British carboniferous bryozoan biogeography

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BRITISH CARBONIFEROUS BRYOZOAN BIOGEOGRAPHY

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A thesis presented for the degree of Doctor of Philosophy
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LIST OF NEW AND REVISED SPECIES

New species

Emended species

ADDENDUM

Taxonomic Nomenclature

a. The names of the new species cited in this thesis, *Rhombopora bancrofti* and *Polypora dendroides*, are provisional only, used for ease of reference within this thesis, and are not deemed valid for taxonomic/ nomenclatural purposes [see article 8b in the *International Code of Zoological Nomenclature*, 3rd Edition (1985) ed. W.D. Ride *et al.*].

b. Throughout this thesis, for *Fenestella tuberculo-carinata* read *Fenestella tuberculocarinata* [see articles 27 and 31d, *ibid.*].

ACKNOWLEDGEMENTS

Most postgraduates gladly welcome the advice and assistance that is invariably offered along the tenuous route from the start of a PhD to that glorious day when the thesis is finally submitted; it is those many people who have provided such support that I would like to thank.

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Many theses would never reach further than the starting stage if it were not for the invaluable assistance of the "boys (and girls) behind the scenes"; the technical support at Durham has been excellent, and I would like to especially thank the three Daves....Dave Asbery, Mr. Fixit himself; Dave Schofield, for keeping me relatively sane; and Dave Stevenson, for maintaining the computer in working order, despite my best (or worst) attempts to "modify" it. Thanks are also due to Gerry Dresser and Alan Carr, whose help in printing off the photographs is most gratefully acknowledged.

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My thanks are also extended to "Fubarite", the Room 223 computer...we've covered a lot of magnetic disc-space together, fought many games of "Battlechess", endured the addiction of "Golf", and even managed to produce some thesis work (occasionally)!

I am very grateful to the Department of Geological Sciences for providing me with so much support over my years in Durham. I am also indebted to the Natural Environmental Research Council for providing a grant to fund this research.

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Finally, I am greatly indebted to my mother, who, amongst the many wonderful things mums do, never did get round to throwing away my collection of "bricks"!

DECLARATION AND COPYRIGHT

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Dedicated to my dad,

Mr. Douglas Billing (1944 - 1978)

who was there when I found my first fossil.

Polyzoa (Bryozoa)....They range from Ordovician to Recent, and are of no geological importance.

D.G.A. Whitten and J.R.V. Brooks,
The Penguin Dictionary of Geology.

Ian Michael Billing

British Carboniferous Bryozoan Biogeography

ABSTRACT

The geographical and temporal distributions of the British Carboniferous Bryozoa have been determined, incorporating data from fieldwork (including localities in Scotland, North England, North Wales, South Wales, and Avon), museum collections, and literature searches. A total of 126 species has been recognised, though further work may reveal some synonymies within this list.

The forty species collected during the fieldwork have been identified by reference to previous taxonomic work; most species can be assigned to established taxonomic descriptions, but two new species, *Rhombopora bancrofti* and *Polypora hexagonaria*, are proposed, and the descriptions of *Rhombopora incrassata* and *Rhombopora similis* are emended. The applicability of Student's t-test to the morphometric analysis of Carboniferous bryozoan species has been studied, and a computer program written to perform this task, incorporating a database of species measurements. A new statistical method, the division t-test, is presented in this thesis; this method is useful in comparing the relative ratios of bryozoan colony parameters. Both the t-test and the division t-test were found to be of use in identifying bryozoan species.

Analysis of the bryozoan faunas in nine regional areas of Britain has been made using the Simpson and Jaccard coefficients of similarity. The resulting coefficients are consistent with the limited distribution capability of many bryozoan taxa, and also match with the known palaeogeography and palaeocurrents of the Carboniferous of northwest Europe.

Plots of species diversity against geographical distribution show a similar pattern to that produced by Tertiary non-planktotrophic larvae-bearing neogastropods. Further, additional plots of species diversity against species longevity produced a pattern consistent with normal background extinction events. A study of bryozoan morphology between different areas and different stages within the Carboniferous indicated that species showed no measurable temporal evolutionary or lateral geographical changes through the Lower Carboniferous. Rather, local environmental stresses are the major architects of bryozoan colony morphology.

PART I : BACKGROUND

CHAPTER 1 : INTRODUCTION AND PREVIOUS RESEARCH

The principal aim of the research presented in this thesis has been to deduce the biostratigraphical and palaeobiogeographical ranges of the commoner British Carboniferous bryozoan taxa. Bryozoans are a very common and important constituent of many Carboniferous marine faunal assemblages, but their study has largely been neglected, in favour of larger, or conversely smaller, fossil groups. Thus bryozoans, because of their combination of small individuals and large colonies, fall between the conventional studies of macro- and micro-palaeontology.

A study of this nature, by virtue of the interweaving of many causes and effects of biogeographical distributions, is inter-disciplinary, and ideas from many schools of thought must be collated. Only by linking different approaches to the topic can a coherent analysis of British Carboniferous bryozoan biogeography be made.

The accompanying flowchart shows the major contributory disciplines which have been incorporated into this thesis.

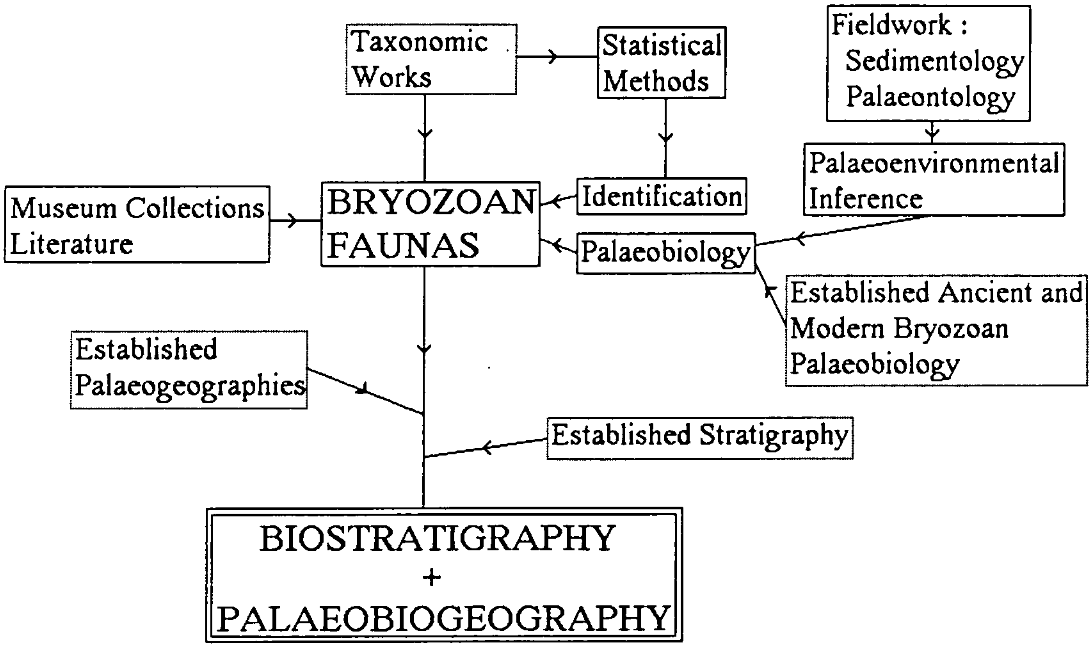


Fig 1.1. Flowchart of the disciplines involved within palaeobiogeography

Established taxonomic works relating to bryozoans

Taxonomic works by far dominate the published literature regarding bryozoans. However, these works are essential to the correct identification of British Carboniferous bryozoans. The most comprehensive summary of British

Carboniferous bryozoan taxonomy is that of Bancroft (1984), in which 41 taxa are revised and discussed. The quality of illustrations and the descriptions are above reproach, and this is undoubtedly a work of major importance. Much of the material from the present study is compared with Bancroft's descriptions, which augment the often poorly illustrated and described initial designations.

In addition to the original species descriptions of various authors (listed in appendix A) large scale taxonomic works of importance include Ulrich's 1890 monograph entitled *American Paleozoic Bryozoa*, which contains high quality illustrations of many hundreds of taxa. Ulrich produced several other papers of great taxonomic importance (1882, 1904, 1905); however, most British Carboniferous bryozoans are absent from American faunas, and are therefore not described, and, conversely, many American taxa are absent in Britain. Also of note is McCoy's 1844 work, *Synopsis of the characters of the Carboniferous Limestone fossils of Ireland* in which over 13 of the commonly occurring taxa are described for the first time.

More recently, the British Museum (Natural History) bulletin *Fenestrate Bryozoa of the Viséan of County Fermanagh* by Tavener-Smith (1973a) described an exceptionally diverse silicified bryozoan fauna of Asbian age. The numerical data provided by Tavener-Smith has been incorporated into species comparisons in this thesis.

Miller has produced some useful reviews and revisions of British Carboniferous bryozoans (1961a&b, 1962a&b, 1963), most notably 1961a, which discussed type specimens of the genus *Fenestella* from Britain. Though the descriptions are rather brief, and the photographs of indifferent quality, this is still a useful work.

Lee (1912) produced a survey of British Carboniferous Trepostomata, and Owen (1966, 1967, 1973) described several new species from Derbyshire, Scotland, and County Tyrone. However, the output of data on British Carboniferous bryozoans, compared with that of Soviet and American and Sino-Japanese contemporaries has been rather scant.

The specimens collected during fieldwork have been identified by reference to the above-cited taxonomic works. Where possible, the original species' descriptions have also been consulted, but such descriptions are usually inadequate. The Trepostomata have proved to be the most difficult group to identify to species level, even though a monograph (Lee, 1912) has been published on British representatives of this group. Thin sections of well-preserved specimens are usually needed for an accurate diagnosis, though statistical analysis of external characters have been used to compared some specimens of *Tabulipora* with those measured by Bancroft (1984).

Statistical methods used in this study

The use of statistical methods in identifying bryozoans has become important, especially in the Fenestrata, where a large number of colonial parameters can be defined. Previous methods involved a simple classification using a "meshwork formula", but this has been shown (Tavener-Smith, 1966) to be of little use in biometrical discrimination. This thesis has built on Tavener-Smith's ideas of using the t-test to discriminate bryozoan species, and computer programs have been written with this aim in mind. Reference is made throughout the fieldwork sections to t-test comparisons of material, with data from Bancroft (1984) and Tavener-Smith (1973a).

Fieldwork conducted during this study

The collection of Carboniferous bryozoan samples was central to the aim of the project; though many museums have well-preserved bryozoan specimens, collections are not usually representative of the complete fauna at the collection locality. Fieldwork, therefore, gave an unparalleled insight into relative abundances of various taxa. Though the absence of a particular species at a locality does not prove the absolute non-occurrence, enough collection time was spent at each locality to indicate that if non-recorded species were present then they were rather rare.

Fieldwork was initially undertaken along the Northumberland coast, giving a continuous succession of the Upper Viséan. Additional field seasons were spent in the Upper Viséan of Fife, Arran and some localities in North Wales, and the whole of the Dinantian was surveyed in South Wales, concentrating on the Gower Peninsula. Local fieldwork included some collecting from Redesdale and Stanhope, in Asbian and lowermost Pendleian strata respectively.

The faunas from Fife, Gower and Arran are described in some detail, since they illustrate both provincial and pandemic bryozoan species. These localities have also provided the specimens on which the statistical identification of bryozoans has been tested. Further, it was necessary to provide descriptions of all the Bryozoa taxa at these three localities to test whether the same species showed variation in different areas and at different stratigraphical horizons. Additional fieldwork localities have been described in an abbreviated form, since the main taxonomic methods are detailed in the above three sections; a full description of the remaining faunas would make the thesis unduly long, and would produce little extra information. Thus, Northumberland, North Wales, Stanhope, Redesdale, and Clitheroe have only the general facies types and faunal lists included, with a discussion of the more important bryozoans which may be present.

The majority of the forty species collected during the fieldwork match well with previous taxonomic descriptions, and show no features requiring emended diagnoses. Where appropriate, these species have been compared with the taxonomic revisions of Bancroft (1984) and Tavener-Smith (1973a). Two new species have been described - *Rhabdomeson bancrofti* (described on page 148) and *Polypora hexagonaria* (described on page 194) - and emended diagnoses have been produced for two species - *Rhombopora similis* (described on page 144) and *Rhombopora incrassata* (described on page 146). A further species of *Eridopora* may be new, but the only specimen is too poorly preserved to allow a formal and accurate identification. This taxon is described on page 73.

In addition to providing bryozoan material, fieldwork allowed an assessment of bryozoan species and their palaeoenvironmental setting, using evidence from sedimentology and general palaeontology; where applicable, such communities have been compared with the Carboniferous communities of Ramsbottom (1978).

The relationship between bryozoan species and facies settlement is discussed throughout the species descriptions. Though the descriptions of the material from Fife, Gower, and Arran show much repetition, often with the same species being described in a fair amount of detail from several different localities, this is an important aspect of the research. It is only by a thorough analysis of a species that any morphological variations can be detected, be they temporal, geographical, or facies related differences.

Repositories of Carboniferous bryozoan specimens

Several large museum collections have been carefully studied as part of the research for this thesis. Museum collections provide a rapid way to collect bryozoan data, but many suffer from several faults. Firstly, the identifications associated with the bryozoan material are not always correct; bryozoans can be difficult to identify to species level, and some assignments given by general palaeontologists employ either incorrect names, or use old synonyms. However, this problem has been overcome by first-hand study of the specimens, which allowed verification of the labels associated with the material.

Secondly, some collections have little detail associated with the specimens, other than a name for the bryozoan. Poor stratigraphical and geographical locality information eliminates some excellent material, since labels such as "Carboniferous

Shales, Ireland" are not useful. Other labels give exact localities (eg. 200m upstream of X), but fail to reveal where location X is sited; for this reason, it has been impossible to place some of the smaller Irish localities. Thus, there are certain species which are known to occur at some time in the Carboniferous, at some place within a certain depositional basin, but their palaeogeographical details cannot be further constrained.

Museums which were visited include the Hancock Museum (Newcastle), the Hunterian Museum (Glasgow), the Royal Scottish Museum (Edinburgh), Glasgow Art Gallery and Museum, the Natural History Museum (London), the Merseyside County Museum (Liverpool), and the collections of the British Geological Survey (Keyworth, Nottingham).

A reference set of British Carboniferous Bryozoa was assembled from various museum collections. This was found to be useful for comparison of material, and was thus an additional aid to species identification.

The use of works referring to Carboniferous bryozoans

As has already been mentioned, there is a scarcity of reliable papers written on British Carboniferous Bryozoa. Young & Young produced a prolific output regarding bryozoan occurrences, mainly within Scotland, and Vine wrote a series of papers on Carboniferous and Permian bryozoa of Yorkshire and Lancashire (1881, 1885, 1888, 1889).

Many Geological Survey memoirs have appendices of fossils in the memoir area, with their localities; though material is very well localised, the bryozoan identifications, in contrast to brachiopod identifications for instance, are rather minimal, usually citing forms such as "*Fenestella* sp.", or "Trepostome indet.". References such as this are usually too general to be of use in biogeographical reconstruction. Mis-identification is an additional obstacle which, unlike museum identified material, is not easy to check without relocating Geological Survey material; in the time available for this project, this has not been possible. Where no other information is available on an area, Memoir identifications have been used, though a "?" next to the locality has sometimes been added.

The work of Jas. Kirkby (1880, 1901) contains stratigraphical ranges for many Fife fossils, including some bryozoans identified to species level, and this data has been incorporated into the succession listings for Fife since some of Kirkby's horizons are now inaccessible.

Palaeobiology of bryozoans

An understanding of bryozoan palaeobiology is essential for biogeographical interpretation; the interplay between bryozoans and sediment can be very important (McKinney *et al.*, 1987), and sediment type can also be of major influence on bryozoan settling behaviour (Taylor, 1977; McKinney & Jackson, 1989; Billing, 1991).

One problem facing bryozoologists is that most of the Palaeozoic orders of Bryozoa are now extinct, so inferences from modern bryozoans may not necessarily hold true for Carboniferous forms. Though three classes of Bryozoa are recognised (the freshwater, soft-bodied Phylactolaemata, the short-chambered Gymnolaemata and the cylindrical-chambered Stenolaemata), the Palaeozoic Bryozoa are represented almost exclusively by the class Stenolaemata (Borg, 1926), of which the only surviving order is the Cyclostomata; unfortunately, the cyclostomes are not common Palaeozoic fossils. In this study, the only cyclostome incorporated into the biogeographical data is *Hederella carbonaria* Condra and Elias (1944), described in Britain by Bancroft (1986b). Ctenostome Gymnolaemates are known from the Ordovician onwards, but they are weakly calcified, and thus are only rarely preserved as fossils. Two ctenostome species have been identified in British Carboniferous rocks.

Bryozoans are aquatic, colonial coelomates, possessing a U-shaped digestive tract, and a retractable lophophore, bearing a series of post-oral ciliated tentacles. Most marine bryozoans possess calcified zooecial chambers, and this is the only portion of the colony which is usually fossilized. Thus, the superficial similarity between bryozoan skeletons, tabulate corals, chaetetids, and calcareous algae can lead to problems in identifying the group. Though Ehrenberg (1831) had erected the taxon Bryozoa, the group was still classified with the corals by some workers (for example, Phillips, 1836 and 1841). Certain specimens of the sclerosponge *Chaetetes* have been described as bryozoans (an assignment thought tentative by Duncan, 1871; this was further nullified in Bassler, 1951, p.G236, and the sclerosponge affinities of certain members of the genus *Chaetetes* was proven by Gray, 1980) and *Cucumulites* from the Mississippian of North America was originally described as a sponge, but has been shown (Nitecki and McKinney, 1975) to be a fistuliporid bryozoan. Further, *Koninckopora* Lee, 1912, was originally assigned to the Trepostomata; however, the lack of internal tabulae or differentiation into an exo- and endo-zone, coupled with the observation that zooecial chambers do not recurve, excludes this genus from the Trepostomata, and it is almost certainly a calcified alga (Wood, 1942). Several specimens from Fife described in Chapter 4 (collected from Randerston and the Billow Ness Marine Band), have proved difficult to assign with confidence to the

Bryozoa, and likewise, they may also prove to be dasycladid algae. Fortunately, externally-observable budding patterns and colony shapes are usually very distinctive in the Bryozoa, and most specimens can be confidently assigned to an order within the phylum.

Tavener-Smith (1969a) demonstrated the presence of an outer epithelium in the Fenestellidae, thus showing an interplay between colonial and autozooecial secretion of the skeleton, and Bancroft (1984) tested this hypothesis with other Carboniferous bryozoan orders. Flexibility of the colony plan as a result of this interplay is shown to be a major factor in bryozoan facies relationships.

McKinney has published recently on inferred palaeobiologies of American Carboniferous Bryozoa. Work on taxa such as *Lyroporella* and *Archimedes* (McKinney, 1977 and 1983) have related colony morphology to environmental adaptive strategies. Where possible in this thesis, some discussion of the inferred life habit of the bryozoans encountered has been made. Palaeozoic bryozoans needed a firm substrate on which to settle, a suitable skeleton to withstand the rigours of their chosen habitat, and a method of ensuring food particles were trapped effectively; much of the variation in colony morphology between different species can be attributed to these needs (for a review see McKinney and Jackson, 1989), though defences against predation may also affect colony morphology (Bancroft, 1986e and 1988b; Southwood, 1985).

Previous work on bryozoan biogeography

Distribution patterns of modern bryozoans were reviewed by Lagaaij and Cook (1973); their overwhelming impression was that Recent bryozoans have very widespread distributions, in contrast to their limited larval dispersals. Cheetham (1960) noted that encrusting bryozoans had greater trans-Atlantic distributions than non-encrusting taxa.

Generic-level studies of Carboniferous and Permian bryozoan global biogeographies have been carried out by June R.P. Ross (1981); see also J.R.P. Ross and C.A. Ross (1990) and C.A. Ross and J.R.P. Ross (1981 and 1985). These studies are useful in illustrating the global patterns of Palaeozoic bryozoan distributions, which they believe are mainly influenced by thermal clines and the configuration of continents. The present study aims to "zoom in" on a single portion of the Southern Laurasian continental shelf, and deduce some biogeographical trends by analysing species distributions within the British Dinantian and Lower Silesian.

Carboniferous palaeogeography

The position of the continents during the Carboniferous has been demonstrated to have a bearing on distributions and migrations of various taxa (Johnson, 1980b; Nudds and Johnson, 1985: Ross, 1990). The latest reconstruction of global Carboniferous geography is that of Scotese and McKerrow, 1990 ; fig. 1.2 shows their reconstruction of the continental configurations for the European region in the late Dinantian. This reconstruction differs slightly from that of Johnson and Tarling (1985), who envisaged a separate South Europe microplate colliding with Laurasia before the suturing with Gondwanaland. However, both Lower Carboniferous reconstructions have the following features in common:

a. Britain is placed in a position just south of the equator,

b. The Laurasian shelf extended from the mid North America, through Britain, and on into the Baltic region,

c. There was a narrowing seaway between Laurasia and Gondwanaland,which closed by the end of the Upper Carboniferous.

It is these three points that are of most relevance to explanations of British Carboniferous bryozoan biogeographies.

The geographical reconstructions of Johnson (1982) for Britain through the Carboniferous have been used in this study; the species distribution maps and geographical zones are plotted on a computer-designed map of the mid-Viséan reconstruction. Johnson's maps for the Tournasian, the mid-Viséan, and the Namurian are redrawn in figs. 1.3 to 1.5. The reconstructions illustrate an archipelagic arrangement of islands, the most prominent of which are the Longford Down Massif, and the Wales-Brabant Massif, which extended into northern France. There was an increasing degree of marine influence over the shelf during the Dinantian, but a Namurian shallowing of the seas and dominance by fluvial deltaic sedimentation. The edge of the continental shelf is inferred to run through north Devon and on through southernmost Ireland; the shelf therefore narrows quite markedly to the west.

A late Asbian facies map of Britain is shown in fig. 1.6, redrawn from Walkden (1987). Platform carbonates developed around the fringes of the Wales-Brabant Massif, over much of the shallowing shelf in Ireland, and on the structurally-high Manx-Cumbria and Askrigg Blocks. Reef facies were developed on the Derbyshire Platform. To the north, sedimentation was greatly influenced by fluviatile run-off from the Laurasian continent (Wilson, 1989).

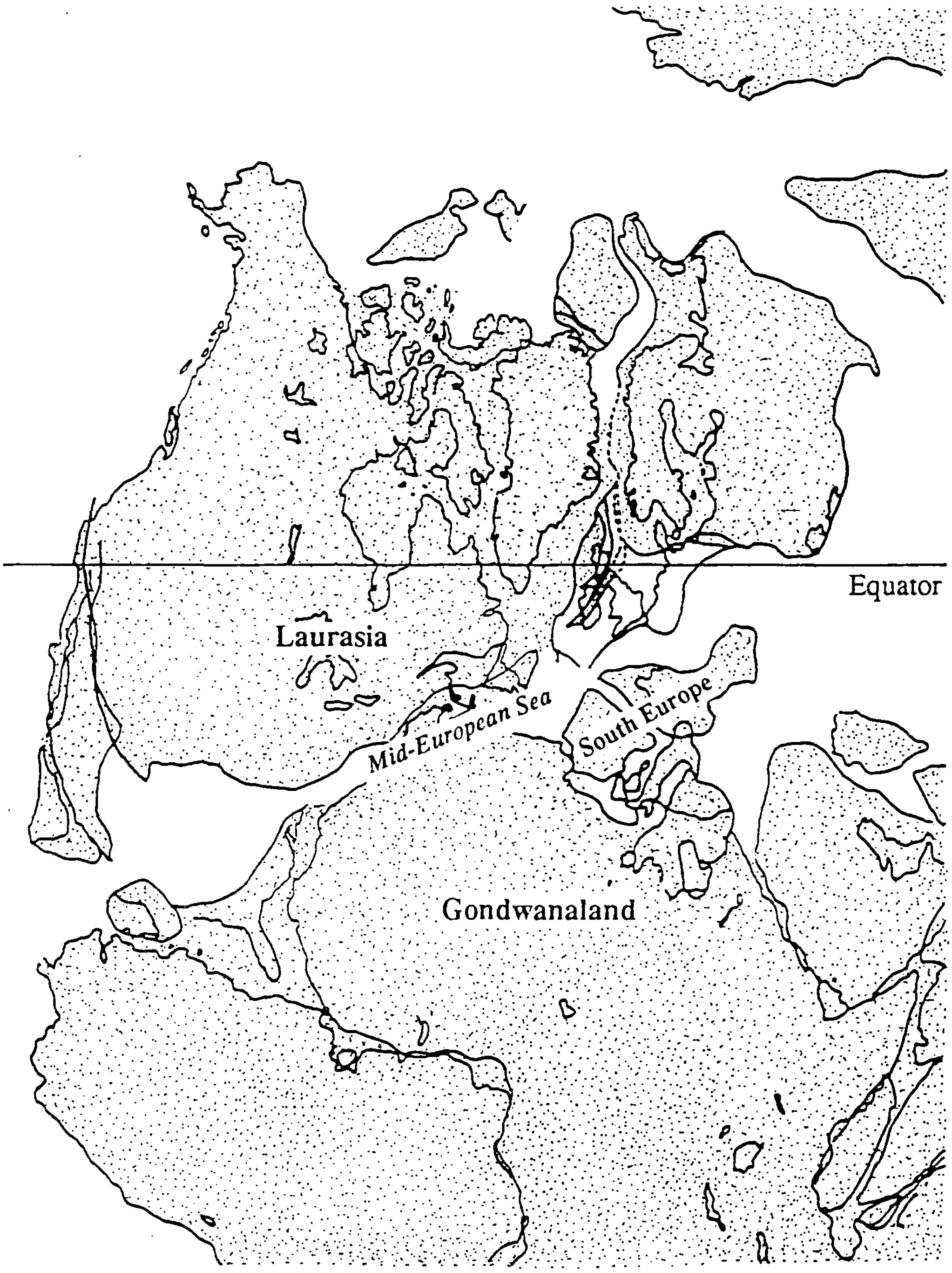


Fig. 1.2. Continental reconstruction for the Upper Dinantian (redrawn from Scotese and McKerrow, 1990)

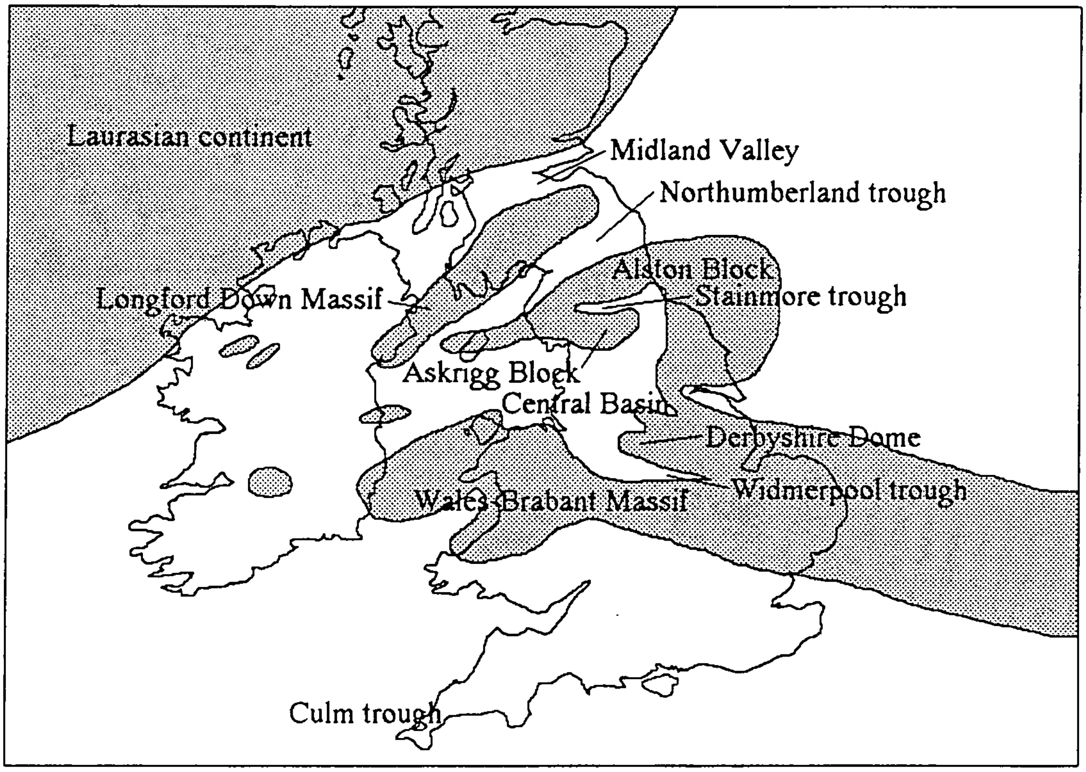


Fig. 1.3. British Tournasian Palaeogeography (redrawn from Johnson, 1982)

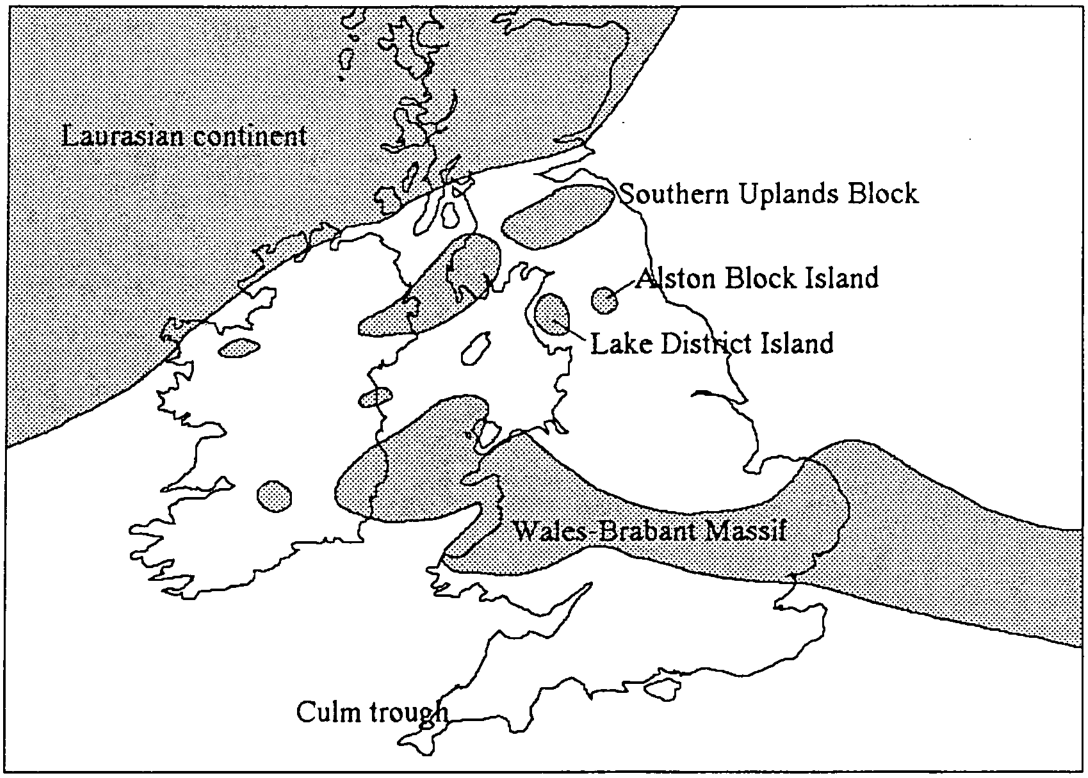


Fig. 1.4. British Viséan Palaeogeography (redrawn from Johnson, 1982)

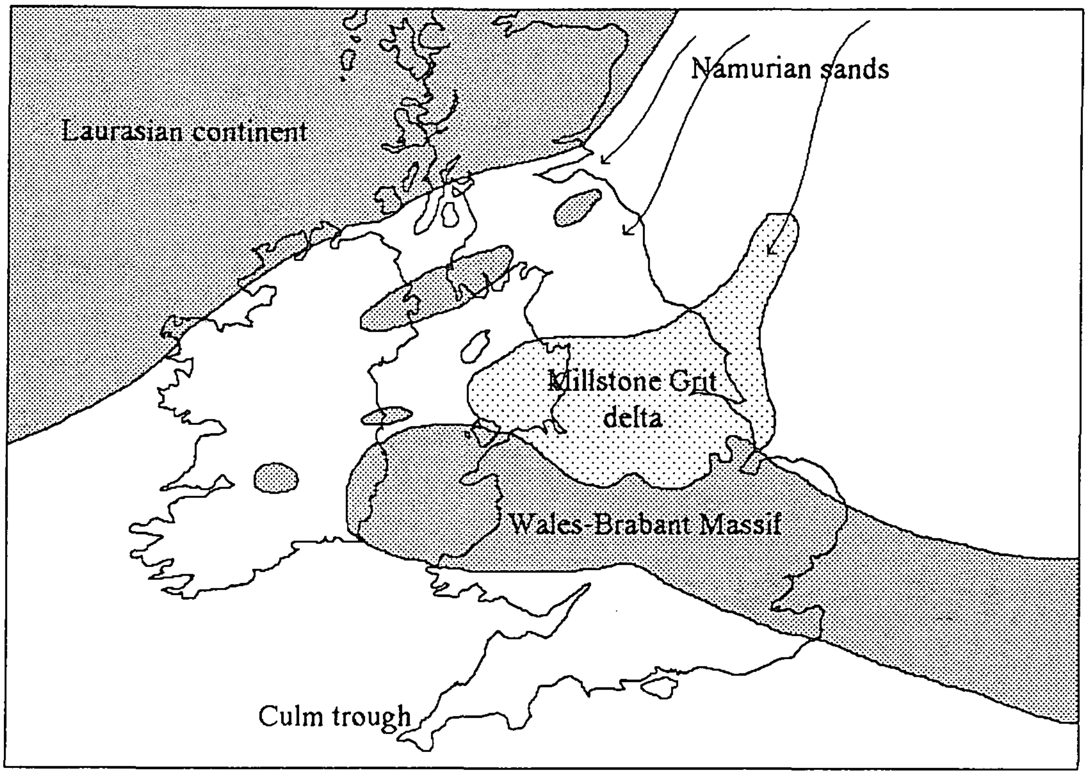


Fig. 1.5. British Namurian Palaeogeography (redrawn from Johnson, 1982)

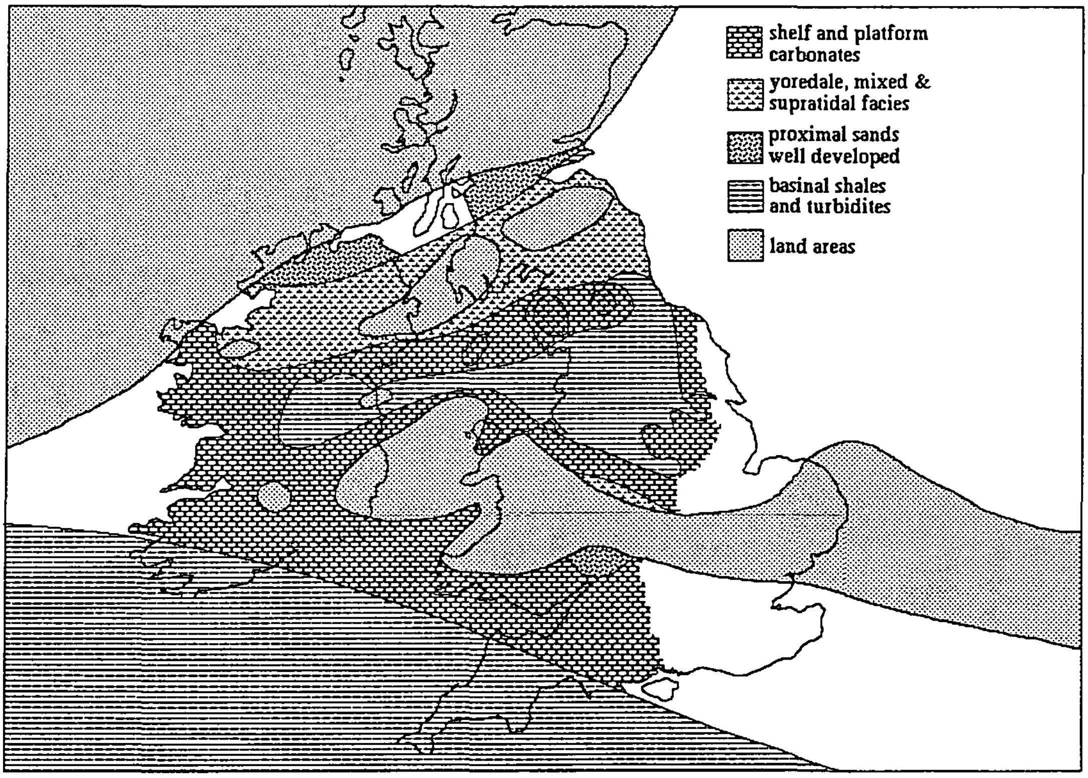


Fig. 1.6. Facies map of Britain in the late Asbian (redrawn from Walkden, 1987)

Carboniferous stratigraphy

The stratigraphical scheme used throughout this thesis is based on that of George *et al.* (1976), Ramsbottom *et al.* (1978), and also incorporates the zones of Vaughan (1905) for the Dinantian, and Ramsbottom (1969) for the Silesian:

SUB-SYSTEM	SERIES	ZONE	STAGE	AGE (Ma)
Lower Silesian	Namurian	G1	Yeadonian	315
		R2	Marsdenian	
		R1	Kinderscoutian	320
		H2	Alportian	
		H1	Chokerian	
		E2	Arnsbergian	
		E1	Pendleian	333
Dinantian	Viséan	D2	Brigantian	
		D1	Asbian	
		S2	Holkerian	
		C2-S1	Arundian	
			Chadian	352
	Tournasian	C1	Courceyan	
		Z1-Z2		
		K		360

Fig. 1.7. Dinantian and Lower Silesian stratigraphical nomenclature

The local stratigraphy of fieldwork areas has been taken from the Geological Survey memoirs for each district, or has used the most recent stratigraphical revision for each area. The questioning of the stratigraphical position of local horizons is beyond the nature of this study, and most assignments have been taken at face value; however, there is some discussion of the stratigraphy of the Carboniferous of Arran. The current study has examined bryozoans ranging in age from the Courceyan to the Arnsbergian; bryozoans younger than this have not been noted.

Bryozoan morphology and classification

An overview of bryozoan morphology is provided in Ryland (1970); this book, though now out of print, is a more suitable introduction to the Bryozoa than the excellent, but rather technical, publication of McKinney and Jackson (1989). Basic introductions to the phylum are included in Clarkson (1986) and Taylor (1985b).

The classification scheme of Boardman *et al.* (1983)is shown below in a modified version of the tables cited in McKinney and Jackson (1989) for the Palaeozoic classes and orders of Bryozoa:

Class **Stenolaemata** BORG, 1926: Cylindrical zooecia, which are elongate, and continue to lengthen throughout ontogeny; the long axis of the chambers is inclined to the overall colony growth direction. Basal and vertical walls are rigidly calcified. Interzooecial communication takes place via an outer epithelium, or, in some cases, through communication pores in the vertical walls. The polypides are enclosed within a membraneous sac; deformation of this sac extrudes the lophophore through the zooecial aperture at the end of the chamber. Range: Lower Ordovician - Recent.

Order **Cryptostomata** VINE, 1883: Colonies may be erect dendritic or bilaminate sheets. Autozooecia are usually short, and may contain basal diaphragms or hemisepta (which are incomplete partitions). Communication pores are not present. The skeleton is typically laminated. Kenozooids (diminutive polypides, which are probably non-feeding) or extrazooecial skeletal material (such as spinose projections) may be present. Range: Lower Ordovician - Upper Permian or ?Cretaceous.

Order **Fenestrata** ELIAS and CONDRA, 1957: Erect colonies with narrow, unilaminate branches. Autozooecia are short, and commonly contain hemisepta, but basal diaphragms are rare. Communication pores are absent. Primary skeleton is granular; extrazooecial skeleton is extensive and comprises laminae pierced by small granular rods. Various heterozooecia, including gonozooecia, may be present. Range: Lower Ordovician - Upper Permian or ?Triassic.

Order **Trepostomata** ULRICH, 1882: Encrusting or erect colonies, with elongate autozooecia, generally containing basal diaphragms and other lateral structures. Communication pores are not present. Laminated skeleton, with extrazooecial material in some taxa. Kenozooecia are common. Range: Lower Ordovician - Upper Triassic or ?Recent.

Order **Cystoporata** ASTROVA, 1964: Colonies may be erect dendritic, or may form bilaminate sheets. Zooecial chambers may be short, lacking basal diaphragms, or long with basal diaphragms. Most autozooecia have a thickened strip (a lunarium) along one side of a thick-walled outer zone; the lunarium may project over the autozooecial aperture. The skeletal structure is laminated, granular, or granular-prismatic, and communication pores may be present. Autozooecia are separated by vesicular extrazooidal skeletal material. Kenozooecia may be present. Range: Lower Ordovician - Upper Permian or ?Cretaceous.

Order **Cyclostomata** BUSK, 1852: Encrusting or erect colonies. Autozooecial chambers are commonly long, and some may contain basal diaphragms or other structures. The skeletal structure is typically laminated, and communication pores are very common. Extrazooecial material is sometimes developed. Gonozooecia are common, and kenozooecia may occur. Range: Lower Ordovician - Recent.

Class **Gymnolaemata** ALLMAN, 1856: Box- or sac-shaped to short cylindrical zooecia, the size of which is fixed early in ontogeny. The long axis of the chambers is parallel to the colony growth direction. Walls can vary from entirely organic to rigidly-calcified. Interzooecial communication takes place by a network of tissue strands (funiculae) through pores in the vertical walls. The lophophore is extruded by deformation of the vertical or frontal walls. Range: Upper Ordovician - Recent.

Order **Ctenostomata** BUSK, 1852: Zooecial walls membraneous or gelatinous, occasionally weakly calcified. The orifice is terminal, and is usually closed by a pleated collar. Heterozooecia are usually absent. Range: Lower Ordovician - Recent.

Summary of the present study

The identification of faunas from eight fieldwork areas has given a coherent view of regional and temporal variations in Lower Carboniferous bryozoan faunas across much of Britain. Additional bryozoan-bearing localities are incorporated from several museum collections and from information recovered from literature searches. By analysing bryozoan faunas from nine geographically-defined regions (see Chapters 12 and 13), it has been possible to produce similarity coefficients for these regions. Several explanations are offered to account for the regional variations, and mathematical models constructed to test the hypothetical effects of current systems on bryozoan distributions.

The variation of bryozoans through time is discussed, and the possibility of regional morphological variations within single species is also addressed. Further, the geographical and temporal distributions of bryozoan species is compared with patterns published for non-planktotrophic larvae-bearing gastropod taxa. The patterns are also compared with distributions discussed by Jablonski (1986) for normal background extinctions.

The use of the t-test in the morphometrical identification of bryozoans is also tested, and reference to this statistical technique is made throughout Part II, which describes bryozoan faunas collected during fieldwork.

CHAPTER 2 : METHODS OF PREPARATION AND PRESENTATION

Specimen Preparation and Examination

Many bryozoan specimens recovered in the field were embedded in the rock matrix, or were obscured by organic growths. Therefore it was necessary to clean some specimens before enough colony detail could be exposed prior to identification. Additionally, sections had to be made through some samples to reveal their internal structure; such sections are essential if certain trepostomes, for instance, are to be identified to species level.

Specimen cleaning

For many specimens, washing, gentle brushing with a soft brush, or directing a jet of compressed air over the specimen would successfully expose colony surface detail. Some samples were cleaned in an ultrasonic bath, with a little detergent added to the water to aid the removal of adhering clay particles.

Those specimens which were obscured by firmly-cemented matrix had to be exposed by mechanical means; careful chipping with finely-pointed dissecting needles was the most successful method of removing the more robust components of the matrix. This technique worked best if the specimen was submerged in a bowl of water, which had the advantage of washing away extracted chippings. During such extractions, the sample was viewed through a binocular microscope.

Some collected samples consisted of disaggregated marly sediments. Boiling these marls in water, to which detergent had been added, proved to be successful in breaking down the clay matrix further. The freed calcareous fauna could then be recovered by sieving. However, such a method is rather vigorous, and only small bryozoan fragments were extracted.

When many bryozoan-bearing shales are split apart, it is usually the obverse surface of fenestellid fronds which remains attached to the shale, while the less informative smooth reverse surface is cleanly exposed. Rather than this being the random case of bread usually landing butter-side down, it is the rougher nature of the obverse surface, with nodes, carinae, and apertures, which deem that this surface is more cohesive. Young (1877) described a method of embedding the exposed reverse surface in a layer of asphalt; on hardening, the remaining shale, which still obscured the obverse surface, could be removed, leaving a fenestellid embedded in asphalt, with an exposed obverse surface. Bancroft (1984) utilised this technique in his specimen preparation, often with great success, but Southwood (1985) recorded less success with his Permian limestone material. A variation of this technique was carried out in this study; experiments were conducted which involved covering the reverse surface of limestone-embedded fenestellids in "Araldite" epoxy-resin. Once the "Araldite" had dried, gentle blows with a chisel could prise the resin and limestone apart, and usually the fenestellid branches remained attached to the epoxy-resin counterpart, revealing the obverse surface detail.

Though the above methods were useful in revealing obverse surface detail, the techniques are all rather time-consuming, and in a large batch of material it is not feasible to prepare each specimen in this way. Thus, most specimens processed for this study remained untreated.

Specimen sectioning

For several taxa, it was necessary to examine the internal morphology. Tangential sections of fenestrate bryozoans, and tangential and transverse sections of cylindrical taxa were therefore made. Small specimens were mounted within blocks of resin, for ease of sectioning.

Specimens were initially ground down on an abrasive wheel to within a millimetre or so of the desired section surface. Polishing and further grinding was carried out using 400 and then 1000-grade silicon carbide grits on a glass plate. Final polishing, where necessary, was carried out with 1μ alumina powder on a rotating lap.

Some specimens were then fixed to glass slides using "Lakeside" resin, and ground down to 30μ thickness. Such thin sections were usually prepared from specimens which were partially-silicified, or which were thought to be recrystallised. Acetate peels were taken from the majority of specimens. Such peels, though lacking the high-resolution of traditional thin sections, have the advantage of being much quicker to produce, and enabled a series of serial sections to be recorded through the specimens.

Specimen surfaces from which peels were to be taken were etched in 10% dilute hydrochloric acid for approximately 15 seconds, and then thoroughly rinsed in cold water. The specimen surface was allowed to dry completely, before being flooded with acetone. A sheet of medium-thickness acetate was then rolled over this surface, excluding air bubbles as far as possible, and allowed to dry for up to half an hour. Smaller specimens were placed directly onto the acetate sheet, a small drop of acetone having been previously placed on the sheet. The resulting peel was carefully but quickly removed, trimmed to size, and "Scotch-taped" between two glass slides to prevent warping of the peel.

Though peels and thin sections can produce useful information about the internal morphology of specimens, much of the material studied was rather recrystallised, and most of the internal structure of the bryozoans had been lost. Thus, several trepostomes encountered in the field could not be identified further than ordinal level, and in some cases even this assignment is tenuous.

The biggest disadvantage of sectioning material, aside from the preparation time, is that it is a destructive technique. Several specimens were therefore examined by exposure to X-rays, to determine if this method could give information regarding the internal structure. However, the density contrast between the laminar and granular calcite, which compose the bryozoan skeleton, and the sparry calcite which usually infills the chambers, was not sufficient to be detected by X-ray absorption. Recently, a new technique involving ultrasound scanning of material (Sinclair and Smith, 1979; Boyde, 1985; Boyde *et al*, 1985) has been developed, and has had some success in producing non-destructive serial sections through opaque teeth and other bony material. It is quite probable than scanning acoustic microscopy could produce similar sections through calcified bryozoan specimens, but this technique remains to be tested.

Microscope facilities

The relatively small size of bryozoan autozooids necessitate the study of specimens under the microscope. For this study, a Wild M8 binocular microscope was used. This particular microscope has excellent optics and lens alignments, allowing a specimen to remain in focus throughout the range of the zoom lens. The magnifications available range from x2.4 (with 10x eyepieces, and a x0.4 objective lens fitted) to x100 (with 20x eyepieces, and the standard x1.0 objective).

An eyepiece graticule allowed measuring of bryozoan zoarial parameters. The graticule is divided into 100 divisions, and most measurements were made at x50; thus, there are 50 graticule divisions in 1mm, with each division representing 0.02mm. Measurements could be gauged to within half a division, thus giving a minimum measuring distance of 0.01mm. For relatively large parameters such as fenestrule lengths, this limit gives a average measurement error of only 1%, but for smaller features such as cyclozooecial diameter, which can be as small as 0.05mm, errors of up to 20% can be expected.

Specimens were initially drawn with the aid of a *camera lucida*, attached to a Leitz binocular microscope, but as Bancroft (1984) pointed out, such an arrangement, which results in lower apparent light levels of the image, makes it difficult to distinguish the less obvious characters. Thus, when inked drawing were produced from the pencilled drafts, it was necessary to re-examine the specimen in order to add the finer detail. All diagrams are shown with a 1mm scale bar.

Thin sections were examined with illumination from the transmitted light base of the Wild microscope, or with Nikon and Olympus polarising binocular microscopes. The clearest detail was provided by the Olympus BH-2 transmitted light microscope, with magnifications of up to x1000.

Photography of specimens

Most specimens were photographed with a camera tube attached to the Wild M8 microscope. An extension tube bearing a x10 eyepiece, attaches into a trinocular tube on the microscope body; the image is then focused by a x0.32 lens which attaches, via a standard T-mount, to an SLR camera. An Olympus OM30 camera body, with an option for automatic exposure control, was used for the photography throughout this study. The field of view is approximately half the length, and a third of the width of the field seen through the x10 eyepieces. The depth of focus can be controlled by the double iris diaphragm on the trinocular tube; values are not cited in standard F-stop numbers, but range from 10 (for fully open) to 1 (virtually closed).

Specimens were illuminated from the left by a low-angle 6Volt/20Watt Wild halogen lamp, giving a uniform illumination spot at 3200K, and from the right by a high-angle 6Volt/10Watt Wild lamp with a colour temperature of 2700K, to fill in unwanted shadows. Both lamps were fitted with daylight blue filters, to create a better contrast on the specimens. A fibre optic ring illuminator, which fits around the microscope objective lens, was used to fill in the shadows on some shots, but this lamp produced a rather yellow light.

Photographic experiments have shown that for ASA 100 black and white film (Ilford and Fuji film were both used), the camera rating should be lowered to ASA 50, to compensate for the artificial light, and the trinocular diaphragm should be set between 2.5 and 3.5. Smaller diaphragm settings produce a greater depth of field, which is useful at high magnifications for bryozoan colonies with considerable relief, but images are usually darker, and require longer exposure times. Shutter release times were usually controlled automatically by the camera, but averaged about 1.5 to 2.5 seconds for shots at x25. The resulting negatives were printed on Ilford "hard" photographic paper, though darker negatives were printed onto Ilford "medium" paper, with a lower exposure time.

Specimens larger than 4cm could not be photographed with the microscope arrangement, and were shot with a Tamron 35-70mm zoom lens attached to the Olympus camera body. Some thin sections were photographed through the trinocular tube of the Olympus BH-2 microscope.

Computer Facilities

The use of the microcomputer in the geological sciences is rapidly becoming more and more widespread. Statistical computing methods are discussed in Chapter 3, and the applicability of microcomputers for the presentation of geological data is the subject of this section.

Most of the computing was conducted on an IBM PS/2 microcomputer, and the various programs executed through the Microsoft Windows Version 3.0 software. An additional four Microsoft programs - Word For Windows (Version 1.1), Excel (Version 2.1c), Paint (Version 2.1), and Paintbrush (Version 3.0) - were used to produce this thesis.

The tabulated values of bryozoan parameters were produced as spreadsheets within the Microsoft Excel program, and were then pasted into the thesis text within the Word word-processing package. Similarly, most of the graphic logs and maps presented in this thesis were designed on the IBM computer. Graphic logs were originally drawn in the Paint program, which allowed the various ornaments to be added, and pasted into the more sophisticated Paintbrush program where the text annotations were included. Once the complete image was finished, maps and logs could again be pasted within the text of the Word documents.

The thesis itself has been produced with Word, and is set in Times Roman 12point type, with a line and a half spacing.

CHAPTER 3 : STATISTICS AND COMPUTER APPLICATIONS

Variation in populations

In an ideal world, a population of any species would consist of absolutely identical individuals. This would make life very easy for taxonomists; if a parameter on a fossil differed from that of another fossil by only a few hundredths of a millimetre, this should indicate a different species. However, in reality, parameters within a population of the same species can vary quite considerably. There are, in fact, several factors which lead to this phenomenon of variation.

In a population which reproduces sexually, there are genetic variations between individuals partly due to DNA switchover during the process of meiosis, which produces the gametes, but mainly from the recombination of DNA from two different parents. Even in populations which reproduce asexually, though, there is still some observable variation between individuals. These differences can be accounted for by randomising factors, which also affect sexually reproducing populations; for instance, imperfect DNA replication during cellular division can create small but significant changes in the makeup of individuals. Further, the microenvironment, the small zone of space around each individual, is never exactly the same in any two given areas, and this can put quite different "stresses" on two otherwise identical individuals living relatively close to each other. These differing stresses will cause the individuals to grow in slightly different ways.

The Normal curve

So, variation is an inevitable feature of a population. However, though the factors which cause variation are random and completely unpredictable (they are said to be "chaotic") studies have shown that if the population is large enough then a plot of parameter size (eg. height) against the frequency of individuals will produce a fairly consistently-shaped graph (fig. 3.1):

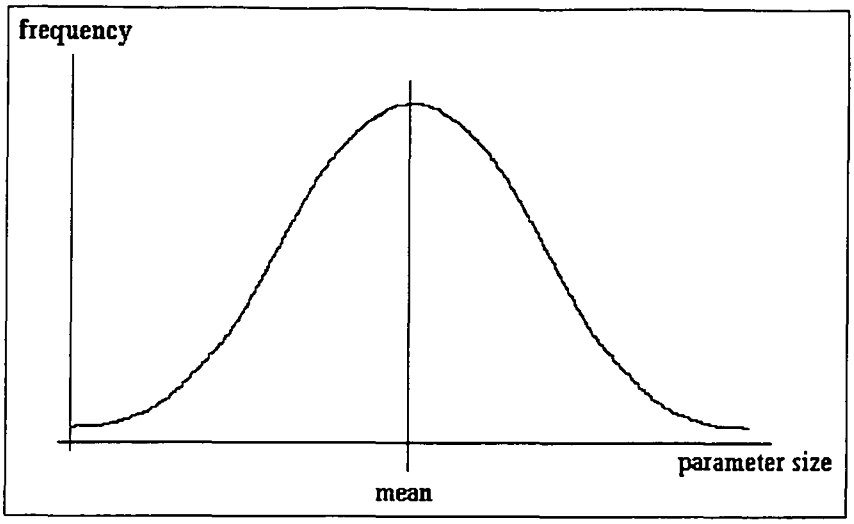


Fig. 3.1. The Normal Curve

This graph is called a Normal curve, since it is the shape most commonly seen in natural population distributions. It is "bell"-shaped, and has several important characteristics.

Firstly, it is symmetrical; thus, the average value for a particular parameter for all the individuals lies exactly in the centre of the bell-shaped curve. In mathematical language, the mean (the population average) is the same as the mode (the most frequently-occurring size). In this case, the mean is defined as :

$$\bar{x} = \frac{\sum_{i=1}^{i=N} x_i}{N}$$

where $\bar{x}$ = the mean

N = the number of measurements

i = each score

Secondly, the symmetrical nature of the curve implies that there are exactly the same number of individuals with a parameter size less than the average as there are individuals with a greater-than-average parameter value. And thirdly, by far the bulk of individuals have parameters which lie quite close to the mean. There are only a few individuals who have parameter sizes at the extremes of the variation, and there is a mathematical gradient between these and the mean.

The actual shape of the curve - the breadth of the "bell" - differs from population to population, depending on how much variation there is within each population. This degree of variation is called the variance, and is an average of the amount by which individuals differ from the mean value. More usually, the variance is expressed as its square root equivalent, the standard deviation, which is given the symbol σ :

variance = average of (mean - individual)^2 or,

$$\sigma = \sqrt{\left[\frac{\sum_{i=1}^{i=N} (\bar{x} - x_i)^2}{N}\right]}$$

If a population has little variation, then σ will be small, and the Normal curve will look rather compressed :

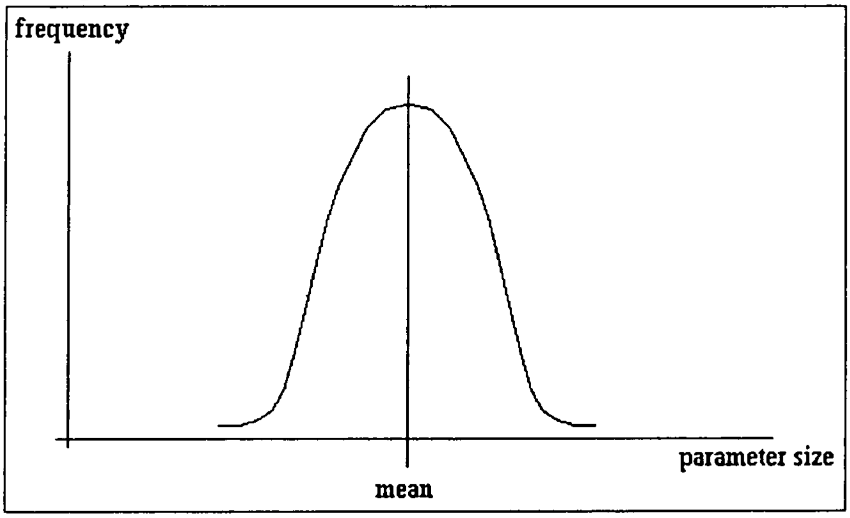


Fig. 3.2. Compressed Normal curve

If, on the other hand, there is a lot of variation within the population, then the "bell" will be much broader :

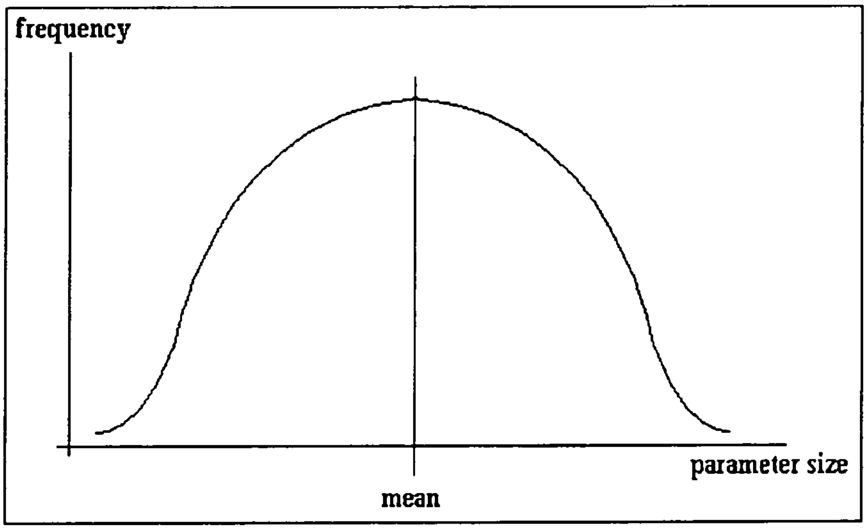


Fig. 3.3. Expanded Normal Curve

However, whatever the value of the standard deviation, all the Normal curves will have the properties outlined earlier.

The actual shapes of the curves may also change depending on the size of the population. The Normal curve, with its mathematical boundaries, strictly defines only a population of infinite size, but populations as small as 30 usually adhere quite closely to its mathematical definition.

The t-test

If a taxonomist has two small populations (usually two sets of specimens) he may wish to test them statistically, to see if they belong to the same larger population, the species :

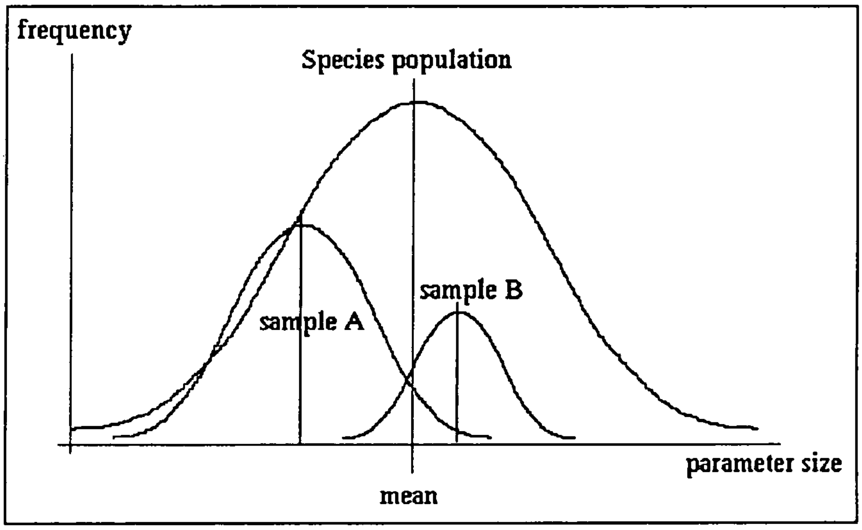


Fig. 3.4. Population overlaps

Two populations will usually have different sizes (N), means ($\bar{x}$), and standard deviations (σ). Several statistical tests have been devised to check the similarity of populations using these three variables. The Chi-squared test compares the variances of two populations, whereas the t-test places more emphasis on the population means. For comparing populations for similarity at species level, the t-test is more useful, since for small samples there is much more error in obtaining the variance than in obtaining the mean.

The t-test assesses the probability of two samples coming from the same population. It has the advantage that it is designed for studies on "small", normally-distributed samples, and requires the following parameters :

The number of measurements, or colonies, N
The mean, $\bar{x}$
The standard deviation, σ

These parameters, in practice, may be found by entering the data on a statistical calculator. In this study, a Sharp EL-506 P was used, which allowed quick entry of data with accurate results.

An average standard deviation of the two samples can then be calculated,

$$\sigma = \sqrt{\left[\frac{\sigma_1^2.(n_1 - 1) + \sigma_2^2.(n_2 - 1)}{(n_1 + n_2 + 2)}\right]}$$

t is then defined as

$$t = \frac{\bar{x}_1 - \bar{x}_2}{\sigma . \sqrt{(1/n_1 + 1/n_2)}}$$

and the value of t is correlated with the Degrees of Freedom ($n_1 + n_2 - 2$) in a set of tables to give a Probability score. The Degrees of Freedom mathematically shape the Normal curve against which the samples are correlated. For this study, a series of computer programs were written to calculate t and the subsequent probability scores for bryozoan data.

The applicability of statistical studies to bryozoans

Though many bryozoan species have been erected on the basis of their external morphology, the characteristic features may be seen only on the best-preserved material. One aim of this project was borne of necessity (since most bryozoans collected by field workers are only moderately-well preserved) and involved designing a method to identify bryozoans to species level using a statistical treatment of their external parameters.

Bryozoan colonies lend themselves to a statistical classification, since there are a relatively-large number of easily-determinable features to measure. The main parameters which have been measured for the rhabdomesonids, the fenestellids, the pennireteporid acanthocladiids, the trepostomes and the cystoporates are illustrated in figs. 3.5 to 3.8. The abbreviations cited are based on those of Bancroft (1984) and utilise the additional terminology of Cuffey (1967), Newton (1971), Tavener-Smith (1973a), and Olaloye (1974). A useful glossary of morphological terms is provided in Boardman *et al.* (1983, p.304-320).

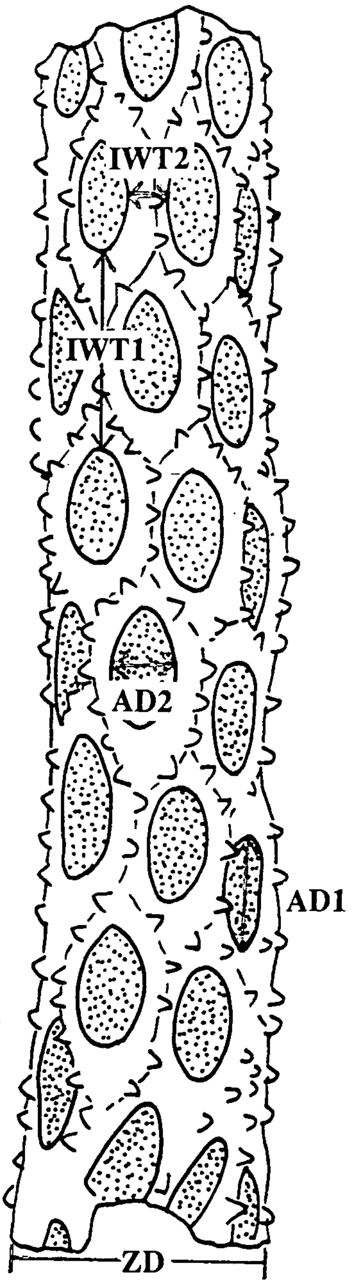


Fig. 3.5. Parameters of rhabdomesids

ZD	Transverse zooecial diameter
AD1	Longitudinal aperture diameter
AD2	Transverse aperture diameter
IWT1	Longitudinal interapertural wall thickness
IWT2	Transverse interapertural wall thickness
(not illustrated)	
ED	Exilazooecial aperture diameter
Z1	Number of apertures in a 1mm^2 area
Z2	Number of apertures in a 2mm line

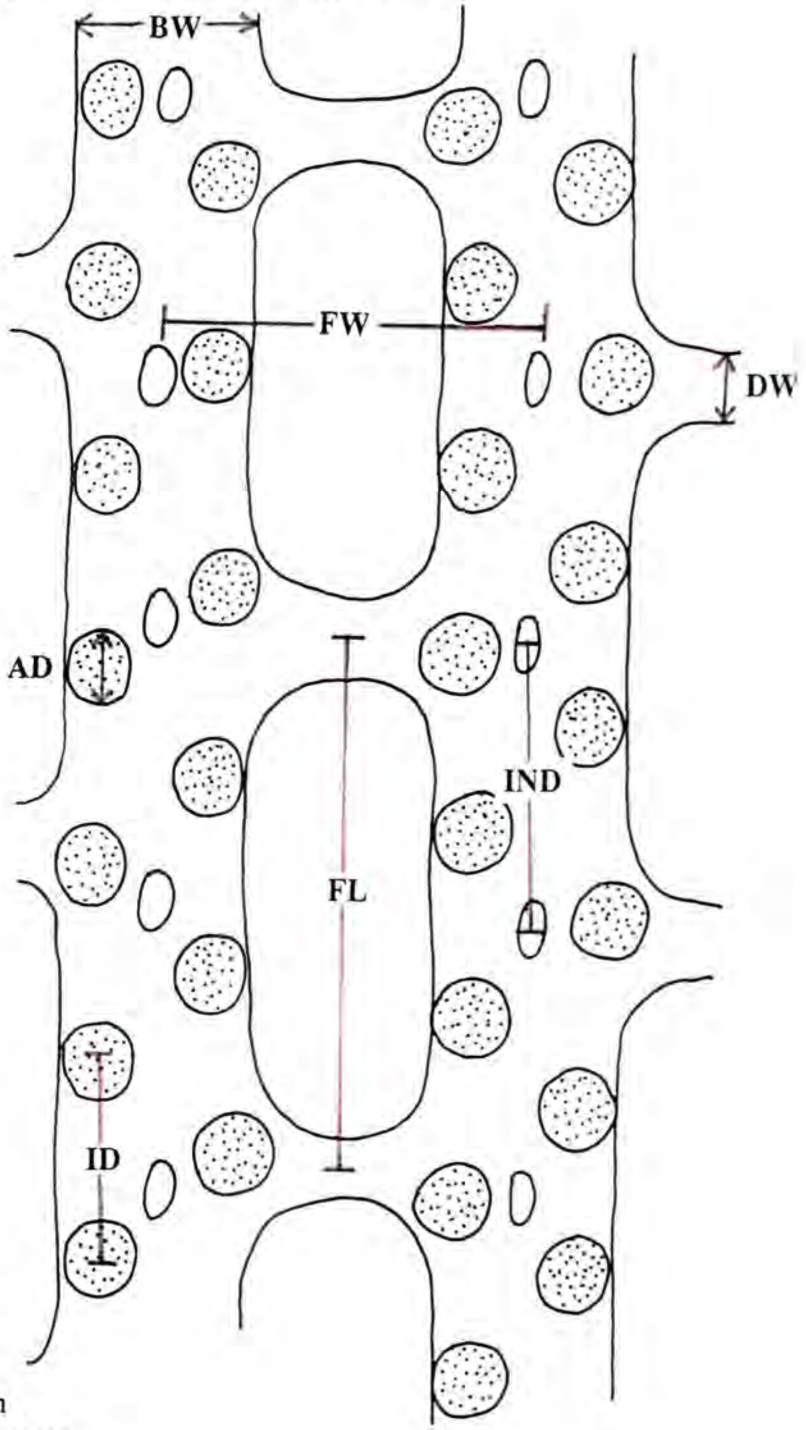


Fig. 3.6. Parameters of fenestellids

BW	Branch width
AD	Aperture diameter
ID	Interaperture distance
FL	Fenestrule width
FW	Fenestrule length
DW	Dissepiment width
IND	Internodal distance
(not illustrated)	
CD	Cyclozooecial aperture diameter
ZB1	Zooecial chamber base length
ZB2	Zooecial chamber base width

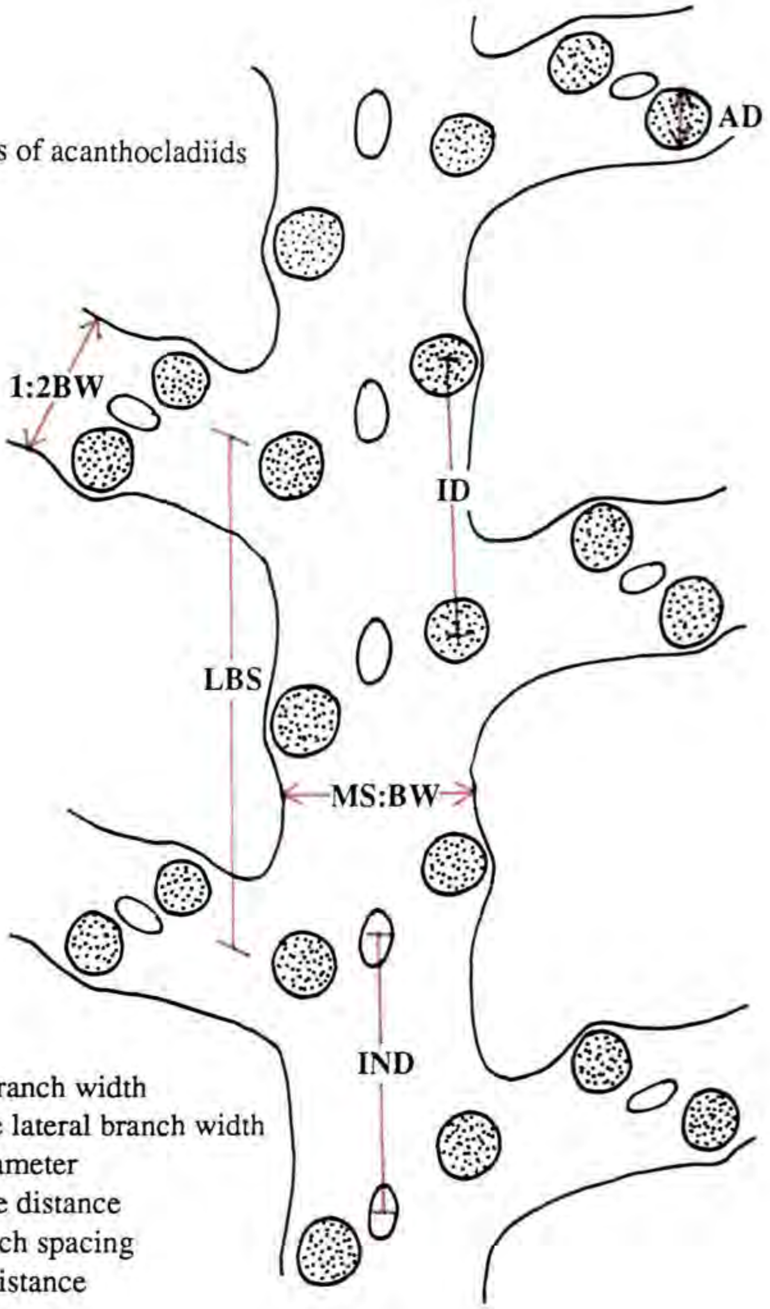
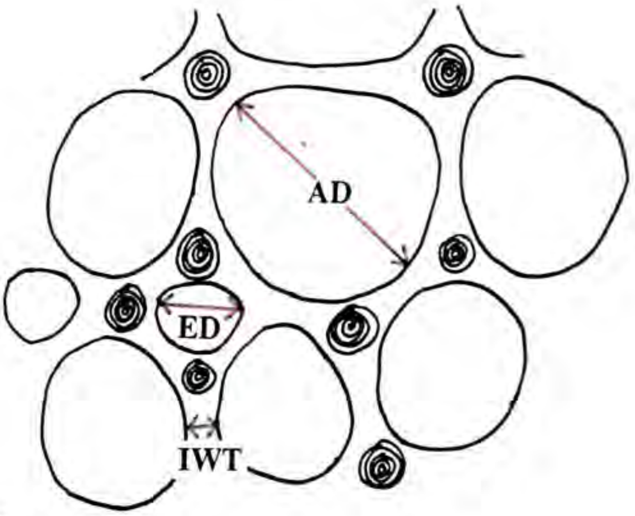


Fig. 3.7. Parameters of acanthocladiids

MS:BW	Mainstem branch width
1:2BW	Non-pinnate lateral branch width
AD	Aperture diameter
ID	Interaperture distance
LBS	Lateral branch spacing
IND	Internodal distance
(not illustrated)	
PBW	Primary branch width
LBW	Lateral branch width
2:1BW	Pinnate lateral branch width
FL	Fenestrule length
FW	Fenestrule width
DW	Dissepiment width
CD	Cyclozooecial aperture diameter

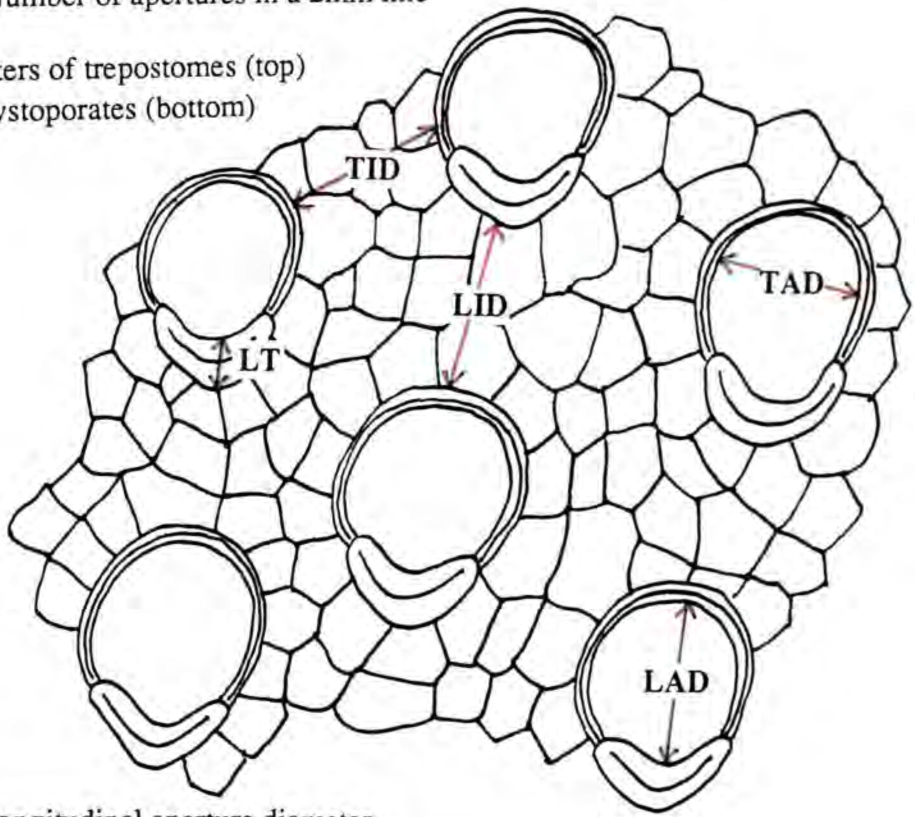


AD	Aperture diameter
IWT	Interapertural wall thickness
ED	Exilazooecial aperture diameter

(not illustrated)

ZD	Transverse branch diameter
Z1	Number of apertures in a 1mm^2 area
Z2	Number of apertures in a 2mm line

Fig. 3.8. Parameters of trepostomes (top) and cystoporates (bottom)



LAD	Longitudinal aperture diameter
TAD	Transverse aperture diameter
LID	Longitudinal interapertural distance
TID	Transverse interaperture distance
LT	Lunarium thickness

McCoy (1844) and Shrubsole (1881) were amongst the first workers to include measurements in their descriptions of bryozoan species. Russian bryozoologists in particular erected a standard classification of certain "key"-features for the fenestrate bryozoans, and this was adopted in the West as the "meshwork formula" of Condra & Elias (1944) or the "micrometric formula" of Miller (1961).

The meshwork formula considers the following parameters :

Number of branches in a 10mm line, perpendicular to growth direction (b)
Number of fenestrules in a 10mm line, parallel to growth direction (f)
Number of apertures in a 5mm line, parallel to growth direction (a)
Number of nodes in a 5mm line, parallel to growth direction (n)

These parameters are usually expressed as ranges :

$$b_{min}\text{-}b_{max} \,/\, f_{min}\text{-}f_{max} \,/\, a_{min}\text{-}a_{max} \,/\, n_{min}\text{-}n_{max}$$

However, this method indicates neither the mean of the data nor the number of specimens measured. Tavener-Smith (1966) noted this failing in the micrometric formula and showed that it was therefore not suitable for the taxonomic classification of bryozoans. Previously, several workers had erected new species based on slight differences in the micrometric formula recorded from only a single specimen. Tavener-Smith proposed the abandonment of the micrometric formula for diagnostic purposes, retaining it only as a simple "tag" on a specimen, and suggested its replacement by a series of means, standard deviations, and the actual number of measurements taken for each parameter on a species. Thus, samples can be statistically compared to each other using Student's t-test.

For a reliable Probability score, it is essential that the data has a normal distribution. This is because the t-score probability curves are derivatives of the Normal distribution curve. The parameters of many fossil groups would usually be expected to show a skewing, since the relative dimensions of most animals change with maturity. However, bryozoan colonies are constructed from a multitude of asexually-budded zooids, and though the gross colony morphology may change as the zoarium grows, the parameters of the individual zooids should remain similar. This hypothesis was tested by Stratton and Horowitz (1976) who measured the astogenetic variability in a frond of *Polypora laevinodata*. They concluded that the seven parameters which they tested (relating to aperture spacing, branch width and fenestrule dimensions) showed no significant difference between the proximal and distal portions of the colony. Thus, the parameters within a bryozoan colony appear to be Normally distributed.

When a bryozoan population from a given horizon is analysed, it is equally important that the inter-colonial parameters are also Normally distributed. This was tested with a study on specimens of *Rhabdomeson gracilis* from Laggan Cottage, Isle of Arran; the results seems to show that bryozoans do have a normal distribution of their parameters. The evidence for this was obtained from considering several aspects of the parameters, including weighted vs. unweighted means, and simple plots of frequency distributions.

One possible additional obstacle in obtaining an inter-colonial mean for use in the t-test is that the mean is usually unweighted; for instance, the inter-colonial mean, based on the intra-colonial means of a batch of several specimens, does not take into account the fact that the mean of colony A may have been derived from only 7 measurements, while that of colony B may have had 28 measurements for the same parameter. Thus, though colony B has a wider number of measurements, giving a more tightly-constrained mean than colony A, the overall inter-colonial mean does not give any extra weighting to B.

If n=number of measurements for a particular parameter on a colony, and N=number of colonies measured, then

$$\text{unweighted mean } x = \frac{\sum_{1}^{N} (\text{colony mean } x)}{N}$$

whereas a new statistical formula was defined as

$$\text{weighted } x = \frac{\sum_{i=1}^{i=N} (n_i \,.\, x_i)}{\sum_{i=1}^{i=N} n_i}$$

In the sample of *Rhabdomeson gracilis* , analysis of the aperture diameter was undertaken, since this parameter had the highest variance (σ=0.0210) . The parameters were as follows :

AS^3 6	n=9	x=0.191mm
AS^3 9	n=7	x=0.234mm
AS^3 12	n=7	x=0.163mm
AS^3 16	n=5	x=0.200mm
AS^3 18	n=5	x=0.208mm
AS^3 19	n=8	x=0.180mm
AS^3 21	n=5	x=0.208mm

Where

$$N=7 \quad n=46$$
$$_{min}=0.163\text{mm}$$
$$_{max}=0.234\text{mm}$$

Calculating the inter-colonial means gave the following results :

unweighted $x = 0.198$mm

weighted $x = 0.196$mm

The fact that there is only a small difference (about 1%) between weighted and unweighted means suggests firstly that the data is evenly distributed, and is therefore suitable for analysis by the t-test, and secondly that it is preferable to calculate an unweighted mean in view of the much simpler numerical procedure.

Likewise, inter-colonial σ is normally unweighted, and calculated as

$$\bar{\sigma} = \frac{\sum_{i=1}^{i=N} (\text{ colony standard deviation } \sigma_i)}{N}$$

A weighted standard deviation was defined in this study by

$$\text{weighted } \bar{\sigma} = \frac{\sum_{i=1}^{i=N} n_i . \left(\frac{\sigma_i}{x_i} \right)}{x . \sum_{i=1}^{i=N} n_i}$$

rather than by

$$\text{weighted } \bar{\sigma} = \frac{\sum_{i=1}^{i=N} (n_i . \sigma_i)}{\sum_{i=1}^{i=N} n_i}$$

since the value of σ depends on x, which the latter formula doesn't take into consideration.

Since

$$\frac{\sigma_i}{x_i} = \text{Coefficient of Variation}$$

then the preferred formula deduces the average intra-colonial coefficients of variation, then divides by the inter-colonial mean, thus giving an accurate weighted standard deviation.

However, as with the mean, very little difference was detected; for example, from the same locality, at the level AS4, and measuring longitudinal inter-wall thickness, which showed the greatest difference between σ (inter-colony) and average unweighted intra-colony σ the results were

$$\text{unweighted } \sigma = 0.0218\text{mm}$$

$$\text{weighted } \sigma = 0.0217\text{mm}$$

A plot of 54 fenestrule lengths of specimens of *Fenestella multispinosa*, from Snook Point in Northumberland, showed an approximation to a Normal distribution curve :

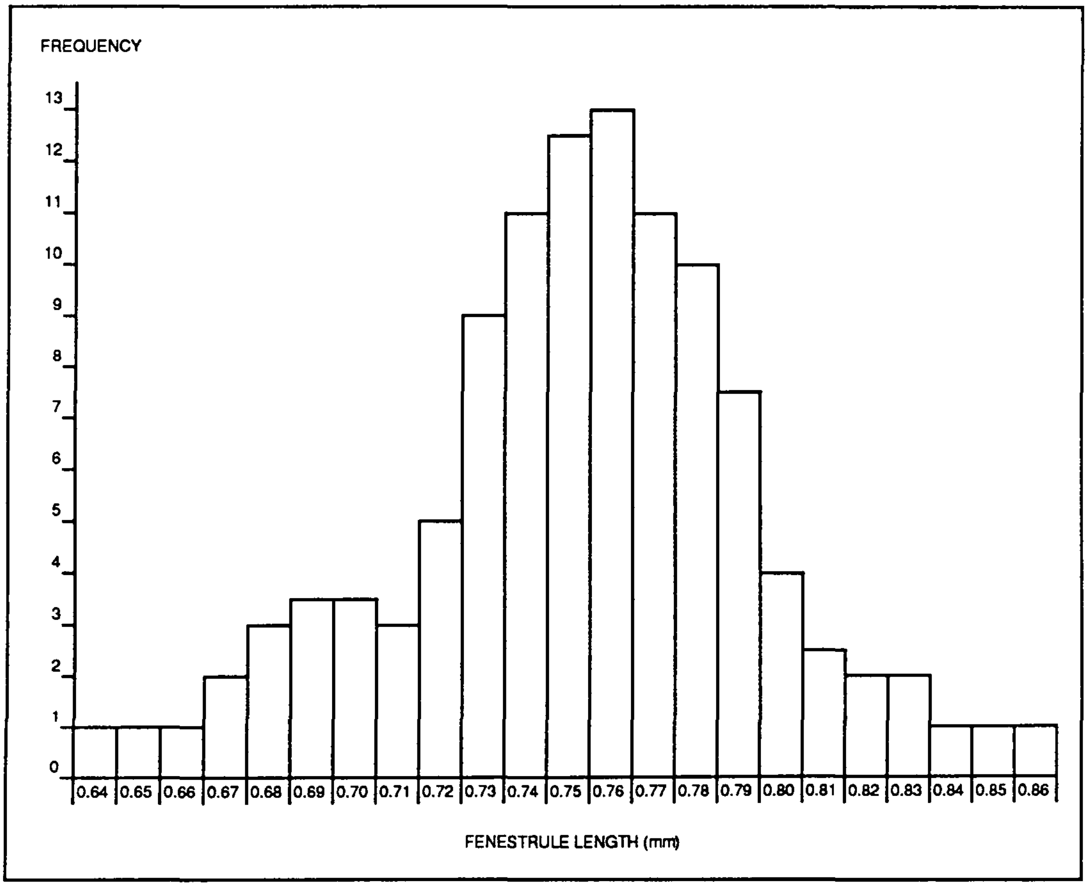


Fig. 3.9. Plot of fenestrule lengths against frequency of occurrence.

Since the data was measured to an accuracy of 0.02mm, the graph is a composite of data plotted in the 0.64-0.66,etc. range, and the 0.65-0.67,etc. range. Hence, the area under the graph is twice the actual frequency of the particular fenestrule length. The graphical mode is approximately 0.762mm, while the mean is 0.751mm; thus, the mode and mean are very close, suggesting an approximately Normal distribution.

Thus, these findings suggest that within bryozoan populations, parameters which are affected by random factors (genetic changes during budding, and micro-environmental fluctuations), seem to have a Normal distribution. The study on the Arran material has also shown that for a sample with over 7 colonies, and over 5 measurements on each colony, the parameters for bryozoans appear to be normally distributed. Thus, it is perfectly valid to apply methods of statistical analysis to bryozoan parameters using Student's t-test.

Computer Programs

As Tavener-Smith showed, the t-test is a very useful statistical method to employ in palaeontology. However, to calculate the values of t, and then to find corresponding values of the probability from standard tables is a very time-consuming job. It was therefore necessary to devise a way to speed up the calculation time, since this project involved a large amount of data. To this end, several computer programs were written, under the following names :

T-FEN : compares specimens with the standards of Bancroft (1984)

T-FEN3 : compares specimens with the standards of Tavener-Smith (1973a)

T.FEN.DIV : a more flexible program, using data stored on disc, allowing any standard to be entered, and files to be built up of representative specimens.

Though the programs use different data sets, the methods for calculating the values of t and then of the probability, are the same in each case. The flow chart (fig. 3.10) outlines the major steps in the T.FEN.DIV program. Symbols used are :

CALCULATION	Automatic action by computer
display	Screen display
option	Response to be entered by user

The main core of the program, once data on a specimen has been entered, deals with alculating the probability, by interpolating the t-score and the degrees of freedom for

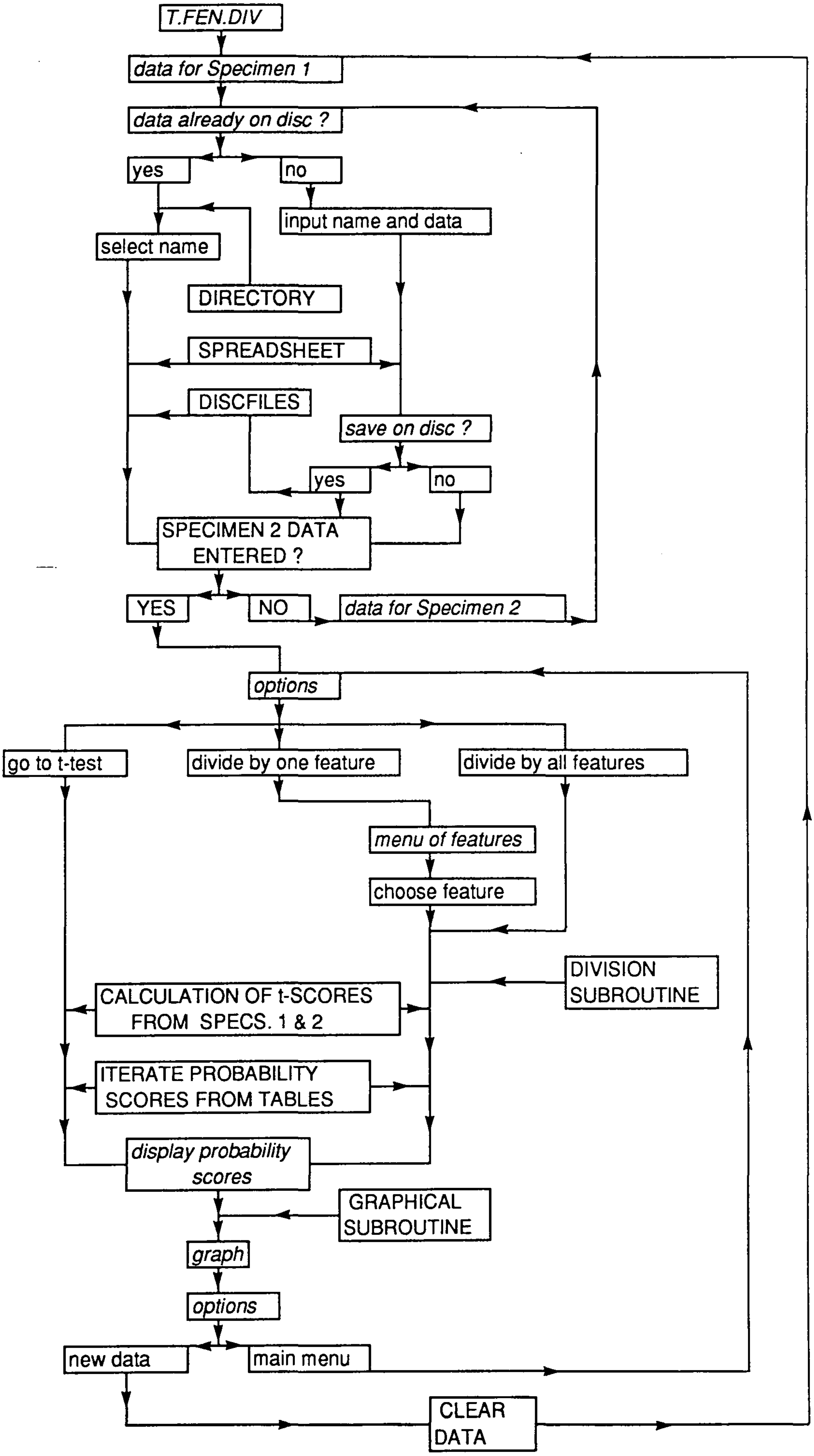


Fig. 3.10. Flow chart of the T.FEN.DIV computer program

the specimens being compared in a set of computer-resident tables. The tables were entered based on data from Hartley & Pearson (1950), which give probabilities correct to 4 decimal places. However, since the probability distribution is not a linear function (in fact, it is a rather complicated integral) it is not accurate enough to use a simple linear interpolation to determine the probability (ie. an "average" of the value between two columns within the tables). Instead, double-entry interpolation is used, as described by Hartley & Pearson :

Let t_{-1}, t_0, and t_1 equal successive tabular values of t such that

$$t_0 <= t <= t_1$$

and then let

$$q = (t - t_0) / (t_1 - t_0)$$

If there are v degrees of freedom, then let v_0 and v_1 be two successive tabular values of v such that

$$v_0 <= v <= v_1$$

then let

$$f = v - v_0$$

Thus the overall probability is calculated from the tables using

$$P(t,v) = P_{00}(1 - q - f + qf) + P_{10}(q - qf) + P_{01}(f - qf) + P_{11}qf$$

where $P_{ij} = P(t_i,v_j)$.

The programs were written in BBC BASIC which is a flexible, if a little outdated language, enabling a combination of numerical and graphical procedures. A model B BBC machine was used, equipped with the memory expander *SHADOW, which was necessary for the size of the programs. The original BBC BASIC program was later transferred onto an IBM PS/2 (model 55 SX) using the KERMIT and HOST facilities on the Durham MTS mainframe system. The acquisition of the program BBASIC from Border Computing and Programming enabled programs written in BBC BASIC to run on the much more powerful IBM-compatible machines. In this way, TFENDIV, the IBM version of T-FEN-DIV was produced, and slightly rewritten such that it is more "user-friendly". TFENDIV is much faster than its precursor, and allows quicker access to a larger number of data files. A copy of the program is lodged with the Department of Geological Sciences, University of Durham, and a listing of TFENDIV is given in the appendix, with instructions on how to load the program.

Using T-FEN, which compares probabilities for Bancroft-cited material, a spreadsheet of probability scores could be obtained in approximately 50 seconds. If the program had been written in FORTRAN, the speeds of results would undoubtedly have been more rapid. However, the results obtained from the programs were very accurate, and correlated exactly with those calculated by hand. The version produced for IBM machines is much quicker, and results are calculated almost instantaneously.

The t-test is very discriminating, which can be a disadvantage when relatively small parameters are being measured, since the accuracy of measuring is a limiting factor; for instance, the aperture diameter has an average value of around 0.10mm for many fenestellids, but the limiting size of the graticule is only 0.01mm, and more normally 0.02mm. Thus, the true error range in aperture diameter is 0.08mm to 0.12mm, but specimens at end points of this range would rate 0.0000 on the probability score when compared to a diameter of 0.10mm.

Thus, it is not practicable to assume that the probability score is an accurate measure of comparison, but should be treated only as a broad indicator of likelihood. When looking at a sample, a score of 0.0000 should not necessarily be taken to indicate that the sample does not belong to the species against which it is being compared. With this method, it is a series of relatively high probability scores which should indicate taxonomic affinities, rather than low scores being used to nullify the affinity. However, the larger the parameter being compared, the smaller the error in measurement, so features such as fenestrule length (which usually ranges from about 0.50mm to over 3.00mm) will have a more reliable probability score than the small aperture diameter, or dissepiment width. In such a case, two samples with a probability score of 0.0000 for the fenestrule length can be considered to be distinct species.

Tavener-Smith (1966) used just one feature to distinguish the affinities of three samples, by analysing the fenestrule width. He followed in the line of thought of Williams (1962) who, when analysing Caradocian brachiopods, suggested that a difference in one feature between samples would be enough to merit the erection of a sub-species, while a difference in two characteristics would indicate a new species. It is believed here that much more caution is needed when using statistical methods to ascertain the affinities of a sample, and that a statistical difference should be coupled with a morphological distinction before a new species can be erected confidently.

One additional feature of T.FEN.DIV, not present in the other t-test programs, is a new statistical method for testing for stunting of a population or of an individual. If a specimen has exactly the same ratio of its parameters, but is smaller than the standard for that species, then the t-test will simply return rather low probability scores. Using such results, a worker may erect an entirely new species for the sample, even though norphologically it may appear identical to the original, larger species. The '.FEN.DIV program overcomes this possible problem by allowing calculations of the t-score based on the ratios of the parameters for the specimen and the standard. Tavener-Smith noted that there was a weak positive correlation between certain features in fenestrate bryozoans. Thus, if a species has a large fenestrule length and interapertural distance, then a stunted representative would be expected to have not only a smaller fenestrule length, but also a correspondingly smaller interapertural distance.

If x_m represents the mean of the feature which the other parameters are divided by, and there are T features which have been measured, then the probability that $spec_1$ is related to $spec_2$ regarding feature m, is

$$P[x_{1m}.x_{2m}] = \frac{\sum_{f=1}^{f=m-1} P\left[\left(\frac{x_{1f}}{x_{1m}}\right).\left(\frac{x_{2f}}{x_{2m}}\right)\right] + \sum_{f=m+1}^{f=T} P\left[\left(\frac{x_{1f}}{x_{1m}}\right).\left(\frac{x_{2f}}{x_{2m}}\right)\right]}{(T-1)}$$

and thus the overall probability regarding all the measured features is

$$P[spec_1.spec_2] = \frac{\sum_{m=1}^{m=T} P[x_{1m}.x_{2m}]}{T}$$

A study on some specimens of *Fenestella tuberculo-carinata* again from the Asbian shales of Arran seemed to show such an instance. The material had external features similar to *Fenestella tuberculo-carinata* but a series of measurements made using a graticule in one of the microscope's eyepieces showed that all the parameters were consistently smaller that those obtained by Bancroft when measuring *F. tuberculo-carinata* (plotted by TFENDIV in fig. 3.11) :

	Fenestella cf. tuberculo-carinata			*F. tuberculo-carinata*
	n	σ	x	x
BW	14	0.0186	0.245	0.30
AD	3	0.0062	0.088	0.09
ID	3	0.0185	0.201	0.23
FL	22	0.0404	0.624	0.73
FW	22	0.0541	0.460	0.57
DW	14	0.0382	0.169	0.20
IND	5	0.0141	0.152	0.20

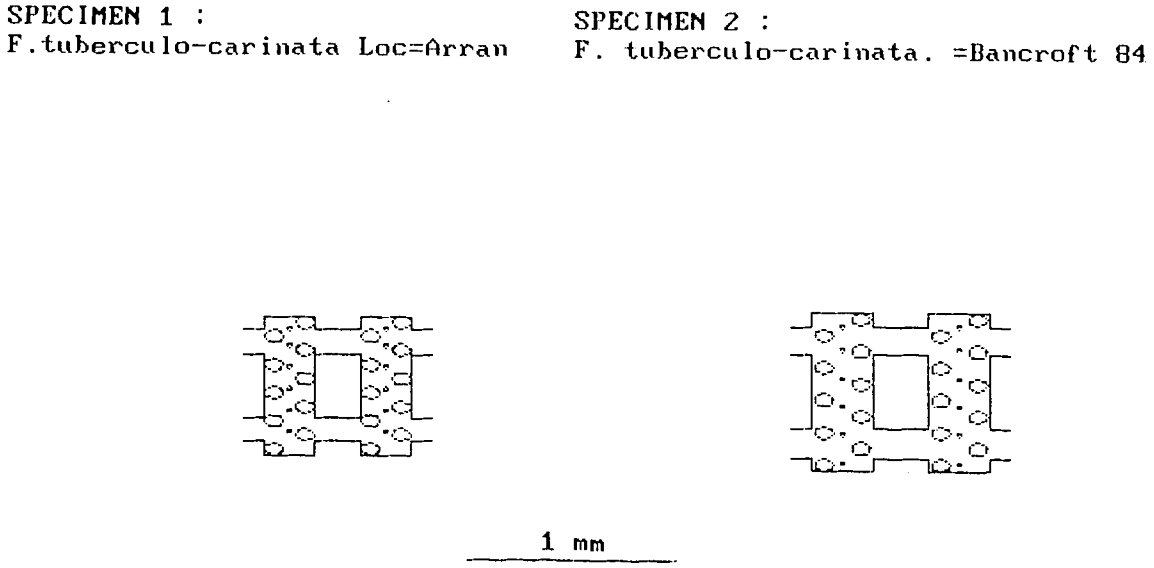
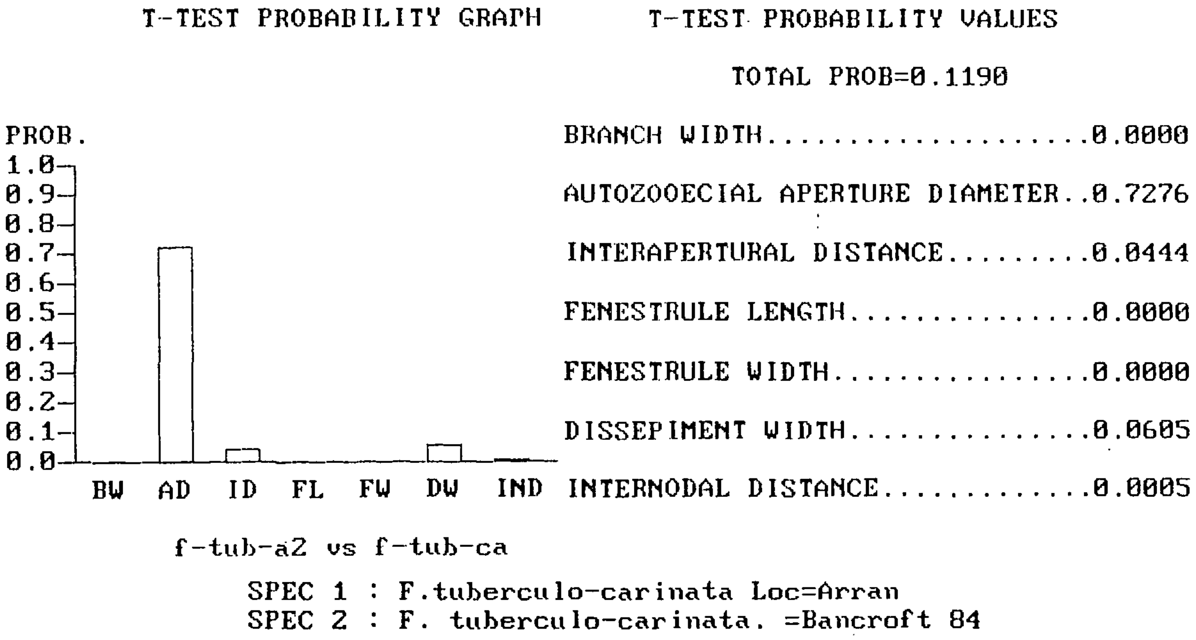


Fig. 3.11. Comparison of *F. tuberculo-carinata* from computer drawing



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T-TEST PROBABILITY VALUES

TOTAL PROB=0.1190

BRANCH WIDTH....................0.0000

AUTOZOOECIAL APERTURE DIAMETER..0.7276

INTERAPERTURAL DISTANCE.........0.0444

FENESTRULE LENGTH...............0.0000

FENESTRULE WIDTH................0.0000

DISSEPIMENT WIDTH...............0.0605

INTERNODAL DISTANCE.............0.0005

f-tub-a2 vs f-tub-ca

SPEC 1 : F.tuberculo-carinata Loc=Arran
SPEC 2 : F. tuberculo-carinata. =Bancroft 84
```

Fig. 3.12. Uncorrected t-test scores between Arran and Bancroft's material

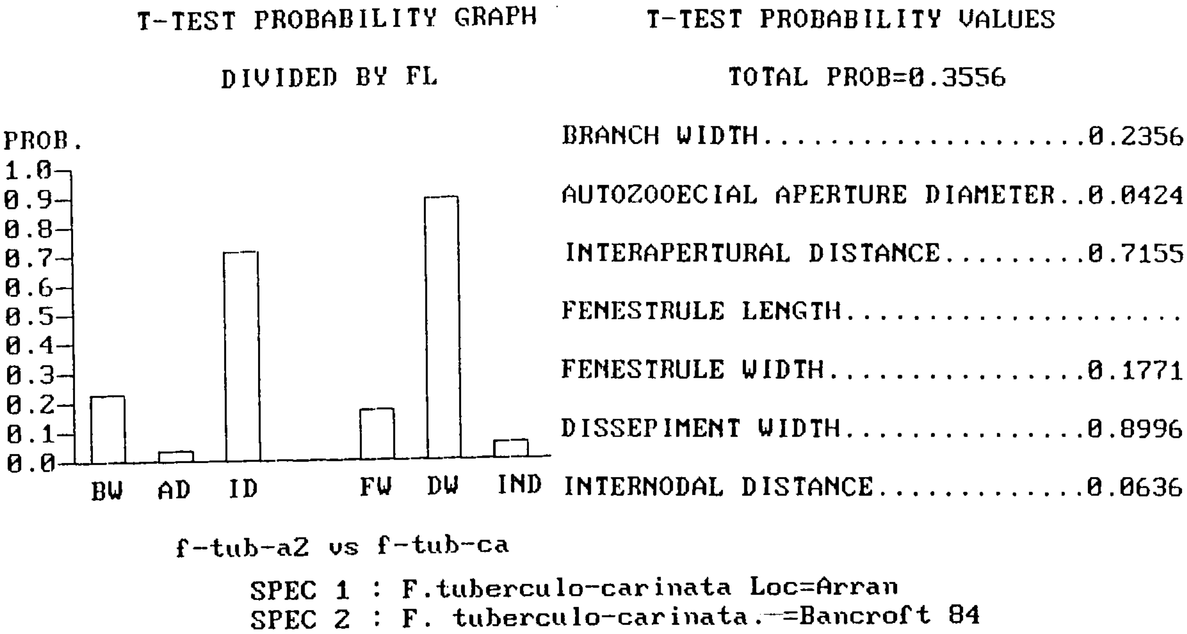
These figures are represented graphically in fig. 3.12, a printout of a representation of the species drawn by the TFENDIV program.

Thus, when a standard t-test was carried out on the material, the resulting probabilities suggested affinities with other fenestellids :

PROBABILITY SCORES USING T.FEN.DIV AND NORMAL t-TEST			
	F. tuberculo-carinata	*F. frutex*	*F. multispinosa*
BW	**0.0000**	**0.4354**	**0.5386**
AD	**0.6892**	**0.7391**	**0.5131**
ID	**0.0200**	**0.0203**	**0.0000**
FL	**0.0000**	**0.0001**	**0.0150**
FW	**0.0000**	**0.0961**	**0.0139**
DW	**0.0455**	**0.0000**	**0.0002**
IND	**0.0001**	**0.0000**	**0.0000**

However, by calculating the ratios for each parameter, and then comparing the specimens and the standards gave quite different results. The TFENDIV program works by taking each feature for the sample and the standard, and dividing throughout the whole range of parameters by the value for that feature. For example, in this case the program would firstly divide all the parameters for the sample by the branch width (0.245mm), and then compare them with the ratios obtained by dividing the parameters of the standard by the standard's branch width (0.30mm), giving the following ratios :

VALUES DIVIDED BY BRANCH WIDTH		
	F. cf. tuberculo-carinata	*F. tuberculo-carinata*
	x	**x**
BW	**1.000**	**1.000**
AD	**0.359**	**1.000**
ID	**0.820**	**0.766**
FL	**2.547**	**2.433**
FW	**1.878**	**1.900**
DW	**0.690**	**0.667**
IND	**0.620**	**0.667**



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T-TEST PROBABILITY GRAPH        T-TEST PROBABILITY VALUES

     DIVIDED BY FL                   TOTAL PROB=0.3556

                          BRANCH WIDTH...................0.2356

                          AUTOZOOECIAL APERTURE DIAMETER..0.0424

                          INTERAPERTURAL DISTANCE.........0.7155

                          FENESTRULE LENGTH...................

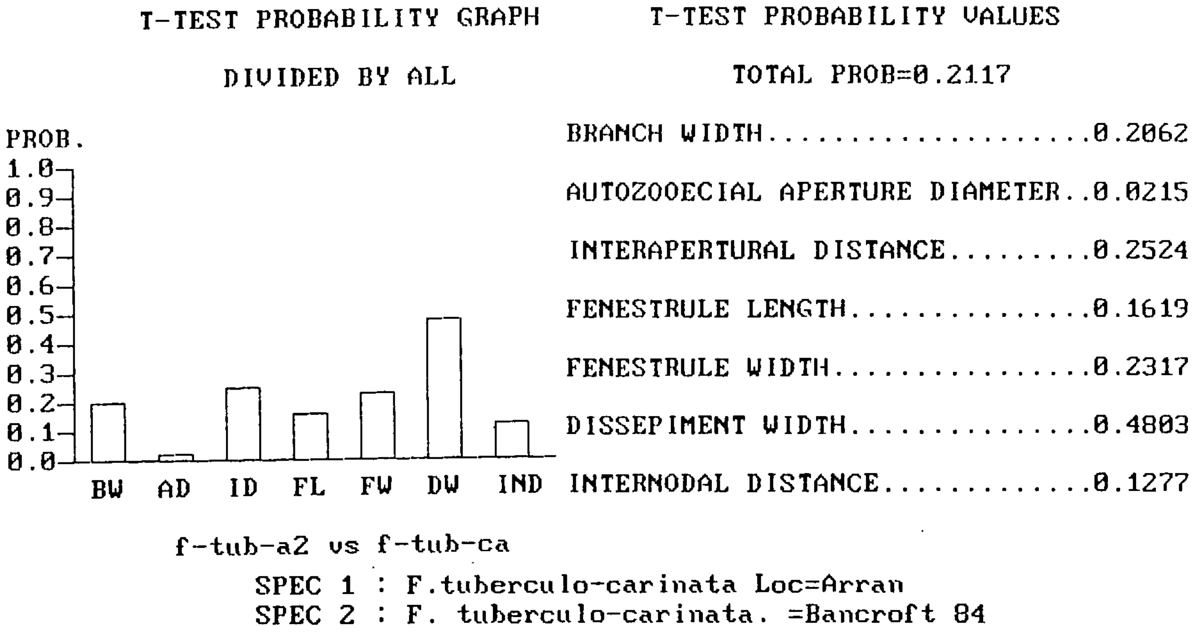
                          FENESTRULE WIDTH................0.1771

                          DISSEPIMENT WIDTH...............0.8996

                          INTERNODAL DISTANCE.............0.0636

     f-tub-a2 vs f-tub-ca
         SPEC 1 : F.tuberculo-carinata Loc=Arran
         SPEC 2 : F. tuberculo-carinata.—=Bancroft 84
```

Fig. 3.13. t-test comparison of material when divided by fenestrule length



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T-TEST PROBABILITY GRAPH        T-TEST PROBABILITY VALUES

     DIVIDED BY ALL                  TOTAL PROB=0.2117

                          BRANCH WIDTH...................0.2062

                          AUTOZOOECIAL APERTURE DIAMETER..0.0215

                          INTERAPERTURAL DISTANCE.........0.2524

                          FENESTRULE LENGTH...............0.1619

                          FENESTRULE WIDTH................0.2317

                          DISSEPIMENT WIDTH...............0.4803

                          INTERNODAL DISTANCE.............0.1277

     f-tub-a2 vs f-tub-ca
         SPEC 1 : F.tuberculo-carinata Loc=Arran
         SPEC 2 : F. tuberculo-carinata. =Bancroft 84
```

Fig. 3.14. Division t-test scores from uncorrected Arran and Bancroft's material

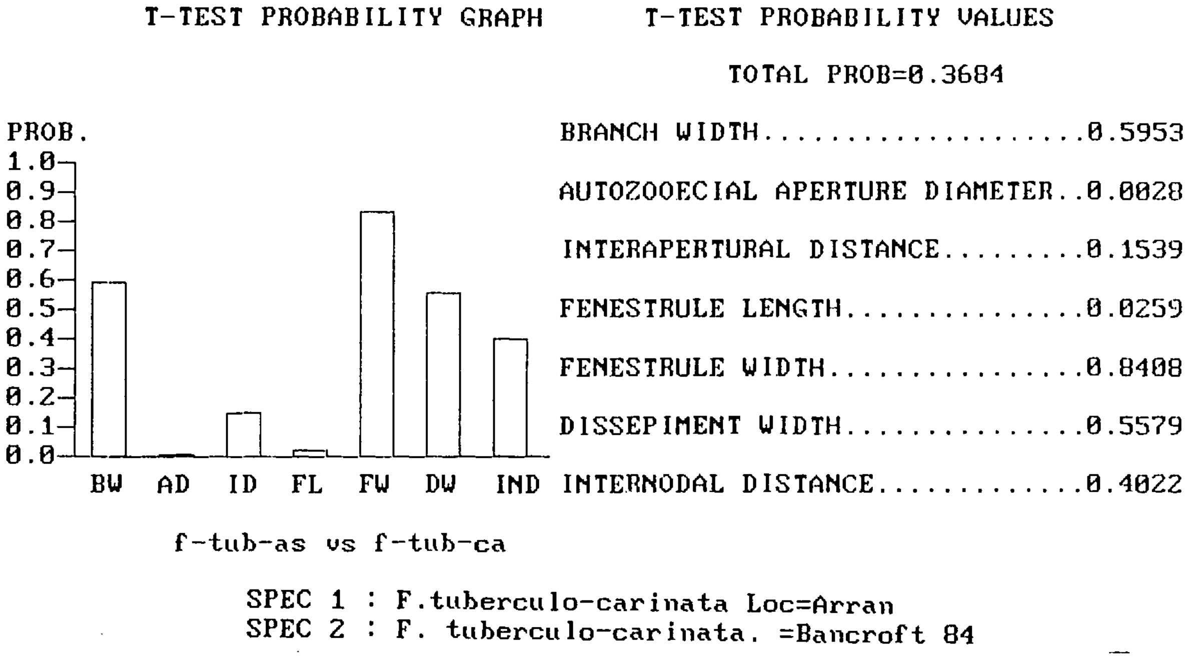
A similar result is obtained when the original data is divided throughout by the fenestrule length of each of the species, and this result is illustrated in fig. 3.13.

The computer repeats these divisions for all the characters, and then calculates an average probability score for each character, together with an overall probability. This result is illustrated in fig. 3.14, indicating that sample F-tub-a2, based on the original measurements of *Fenestella* cf. *tuberculo-carinata* from Laggan Cottage is, in fact, a scaled-down version of the more usual *F. tuberculo-carinata* from the Midland Valley. Division test comparisons with other species of *Fenestella* produced the following results:

PROBABILITY SCORES USING T.FEN.DIV AND DIVIDING BY ALL			
	F. tuberculo-carinata	*F. frutex*	*F. multispinosa*
BW	0.1795	0.0653	0.0346
AD	0.0111	0.1648	0.1284
ID	0.1952	0.0106	0.0000
FL	0.1514	0.0137	0.0551
FW	0.2057	0.0814	0.0602
DW	0.4477	0.0000	0.0000
IND	0.0987	0.0000	0.0000
TOTAL	0.2159	0.0380	0.0442

It can be seen from the above tables that had the normal t-test been used, then the specimens would not have been assigned to *Fenestella tuberculo-carinata*, but more likely to *F. frutex* or *F. multispinosa*. However, the specimens actually possessed features which were very typical of *F.tuberculo-carinata*, so it is interesting to see that when the ratios are compared, the true affinity of the specimens is highlighted.

Further analysis of the material, coupled with measurements on other species, showed that the specimens from Arran were not actually stunted: rather, the microscope graticule had been incorrectly calibrated, so all measurements were reduced by a factor of x0.8 ! A t-test comparison of the corrected measurements of the Arran material with Bancroft's "standard" *F. tuberculo-carinata* is shown in fig. 3.15, indicating that the material is, indeed, referable to this species. It is also important to note that the division t-test scores (fig. 3.16) are the same for the correctly-scaled material as for the scaled-down measurements, indicating the validity of this method. The division t-test method, originally developed to solve the problem



T-TEST PROBABILITY GRAPH

T-TEST PROBABILITY VALUES

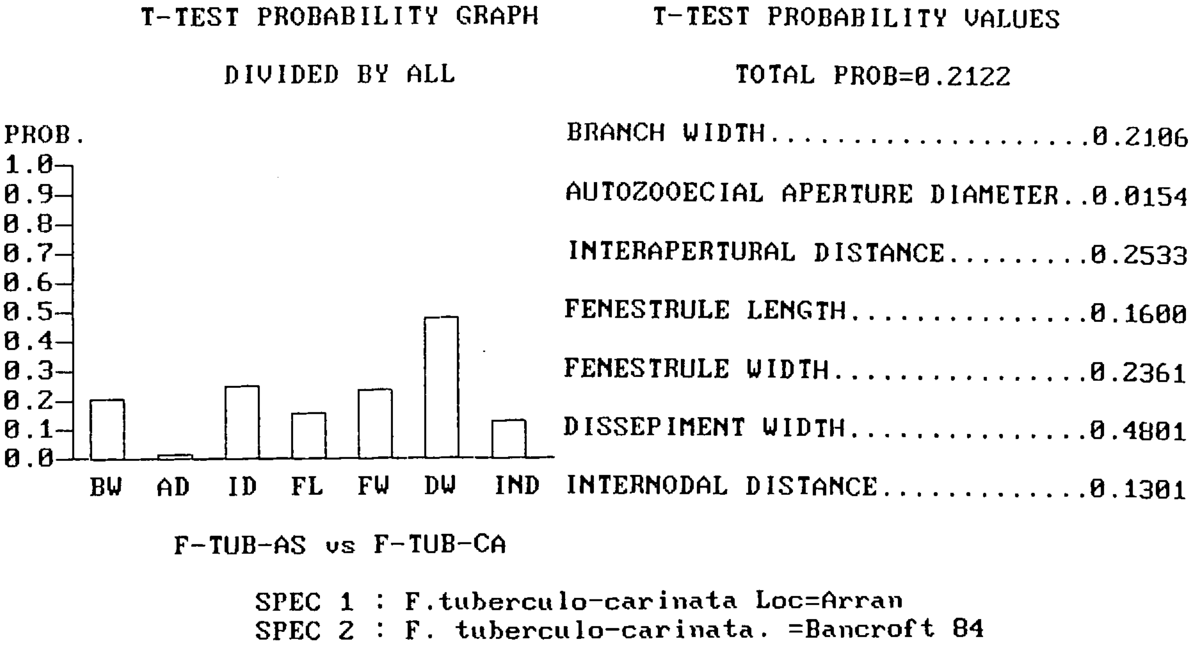
TOTAL PROB=0.3684

BRANCH WIDTH....................0.5953
AUTOZOOECIAL APERTURE DIAMETER..0.0028
INTERAPERTURAL DISTANCE.........0.1539
FENESTRULE LENGTH...............0.0259
FENESTRULE WIDTH................0.8408
DISSEPIMENT WIDTH...............0.5579
INTERNODAL DISTANCE.............0.4022

f-tub-as vs f-tub-ca

SPEC 1 : F.tuberculo-carinata Loc=Arran
SPEC 2 : F. tuberculo-carinata. =Bancroft 84

Fig. 3.15. Corrected t-test scores between Arran and Bancroft's material



T-TEST PROBABILITY GRAPH

DIVIDED BY ALL

T-TEST PROBABILITY VALUES

TOTAL PROB=0.2122

BRANCH WIDTH....................0.2106
AUTOZOOECIAL APERTURE DIAMETER..0.0154
INTERAPERTURAL DISTANCE.........0.2533
FENESTRULE LENGTH...............0.1600
FENESTRULE WIDTH................0.2361
DISSEPIMENT WIDTH...............0.4801
INTERNODAL DISTANCE.............0.1301

F-TUB-AS vs F-TUB-CA

SPEC 1 : F.tuberculo-carinata Loc=Arran
SPEC 2 : F. tuberculo-carinata. =Bancroft 84

Fig. 3.16. Division t-test scores between corrected Arran and Bancroft's material

of the "small" Arran bryozoans, has been incorporated in many bryozoan studies in this thesis, and has proved to be a useful statistical tool.

In summary, the t-test as developed in work for this thesis, appears to be a very useful tool in the identification of bryozoans. Since populations are normally-distributed, accurate t-test scores can be obtained using the various computer programs. Additionally, even with only a relatively small number of measurements on a relatively small population, a fairly confident probability score can be calculated, which should make this type of statistical method very useful to practical research workers.

PART II : FIELDWORK LOCALITIES

CHAPTER 4 : EAST FIFE

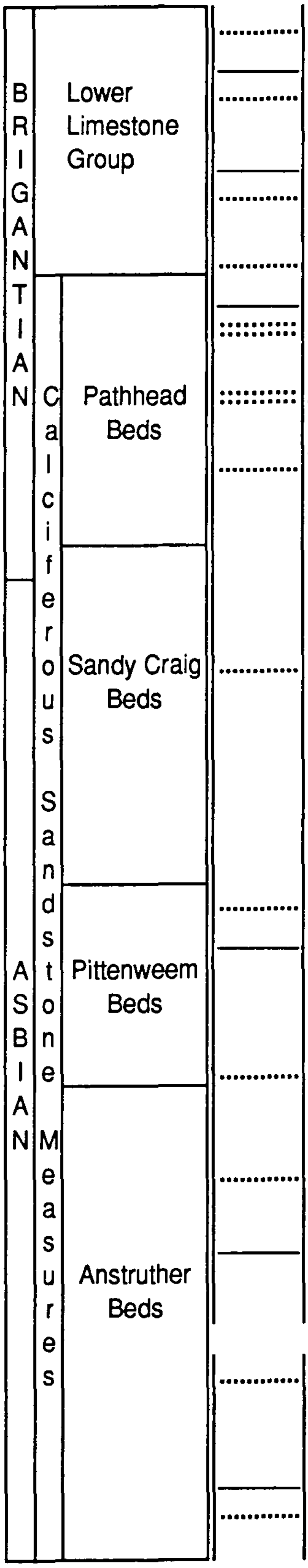
Stratigraphy and Palaeogeographical Setting

East Fife provided a good area for the collection of Carboniferous bryozoans for this study, since sediment types and facies are similar to those of Northumberland, where a previous field season had been spent. The coastal exposure in Fife is very good, and the section of coast between St. Andrews and St. Monance was surveyed as comprehensively as time and weather would allow. The Geological Survey's Memoir on the area (Forsyth & Chisholm, 1977) provided useful information on the marine horizon localities, giving eight-figure grid references, but sadly sand and sea have obscured some important horizons.

East Fife represents a nearshore sequence, lying to the east within the Midland Valley trough, dominated for much of the Dinantian by cyclic deltaic sedimentation. To the north lay the supercontinent of Laurasia, and to the south the Southern Uplands Block, with a link through to the Tweed and Northumberland basins. Research by several workers on faunal migration (Nudds & Johnson, 1985; Wilson, 1989) suggests that there was a prevalent ocean current from the east, and certainly this corresponds with eastward sediment transport patterns from the deltaic sequences (Wilson, 1989). The Southern Uplands Block was thought to have been of low relief (very little Carboniferous sediment was derived from it), and should not have presented a great barrier to faunal migration round the eastern margin.

The stratigraphical table lists the major marine horizons in East Fife (fig. 4.1). Those shown in bold type yielded bryozoans during the fieldwork, and are described in this chapter. The table shows grid references, localities, and locality abbreviations used in this study. The remaining horizons are indicated in light type and have a dashed line in the formation column; those which were surveyed during this study but yielded no bryozoans have "no bryozoans found" after the name. The table is compiled from Forsyth & Chisholm (1977) and from George *et al.* (1976), but the Asbian/Brigantian boundary is not actually well-constrained; all of the Lower Limestone Group is known to be Brigantian from both goniatite (Currie, 1954) and miospore (Neves *et al.*, 1973) evidence, and much of the Calciferous Sandstone Measures are Asbian. The boundary probably lies between the West Braes Marine Band and the Boat Harbour Marine Band.

Fig. 4.2 shows the position of the bryozoan collection localities from the East Fife coast.



Formation	Grid ref.	Locality	Abbr.
Upper Kinniny Lst.			
Mid Kinniny Lst.	**NO 5296 0169**	**St. Monans**	**MMK**
Mill Hill Lst.			
Charlestown Main Lst	**NO 5372 0220**	**Pathhead**	**PCM**
St. Monance Little Lst.			
St. Monance Brecciated Lst	(no bryozoans found)		
St. Monance White Lst.	**NO 5241 0146**	**Partan Craig**	**PCB**
Pathhead Marine Bands	**NO 5379 0213**	**Pathhead**	**PMW**
Ardross Lsts.			
West Braes Marine Band			
Boat Harbour Marine Band			
St. Andrews Castle M.B.	(no bryozoans found)		
Witch Lake Marine Band	**NO 542 153**	**Rock & Spindle**	**RSW**
	NO 526 158	**Maiden Rock**	**MRW**
Cuniger Rock Marine Band	(no bryozoans found)		
Chain Road Marine Band	(no bryozoans found)		
Billow Ness Marine Band	**NO 5609 0279**	**Pittenweem**	**PBN**
Anstruther Wester M.B.			
Randerston Lst. No.5	**NO 6133 1133**	**Randerston**	**RRL**
Wormistone Lsts.			

Fig. 4.1 Stratigraphy and Bryozoan Localities in East Fife

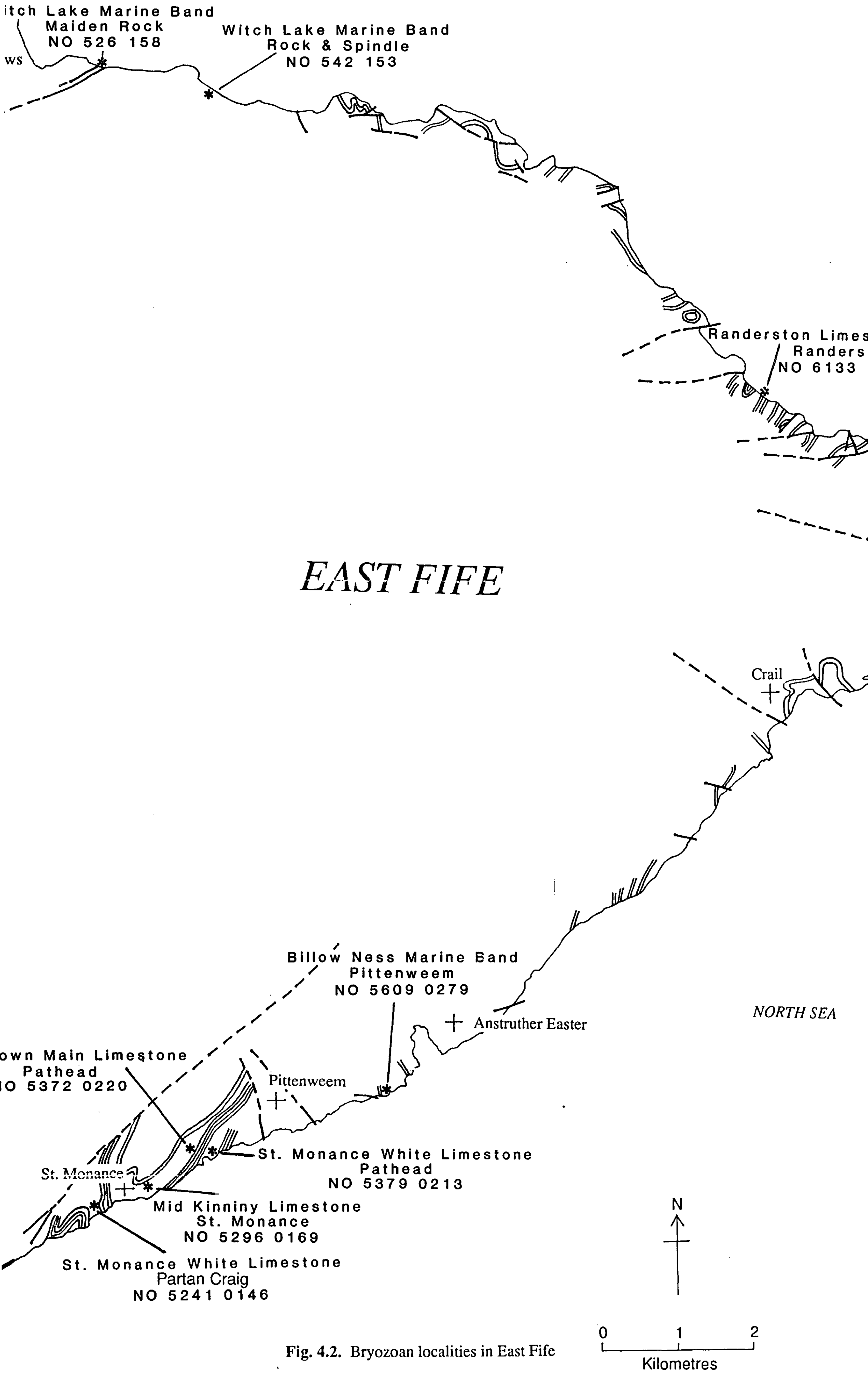


Fig. 4.2. Bryozoan localities in East Fife

The succession of beds at East Fife is actually the thickest Dinantian sequence in the Midland Valley (George *et al.*, 1976, p50.) and Forsyth & Chisholm (1977) give the following thicknesses :

Lower Limestone Group	180m (approx.)
Pathhead Beds	311m
Sandy Craig Beds	557+m
Pittenweem Beds	220+m
Anstruther Beds	813+m

Though several workers have catalogued the Carboniferous fauna and flora of East Fife, bryozoans are usually deal with in only a superficial manner. Kirkby (1880) gave the most thorough account of the fauna, and identified several bryozoans down to species level; however, his collection was dispersed after his death, so it has not been possible to trace the specimens which he had recovered from the area. Wilson (in Forsyth & Chisholm, 1977) gave listings of several bryozoans, with horizons and localities recorded, but in only a few instances did he identify them beyond generic level. The bryozoan record of both these workers are given in the stratigraphical range table (fig. 4.10) at the end of this chapter.

Randerston Limestone No. 5

GRID REFERENCE : NO 6133 1133
AGE : Asbian

The Randerston shoreline is noted for the occurrence of a series of limestones of early Asbian age, known as the Randerston Limestones. During the season of study in Fife, most of these limestones were examined, but many were not wholly marine, being dominated by *Schizodus* bivalves and gastropods. Though the Geological Survey Memoir of the district (Forsyth & Chisholm, 1977) records the occurrence of various bryozoans in the limestones, the exact horizons are not listed. In this present survey, bryozoans were encountered only in the Randerston Limestone no. 5.

This limestone is a grey micrite, about 50cm thick, with a diverse fauna of brachiopods, crinoids, and some poorly preserved tube-like structures approximately 1cm by 0.2cm^2 in volume. Under the microscope, it is seen that these "tubes" are covered in a mosaic of polygonal-walled zooids, often with thicker stylet-like structures at wall meeting-points (fig. 4.5a). It is believed that the "tubes" may actually be bryozoans; the faunal list of Kirkby (1880) lists *Stenopora* (now *Stenodiscus*) from the Randerston section.

Certainly, the cylinders are reminiscent of trepostomes, with polygonal interzooecial walls, but if they are bryozoans then they appear to have been rolled in the sediment prior to burial, removing the outermost layer of the skeleton, since the interchamber walls are rather thin. Chamber diameters can be varied, ranging from 0.12mm to 0.20mm, and the chambers (possibly autozooecial chambers) are irregularly arranged.

Acetate peels were prepared from one sample (fig. 4.5b), taken at successive intervals through the rock, and displaying various levels through the fossils. However, the fossils are rather recrystallised, and the wall-structure, which could have been indicative of trepostome affinities, had been destroyed. The peels did show, though, that the fossils are composed of chambers apparently curving upwards from an axial region. No hemisepta or diaphragms were seen.

The general size of the fossils, and the polygonal walls suggest that they are actually trepostomes of some sort, but the recrystallisation of the internal structures means that it is not possible to conclusively prove this. Examination of better-preserved specimens may show the material to belong to the dasycladid algae. The genus *Koninckopora* bears some similarity to the Randerston specimens, and Wood (1942) demonstrated that *Koninckopora* was most probably an alga, and not a bryozoan as Lee (1912) had tentatively suggested.

The fauna of Randerston Limestone no. 5 seems to be fairly nearshore, especially since small fragments of driftwood are abundant, with lingullelid brachiopods and various high-spired gastropods, together with some strongly growth-line ornamented bivalves and smooth ostracods. The community is referable to the *Modiolus* Community of Ramsbottom (1978), but perhaps not as hypersaline as is typical of this assemblage. The abnormal salinity of this environment may indicate that the possible trepostome specimens are more likely to belong to the dasycladid algae.

The Billow Ness Marine Band

GRID REFERENCE : NO 5609 0279
AGE : Asbian

At Pittenweem, in a small cutting at the top of the high water mark, there is a sequence of shales and ironstones, representing the Billow Ness Marine Band. The fauna is, as in the Randerston Limestone No. 5, typical of a nearshore environment, with possibly hypersaline conditions, as an algal limestone, together with ostracod-rich shales and a *Lingula* band are developed (a graphic log of this section is given in fig. 4.3).

One ferruginous limestone, towards the top of the sequence, contained algal nodules and one possible bryozoan (fig. 4.5c. and fig. 4.5d); this is a rather poorly-preserved specimen measuring 6cm in length, with rounded chambers and thick "interzooecial walls".

These "chambers" have an unusual structure, being infilled by two types of calcium carbonate, an outer, thin white porcellanaceous layer, and an inner fill of coarser grey carbonate. The chambers are surrounded by the grey matrix of the micritic limestone, and also by carbonaceous filaments.

The rounded shape of the chambers, and the nature of the material between them, suggests that this is not actually a bryozoan. However, its exact taxonomic affinities are still not certain, though the specimen may be a calcified dasycladid algae. Unfortunately, the material is not particularly well-preserved, and a thin section would therefore reveal little information about the internal structure.

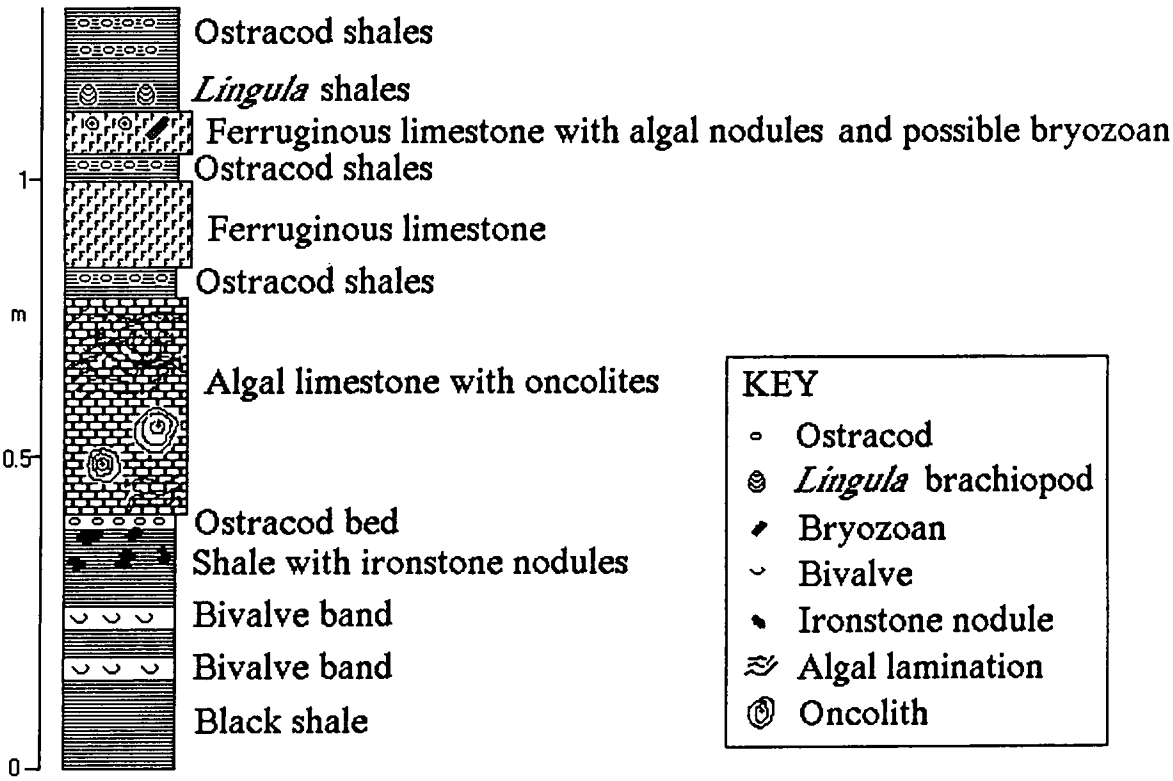


Fig. 4.3. Graphic Log of the Billow Ness Marine Band

The Witch Lake Marine Band
Maiden Rock & Rock and Spindle

GRID REFERENCE : NO 526 158
AGE : Asbian

The two localities, Maiden Rock and the Rock & Spindle, expose the same horizon, a red limestone approximately 15cm thick. By the Rock and Spindle, only scattered blocks of this limestone were recovered, but at Maiden Rock the horizon is better developed, and occurs sandwiched between two metres of a shale which yields some plant remains.

The red limestone contains abundant crinoid ossicles, especially nearer the top of the unit, and hence it was formerly known as the Encrinite Bed. Fenestellid bryozoans are also very abundant in this top layer, but were only visible on weathered surfaces. They occur as relatively well-preserved fan- and half-cone- shaped colonies.

The Witch Lake Marine Band also occurs about 250m east of the Maiden Rock at NO 529 157. The limestone band is not as well-developed, and thinner, more irregular bands and lenses occur, with a fauna of bivalves, brachiopods, and crinoids. The thickest limestone is particularly rich in these taxa, but this locality did not yield any bryozoans.

The relatively large size of the bryozoan colony fragments recovered at the first two localities, and their absence from the third, suggests that they were found almost *in-situ* in a rather local bryozoan bank. The whole of this marine unit, though, has a very wide distribution across Fife.

Jas W. Kirkby (1880) mentions finding *Fenestella tuberculo-carinata* and *Stenopora tumida* at this locality. Only material referable to the former was found in the fieldwork conducted for this thesis. Kirkby also records the occurrence of this horizon at Pittenweem, and here *Fenestella plebeia* and *F. morrisi* are reported to occur in addition to *Fenestella tuberculo-carinata.*

Fenestella tuberculo-carinata

The parameters for the specimens from the Witch Lake Marine Band are given in the table on the following page:

	Fenestella cf. tuberculo-carinata			*Fenestella tuberculo-carinata*	
	MRW1				
	n	σ	x	x	T.FEN.DIV PROB
BW	6	0.0138	0.296	0.30	0.7574
AD	15	0.0200	0.121	0.09	0.0000
ID	17	0.0193	0.240	0.23	0.1642
FL	16	0.0561	0.671	0.73	0.0157
FW	15	0.0344	0.556	0.57	0.4208
DW	15	0.0100	0.129	0.20	0.0000
IND	10	0.0227	0.128	0.20	0.0000

Specimens are moderately well-preserved, enabling confident descriptions, but most colonies show only the reverse surface. Examples showing the obverse surface were not common, and those that did were usually obscured by matrix such that only the carina was clearly visible. Specimen MRW1 (fig. 4.7a; Plate 2, fig. g.) was by far the best-preserved example, and its measurements are outlined in the table. However, even this specimen has been weathered, with many peristome rims and carinal nodes being removed.

The specimens of *Fenestella tuberculo-carinata* have thick branches and a very prominent, rather broad median carina. This carina is ornamented by very closely-spaced nodes (av. internodal distance is about 0.128mm) which are unfortunately rather weathered in all the examples collected. The carina, like the branches, can be gently sinuous, but the branches are more usually rather straight and sub-parallel; extra branches form by bifurcation and are quickly accommodated within the regular meshwork. Branch sides slope steeply away from the carina.

Dissepiments on the obverse surfaces are seen to be only of moderate width, but do show considerable flaring towards the branches. Often they have a poorly-defined median carina, and this is noticeable in that it also flares towards the carinae of the main branches, irrespective of whether there is an aperture developed at the dissepiment/branch junction. Dissepiments appear virtually flush with the branches on the obverse surface.

Apertures are very prominent, and are sunk into the branch sides; well-preserved apertures show thick peristome rims, which sometimes project into the fenestrules. There are about 3 to 4 apertures per fenestrule.

The reverse surfaces can be very variable in appearance. Branches are usually sub-parallel and straight (fig. 4.7b; Plate 2, fig. e.), only occasionally becoming regularly-sinuous, developing a hexagonal "honeycomb" pattern. Usually pustules are developed in closely-spaced longitudinal rows, but sometimes the reverse surfaces appear to be smooth, possibly due to weathering. Seen from the reverse surface, dissepiments are slightly depressed or flush with respect to the branches, and all appear to be smooth and well-rounded. They flare only a little towards the branches, and have a more bar-like appearance.

The specimens from the Witch Lake Marine Band compare well with *Fenestella tuberculo-carinata* Etheridge Jun. 1873, most noticeably in possessing a broad median carina, in having prominent apertures with thick peristome rims, and in possessing very flared dissepiments. However, the specimens differ from the descriptions of Bancroft (1984) in several ways:

Statistically, the TFENDIV division t-test shows a close match to *Fenestella tuberculo-carinata* : an overall probability score of 0.1364 was obtained (cf. vs. *F. plebeia* ,0.0376 ;vs. *F. multispinosa* ,0.0166), but in several parameters the specimen MRW1 departed from the standards. Aperture diameter comparisons rated a t-test probability of 0.0000; this is probably because many of the apertures were weathered, and so appeared to be larger than they were originally. The dissepiment width also scored 0.0000, since MRW1 had an average width of only 0.128mm whereas the standards have an average of 0.20mm. An explanation may be that not all of the dissepiment is exposed, but measurements on the reverse surfaces of other specimens still fell within a range from 0.13mm to 0.18mm. The internodal distance rated a probability of 0.0000: nodes on MRW1 are very close, being on average 0.128mm apart, compared to 0.20mm for the standard *F. tuberculo-carinata* which is still close by comparison with most fenestellids.

The very close nodes and the narrow dissepiments are departures from Bancroft's established standard *F. tuberculo-carinata* which have been picked out statistically. There are, however, other features which differ from the standard. The specimens from the Witches Lake Marine Band tended to have straight branches, whereas those of *F. tuberculo-carinata* Etheridge Jun. are sinuous, and give a typical honeycomb appearance to the meshwork on the reverse surface; this was only partially developed within the specimens collected. Also, the pustulose ridges seen on the reverse surfaces are not typical of *Fenestella tuberculo-carinata* and are more commonly seen on *F. plebeia* which also has straight branches and relatively thin dissepiments. Thinner dissepiments, though, may be an adaptation to life in lower-energy environments, where strength of the meshwork is not as important as in higher-energy settings.

The Witch Lake Marine Band is considered to be Middle Asbian in age; by contrast, Bancroft (1984 & 1987) viewed *F. tuberculo-carinata* to have a stratigraphical range from Lower Brigantian to Pendleian. Thus it is possible that the specimens from the Witch Lake Marine Band represent precursors to the main stock of Midland Valley *F. tuberculo-carinata* , and may have evolved from a *F. plebeia* population, though a possible occurrence of *F. tuberculo-carinata* has been reported in Holkerian strata at the Ash Fell road cutting in Cumbria (Natural History Museum collections).

St. Monance White Limestone
Pathhead

GRID REFERENCE : NO 5379 0213
AGE : Brigantian

On the foreshore at Pathhead, in a low cliff, there is a small exposure of a very white limestone, the St. Monance White Limestone. The limestone is approximately 2.5m thick, and contains a 70cm-thick brown dolomitic layer. Many *"Lithostrotion"* (now *Siphonodendron*) coral colonies are present, and several bryozoan colony fragments were also recovered at three horizons. The material is only moderately well-preserved, and often coated by brown dolomitic stains. However, the following taxa were recognised :

Fenestella tuberculo-carinata
Tabulipora urii
Tabulipora sp.indet.
Rhabdomeson gracilis

Environmentally, the St. Monance White Limestone probably represents a very clastic-free reef flank setting, inhabited by *Siphonodendron* colonies, crinoids, and productid brachiopods. The coral-calcarenite community of Ramsbottom (1978) matches this limestone fairly well; in addition, acetate peels showed that algal structures are also preserved in addition to the more visible shelly fragments.

The overlying dark-grey shales may represent a time of clastic input into the area, or could represent a facies switch to lagoonal deposits. Thin-shelled and broad-ribbed rhynchonellid brachiopods are accompanied by spinose productids, and are rather abundant at certain levels within the shale. One horizon yielded bryozoans, but appeared to be monospecific; only the ubiquitous *Fenestella tuberculo-carinata* was recovered.

Bryozoans of the St. Monance White Limestone at Pathhead

Bottom levels of the Limestone

Bryozoans are not abundant, but three specimens of a trepostome were recovered, together with two fenestellid fragments. The trepostome is an encrusting form, with rounded apertures separated by polygonal walls. The specimens are rather weathered, and only a few patches of the colonies show the originally-sharp interzooecial walls and vague acanthopores (stylets). There do not appear to be a great number of exilazooecia. One specimen appears to have encrusted the outside of a productid brachiopod shell, and to have also covered two broken brachiopod spines which lay on the shell (specimen $\mathrm{PMW_{B}3}$). Acetate peels of specimen $\mathrm{PMW_{B}2}$, a large (1cm by 2cm) flat, encrusting colony, showed that the specimen is made up of several layers encrusting each other, but recrystallisation has destroyed much of the internal structure to such a degree that it is not even possible to show conclusively that the specimen is a trepostome.

Two fenestellid fragments were recovered. These appear to be referable to *Fenestella tuberculo-carinata*, despite being heavily secondarily-calcified. In his 1882 paper, J. Young discussed the nature of *Fenestella tuberculo-carinata*, and noticed the secondary calcification in older specimens; the apertures become partially sealed by a translucent calcite plate. Specimen $\mathrm{PMW_{B}5}$ (fig. 4.8c) shows an obverse surface with heavy calcification which occluded most of the apertures, but some are still visible through the calcite coatings, though the calcite plates of Young (1882) are not visible. Both specimens show greater thickening of the branches and dissepiments than the "normal" species, and this leads to a very finely-striated meshwork with oval to circular fenestrules. The carina and nodes are not visible externally.

Acetate peels of specimen $\mathrm{PMW_{B}4}$ (the original colony is shown in fig. 4.8b) showed very little of the internal structure; strongly striated skeletal material was visible, and a series of dark spots in the centre of the branches, probably the internal representation of the nodes, were seen, but not the traces of zooecial boundaries. If the dark spots do represent nodes, then they are very closely-spaced indeed (0.08-0.12mm, cf. *Fenestella tuberculo-carinata* 0.19-0.21mm).

Statistical measurements, however, show that there is a good comparison with *Fenestella tuberculo-carinata* :

	Fenestella cf. tuberculo-carinata PMW-B5			*Fenestella tuberculo-carinata*		vs. MRW1
	n	σ	**x**	**x**	**PROB**	**PROB**
BW	6	0.0137	0.303	0.30	0.8265	0.4498
AD	5	0.0098	0.112	0.09	0.0004	0.3770
ID	5	0.0219	0.240	0.23	0.3547	1.0000
FL	13	0.0499	0.682	0.73	0.0514	0.6025
FW	5	0.0522	0.500	0.57	0.0328	0.0185
DW	9	0.0724	0.333	0.20	0.0000	0.0000
				TOTAL	0.2110	0.4080

Features which are unaffected by secondary calcification (ID, FL, FW) score highly against Bancroft's average *Fenestella tuberculo-carinata*, but the highest correlation is with branch thickness. Dissepiments, though, are clearly seen to be much thicker in PMW$_B$5. Excellent correlation scores resulted from a comparison with other Fife material, most notably with the limestone-preserved MRW1 from the Witch Lake Marine Band.

Top levels of the Limestone

The following five specimens were recovered :

PMW^T 1 *Fenestella tuberculo-carinata*.. Well preserved reverse.
& *Rhabdomeson gracilis* .
2 *Tabulipora urii* ? Moderately well-preserved. Ironstained.
3 *Rhabdomeson gracilis*. Poorly-preserved. Ironstained.
4 Fenestellid reverse fragments (one striated) & *Tabulipora*. Poorly-preserved.
5 *Fenestella tuberculo-carinata*. Large colony fragment. Poor to moderate preservation.

Specimens referable to *Fenestella tuberculo-carinata* are very similar to those from the lower, more clay-rich portion of the limestone. They all appear to be heavily calcified such that the reverse surfaces are smooth, rather than possessing the classic striated reverse, but one specimen has been partially weathered, and shows some broad longitudinal striae. Calcification has lead to very rounded fenestrules; John Young (1882) noted that it was in greyish-white limestones that *Fenestella tuberculo-carinata* occurred in thickened fronds with zigzag branches, giving a hexagonal appearance to the meshwork; certainly this appearance is true for specimens from the St. Monance White Limestone (for example, specimen PMW^{T}5, Plate 2, fig. f.), and such thickening may have been due to a plentiful supply of dissolved carbonate in the environment. In Young's "most perfect aspect" of the species, the reverse surfaces develop large rounded tubercules at each angle of the hexagonal meshwork. This is seen very clearly in specimen PMW^{T}1 (fig. 4.8a).

Several examples of the cryptostome *Rhabdomeson gracilis* were found (Plate 2, fig. a.). They were rather weathered, but showed the very regular rhombic arrangement of rounded apertures of equal size on a relatively slender branch. The central rod characteristic of this genus was not visible, nor were the stylets, but the zooecial arrangement clearly assigns the specimens to this species.

Two specimens referable to *Tabulipora urii* were also noted. Both specimens had relatively broad cylindrical colonies (PMW^{T}4 approx. 2.4mm diameter : PMW^{T}2 approx. 3.8mm diameter) and were covered in a mosaic of irregularly-arranged, polygonal autozooecial apertures. Exilazooecia were not demonstrable, but this may be because the specimens were, again, rather weathered, suggested by the moderately-thick appearance of the eroded endozone walls. The material also appeared too weathered for a thin section to show any extra detail at the expense of destroying the sample. However, the broad diameter of the colonies, coupled with the scarcity of exilazooecia, and the sub-rounded shape of the apertures suggests that the specimens be assigned to *Tabulipora urii*, which is common in the Scottish area.

Shales overlying the Limestone

Only one species of bryozoan was discovered in the shales; all fragments recovered appear to be referable to *Fenestella tuberculo-carinata*. PMW^{S}1 (Plate 2, fig. h.) is particularly well-preserved, and shows a moderately-open meshwork with thick branches and a very prominent median ridge on each branch, which is ornamented by very closely-spaced nodes. Branch sides slope very steeply away from the median ridge, and flared, moderately-thick dissepiments are sunk beneath the ridge crests. Apertures are round to oval, and there are four apertures per fenestrule. One aperture appears at each dissepiment-branch junction, and is elevated above the other three apertures. Thus, on colonies still partially covered in matrix, only the median ridge, the flared dissepiments, and these elevated apertures can be seen (for example, on PMW^{S}2).

Measurements on specimens gave very good correlations with Bancroft's averaged data :

	Fenestella cf. tuberculo-carinata			*Fenestella tuberculo-carinata*				
	PMW-S1						vs PMW-B5	vs MRW1
	n	σ	x	x	PROB	DIV.	PROB	PROB
BW	15	0.0361	0.335	0.30	0.0153	0.5306	0.0580	0.0248
AD	12	0.0099	0.108	0.09	0.0002	0.0900	0.4978	0.0593
ID	15	0.0252	0.217	0.23	0.1530	0.0066	0.1078	0.0091
FL	19	0.0445	0.826	0.73	0.0001	0.5139	0.0000	0.0000
FW	19	0.0716	0.583	0.57	0.6040	0.0353	0.0327	0.2142
DW	16	0.0380	0.223	0.20	0.1326	0.6196	0.0001	0.0000
IND	18	0.0441	0.226	0.20	0.0824	0.5299		0.0000
				TOTAL	0.1411	0.3323	0.1161	0.0439

The only parameters which differ significantly from *Fenestella tuberculo-carinata* are the aperture diameter and the fenestrule length. Clearly, PMW^{S}1 has much larger fenestrules than Bancroft's average, but still within the reported colony mean range. Aperture diameter, likewise, is larger than Bancroft's average, but low probabilities are to be expected because of the low accuracy to which such relatively-small features can be measured.

Comparing PMW^{S}1 with the secondarily-calcified PMW$_{B}$5 from the base of the St. Monance White Limestone, a lower probability score is obtained, and an even lower score against the Witches Lake Marine Band sample MRW1. Thus, the statistics reinforce the observations that the morphology of the same species is very different in the limestone and in the shales, with the limestone-preserved specimens having a stouter meshwork with much thicker dissepiments.

Interestingly, branch thicknesses were actually greater in the quieter-water dwelling specimens from the shale, despite there being no evidence of secondary calcification. It is possible that the extra thickness of the branches could be due to compaction during diagenesis, but the specimens actually appear to be remarkably uncrushed.

St. Monance White Limestone
Partan Craig

GRID REFERENCE : NO 5241 0146
AGE : Brigantian

In a small bay near St. Monans there is a long ridge-like outcrop of a grey, knobbly-weathering limestone, the westerly outcrop of the St. Monance White Limestone. It is a unit approximately 2.5m thick, underlain by a shelly mudstone. The limestone is rich in crinoid columnals, and has localised patches of coral development, with *Siphonodendron* colonies and small specimens of *Dibunophyllum*, but corals are not as abundant as at the Pathhead exposure. Other fossils are rare, but productid brachiopods and fish teeth were seen. Bryozoans are present, but they are rather scarce; fenestellids and tabuliporids were found, together with a possible trepostome of uncertain affinities.

Correlations of the St. Monance White Limestone outside of Fife are uncertain. However, the St. Monans Brecciated Limestone, which overlies the White Limestone by as little as 4m, is a persistent marker horizon, and has been correlated with the Hurlet Limestone of the Midland Valley (Forsyth & Chisholm, 1977).

At this locality, material was quite probably derived from a high-energy crinoid bank. Hence bryozoans would have been rare on account of the turbulent water currents which crinoids favoured; those that do occur appear to have been thickened to cope with the currents, in a manner similar to at Pathhead, with which the fauna compares favourably.

Bryozoans of the St. Monance White Limestone at Partan Craig

Recrystallization has made identification of the bryozoans rather difficult. Three fragments of fenestellid bryozoans were found, all three looking rather different :

PCB1 (fig. 4.6c) is an obverse surface of a frond, characterised by rounded branches with a broad median ridge, and small (0.10mm) widely-spaced apertures (ID approx. 0.30mm). Branches are rather thick (0.40mm) as are the dissepiments (0.26mm - 0.40mm). The one fenestrule preserved is rather rounded, and measured 0.78mm by 0.64mm. There are 3 to 4 apertures per fenestrule. The specimen is probably referable to *Fenestella tuberculo-carinata* but it would be dangerous to assign it positively to this species on the basis of the one small fragment studied.

PCB2 (fig. 4.6b) is a colony reverse-surface fragment, with rounded, sub-parallel branches connected by rather straight dissepiments. The branches are broad (approx.

0.35mm) and occasionally show longitudinal striae. Dissepiments are bar-like, regularly-placed, slightly sunk beneath the branch crests, and ranging from 0.15mm to 0.20mm in thickness. The fenestrules are rather rounded, and average 0.60mm by 0.50mm.

PCB8 (fig. 4.6a; Plate 2, fig. i.) is a very thick-branched specimen (branch thickness approx. 0.57mm), showing a frequently-bifurcating reverse surface. The branches are very round, and ornamented by faint longitudinal striae. Dissepiments are correspondingly thick and stubby, measuring 0.40mm in diameter, and are virtually flush with the branch crests. Fenestrules are long (1.40mm to 1.90mm) but relatively narrow (approx. 0.90mm), and have well-rounded margins. There appear to be the bases of several *Palaeocorynae* spines on the fragment. The dimensions of this colony suggest that it is probably a *Polypora* of some sort, fitting closely with *Polypora dendroides*. The 1977 Institute of Geological Sciences' Memoir on East Fife (Forsyth & Chisholm) actually cites *Polypora dendroides* in the appendix (the only named species) with all specimens having been obtained from the St. Monance Brecciated Limestone. It is therefore interesting to find this species in the slightly older White Limestone. Its occurrence in these rocks extends both the geographical and temporal range of this species.

The cryptostome *Rhabdomeson gracilis* is represented by a small colony fragment, but within this fragment it is possible to see the regular rhombic arrangement of the apertures, separated by relatively thin interapertural walls. Apertures are rounded and of equal size around the colony. Between each aperture there are the weathered bases of stylets. From the broken end of the colony, there is a suggestion of the axial rod characteristic of this genus. Parameters are as follows :

	PCB7 :Partan Craig, Fife			Bancroft (1984)		
	Rhabdomeson gracilis			*R. gracilis*	PROBABILITY SCORES	
	n	σ	x	x	T-FEN	T.FEN.DIV
ZD	1		1.000	0.76		
Z2	1		5.000	4.77		
AD1	9	0.0133	0.180	0.21	0.0013	0.0050
AD2	7	0.0099	0.131	0.10	0.0000	0.0077
IWT1	7	0.0200	0.237	0.24	0.8187	0.0493
IWT2	7	0.0140	0.134	0.09	0.0000	0.0074
				TOTAL	0.2050	0.0174

The specimen falls within the ranges cited by Bancroft for the species, though the transverse colony measurements (Aperture Diameter 2, and InterWall Thickness 2) are greater than average, possibly representing an adaptation for survival in more turbulent waters; *Rhabdomeson gracilis* is more usually a tranquil-water dwelling species.

Several trepostome colony fragments were collected, in varying degrees of preservation (Plate 1, fig. g.). Though morphology of the colony varies from flat encrusting representatives through to erect forms, the autozooecial architecture is similar in all cases. Apertures are sub-rounded, and irregularly-developed over the surface of the colony. Interapertural walls are moderately thick, and have a slight "beaded" appearance. Exilazooecia are irregularly-placed within the colony, and do not appear to cluster in maculae. Poorly-developed stylets occur at interzooecial wall junctions. Specimen PCB9 is an erect, cylindrical form with a colony diameter of 2.90mm. This broad diameter, coupled with the lack of maculae and the sub-rounded, relatively-large apertures point to this species being *Tabulipora urii*.

Two perplexing specimens are PCB5 and PCB6, which are elongate, buff-coloured impressions within the rock, approximately 4mm in width. These impressions curve into the matrix, suggesting that they are the moulds of a cylindrical fossil, and are ornamented by irregularly-developed, relatively small black speckles, which may have been colony apertures. The moulds could be fragments of a dissolved trepostome colony, but it is impossible to identify them with certainty, and their true affinities remains a mystery.

Charlestown Main Limestone
Pathhead

GRID REFERENCE : NO 5372 0220
AGE : Brigantian

The Charlestown Main Limestone outcrops at Pathhead, approximately 70m south-west from the St. Monance Brecciated Limestone, from which it is separated by a sequence of barren black shales containing ironstone nodules. It is a brown dolomitic limestone 1.75m in thickness, with patches of dolomite crystal growth, and occasional undolomitised levels. Crinoid columnals are especially abundant, and constitute virtually all of the fauna. A few productid brachiopods were noted, mainly within shale partings, and one rhabdomesid bryozoan was recovered.

The crinoid columnals are disarticulated and slightly rounded, suggesting that they had been rolled in a high-energy environment prior to burial. Additionally, the brachiopod spines which are present have been rather fragmented.

The one rhabdomesid fragment recovered also appears to have been rolled, since only the stubby bases of the stylets remain. Parameters from specimen PCM1 (Plate 2, fig. c.) are given below:

				Rhabdomeson gracilis				*Rhombopora incrassata*	
	PCM1			Bancroft		PCB7		Tears Point, Gower	
	n	σ	x	x	div. t-test	x	div. t-test	x	div. t-test
ZD	1		1.040	0.76		1.000		0.60 - 1.36	
Z2	5	0.4899	3.600	4.77		5.000		4 - 6	
AD1	11	0.0476	0.225	0.21	0.0001	0.180	0.2367	0.177	0.0675
AD2	12	0.0099	0.152	0.10	0.0004	0.131	0.0082	0.115	0.0637
IWT1	11	0.0425	0.304	0.24	0.0129	0.237	0.2056	0.318	0.0267
IWT2	10	0.0280	0.190	0.09	0.0000	0.134	0.0791	0.126	0.0140
Total					0.0033		0.1324		0.0430

The specimen seems to be referable to *Rhombopora incrassata* Ulrich, 1890; it possesses equal-sized rounded apertures (with hemisepta visible in some), regularly arranged in a spirally-budded rhombic pattern around the colony. Interzooecial walls are very thick, and are ornamented by rows of small stylets. The colony is rather broad, having a diameter of 1.04mm. Apertures are widely-spaced, averaging 3.6 per 2mm line . Most importantly, a thin section revealed budding from a central zone, rather than an axial rod, indicating that the specimen belongs to the genus *Rhombopora* rather than to *Rhabdomeson.*

The arrangement of the apertures is similar to that of *Rhabdomeson gracilis*, and statistical comparisons with this species have been included in the table. Though there is little match with the parameters reported by Bancroft (1984), a specimen of *R. gracilis* from the St. Monance White Limestone at Partan Craig (PCB7) showed similar ratios (but not actual parameter lengths) with PCM1. This highlights a vulnerability of the division t-test, when different species adopt a similar ratio of their parameters. The division t-test scores compared with the specimens of *Rhombopora incrassata* from Tears Point in South Wales (see Chapter 6) are only moderately high, but Student's t-test score between PCM1 and the Welsh material is 0.1249, confirming the affinities of the specimen.

Mid Kinniny Limestone
St. Monans

GRID REFERENCE : NO 5296 0169
AGE : Brigantian

The Mid Kinniny Limestone outcrops in a small cliff on the foreshore at St. Monans. The sequence consists of deltaic sandstones, thin shales, and the Mid Kinniny Limestone itself, which forms a patchily-dolomitised unit just over one metre thick. The beds dip inland, and the topmost surface of the limestone has become well-exposed; it is from this horizon that a very diverse bryozoan fauna was collected, with the following species being identified :

Rhabdomeson gracilis
Fenestella cf. bicellulata
Fenestella tuberculo-carinata
Penniretepora spinosa
Tabulipora urii
Tabulipora cf. howsii
Eridopora sp. nov. ?

Environmentally, the facies represents a lagoonal phase developed over a subsided delta top. The graphic log (fig. 4.4) of the section illustrates a transgressive episode flooding the vegetated delta top, with initial colonisation by chonetid brachiopods (Cumming, 1928, called it the *Chonetes* Limestone) before the establishment of a nearby backreef facies from which the fauna of the uppermost limestone is probably derived. The high diversity, and taxa present, are indicative of Ramsbottom's (1978) Mud Community.

The Mid Kinniny Limestone was the stratigraphically highest bed surveyed during the Fife fieldwork. It is actually a very widespread bed throughout east Fife (Forsyth & Chisholm, 1977, p79), but its correlations within the Midland Valley are not certain; it may correlate with the Second Hosie Limestone to the West, and the Bilston Burn Limestone to the East (George *et al.*, 1976).

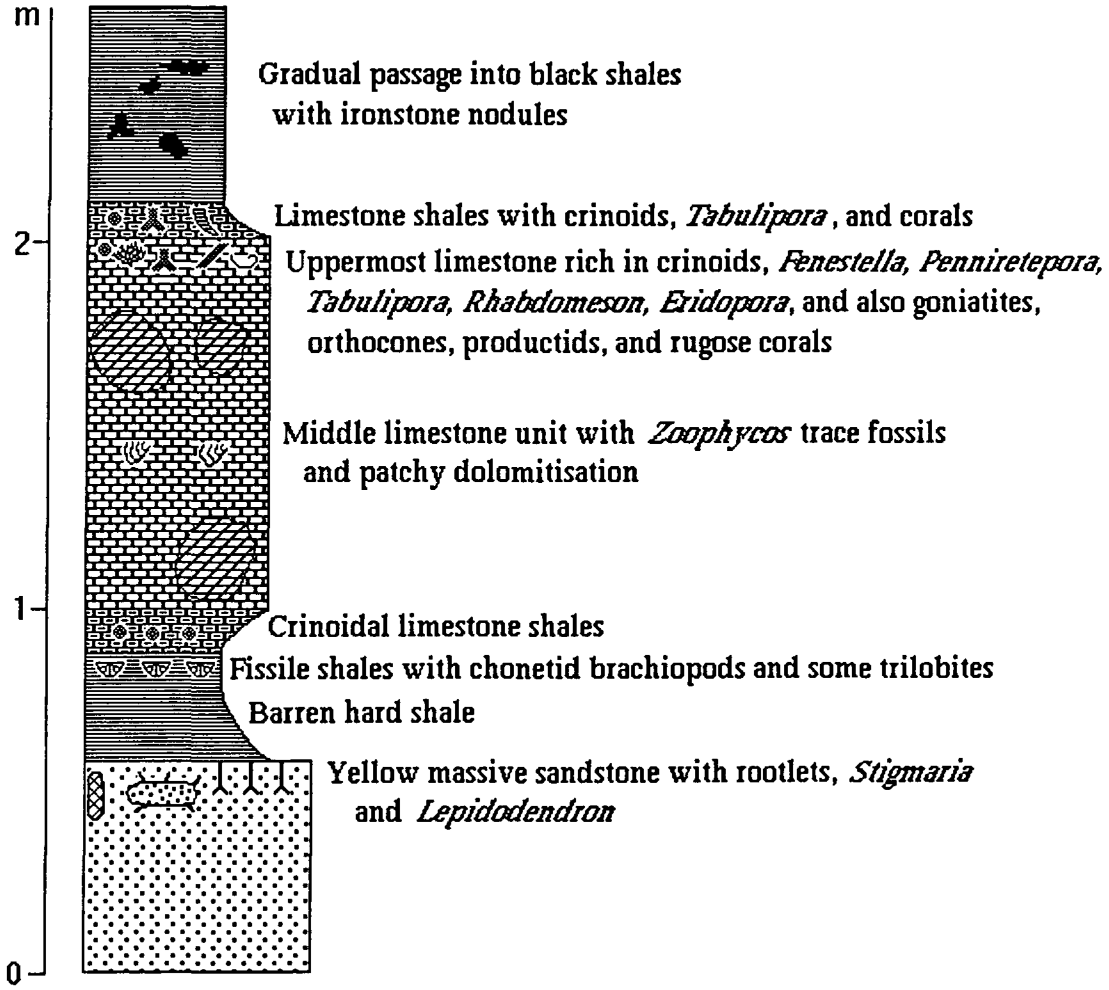


Fig. 4.4. Graphic log of the Mid Kinniny Limestone

Bryozoans of the Mid Kinniny Limestone

Rhabdomeson

Several specimens referable to *Rhabdomeson gracilis* were found in the Mid Kinniny Limestone (Plate 2, fig. b.). Despite being almost completely recrystallized, they are still identifiable as *R. gracilis* on account of the slender, straight cylindrical colony, and the regular rhombic arrangement of equal-sized autozooecial apertures. The table below shows that the measured parameters match very closely those of Bancroft's averages for *Rhabdomeson gracilis*:

	Mid Kinniny Limestone	**Bancroft (1984)**
	Rhabdomeson gracilis	*Rhabdomeson gracilis*
	range	**x**
ZD	**approx. 0.60**	**0.61 ?**
AD1	**0.20 - 0.24**	**0.21**
AD2	**0.10 - 0.12**	**0.10**
IWT1	**approx. 0.22**	**0.24**
IWT2	**approx. 0.10**	**0.09**

The muddy environment of the Mid Kinniny Limestone was probably similar to that of the shales from which most of the material Bancroft examined was collected. This similarity in facies could account for the higher correlations between the Mid Kinniny Limestone specimens of *R. gracilis* and Bancroft's examples, than for those of the same species from the relatively high-energy conditions of the St. Monance White Limestone.

Penniretepora

Two examples of *Penniretepora* were found; on MMK30 there is a colony fragment approximately 3mm long (fig. 4.9b; Plate 2, fig. j.), showing a strongly longitudinally-striated reverse surface of a main branch, with several stubby secondary branches diverging at an angle of about 70°. These lateral branches are almost flush with the reverse surface, and opposing branches are slightly offset, but never by more than half an inter-branch distance. Lateral branches have well-defined junctions with the mainstem, and there is no branch flaring at these junctions.

MMK28 (fig. 4.9a) is a larger colony fragment, being 9mm long, and is not as well-preserved, with much of the original striation now not visible. The mainstem curves gently, and there is a relatively long 2:1 branch with a small tertiary branch on it.

The dimensions for both specimens are given below.

	Penniretepora spinosa						
	MMK 30			**MMK 28**			**Bancroft**
	n	**σ**	**x**	**n**	**σ**	**x**	**x**
MS;BW	**3**	**0.0163**	**0.320**	**3**	**0.3130**	**0.313**	**0.25 - 0.33**
2:1;BW				**1**		**0.300**	**0.26 - 0.30**
1:2;BW	**7**	**0.0259**	**0.191**	**12**	**0.0300**	**0.221**	**0.18**
LBS	**5**	**0.0845**	**0.632**	**10**	**0.0127**	**0.700**	**0.62**

The specimens tally closely with Bancroft's parameters for *Penniretepora spinosa* and zoarial features, including non-flaring lateral branches, confirm this diagnosis.

Fenestellids

Fenestellid bryozoans are moderately abundant, and seem to fall into two distinct species: a long-fenestruled, frequently-branching form, and a squat-fenestruled, parallel-branched species.

The long-fenestruled form is the slightly less common of the two, with six specimens being recovered. Most of these are rather poorly-preserved reverse surfaces, but one fragment showing an obverse surface was found. This specimen (MMK26) shows a very prominent median ridge on each branch, but virtually all detail of the apertures has been lost. At lower magnifications, faint impressions of apertures can be seen, showing them to be relatively large circular structures, surrounded by peristomes, but this detail is lost at higher magnifications.

Branch sides slope steeply away from the median ridge, and apertures are set relatively low down on the branches, flush or slightly projecting into the fenestrules. One aperture is usually positioned at the dissepiment/branch junction. Branches themselves are slightly sinuous, and bifurcate frequently in a "tuning fork" pattern, the meshwork quickly accommodating the extra branches.

Dissepiments are depressed well below the branch crests. They are moderately-thick, and flare slightly at their junctions with the branches.

The other specimens show mainly smooth reverse surfaces, but this smoothness may well be due to recrystallization, since MMK32a shows a strongly longitudinally-striated reverse surface.

Parameters and comparisons for MMK26 are given below:

	Fenestella tuberculo-carinata					PROBABILITY SCORES	
	Mid Kinniny Limestone				Bancroft	Bancroft	MRW1
	n	σ	range	x	x	t-TEST	t-TEST
BW	5	0.0098	0.28 - 0.30	0.288	0.30	0.4343	0.4007
AD	4	0.0100	0.10 - 0.12	0.110	0.09	0.0026	0.3498
ID	5	0.0294	0.24 - 0.32	0.276	0.23	0.0027	0.0101
FL	8	0.0357	0.68 - 0.80	0.765	0.73	0.2194	0.0006
FW	9	0.0632	0.40 - 0.60	0.480	0.57	0.0047	0.0021
DW	6	0.0137	0.12 - 0.16	0.143	0.20	0.0033	0.0342
					TOTAL	0.1112	0.1329

The parameters fall within the ranges of Bancroft's averages for *Fenestella tuberculo-carinata*, though the dissepiments appear somewhat thinner than normal. Statistically and morphologically, MMK26 compares favourably with specimen MRW1 from the Witch Lake Marine Band, which is also inferred to have formed in a rather muddy limestone facies. It is interesting to note that though correlations with Fife shale facies representatives (PMW^{S}1 and PMW^{S}2) give similar total probability scores (0.1328 and 0.1390), these are boosted by a high score for the aperture diameters, and would otherwise have been much lower. The secondarily-calcified PMW$_{B}$5 from the St. Monance White Limestone gave a good correlation spread, and averaged 0.2814. Zoarially, the broad, rounded apertures and strong median ridge with steeply sloping branch sides point to these specimens being referable to *Fenestella tuberculo-carinata.*

Twelve colony fragments of the smaller meshworked species were found, in varying states of preservation. Most of the specimens appear to show the reverse surface, but MMK43 shows an obverse surface. Unfortunately, the specimen is rather badly recrystallized, and all detail of the apertures has been lost. However, it is possible to see a thin carina running down the centre of the branches. Branch surfaces are gently rounded, and thin, bar-like dissepiments are sunk well below the branch crests. Fenestrules are rectangular, and average 0.45mm in length, and 0.38mm in width.

The best-preserved specimen is MMK44 (Plate 2, fig. d.), which shows a planar, outward-fanning colony with a close-packed meshwork. Branches are gently sinuous, but remain sub-parallel. The reverse surfaces of the relatively thin branches (0.21mm in diameter) are strongly striated in the better-preserved portions of the colony, and dissepiments are sunk beneath the branch crests, though not as much as on the obverse surface. The colony branches by low-angle bifurcations, so new branches are not usually fully accommodated into the meshwork until two or three fenestrule lengths.

Parameters are given below for specimen MMK 44, for inter-colony averages from five specimens, and a total summation from all five specimens:

	Fenestella bicellulata									
	MMK 44			MMK averages			MMK totals			Bancroft
	n	σ	x	n	σ	x	n	σ	x	x
BW	12	0.0125	0.213	5	0.0069	0.225	27	0.0189	0.220	0.18
FL	12	0.0221	0.447	5	0.0268	0.479	30	0.0381	0.464	0.42
FW	13	0.0166	0.382	5	0.0177	0.395	28	0.0290	0.389	0.36
DW	12	0.0137	0.077	5	0.0052	0.086	29	0.0152	0.084	0.08

	Probability scores vs. Bancroft (1984)					
	MMK 44		MMK averages		MMK totals	
	t-PROB	DIV	t-PROB	DIV	t-PROB	DIV
BW	0.0000	0.0000	0.0000	0.0012	0.0000	0.0000
FL	0.0756	0.1187	0.0123	0.1203	0.0001	0.0542
FW	0.0129	0.1127	0.0118	0.1106	0.0001	0.0493
DW	0.5081	0.0385	0.3146	0.2749	0.2559	0.1489
TOTAL	0.1491	0.0675	0.0847	0.1267	0.0649	0.0627

The specimens compare favourably with Bancroft's analysis of *Fenestella bicellulata*, but most noticeably, branches are thicker than normal; even though they are only 0.04mm thicker, this is enough to return low probability scores for the colonies. Interestingly, correlations with *Fenestella frutex*, with which Tavener-Smith (1973a) had suggested *Fenestella bicellulata* was conspecific, returned total probabilities of 0.0000 for both Tavener-Smith's data, and that of Bancroft.

The higher division probability from the colony averages shows that though the specimens are slightly stouter than Bancroft's averages, the meshworks have roughly the same proportions.

Trepostomes

Trepostomes are numerically the most abundant bryozoan group from the Mid Kinniny Limestone. Two forms appear to be present; branching, relatively slender cylindrical bryozoans with thick interzooecial walls, and rarer sheet-like forms which have thin interzooecial walls and larger apertures.

Cylindrical colonies, best represented by MMK41 (Plate 1, fig. i) and MMK13 (Plate 1, fig. h.), are probably referable *Tabulipora urii.* They have a variable morphology; in weathered specimens, the interzooecial walls appear rather thick (up to 0.12mm) and are rounded, both on their sides (giving apertures a sub-rounded shape) and on their tops. MMK41 shows a transition to unweathered portions of the colony where interzooecial walls form sharp polygonal ridges around the depressed apertures, and the walls are only 0.05mm thick. As the aperture deepens, there is a change from the sharp angular nature of the interzooecial wall to a thicker, more rounded appearance.

Autozooecial apertures are irregularly arranged and closely spaced. They are relatively small, being on average 0.25mm in diameter. As Bancroft (1984) mentioned, on some cylindrical colonies, in addition to thicker walls, the apertures are more oval than rounded, and are elongated parallel to the branch margins.

Exilazooecia are fairly common, but do not usually cluster in maculae. MMK 14, however, shows a well-developed cluster of about eight exilazooecia into an elevated monticule; this is not typical and more usually exilazooecia occur singly or in groups of two or three.

Stylets are poorly developed at the interzooecial wall junctions, and it was not possible to see any of Bancroft's "type c" stylets along these walls. Colonies form branching, sometimes sinuous, solid cylinders, ranging from approximately 2mm to 4mm in diameter. The longest colony fragment found was 18mm in length.

A summary of the measured parameters is given on the following page:

	Mid Kinniny Limestone			Bancroft (1984)
	Tabulipora urii			*Tabulipora urii*
	n	σ	x	x
AD	11	0.0323	0.249	0.27 ?
IWT			0.05 - 0.12	0.06
Z2			6 - 7	6.70
ZD	13	0.5289	2.920	3.63

The solid cylindrical dendritic colony form, coupled with the relatively small apertures point to this species being *Tabulipora urii.* Recrystallization has destroyed all internal features, though, and acetate peels showed nothing of the nature of the interzooecial walls, which are very important in correctly identifying members of the order Trepostomata.

Sheet-like forms, represented by MMK37 and MMK39 (Plate 1, fig. j.), are distinguished from the cylindrical forms not only by the colony shape, but by the zoarial features. Interzooecial walls are thinner and more angular than in *Tabulipora urii*, being sharp and ridge-like. When weathered, walls can be up to 0.10mm in thickness, but more usually range from 0.04mm to 0.05mm when unweathered.

Autozooecia are irregularly arranged, but usually conform to a crude hexagonal pattern, with each zooid being surrounded by six others. However, there are commonly patches where this hexagonal arrangement is lost, and autozooecial apertures become rhombic in shape. Apertures are moderately large, averaging 0.311mm in diameter.

Exilazooecia are notably scarce, occurring only occasionally as "space-fillers"; they are found singly, and do not cluster into maculae. Stylets are not prominent, but there is some thickening at interzooecial wall junctions, forming broad stylets which rise slightly above the level of the walls.

MMK37 shows a fully developed colony; it is a large, crushed sheet-like structure, which prior to burial and compaction would have formed a broad, hollow cylindrical colony, with irregular branches ranging from approximately 6mm to 10mm in diameter.

Measurements taken from MMK 39 are given on the following page:

	Mid Kinniny Limestone			Bancroft (1984)
	Tabulipora cf. howsii ?			*Tabulipora howsii*
	n	σ	x	x
AD	13	0.0373	0.311	0.29
IWT			0.04 - 0.05	0.06
Z2			5 - 6	7.00
ZD			6.0 - 10.0	7.0 - 22.0

The affinities of these two specimens is not clear. The large colony form is similar to that described by Bancroft (1984) for *Tabulipora howsii* (Nicholson), but the specimens have thinner, more angular interzooecial walls than Bancroft reports for this species, and lack the abundant exilazooecia which are very common in *T. howsii*. Thin interzooecial walls are characteristic of *Tabulipora tenuimuralis* (Lee), but without a thin section, the nature of these walls, which is crucial to identification, cannot be seen. Since recrystallization has destroyed all internal features, the taxonomic position of these specimens must remain in some doubt.

Eridopora sp. nov.?

Only one specimen referable to *Eridopora* was found, a small colony fragment measuring 6mm by 3mm. MMK30 (Plate 1, fig. k.) is assigned to the genus *Eridopora* Ulrich, 1882, on account of the very prominent hood-like lunaria which arch over the zooecial apertures. The specimen is moderately well-preserved for the locality, and forms a thin sheet-like colony. With lighting at a low oblique angle it is possible to ascertain features of the colony surface.

Apertures are rounded, having a slightly-pointed distal end, the closest they approach to the classic eridoporan sub-triangular shape, and covered at the proximal end by very prominent lunaria. Compared to other described eridoporids, the apertures are rather small. The autozooecial apertures are arranged in a fairly regular rhombic pattern, developing in sub-parallel longitudinal rows, and are very widely separated by areas of vesicular tissue, preserved as a polygonal mosaic of calcite between the zooids.

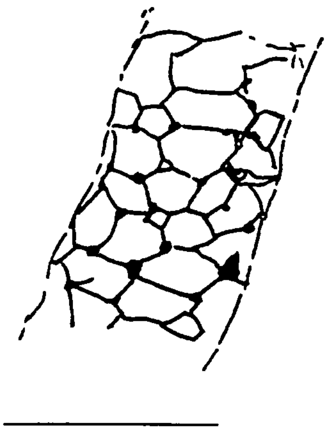
Lunaria are very long (0.205mm), and are sub-triangular in shape, sometimes possessing a very sharp crest. They rise prominently above the zoarial surface, giving the impression of a series of pyramidal peaks on the colony. Monticules appear to be absent, but this cannot be proved from such a small colony fragment.

A summary of the parameters is given below :

	MMK 30			Bancroft (1984)					
	Eridopora sp.			*Eridopora cf. beilensis*			*Eridopora macrostoma*		
	n	σ	x	x	PROB	DIV.	x	PROB	DIV
Z1	3		4.000	6.50			4.73		
Z2	1		4.000	4.50			4.10		
LAD	5	0.0449	0.268	0.32	0.0000	0.0089	0.41	0.0000	0.0327
TAD	6	0.0249	0.267	0.39	0.0000	0.0004	0.39	0.0000	0.0360
LID	4	0.0384	0.165	0.10	0.0018	0.0830	0.09	0.0001	0.2362
TID	6	0.0269	0.223	0.15	0.0002	0.0592	0.12	0.0000	0.1780
LT	4	0.0087	0.205	0.18	0.2134	0.0093	0.09	0.0000	0.0162
				TOTAL	0.0431	0.0323	TOTAL	0.0000	0.0998

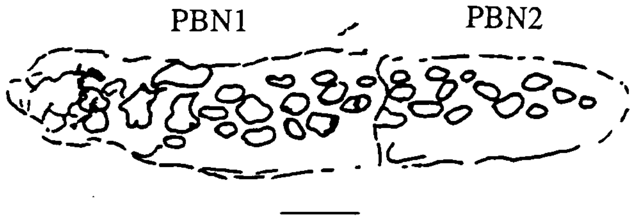
References to the genus *Eridopora* are rather scarce. Ulrich first described the genus in 1882, with *Eridopora macrostoma* as the type species. Perry & Horowitz (1963) recorded this species from the Middle Chester (= Brigantian) of Indiana, Perry having earlier found *Eridopora beilensis* in Virgillian (= Stephanian) strata in Kansas (Perry & Perkins, 1962); they remarked that both species had not been recorded outside of those two states. Bancroft (1984) discovered *Eridopora* in the Arundian strata of Ashfell Edge (*Eridopora macrostoma*) and in Arnsbergian shales at Hirst (*E. macrostoma* and *E.* cf. *beilensis*). Specimen MMK30 from the Brigantian Mid Kinniny Limestone is similar to *Eridopora beilensis* in that it has very long and prominent lunaria.

However, Bancroft's specimens of *E.* cf. *beilensis* differed from the Kansas representatives only in having smaller apertures: MMK30 has even smaller apertures which are also very widely-spaced. These differences are borne out in the table, which compares the Fife material with Bancroft's standards; MMK30 can be seen to differ considerably from these two species. However, with the paucity of data on the genus, it would probably be unwise to erect a new species based on just the one colony fragment, so the taxonomic position of MMK30 must remain in doubt, save that it has closer affinities with *Eridopora beilensis* than with *E. macrostoma.*



a. Weathered trepostome RRL4

b. Acetate peel of trepostome RRL8



c. Possible bryozoan?

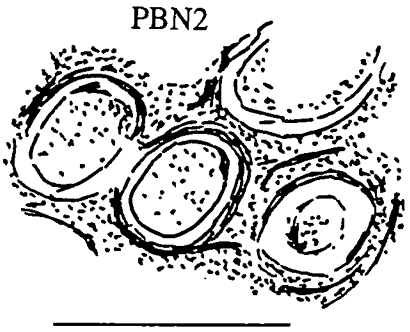
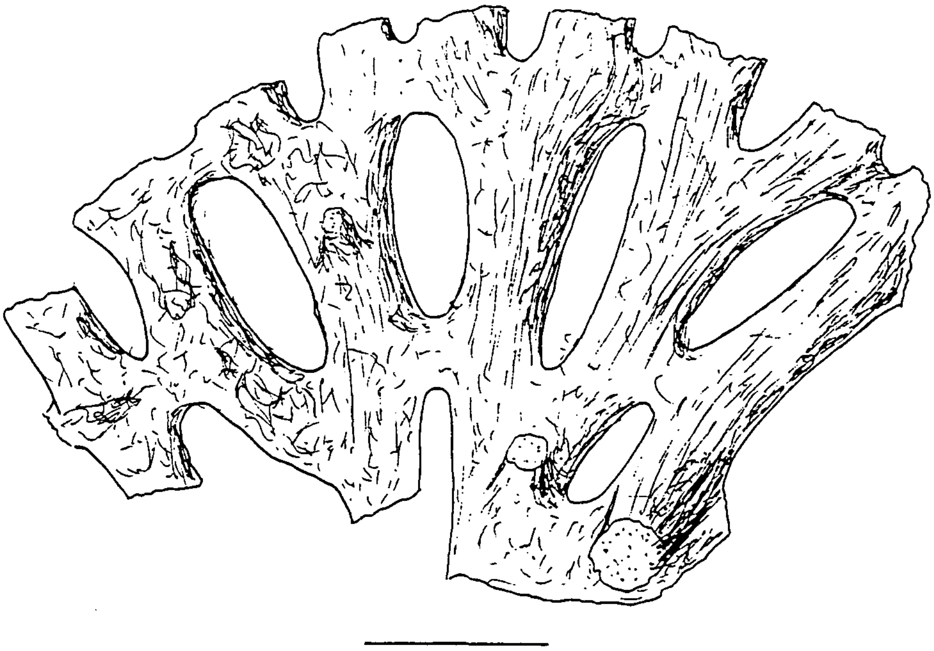
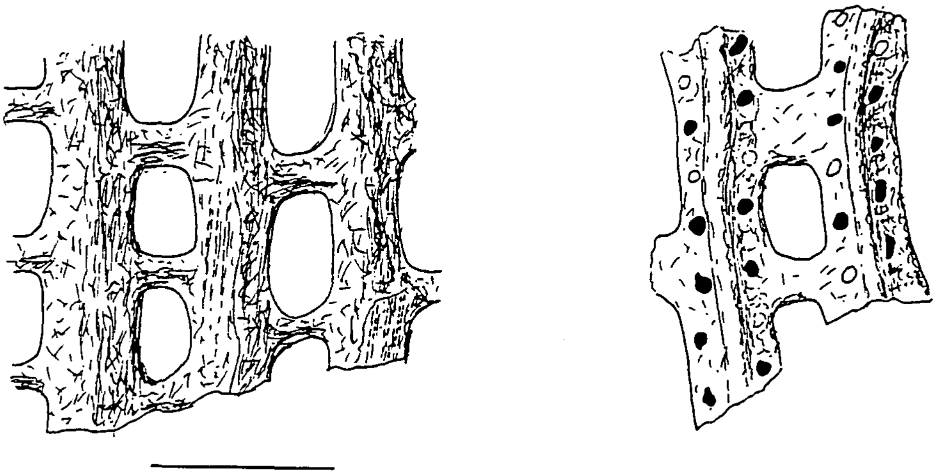


Fig. 4.5. ?Bryozoans from the Randerston Limestone and Billow Ness



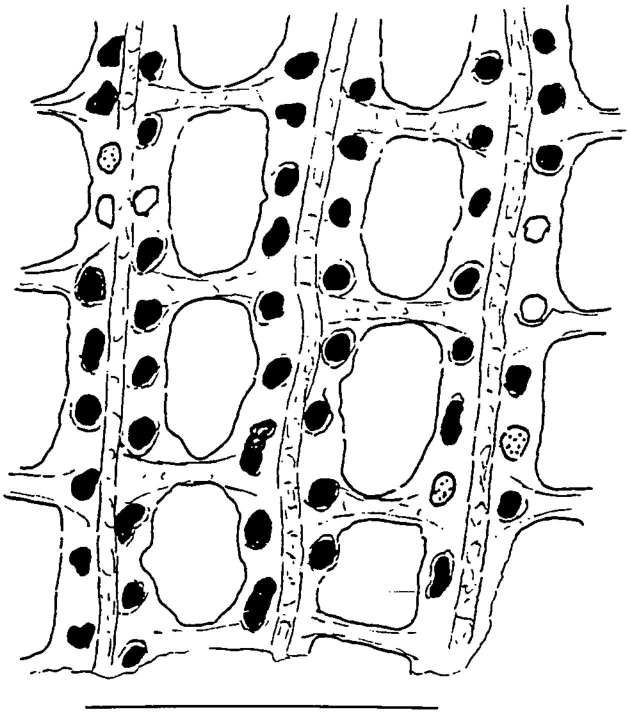
a. *Polypora dendroides* reverse surface PCB8



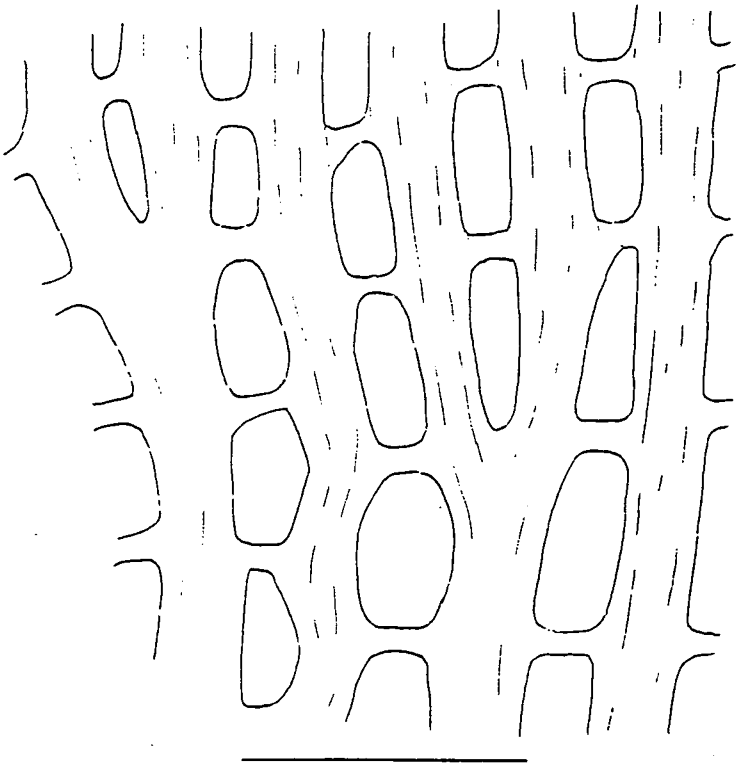
b. *Fenestella* sp. reverse surface PCB2

c. *Fenestella tuberculo-carinata* ?
obverse surface PCB1

Fig. 4.6. Bryozoans from St. Monance White Limestone

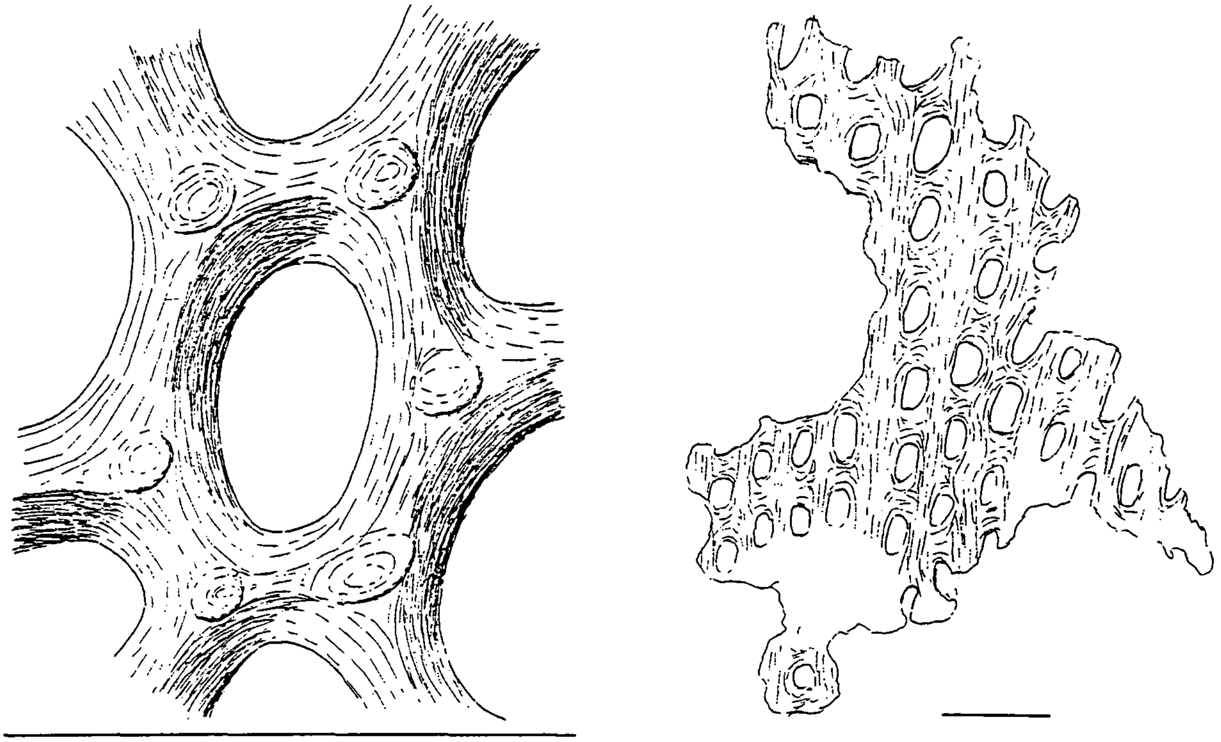


a. *Fenestella tuberculo-carinata* obverse surface MRW1



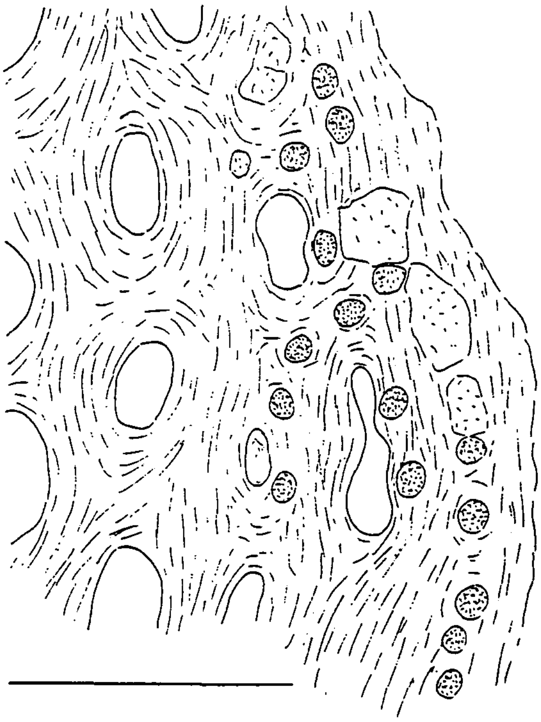
b. *Fenestella tuberculo-carinata* reverse surface MRW3

Fig. 4.7. *Fenestella tuberculo-carinata* from the Witch Lake Marine Band



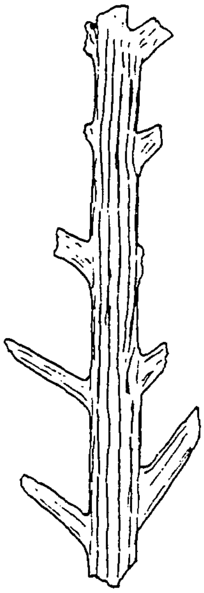
a. *Fenestella tuberculo-carinata* hexagonal reverse surface PMW^{T}1

b. *Fenestella tuberculo-carinata* reverse surface PMW$_{B}$4



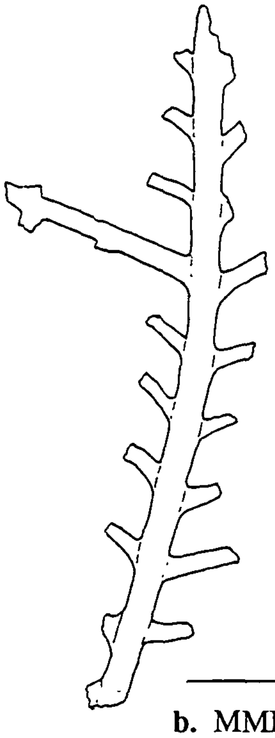
c. *Fenestella tuberculo-carinata* secondary-calcified obverse surface PMW$_{B}$5

Fig. 4.8. *Fenestella tuberculo-carinata* from the St. Monance White Limestone

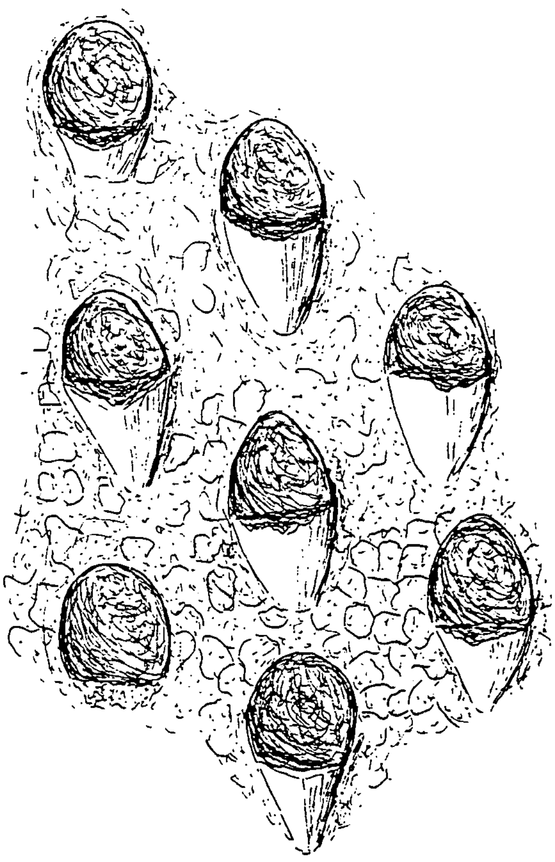


a. MMK28

Penniretepora spinosa
reverse surfaces



b. MMK30



c. *Eridopora* sp. nov.? MMK30

Fig. 4.9. Bryozoans from the Mid Kinniny Limestone

Distribution of Bryozoans in East Fife

The accompanying table outlines the occurrences and stratigraphical time ranges known for bryozoans found in East Fife. Data comes from three sources, and is shown as follows :

Sources of data

○ This study
☐ Kirkby, 1880
× Forsyth & Chisolm, 1977

Thirteen taxa identifiable to species level are included, together with two genera unknown, or unidentified, at species level, and a range for the order Trepostomata. Ranges for individual species are shown by the broken lines, while the ranges at generic or ordinal level are indicated by continuous lines.

There is an increase in bryozoan diversity through the Asbian and Brigantian in East Fife, reflecting the onset of longer-lived, less shoreward carbonate environments during the formation of the Lower Limestone Group. The beds of the Calciferous Sandstone Measures are dominated by nearshore deltaic environments, with occasional shorter-lived episodes of marine influence. Many of the so-called Marine Bands of this series, especially in the Anstruther Beds, are not actually representative of normal marine salinities, and are either brackish water (often indicated by the presence of ostracods and bivalves) or hypersaline (with the common occurrence of algae).

Fully marine conditions were developed during the Lower Limestone Group, and this is reflected in the greater diversity of bryozoan species; in the Mid Kinniny Limestone, for instance, eight different species were recorded. The cryptostome *Rhabdomeson gracilis*, which is normally a mud-dwelling species (Bancroft, 1984), and the similar facies-dwelling genus *Penniretepora* (McKinney & Gault, 1980 ; McKinney and Jackson, 1989) occur; their co-occurrence with *Polypora dendroides* brackets the facies to McKinney & Jackson's "lee side of shoals", perhaps indicating the presence of off-shore shoals.

The ubiquitous *Fenestella tuberculo-carinata* appears to be the most widely-distributed species found in Fife, tallying with data from other parts of the Midland Valley. It thus appears to be occupying the niche normally filled by *Fenestella plebeia*, which, though present in the Midland Valley, is not as common as in other areas within Britain. There is some evidence that *Fenestella tuberculo-carinata* is descended from *Fenestella plebeia* (discussed in the section on the Witch Lake Marine Band), but the exact reasons for the success of this species are not certain. The regular spacing of the dissepiments, coupled with the sinuosity of the branches,

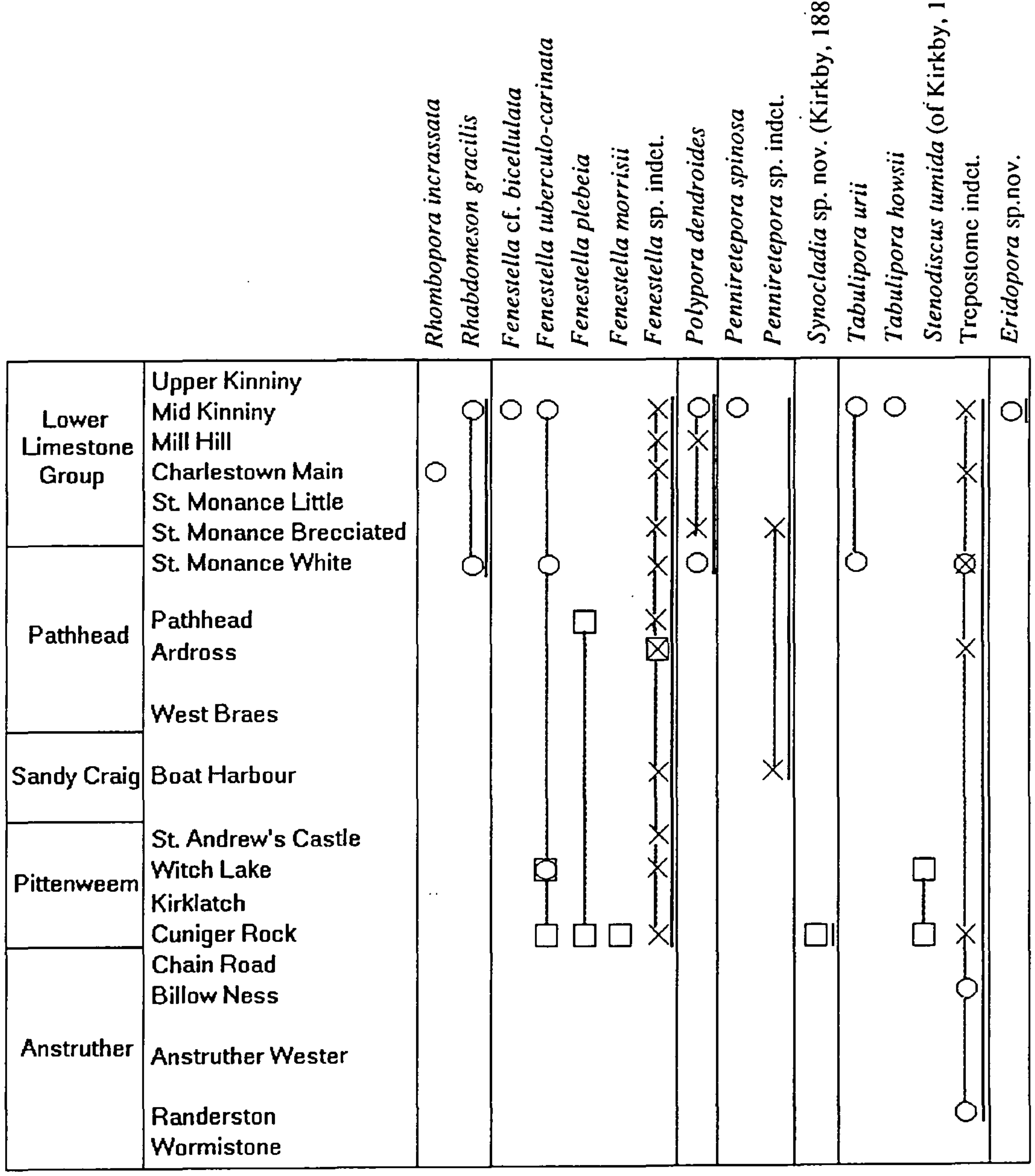


Fig 4.10. Stratigraphical ranges of bryozoans from East Fife

enabled the species to form sturdy hexagonal meshworks, perhaps allowing greater success in more turbulent waters. Representatives from more muddy deposits share the same regular disposition of the dissepiments, but usually lack the hexagonal meshwork or secondary thickening; thus, the colony plan of the species is relatively flexible, allowing it to survive, and occasionally flourish, in a wider variety of facies than normal.

Trepostomes are also very tolerant of salinities and facies, and are the stratigraphically earliest bryozoans to be found in the Carboniferous of East Fife; however, the specimens collected from the Anstruther Beds may not belong to the Bryozoa. Again a wide variety of colony growth forms undoubtedly helped the group achieve its success, and even in the Lower Limestone Group, trepostomes still form the most numerically abundant taxon.

In summary, the introduction of more stable carbonate environments enabled a wider range of bryozoans to inhabit the East Fife area during the Carboniferous, without displacing the earlier pioneering taxa.

CHAPTER 5 : ARRAN

Stratigraphy and Palaeogeographical Setting

The Isle of Arran contains the most westerly outcrop of Carboniferous rocks in the Midland Valley Trough, excepting a small patch on the east side of Kintyre, and it is a link between the Midland Valley of Scotland and the Northern Ireland Carboniferous successions. Carboniferous strata probably once covered much of the island, but earth movements and erosion, especially that associated with Tertiary tectonism, has reduced the outcrop to a relatively small area along the northeast coast and in the centre of Arran.

Rocks of the Old Red Sandstone facies pass conformably into Carboniferous fluvial and deltaic sediments, interbedded with volcanic rocks, as is seen at Corrie, with a few thin, crinoidal limestones, and one thick white limestone, the Corrie Limestone (stratigraphically equivalent to the Hurlet Limestone of the Midland Valley). The Corrie Limestone has a fairly sparse fauna, dominated by gigantoproductid brachiopods, and no bryozoans were recorded. Further along the Corrie shore, there is a passage once more into deltaic sediments with a few thin limestones, one reportedly yielding *Semiplanus latissimus* (possibly identifying it as equivalent to the Index Limestone) and non-marine bivalve bands before unconformably overlying Permian aeolian beds are reached.

The Corrie sequence, measuring approximately 450m in thickness, is a condensed expression of the Carboniferous on the island. To the north, at Laggan, another sequence of Carboniferous rocks occurs, and this too is rather condensed, though slightly thicker (approximately 800m), with the Carboniferous Limestone Series measuring 350m in thickness (Steele, 1978). Even though the areas of Laggan and Corrie are now separated by only about eight miles, they occur on different sides of a broad anticline, and are difficult to correlate. It is probable that local tectonic blocks provided much control over sedimentation, and Arran may well have formed a shallow ridge in the Midland Valley; this idea is supported by the general thinning of sediments in the Midland Valley towards the Isle of Arran and Kintyre.

The first major interruption to Lower Carboniferous deltaic sedimentation is shown at Laggan Cottage, where there is an outcrop of marine shales bearing abundant bryozoans, and limestones containing gigantoproductid brachiopods. These marine beds are correlated with the Corrie Limestone, at the base of the Lower Limestone Group. Further north, another prominent limestone is found, thinner but distinctively red in colour, and containing an abundant fauna of well-preserved bryozoans. Stratigraphically-higher limestones do occur, but are not well exposed.

Stratigraphical correlation with the mainland has proved to be difficult. The Laggan Cottage and Corrie limestones are equivalent, and correlate with the Hurlet Limestone, making them Lower Brigantian in age (this study ; Gunn, 1903 ; George *et al.*, 1976); this correlation is part-based on the abundance of *Gigantoproductus giganteus* which MacGregor (1948) reported to be common at the level of the Hurlet Limestone in the Midland Valley. Steele (1978) thought that this horizon was that of the Hosie Limestone, basing his evidence on the fact that the Laggan and Corrie limestones are the thickest on the island. However, the Hosie Limestone is more probably represented by a series of thin limestones and calcareous shales occurring approximately 40m above the Laggan limestone, in which the bivalve *Sanguinolites variabilis* was recorded by Hind, in Gunn *et al.* (1903); MacGregor (1948) cites this species as characteristic of beds in the stratigraphical vicinity of the Top Hosie Limestone.

The red limestone of north Laggan is more problematical, and Steele, in contradiction to Gunn, labelled the limestone as equivalent to the lowermost Pendleian Castlecary limestone. The macrofaunal lists from the limestone have been studied, and there appear to be no stratigraphically-diagnostic macrofossils, but the abundance of the brachiopod *Semiplanus latissimus* suggests a correlation with MacGregor's Midland Valley Index Limestone horizon; further, the reported occurrence (Peach, in Gunn *et al.*, 1903) of the productids *Dictyoclostus costatus* and the smaller *Eomarginifera longispinus* in the red limestones confirm these beds as belonging to either the Limestone Coal Group, or the Upper Limestone Group. The Castlecary Limestone is probably represented by the "Cephalopod" Limestone, some 4.5 metres higher, based on the reported occurrence of *Tylonautilus nodiferus* . Neves *et al.*, 1973, in their study of miospore zonation of the Midland Valley, sadly omitted to sample Arran, so the exact horizon of the red limestone must remain in some doubt.

The table on the following page, based on data from Steele, Gunn, and MacGregor, outlines the proposed stratigraphy of the Carboniferous of Arran. The horizons from which bryozoans were collected have been highlighted in bold text.

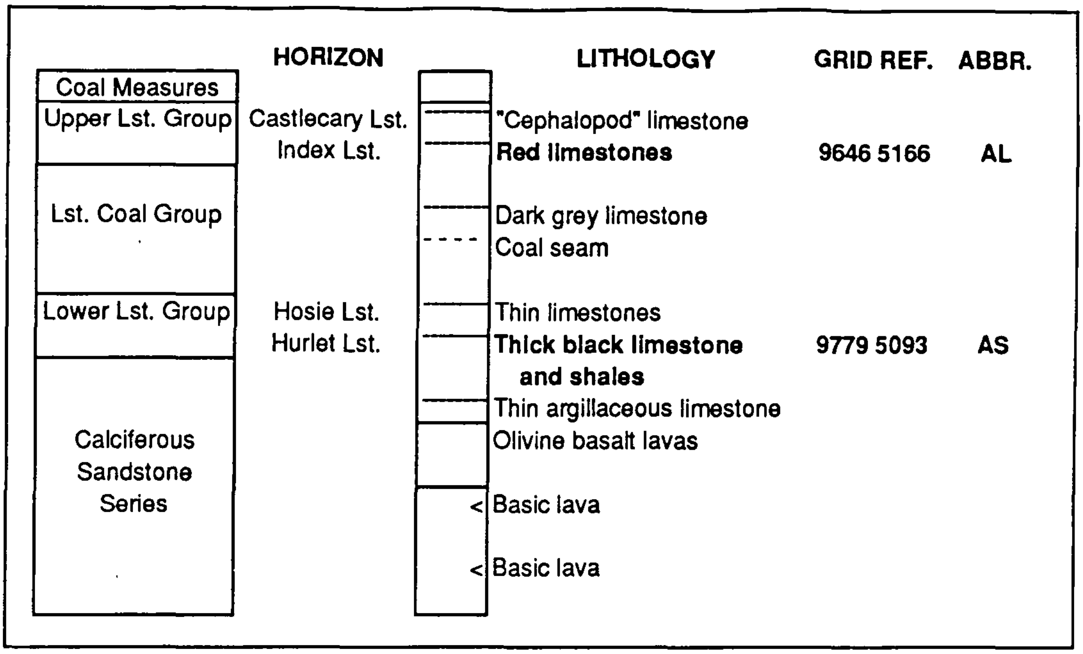


Fig. 5.1. Stratigraphy and bryozoan localities of the Carboniferous rocks on Arran.

The Hurlet Shales

GRID REFERENCE : NR 978 510
AGE : Brigantian

About 200m northwest of Laggan Cottage, a sequence of thick deltaic sandstones is interrupted by about 7m of shales and limestones. This sequence is palaeo-ecologically important, since the fossils within represent a pioneering fauna inhabiting an older, submerged delta-top environment. The fauna is believed to be *in-situ*, since the productid brachiopods are found in life position, and colonies of the bryozoan *Rhabdomeson gracilis* are only partially fragmented. In addition, many of the bryozoan colonies still have delicate lateral branches attached, and these would have been destroyed if the colonies had been transported any distance.

Environmentally, the shales and limestones probably represent a nearshore deposit, but water depths are problematical, since photic-zone-dwelling corals are notably absent. However, the great diversity of the fauna suggests that the community was a shelf-dwelling one, and the abundance of brachiopods, crinoids, bryozoans and some gastropods points to it being referable to Ramsbottom's (1978) Mud Community; the top limestones, which contain abundant *Gigantoproductus* specimens, would then be referable to the slightly shallower-water, or more clastic-free, Brachiopod Calcarenite Community.

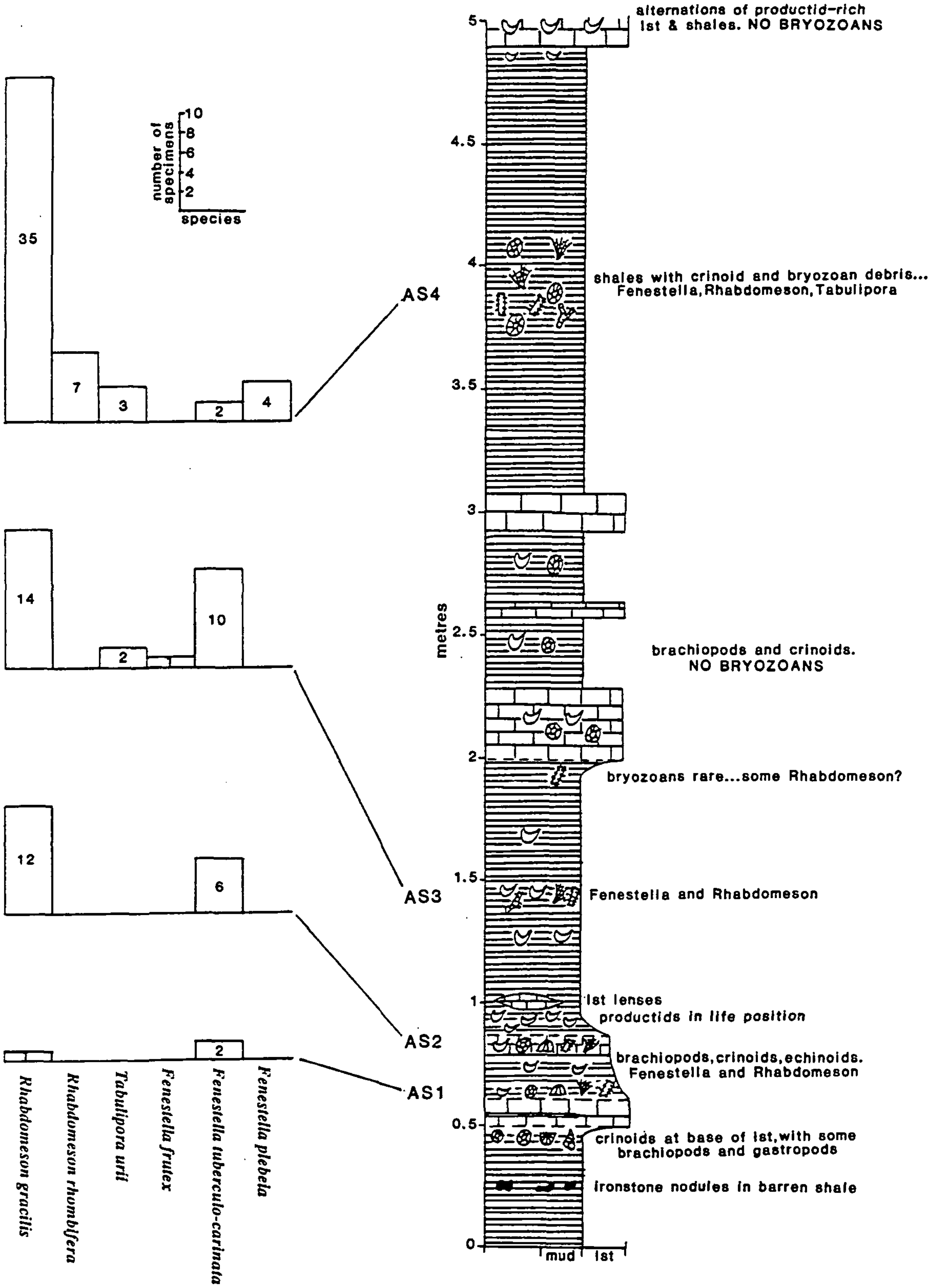


Fig. 5.2. Graphic log of the Hurlet Shales

A study was made through the section, with collections of bryozoans made at four distinct horizons. A graphic log has been produced (fig. 5.2), which details lithological change, and the changes in the fauna. Several bryozoan species were recorded :

Rhabdomeson gracilis
Rhabdomeson rhombifera
Tabulipora urii
Fenestella frutex
Fenestella tuberculo-carinata
Fenestella plebeia

There appear to be distinct changes in the fauna up the succession, which are discussed later, but the systematics described for each species are applicable throughout the whole sequence.

Rhabdomeson gracilis

This species forms by far the most abundant bryozoan taxon from the shales. The specimens are referable to *Rhabdomeson gracilis* on account of the regular rhombic arrangement of equal-sized apertures around a circular, moderately-slender colony (Plate 1, figs. a. and b.). A list af averaged parameters are given below. The material was actually measured from four distinct horizons within the shales, and this table (fig. 5.4) can be found in the section discussing variations within the marine horizon.

Rhabdomeson gracilis			
	Averages for AS shales		**Bancroft**
	x	**n**	**x**
ZD	**0.787**	**23**	**0.61?**
AD1	**0.196**	**23**	**0.21**
AD2	**0.097**	**23**	**0.10**
IWT1	**0.205**	**23**	**0.24**
IWT2	**0.11**	**23**	**0.09**

Apertures are slightly oval, measuring on average 0.20mm by 0.10mm, with their long axes parallel to the length of the colony. They are moderately well-spaced, and are arranged in a regular rhombic pattern. Interapertural walls are moderately-thick, averaging 0.21mm lengthways, and 0.11mm transversely. Stylets are not well-preserved on the walls, but single, large rounded stylets do occur.

Some specimens have broken tips, and show the axial rod, which is characteristic of this genus. Several colonies are over 1.5cm long, and branching is sometimes seen. AS⁴22 shows a partial "tuning-fork"-like bifurcation, and towards the tip of the colony, a lateral branch is developed, diverging at an angle of 60 degrees from the mainstem.

From the list of parameters, a close match to Bancroft's averages for *Rhabdomeson gracilis* can be seen. However, the samples differ most significantly in possessing higher transverse inter-aperture wall values, but lower longitudinal inter-aperture wall thicknesses. Thus, the Arran material has apertures which are "compressed" together longitudinally, but in other respects the specimens are undoubtedly referable to *Rhabdomeson gracilis.*

Rhabdomeson rhombifera

Rhabdomeson rhombifera occurs only in the top portions of the Hurlet shales, and coexists with *Rhabdomeson gracilis.* The colonies are more slender than *R. gracilis*, being only about 0.48mm in diameter (fig. 5.7c; see also Plate 1, fig. a. for a comparison of the two species). Parameters are given below :

Rhabdomeson rhombifera		
	Arran	**Bancroft**
	range	**range**
ZD	**0.48**	**0.49**
AD1	**0.30 - 0.40**	**0.28 - 0.47**
AD2	**0.10 - 0.12**	**0.12 - 0.19**
IWT1	**0.38 - 0.46**	**0.23 - 0.43**
IWT2	**0.05 - 0.06**	**0.06 - 0.18**
Z2	**3**	**3 - 4**

Apertures are regularly arranged, in a stretched rhombic pattern. They are very elongate, having an oval outline, occasionally with pointed proximal and distal margins, and almost straight lateral margins. Though there are variations in size (from 0.30mm to 0.40mm), it is difficult to see the regular grading around the zoarium. Similarly, interapertural walls vary in thickness, but they are all rather thin in the transverse direction. It is not possible to see stylets on the colonies, but they have probably been weathered away.

A comparison of the parameters with Bancroft's averages shows a good correlation, but the apertures may be narrower than usual. Coupled with narrow interaperture wall thicknesses, this implies that the apertures are stretched apart, being closer transversely, but further apart longitudinally, than average.

Specimens are assigned to this species on the basis of rhombically-arranged apertures around a slender cylindrical colony, the apertures being elongate and rather variable in size.

Tabulipora urii

Several specimens referable to this species were found in the shales, towards the top of the logged section. Fragments of cylindrical, dendritically-branching colonies occur, this branching pattern being best developed in specimen AS^{4}32 (Plate 1, fig. f.). These trepostomes are characterised by the irregular arrangement of the autozooecia, which are also rather variable in diameter, averaging 0.184 on specimen AS^{4}32, the best preserved example. This diameter is rather smaller than Bancroft's cited averages for *Tabulipora urii*, but the thin interzooecial walls (0.06mm) and spacing of the autozooids (9 in a 2mm line), coupled with the random distribution of exilazooecia, point to the specimens being referable to this species. Further, the parameters actually give the best fit with this species, compared with other species of *Tabulipora*. Parameters are given below :

	Hurlet Limestone, Arran			Bancroft
	Tabulipora cf. urii			*Tabulipora urii*
	n	σ	x	x
ZD			1.20 - 2.20	3.63
AD	10	0.0196	0.184	0.27
IWT	10	0.0178	0.062	0.06
ED	10	0.0135	0.087	0.09
Z2			9	6 - 7

From the internal morphology, it was not possible to prove the taxonomic affinities of the specimens, since recrystallization has destroyed most of the internal structure. Acetate peels and polished sections of AS^{3}4 showed radiating endozone walls developed from an axial region, but did not show whether ring septa were present. The presence or absence of ring septa is of taxonomic importance, since the genus *Tabulipora* possesses such septa, whereas the similar-looking genus *Stenodiscus* does not. Thus, the material is assigned to the species *Tabulipora urii* on external parameters alone.

		Fenestella frutex							*Fenestella tuberculo-carinata*							*Fenestella plebeia*						
HORIZON		**BW**	**AD**	**ID**	**FL**	**FW**	**DW**	**IND**	**BW**	**AD**	**ID**	**FL**	**FW**	**DW**	**IND**	**BW**	**AD**	**ID**	**FL**	**FW**	**DW**	**IND**
AS4	**x**								0.309	0.106	0.225	0.727	0.569	0.204		0.391	0.123	0.280	1.398	0.831	0.166	
	σ								0.0160	0.0063	0.0125	0.0484	0.0670	0.0779		0.0297	0.0104	0.0128	0.0700	0.0671	0.0298	
	σ2								0.0005			0.0002	0.0105	0.0160		0.0303			0.0177	0.0092	0.0203	
	n								8	4	2	15	8	16		22	4	5	28	17	29	
	N								2	1	1	2	2	2		4	1	1	4	4	4	
AS3	**x**	0.219			0.581	0.450	0.088		0.316	0.121	0.248	0.784	0.587	0.228	0.190							
	σ	0.0063			0.0063	0.0500	0.0089		0.0179	0.0059	0.0059	0.0371	0.0486	0.0213	0.0160							
	σ2								0.0142			0.0261	0.0858	0.0476	0.0133							
	n	2			2	2	4		27	3	6	87	58	33	18							
	N	1			1	1	1		5	1	1	10	10	5	3							
AS2	**x**								0.285	0.104	0.281	0.735	0.581	0.226	0.169							
	σ								0.0183	0.0056	0.0243	0.0558	0.0355	0.0160	0.0120							
	σ2								0.0144			0.0589	0.0724	0.0483								
	n								16	7	8	51	37	20	6							
	N								3	1	1	6	6	3	1							
AS1	**x**								0.317			0.829	0.551		0.214							
	σ								0.0153			0.0936	0.0445		0.0324							
	σ2								0.0065			0.0490	0.0195									
	n								13			11	10		8							
	N								2			2	2		1							

Fig. 5.3. Parameters of the fenestellids from the Hurlet Shales

Fenestellids

The genus *Fenestella* is relatively common in the shales, and three species have been recognised from this locality. *Fenestella tuberculo-carinata* is the most commonly-occurring form, but *Fenestella plebeia* occurs in the uppermost shales, and one small fragment referable to *Fenestella frutex* was found.

Fig 5.3 is a table of the parameters for *Fenestella* from the four horizons within the logged section.

Fenestella frutex

The sole fragment is rather poorly-preserved, and shows a few moderately-narrow, straight, sub-parallel branches joined by rather thin, bar-like dissepiments which do not flare at the branch margins (fig. 5.7b). The dissepiments are slightly depressed beneath the branch crests. Recrystallization has almost obliterated any ornamentation, but faint longitudinal striae may be seen on the reverse surface of the colony.

	Arran, Hurlet horizon			Bancroft			
	Fenestella frutex			*F. frutex*		*F. multispinosa*	
	n	σ	x	x	t-TEST	x	t-TEST
BW	2	0.0063	0.219	0.24	0.1658	0.24	0.3004
FL	2	0.0063	0.581	0.58	0.9720	0.65	0.0144
FW	2	0.0500	0.450	0.44	0.7345	0.49	0.1625
DW	4	0.0089	0.088	0.11	0.0121	0.13	0.0017
			TOTAL		0.4711		0.1190

Statistically, even the few measurements obtained show a very high probability correlation with *Fenestella frutex*, as measured by Bancroft, and a total probability of 0.2410 was obtained when the specimen was compared against Tavener-Smith's Carrick Lough material. The dissepiments and branches, though, are thinner than usual, but this may be an artefact of preservation, since the meshwork is still partially-buried in the matrix; thus the maximum diameters for branch and dissepiment width may not have been recorded. In contrast, the fenestrule lengths and widths, which are not affected by partial burial of the specimen, show excellent correlations.

Comparisons with *F. multispinosa*, a form often confused with *F. frutex*, are included, and show lower probabilities. Thus, the fragment is almost certainly that of *Fenestella frutex*.

Fenestella plebeia

Several fragments referable to this species were found in the uppermost portions of the logged section. These forms are characterised by stout branches, which are sub-parallel, slightly rounded, and occasionally bifurcating. The reverse surfaces are strongly ornamented by longitudinal striations which have been highlighted by the weathering of the specimens. Occasionally, node-like expansions may be seen, but these, unlike carinal nodes, are irregularly distributed, and may simply be artefacts of diagenesis. The branches are very broad (0.39mm), but they may actually have been flattened during burial and compaction of the shale, since the obverse surface recorded curved only gently, rather than being steep-sided as is more typical of the species.

The obverse surfaces bear two rows of circular apertures on each branch, with five apertures per fenestrule (fig. 5.7a). The apertures are of moderate diameter (0.12mm) and are flush with the branch margins; though they possess thin, complete peristomes, these rims do not appear to project into the fenestrules. A thin, slightly-sinuous keel runs down the centre of each branch, but no nodes appear to have been preserved.

Dissepiments are much thinner than the branches, being 0.17mm in diameter. They flare slightly towards the branch margins, and are flush to slightly depressed below the crests of the reverse branch surfaces, and are moderately depressed below those of the obverse surfaces. On their reverse surfaces, the dissepiments are slightly striated (Plate 1, fig. d.). Fenestrules are long and relatively narrow, and are sub-rectangular in outline.

Fenestella plebeia						
	Arran, Hurlet horizon			Bancroft	PROBABILITY SCORES	
	n	σ	x	x	t-TEST	t-DIV
BW	22	0.0297	0.391	0.30	0.0000	0.0305
AD	4	0.0104	0.123	0.11	0.0478	0.0971
ID	5	0.0128	0.280	0.26	0.0323	0.0706
FL	28	0.0700	1.398	1.02	0.0000	0.0896
FW	17	0.0671	0.831	0.60	0.0000	0.0827
DW	29	0.0298	0.166	0.16	0.2865	0.0613
				TOTAL	0.0611	0.0720

Though the colonies have all the characteristics of *Fenestella plebeia* (McCoy), most notably in possessing 4 to 5 apertures per fenestrule, sub-parallel, striated branches, relatively thin dissepiments, and thin circular peristomes, statistically correlations are poor with both Bancroft's and Tavener-Smith's data on the species. Branch widths, fenestrule lengths and widths are much higher than average, but do actually fall at the extreme end of Bancroft's cited ranges. A relatively low division-probability score indicates that the specimens are not merely "scaled-up" versions of an average *Fenestella plebeia*. However, this species is the commonest form of the genus *Fenestella* recorded in the Carboniferous of Great Britain, and such a wide geographical occurrence, coupled with the species longevity, would have produced a considerable amount of variation. A similar degree of variation has been noted by Cuffey (1967) in the common American bryozoan taxon *Tabulipora carbonaria*. Such variation is substantiated by Bancroft's (1984) coefficients of variation for the Fenestellidae; *Fenestella plebeia* has amongst the highest coefficients of variation for its parameters within the genus *Fenestella*.

Thus, though the material from Arran is much stouter than usual, it is still referable to the species *Fenestella plebeia*.

Fenestella tuberculo-carinata

Fragments of this species form the bulk of the *Fenestella* population and, like *Rhabdomeson gracilis*, occur throughout the logged section.

Specimens can be recognised by relatively stout branches which are gently sinuous. Dissepiments are staggered on opposite sides of branches at roughly half-fenestrule intervals, and when seen from the reverse surface, this results in a typical hexagonal "honeycomb" pattern (Plate 1, fig. c.). This pattern is accentuated by the rather thick nature of the dissepiments, and secondary calcification of the meshwork. In addition, reverse surfaces have rounded branches and dissepiments, and the dissepiments are flush with the branch crests. Some specimens show the typical thickened "tubercules" of Young (1882) at the branch/dissepiment junctions on the reverse surface.

Only a few specimens showing the obverse surfaces were found (fig. 5.6, a. and b.). Branches appear to be rather thick, and surfaces slope fairly steeply away from a prominent median ridge. The ridge is gently sinuous and ornamented by oval, moderately large, closely-spaced nodes. Autozooecial apertures are fairly large, and are pronounced with thick peristomes, which abut onto the median ridge and project into the fenestrules. Apertures are very closely-spaced, and there are about four per fenestrule. At branch bifurcations, the splitting branches diverge from each other at a fairly gentle angle, rather than recurving in the usual "tuning fork" pattern. The bifurcation of the median ridge, though, does adopt the tuning-fork pattern, so the "smoothing" of the branch bifurcations is probably a result of secondary calcification of the meshwork. An aperture is placed in the angle of the branch fork.

Dissepiments are moderately well-sunk beneath the obverse surface branch crests, but because of the steep slopes of the branch sides, they are actually flush with the branch margins. From the obverse surface, fenestrules have a more oval appearance, as the dissepiments flare quite considerably at the branch margins. Carinae were not observed on the dissepiments.

The statistics of these specimens are discussed in Chapter 3, exemplifying the use of the division t-test routine for showing true species affinities. In this case, the original measurements were x0.8 smaller than they should have been. A corrected table of results is given below :

Fenestella tuberculo-carinata						
	Arran, Hurlet horizon			Bancroft	PROBABILITY SCORES	
	n	σ	x	x	t-TEST	t-DIV
BW	14	0.0235	0.306	0.30	0.5820	0.1978
AD	3	0.0080	0.111	0.10	0.0015	0.0110
ID	3	0.0234	0.251	0.23	0.1249	0.2234
FL	22	0.0507	0.780	0.73	0.0202	0.1548
FW	22	0.0679	0.575	0.57	0.8362	0.2255
DW	14	0.0480	0.211	0.20	0.5436	0.4673
IND	5	0.0179	0.190	0.20	0.3692	0.1144
				TOTAL	0.3539	0.1992

Statistically and morphologically, the specimens show a very close match to Bancroft's emended descriptions of *Fenestella tuberculo-carinata.* Good correlations compared to results of the same species comparisons from other areas, are probably because of collection bias in Bancroft's data; most of his material seems to have been collected from shale facies within the Lower Limestone Group of the Midland Valley. Thus, with respect to the facies and stratigraphical age of the locality, the Arran material and Bancroft's material are very similar.

Faunal Changes within the Hurlet Marine Horizon

Bryozoans were sampled at four horizons within the basal shales of the Lower Limestone Series at Laggan. An equal amount of collection time was spent at each horizon, so there is probably no sample bias in collecting by this method. There are

Rhabdomeson gracilis					Hurlet horizon, Laggan, Arran			
		N	n	x	σ1	σ2	x-min	x-max
AS4	ZD	6	8	0.768	0.0880		0.700	0.960
	AD1	6	65	0.187	0.0061	0.0152	0.179	0.197
	AD2	6	69	0.087	0.0068	0.0095	0.076	0.094
	IWT1	6	66	0.207	0.0179	0.0218	0.180	0.238
	IWT2	6	71	0.102	0.0155	0.0149	0.090	0.129
AS3	ZD	7	8	0.777	0.0965		0.700	0.960
	AD1	7	46	0.198	0.0210	0.0180	0.163	0.234
	AD2	7	40	0.096	0.0132	0.0089	0.080	0.120
	IWT1	7	40	0.196	0.0244	0.0218	0.147	0.220
	IWT2	7	37	0.114	0.0201	0.0149	0.074	0.136
AS2	ZD	9	15	0.810	0.0907		0.720	1.020
	AD1	9	86	0.205	0.0163	0.0167	0.178	0.240
	AD2	9	76	0.103	0.0066	0.0116	0.091	0.112
	IWT1	9	67	0.213	0.0146	0.0235	0.195	0.249
	IWT2	9	83	0.113	0.0133	0.0142	0.090	0.123
AS1	ZD	1	2	0.770				
	AD1	1	7	0.166		0.0090		
	AD2	1	7	0.117		0.0070		
	IWT1	1	5	0.180		0.0179		
	IWT2	1	3	0.093		0.0094		

Fig. 5.4. Parameters of *Rhabdomeson gracilis* from the Hurlet Shales

certainly distinct faunal changes within the five metres of logged sediment, perhaps representing increasing marine influence over a previously deltaic shoreline. The graphic log (fig. 5.2) shows lithological and faunal changes in the shales.

Within the first metre of the succession (levels AS^1 and AS^2), bryozoans are rather scarce, and only *Rhabdomeson gracilis* and *Fenestella tuberculo-carinata* were recorded, despite marine conditions having been established within the first forty centimetres of shales. By 1.5m in the succession (level AS^3) bryozoans are more abundant, but still dominated by *Rhabdomeson gracilis* and *Fenestella tuberculo-carinata*, though one specimen of *Fenestella frutex* and some *Tabulipora urii* fragments were recovered. A general decline in faunal diversity at 2.5m may suggest an increased terrigenous influence, which could account for the cessation of limestone production, and only brachiopods and crinoids were found. However, by 4m (level AS^4), conditions were more conducive for bryozoans, and a fairly diverse and abundant fauna was established, with *Rhabdomeson gracilis* still the dominant species, though the more slender *R. rhombifera* occurs. *Tabulipora urii* is moderately common, and *Fenestella plebeia* makes its first appearance. *Fenestella tuberculo-carinata* also occurs, but it is not as common as lower in the sequence; however, the small sample sizes mean that it is not possible to determine whether *F. plebeia* competitively replaced *F. tuberculo-carinata.*

All the specimens were recovered from shale facies, which consisted of apparently similar rock types. The fossil material is *in-situ*, so factors other than current-sorting or substrate differences must be inferred to account for the changes. Changes in the salinity may be one possible reason for the differences between the sample points; modern bryozoans are fairly stenohaline (Ryland, 1970), but certain forms are euryhaline, being tolerant of salinity extremes from 1 part per thousand to over 35 parts per thousand. However, such forms usually show a decline in numbers with increased salinity, and if *Rhabdomeson gracilis* were a euryhaline species, then its numerical increase at the diverse AS^4 level would not normally be expected.

The size of modern cheilostome bryozoan autozooids has been shown to be affected by temperature differences (Okamura and Bishop, 1988); the colder the water, the longer the autozooid chamber. Whether this model can be applied to extinct Palaeozoic forms is not certain, but a study of zoarial parameters was conducted on the Arran material. Up the succession, there is actually a decrease in autozooid length (inferred from interaperture distance) in *Fenestella tuberculo-carinata*, but the small sample size means no great significance can really be applied to this. Further, associated length features such as fenestrule length showed no significant trends, as is highlighted in the following table, derived from fig. 5.3 and fig. 5.4:

	Rhabdomeson gracilis	*Fenestella tuberculo-carinata*
LEVEL	AD1 + IWT1	ID
AS4	0.394	0.225
AS3	0.394	0.248
AS2	0.418	0.281
AS1	0.346	

In the species *Rhabdomeson gracilis* zooid length was estimated from the sum of longitudinal aperture diameter and inter-zooecial wall thickness. The data showed no significant trend up the succession. Therefore, the hypothesis that faunal changes may be due to palaeotemperature differences is not substantiated by the data.

It is possible that the logged section represents changes in the pioneering faunas. *Rhabdomeson gracilis* and *Fenestella tuberculo-carinata* appear to be generalists, lacking the thin skeletal architecture, or autozooecial differentiation seen in many bryozoan taxa. The stouter meshworks of the two forms could additionally be best adapted to life in more nearshore, turbulent conditions. Thus, the introduction of *Fenestella frutex*, a less regularly-meshworked form of *Fenestella plebeia*, *Tabulipora urii*, and the slender *Rhabdomeson rhombifera* may be a natural ecological succession, without having to infer environmental shifts.

However, modern ecological successions appear to reach faunal maturity relatively rapidly; there is, though, no way of accurately establishing the time-scale over which the shale sequence in Arran was deposited. It may be worth while, though, attempting to estimate the order of magnitude of the rates of deposition :

Data from T.N. George *et al.* (1976) shows

Courceyan to Middle Arundian = approx. 13Ma.
In South Wales, a sequence of shales and limestones from these stages = 450m
Therefore, 5m of sediment (the thickness on Arran) = approx. 150,000 years

Brigantian = approx. 25Ma.
In Dungannon, mudstones of this stage = 200m
Therefore, 5m of sediment = approx. 625,000 years

Thus the succession logged on Arran possibly represents deposition measurable in hundreds of thousands of years. Modern ecological studies obviously cannot chart faunal successions over this scale of time for newly-created marine habitats, but

Keough (1984) performed studies on cleared patches off the Australian coast, with some interesting implications for bryozoan workers.

Cleared areas which were adjoined by existing communities ("non-isolate patches") were initially encrusted by bryozoans and polychaete worms (forms with free-swimming larvae) but were soon over-encrusted by the slower-growing, but better-adapted, sponges and colonial tunicates invading from the surrounding areas. However, areas surrounded only by water ("isolate patches") depended on their size as to which taxa were most successful in colonising the zone. Small isolate patches were dominated by bryozoans, while bryozoans co-existed with tunicates and sponges on the larger patches.

Thus, modern bryozoans appear to be good colonisers but poor competitors. How far this model can be applied to Palaeozoic bryozoans is not certain, since modern bryozoans are evolutionary-distant from the Palaeozoic stenolaemata. Many of the Palaeozoic bryozoans appear to have been non-brooding, thus probably produced longer-lived free-swimming larvae; some, though, seem to have developed ovicells, especially within the order Fenestrata. The abundance of bryozoans in many Palaeozoic communities certainly points to their being good competitors, at least within the mineralized taxa; it is not possible to ascertain competitive effectiveness with the unmineralized sessile organisms with which they co-existed.

Problems also exist with extrapolating Keough's patch models to a larger scale, that of a newly-created marine zone. With a gradual relative sea-level rise, the new marine areas would be in constant communication with previously-established communities. However, a rapid marine incursion would create a large-scale isolate patch of the type favoured by modern bryozoans.

In summary, the lack of data on modern bryozoan colonisation rates, and the uncertainty of Carboniferous sedimentation rates and sea-level changes means that the exact causes of the bryozoan community evolution must remain unresolved. However, the introduction of more slender forms towards the top of the succession suggests that palaeocurrents could have slackened, perhaps as a result of deepening water associated with a relative rise in sea level through the sequence.

The Index Limestone

GRID REFERENCE : NR 9646 5166

Approximately 1.7km northwest of Laggan Cottage, a sequence of relatively-thin (approx. 0.75m thick), seaward-dipping red coloured limestones occur. There are three posts of this limestone, separated by thin shales, and underlain by purple mottled, barren shales. The red colour is due to hematite staining within the matrix, and a thin section showed the abundance of randomly-occurring hematite opaques. The hematite staining is thought to be caused by a diagenetic percolation of groundwater from the overlying, iron-rich aeolian Permian sandstones.

The fauna has largely recrystallized, so only external detail is preserved but the fossils recovered were weathered out quite clearly on the exposed bedding planes of the sea-washed section. Latissimoid productids referable to *Semiplanus latissimus* are rather common in the limestones, suggesting the correlation of the beds with the Index Limestone (Pendleian). Bryozoans are also very common, and the following forms were found :

Septopora carbonaria
Fistulipora incrustans
Fenestella tuberculo-carinata

The colonies can actually be fairly large, with some specimens of *Fistulipora* up to 12cm in diameter, and large fenestellid fans preserved. Thus, the fauna is probably a disturbed *in-situ* fauna; the encrusted substrate for the cystoporates was not observed. A relatively high-energy environment is inferred for the horizon, since the more delicate bryozoans seen in the Hurlet shales were not found; turbulent waters would favour the stouter bryozoans found here. Applying the McKinney (1989) facies distribution model for Carboniferous sequences, the fenestrate bryozoan fauna is typical of that found seaward of shoals, and above storm wave base. This facies is not inconsistent with palaeoenvironments suggested by the other faunal constituents, which suggest a shallow-water Brachiopod Calcarenite Community structure. Again, comparing this sequence with the Hurlet shales, the lack of corals (save for a possible zaphrentid recorded by Gunn) is interesting; light in these waters may have been reduced by a relatively-high clastic input.

Septopora carbonaria

Several fragments from two colonies were found which are referable to the genus *Septopora* on account of the colonies having two rows of apertures on each branch, and in possessing lateral branches (with the appearance of dissepiments) also with two rows of apertures. The colony meshwork appears very similar to that of a normal fenestellid, with broad branches joined by the dissepiment-like secondary branches .

The form of the colony is not certain, but the preserved fragments indicate a radiating, planar fan-like shape (Plate 1, fig. e.). Likewise, initial stages of the colony are not known, but the more distal portions comprise a regular meshwork of fairly closely-spaced, sub-parallel, straight or gently-curved primary branches, linked by regularly-spaced secondary branches. The branching pattern, however, is not simple; primary branches are generated mainly from a poorly-defined trunk zone, and diverge from this at angles of 15° to 30° (fig. 5.9). Several primaries can been seen to fuse and terminate with secondary branches, and for two primaries to apparently fuse together as one single primary(fig. 5.10, a. and b.). Both primary and secondary branches are well-rounded on the obverse surface, and striations are not apparent.

Secondary branches are almost as broad as primary branches (primary branch width approx. 0.48mm : secondary branch width approx. 0.46mm), and form dissepiment-like cross-struts between the primaries. Angles of divergence can be as low as 60° , but most are perpendicular to the primaries. They are regularly-spaced, and in specimen AL2/10 chevron-like fusions between opposing branches are sometimes developed; however, no such chevroning, which is usually typical of the American forms of *Septopora*, was observed in the tighter meshwork of AL3/24/25. No tertiary branches have been observed.

Two rows of very closely-spaced autozooecial apertures are developed on the obverse surfaces of the primary branches. Apertures are usually circular, but may be slightly oval, and are moderately-sized (approx. 0.14mm in diameter). They are set flush on the branch surface, and apertural rims do not seem to be developed. There are between four and five apertures per fenestrule, and they abut the median ridge, but do not indent the fenestrules.

Apertures on the secondary branches are more irregularly arranged, but usually grow in rows of two; sometimes three rows may be developed, most noticeably at the fused boundary between two secondary branches, where a third row develops between the normal two rows (fig. 5.10c).

Cyclozooecia are sporadically developed, but in certain parts of the colony they may be locally abundant. They have much smaller apertures than the autozooecia, being on average 0.06mm in diameter, and are randomly distributed, some apparently growing on the median ridge, but more often on primary branches, secondaries, or at the junctions between the two types.

On primary branches, a poorly-defined median ridge separates the two rows of apertures; it is never sharp or strong, and is more usually just a broad aperture-free central zone. Nodes may sometimes develop, and when they do they are fairly large, oval, and closely spaced (0.32mm). Very rarely, a median ridge is developed on the secondary branches; a single node, or a pair of nodes, may also occur, and often grow even in the absence of a median ridge.

Fenestrules can be very variable in shape, dependent on how the secondary branches diverge from the primaries. They are invariably well-rounded, and range in shape from circular to elliptical either with the long axis of the ellipse parallel to the primary branches, or in the case of squat fenestrules, with the axis parallel to the secondaries. Axial ratios actually average longitudinal:transverse 1.2:1, but may be up to 1.8:1.

The averaged parameters for five colony fragments are given below :

Septopora carbonaria						
	Index Limestone, Laggan			Bancroft, 1987	PROBABILITY SCORES	
	n	σ	x	x	T-FEN	T.FEN.DIV
PBW	5	0.0680	0.479	0.44	0.3670	0.1729
AD	5	0.0146	0.141	0.13	0.2403	0.1387
ID	5	0.0248	0.213	0.27	0.0025	0.1656
FL	5	0.1235	0.925	1.18	0.0187	0.2153
FW	5	0.1720	0.758	0.78	0.7602	0.2043
SBW	5	0.0624	0.458	0.33	0.0065	0.0117
IND	5	0.0511	0.324	0.44	0.1266	0.2792
CD	5	0.0121	0.064	0.07	0.4324	0.1773
				TOTAL	0.2443	0.1706

Two species of *Septopora* have been described previously from the British and Irish Carboniferous: Tavener-Smith (1973a) described *Septopora hibernica* from the Asbian of Carrick Lough, County Fermanagh, and Bancroft (1987a) evaluated *Septopora carbonaria*, an Asbian to Brigantian ranging species from the Midland Valley and Northumberland. Of the two species, the material from Arran corresponds very closely with the parameters cited by Bancroft for *Septopora carbonaria.* In contrast to *Septopora hibernica*, both have a median ridge with carinal nodes, and both have fairly common cyclozooecia. The table of values shows that parameters also match extremely closely, considering the wide variations in morphological material that Bancroft included in his averages. This variability is shown by the internodal distance, which though differing by nearly 30%, still record probabilities of 0.1266, since Bancroft obtained very large coefficients of variation for this parameter. Similarly, secondary branch widths are rather different, but again a probability of 0.0066 results from a very high coefficient of variation.

For the species as a whole, the coefficients of variation which Bancroft cites are actually very high, and the specimens described in his paper encompass some very different morphologies; it is quite likely that *Septopora carbonaria* (*sensu* Bancroft) encompasses several biological species. Certainly, the British examples of *Septopora* which have been observed in this study range from those with a very acanthocladiid-like morphology of several mainstems and chevroning secondary branches, to those such as the Arran examples with a more fenestellid-like appearance, with very regularly-spaced meshworks. The Arran specimens also differ from the Bancroft described material in lacking peristomal rims, though this could of course simply be a preservational feature.

It is worth entering into the *Septopora/Lanarkopora* controversy of Bancroft and Graham. Graham (1975) reviewed the Scottish Carboniferous acanthocladiid bryozoans, and quite correctly realised that Etheridge's (1873) *Synocladia carbonaria* was not referable to the genus, since branches carried only two, and not three, rows of apertures. However, he did not place the taxon in the genus *Septopora* (Prout) since the material he had studied had carinate secondary branches, while those of the type species *Septopora cestriensis* (Prout) did not. Bancroft argued that this difference was not of sufficient taxonomic merit to erect the new genus *Lanarkopora*; work on the specimens from Arran certainly substantiates the arguments of Bancroft, since some of the secondary branches on colonies are carinate, while others on the same colony do not have carina, and some may even possess nodes while lacking a carina.

It is therefore proposed that Bancroft's placing of *Lanarkopora* as a junior synonym with *Septopora* be upheld. However, it is quite probable that further study will not only record more specimens of *Septopora* since the genus can, at a quick glance, be mistaken for *Fenestella* or sometimes *Polypora*, but may also show that *Septopora carbonaria* (*sensu* Bancroft) actually comprises several species.

Cystoporates

Many cystoporate fragments were found in the Index Limestone. Recrystallisation and haematite impregnation have destroyed many of the external and internal features, but the matrix infilling the zooecial chambers contrasts with the lighter red colour of the calcite forming the original cystiphragmaceous interzooecial walls. Though these cystiphragms are no longer visible, either on the specimens or in cross sectional acetate peels, the specimens are ascribed to the Cystoporata on account of the circular apertures separated by very wide interzooecial walls which suggest their former presence.

Colonies occur as unilaminar sheet-like forms, up to 2mm in thickness, but none were observed encrusting any other fossil; it is quite likely that they had originally lived on soft plant fronds which have not been preserved. One specimen, AL36 (fig. 5.8c), shows the initial stages of a colony. It forms a domed structure, approximately 2mm in diameter, with prominent circular to oval autozooecial apertures, each with obvious, slightly-elevated peristome rims completely surrounding them. Apertures are less well-defined towards the colony periphery, and represent the partially-calcified growing edge. On the more mature colonies, the domed aspect is lost, and the more usual sheet-like appearance develops. Specimen AL37/39, in contrast to AL36, formed a colony at least 12cm in diameter.

Autozooecia are widely-spaced, randomly arranged, and are circular to slightly oval, having an average diameter of about 0.30mm. On the better-preserved specimens such as AL19, small lunaria are developed partway around the proximal side (by definition) of the apertures. They are not very prominent, and unlike *Eridopora*, they do not actually cover part of the apertures. They do, however, form slight elevations above the colony surface. Aperture-free monticules are commonly developed, but it was not possible to determine how regular their occurrence was. In fact, no specimens were deemed sufficiently well-preserved to merit a full set of measurements being taken; however, the number of apertures in a 2mm line (Z2) has been estimated at 4.5.

The lack of polymorphic zooecia, the small lunaria, the common monticules and the large, well-spaced apertures all suggest that these specimens are referable to the genus *Fistulipora*, and are not inconsistent with Bancroft's emended diagnosis for *Fistulipora incrustans* (Phillips), the only species recorded in British Carboniferous rocks.

Fenestella tuberculo-carinata

A large number of bryozoan fragments referable to *Fenestella tuberculo-carinata* were found. Despite much variation in the size of the meshwork, all of the specimens were assigned to this species on the basis of the very prominent median ridge with very obvious, closely-spaced nodes, and the large apertures with thick peristome rims which project slightly into the fenestrules.

Branches are quite broad (0.30mm to 0.36mm) and are sub-parallel, with new branches being added by bifurcation. Along the crest of each branch, there is a very prominent, broad median ridge, usually ornamented with variable-sized nodes, which may be circular or oval (fig. 5.8a). These nodes are very closely spaced (0.27mm to 0.29mm), and sometimes are elevated well above the crest of the median ridge.

Branch sides slope quite steeply away from the median ridge, but actually appear to flatten out, due to the development of relatively large autozooecial apertures (diameter ranges from 0.10mm to 0.13mm) with rather thick peristomes. The peristome rims are complete, and often indent the edges of the fenestrules. Apertures are usually circular, and there are between three and five per fenestrule. One aperture is invariably placed in the angle of the fork formed by branch bifurcation.

Dissepiments are thick (0.20mm to 0.25mm) and short; they also flare considerably towards the branch margins. They are only slightly depressed beneath the branch crests on the obverse surface. Some dissepiments actually have a median carina of their own, and these carinae join the main median ridge at right angles, without the flaring associated with the actual dissepiments; specimen AL32 (Fig. 5.8b) shows a good example of this phenomenon.

Fenestrules are usually elongate, being rather narrow and having well-rounded extremities. They vary in shape from fairly squat-rectangular, to elongate-ellipsoidal forms.

Reverse surfaces are variable in their morphology. Specimen AL16 has a thickened meshwork, and reverse surfaces are smooth and well-rounded, with some dissepiments not only flush with but actually elevated above the level of the branches. Fenestrules still appear sub-rectangular, and the meshwork has not developed the hexagonal appearance typical of this species elsewhere, though specimen AL26 comes close to this morphology.

Measurements taken from two end-members of the meshwork size spectrum are given below :

Fenestella tuberculo-carinata

	AL 1			AL 12			Bancroft, 1984
	n	σ	x	n	σ	x	x
BW	6	0.0247	0.364	12	0.0144	0.315	0.30
AD	5	0.0059	0.125	12	0.0144	0.105	0.09
ID	8	0.0199	0.204	12	0.0199	0.215	0.23
FL	3	0.0449	1.248	12	0.0458	0.798	0.73
FW	5	0.0746	0.650	12	0.0287	0.453	0.57
DW	3	0.0057	0.244	12	0.0936	0.198	0.20
IND	4	0.0255	0.276	13	0.0298	0.294	0.20

A series of probability comparisons has also been compiled, raising some rather interesting considerations (fig. 5.5). Though specimens AL1 and AL12 score very low on the straight t-test, the division probability returns quite a high comparison, with a relatively even spread of correlations, suggesting that the meshwork ratios of the two specimens are similar; this justifies their conspecificity, even though their actual parameters appear to be rather different. Further, the rather large AL1 shows affinities with *Fenestella tuberculo-carinata* from the division analysis (but not on a

	AL1 vs. AL12		AL1 vs. *F. tub.-car.*		AL 12 vs. *F. tub.-car.*	
	t-PROB	DIV	t-PROB	DIV	t-PROB	DIV
BW	0.0004	0.0502	0.0007	0.1599	0.1497	0.0444
AD	0.0174	0.1684	0.0000	0.3392	0.0084	0.0370
ID	0.1918	0.3009	0.0118	0.0000	0.0329	0.0077
FL	0.0000	0.0068	0.0000	0.0008	0.0116	0.0374
FW	0.0000	0.0173	0.0400	0.0901	0.0000	0.0000
DW	0.1319	0.2726	0.0792	0.3686	0.9143	0.1817
IND	0.3520	0.1480	0.0001	0.1759	0.0000	0.0000
TOTAL	0.0991	0.1378	0.0188	0.1621	0.1596	0.0440

	F. plebeia vs. F. tub.-car.		AL1 vs. *F. plebeia*		AL 12 vs. *F. plebeia*	
	t-PROB	DIV	t-PROB	DIV	t-PROB	DIV
BW	1.0000	0.0029	0.0000	0.0934	0.0055	0.0000
AD	0.0000	0.0156	0.0110	0.1201	0.2513	0.0028
ID	0.0000	0.0012	0.0000	0.0000	0.0000	0.0024
FL	0.0000	0.0101	0.0034	0.1690	0.0000	0.0594
FW	0.0740	0.0108	0.0415	0.1104	0.0000	0.0219
DW	0.0000	0.0000	0.0000	0.0001	0.0001	0.0089
IND	0.0000	0.0000	0.0004	0.0027	0.0000	0.0006
TOTAL	0.1534	0.0058	0.0080	0.0708	0.0367	0.0137

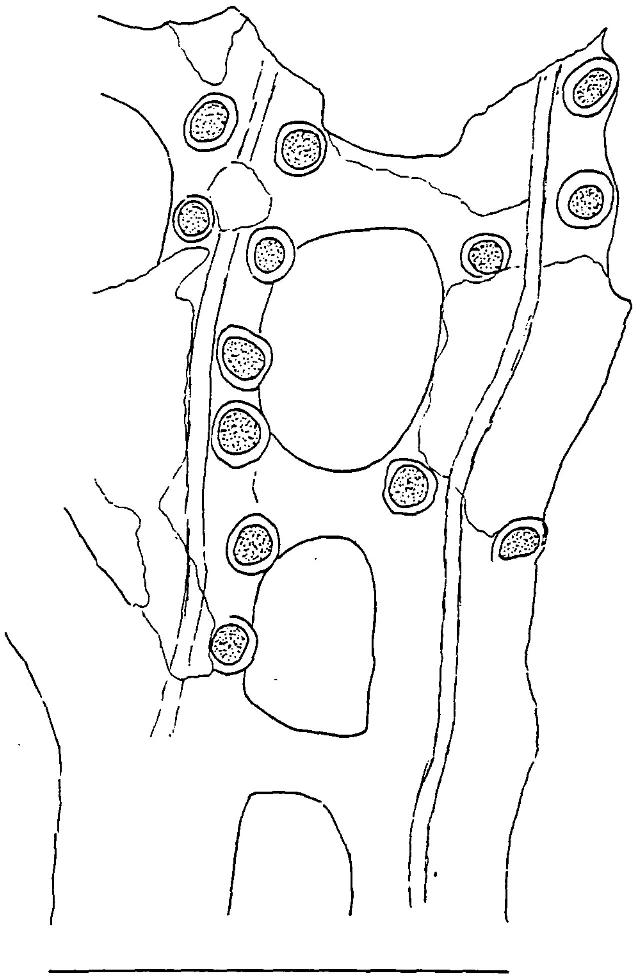
	F. multi. vs. F. tub.-car.		AL1 vs. *F. multi.*		AL 12 vs. *F. multi.*	
	t-PROB	DIV	t-PROB	DIV	t-PROB	DIV
BW	0.0000	0.0075	0.0000	0.0101	0.0000	0.0064
AD	1.0000	0.0000	0.0000	0.0152	0.0000	0.0111
ID	0.0000	0.0000	0.0000	0.3156	0.0000	0.1266
FL	0.0000	0.0156	0.0000	0.0641	0.0000	0.0016
FW	0.0000	0.0256	0.0000	0.0377	0.0025	0.0001
DW	0.0000	0.0002	0.0000	0.1116	0.0000	0.0043
IND	0.0000	0.0000	0.0001	0.1535	0.0000	0.1023
TOTAL	0.1429	0.0070	0.0000	0.1011	0.0004	0.0360

Fig. 5.5. t-test Scores for Arran end-members of *Fenestella tuberculo-carinata*

straight t-test), while AL12, which is more typical of most of the Midland Valley forms, has a good probability comparison with Bancroft's average *Fenestella tuberculo-carinata.*

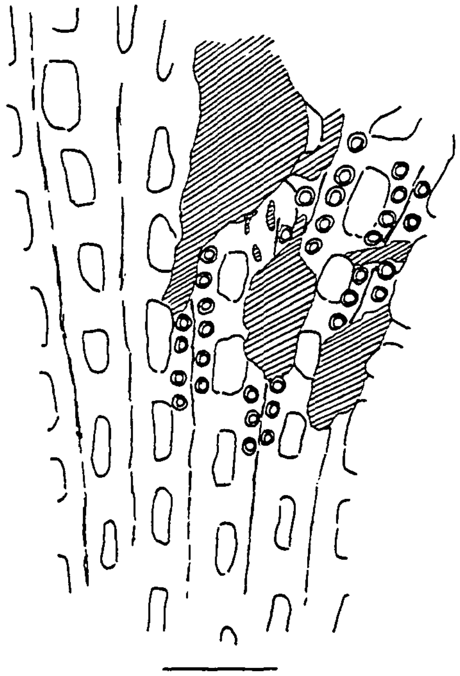
Comparisons with other species of *Fenestella* are also included. The stoutness of AL1 could have suggested that it was actually a representative of *Fenestella plebeia,* but both the t-test and the division analysis rule out this correlation. Also, AL12 could conceivably have belonged to the species *Fenestella multispinosa,* but again both the t-test probabilities, and those from the division routine, seem to disprove this link.

In summary, the specimens from the Index Limestone, though variable in meshwork size, correspond well with *Fenestella tuberculo-carinata* from both morphological and statistical considerations.

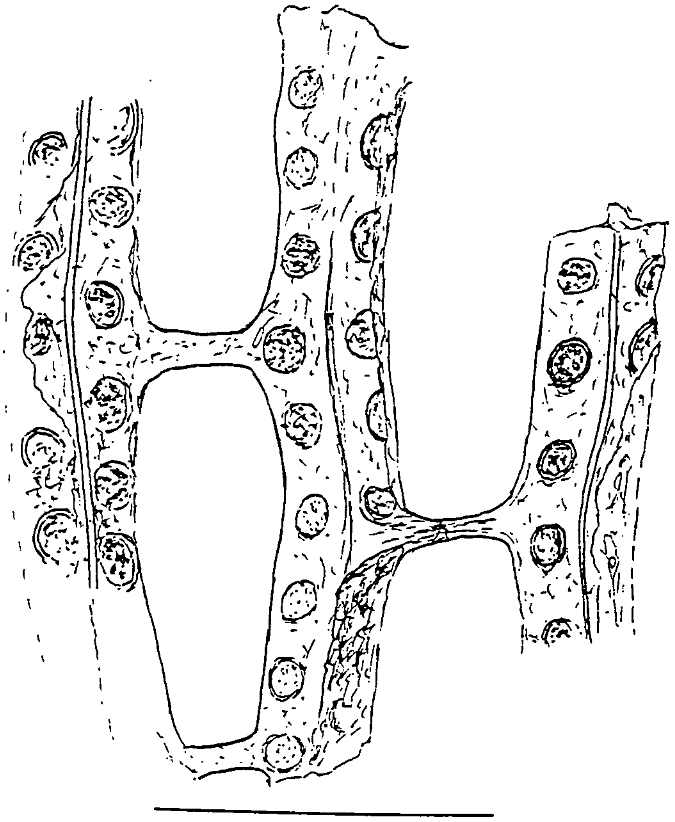


a. *Fenestella tuberculo-carinata* obverse surface detail $AS^4 38$

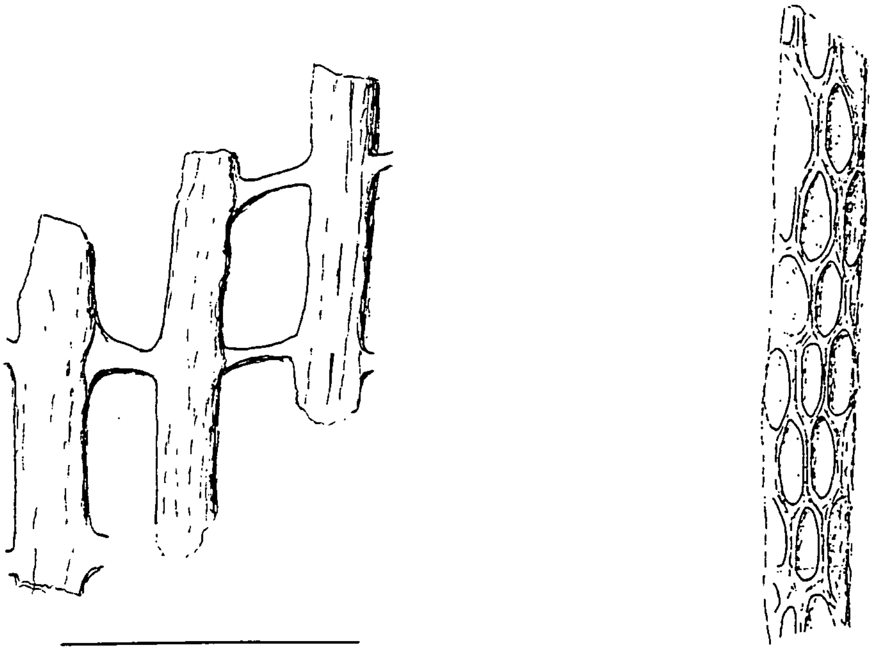
Fig. 5.6. *Fenestella tuberculo-carinata* from the Hurlet Shales



b. *Fenestella tuberculo-carinata* obverse surface $AS^4 38$



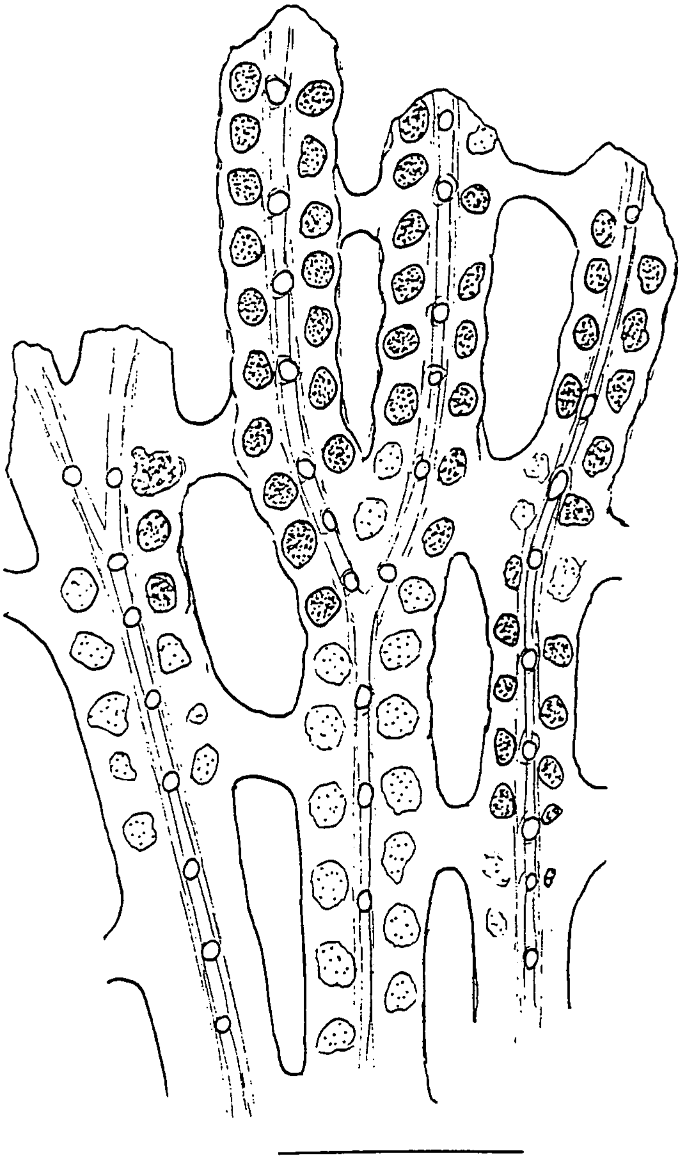
a. *Fenestella plebeia* obverse surface AS^{4}26



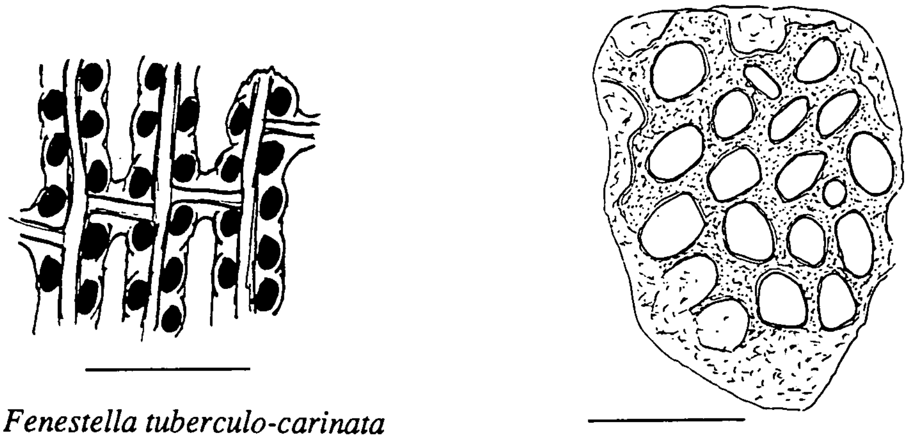
b. *Fenestella frutex* reverse surface AS^{3}8

c. *Rhabdomeson rhombifera* AS^{4}5

Fig. 5.7. Bryozoans from the Hurlet Shales



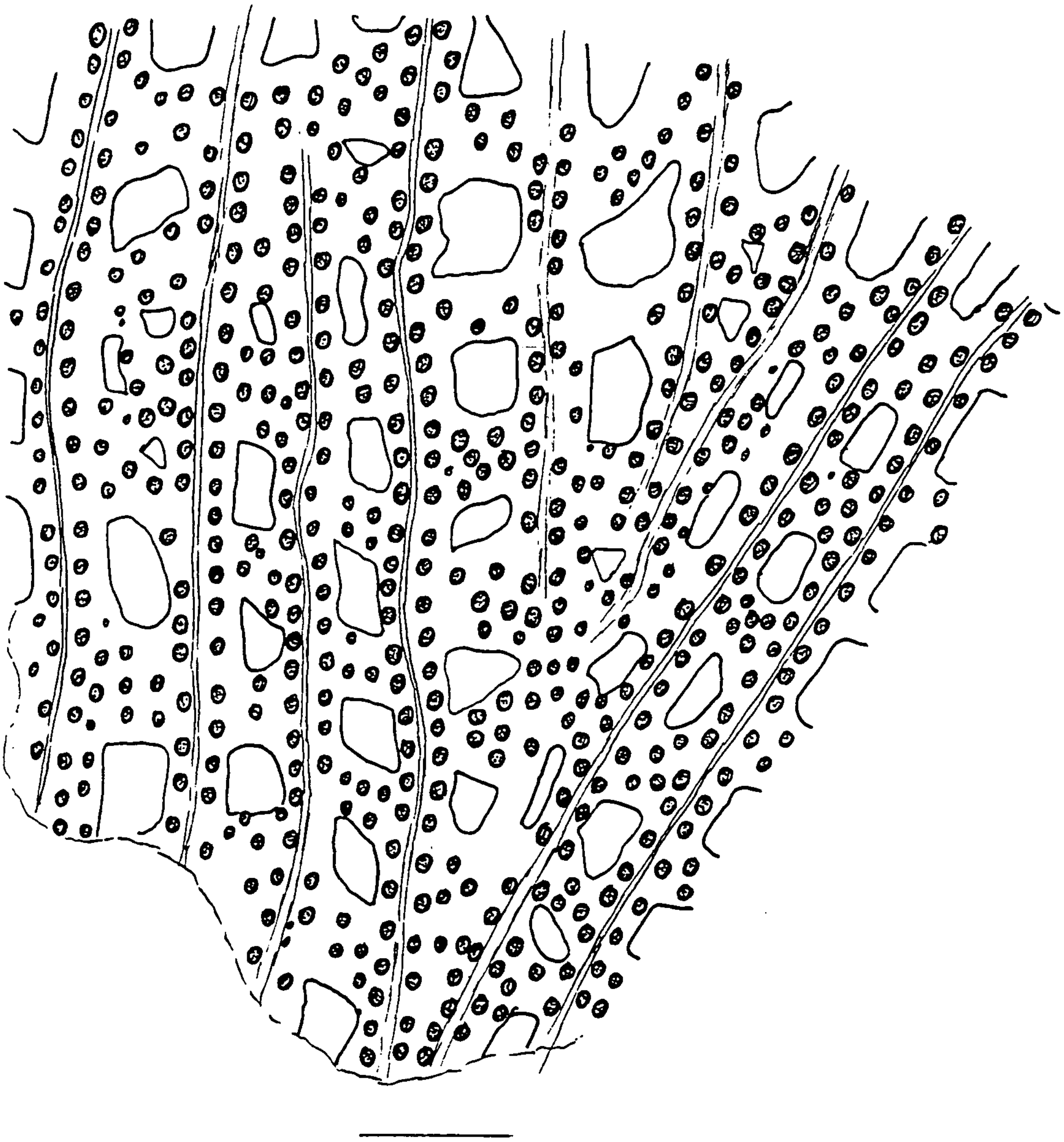
a. *Fenestella tuberculo-carinata* obverse surface AL46



b. *Fenestella tuberculo-carinata* showing carinate dissepiments AL32

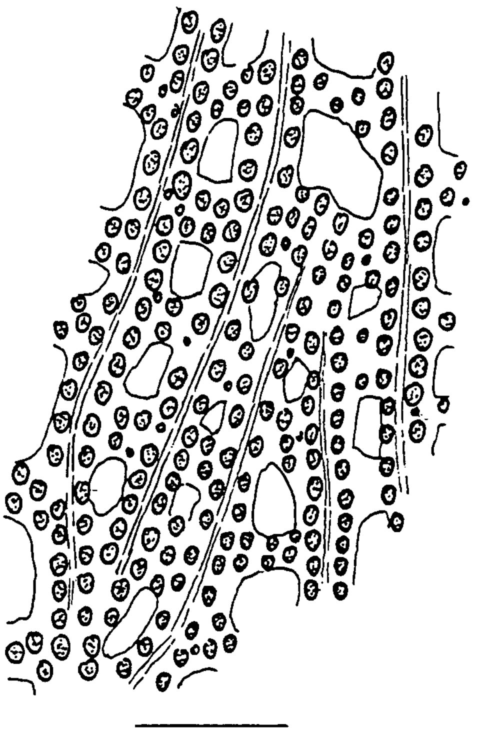
c. *Fistulipora incrustans* AL36

Fig. 5.8. Bryozoans from the Index Limestone

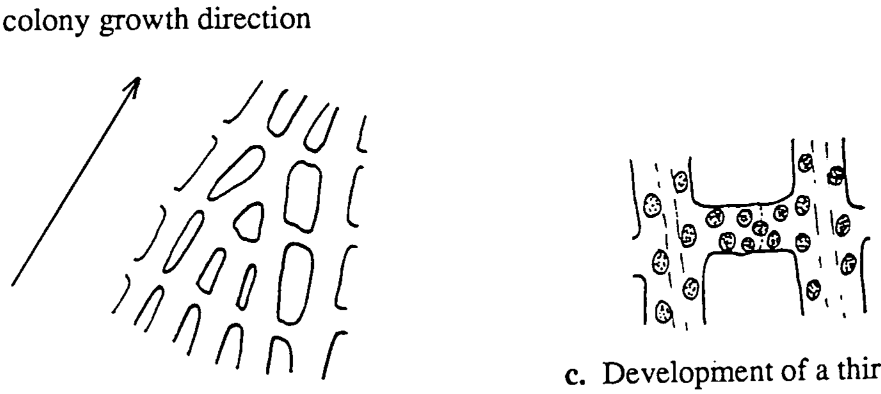


Septopora carbonaria obverse surface AL24

Fig. 5.9. *Septopora carbonaria* from the Index Limestone



a. *Septopora carbonaria* obverse surface AL24



b. Branch fusion in *Septopora*

c. Development of a third row of apertures in *Septopora*

Fig. 5.10. *Septopora carbonaria* from the Index Limestone

CHAPTER 6 : SOUTH WALES AND AVON

Stratigraphy and Palaeogeographical Setting

The region encompassing South Wales and Avon was part of an area of shallow marine shelf during much of the Lower Carboniferous, lying on the southern margin of St. George's Land. The Dinantian succession is known to thin quite considerably where it onlaps onto this long-lived island, as is illustrated in George (1970). An area of deeper sea lay to the south and west of the area, beyond the Culm Trench of Devon and Cornwall (the inferred edge of the continental shelf is illustrated in fig. 13.9). Drainage from the northern Laurasian continent, which provided much of the terrigenous input during the Devonian, virtually ceased in the Lower Carboniferous in this region, and carbonate platforms were able to develop. Terrigenous input resumed on a large scale in the Namurian, with fluviatile sediments similar to those of the Upper Old Red Sandstone being formed. Some marine horizons are present, though, often with an abundant marine fauna.

Most of the material collected during the season of fieldwork was from the Gower Peninsula, which represents a fairly thick accumulation of Dinantian deposits, dominated by shelf carbonates. The basal sequences, the Cefn Bryn Shales (formerly the Lower Limestone Shales), represent a period of some terrigenous input; George (1970) believes that the clastics were derived from south-flowing streams running off St. George's Land. Figure 6.1 illustrates the stratigraphy of the Gower region, showing a comparison of T. N. George's stratigraphies of 1969 and 1976. In the Gower region, there is a fairly complete Dinantian succession, but further northward, local unconformities are more common. The approximate thicknesses of the units in the Gower region are as follows :

Oystermouth Beds	60 - 120m
Oxwich Head Limestone	180m
Hunts Bay Oolite	270 - 330m
High Tor Limestone	150m
Caswell Bay Mudstone	3 - 7m
Caswell Bay Oolite	20 - 50m
Penmaen Burrows Lst Group. (Langland Dol. - Shipway Lst.)	150m
Cefn Bryn Shales	150m

		ZONE	STRATIGRAPHY		LOCALITY AND ABBREVIATION	GRID REF.
			George et. al. 1976	George 1969		
VISEAN	BRIGANTIAN	D3	Oystermouth Beds	Black Lias	Black Lias Quarry (BLQ)	SS 615 884
		D2	Oxwich Head Limestone	Crinoidal lsts.,clays, some thin coals and pseudobreccias		
	ASBIAN	D1				
	HOLKERIAN	S2	Hunts Bay Oolite	Pisolites,algal lsts. towards top, main mass formed of light oolite	Red Chamber (RC) Mewslade Bay (MB)	SS 422 868 SS 419 872
	ARUNDIAN	C2 S1	High Tor Limestone	Coarse crinoidal lsts.		
	CHADIAN		Caswell Bay Mst.	Modiola phase		
		C1	Caswell Bay Oolite	Caninia Oolite	Tears Point (TP)	SS 408 871
	COURCEYAN		Langland Dolomite	Laminosa Dolomite		
TOURNASIAN			Tears Point Lst.			
		Z2	Shipway Limestone			
		Z1		Dolomitized crinoidal lsts.	Three Cliffs Bay (TCB)	SS 535 880
		K	Cefn Bryn Shales	Lower Limestone Shales	Avon Gorge (AG) Stackpole Quay (SQ)	ST 556 746 SR 994 960

Fig. 6.1. Stratigraphy of South Wales and Avon

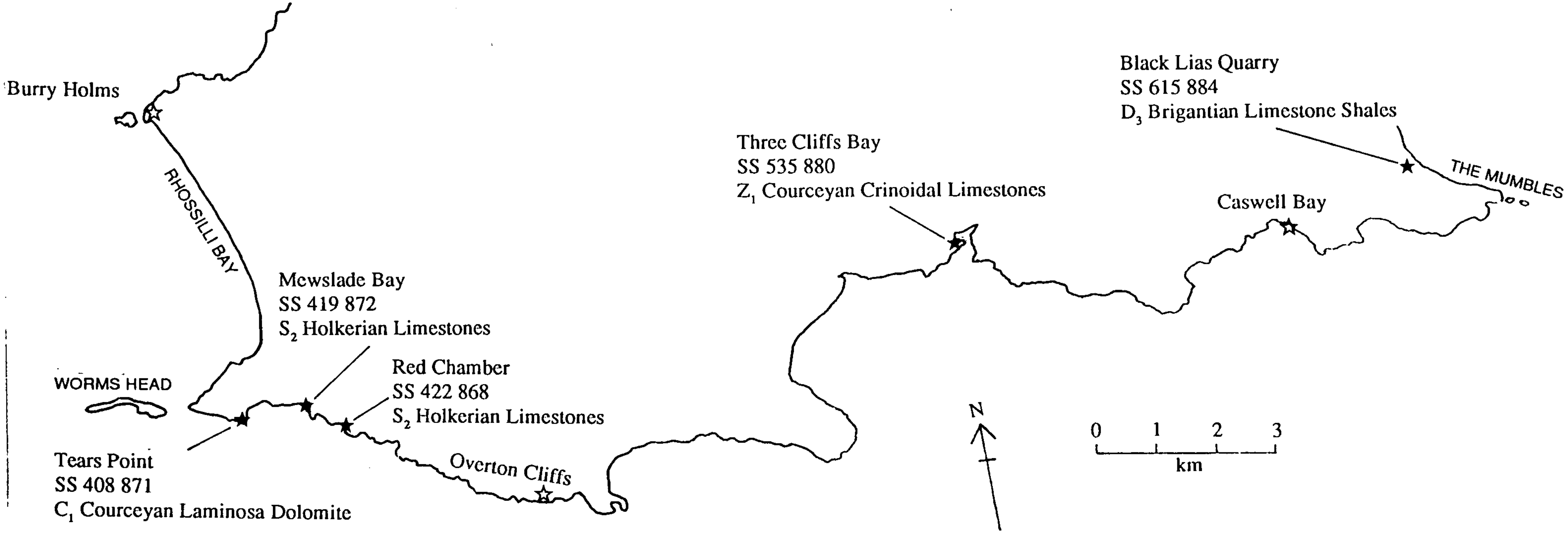


Fig. 6.2. Bryozoan localities on the Gower Peninsula

Ramsay (1987) discussed the depositional settings of the Dinantian facies in Gower, and concluded that the Courceyan represented a phase of transgressive deposition, followed by a regressive episode in the Chadian. Arundian deposits are typical of a further transgressive sequence, with post-transgression low energy barrier-inlet-lagoon complexes, succeeded by an increase in depth during the lower Holkerian as a wave-dominated ramp developed. The Holkerian is terminated by an erosion surface and palaeosol, though there were two additional regressive phases within this stage.

Localities which yielded bryozoans are also shown in figure 6.1, indicated in bold type and placed at their appropriate stratigraphical level. The localities in Gower are additionally indicated in figure 6.2, with areas yielding bryozoans being shown with a black star, and those in which bryozoans were not found are indicated by a white star. Two further sites were visited in the region; Stackpole Quay near Pembroke, and the Avon Gorge in Bristol. Though there are some differences, most noticeably in the frequency of end-stage unconformities in the Avon Gorge, the sequences in the two areas are broadly comparable with that in Gower.

The Avon Gorge

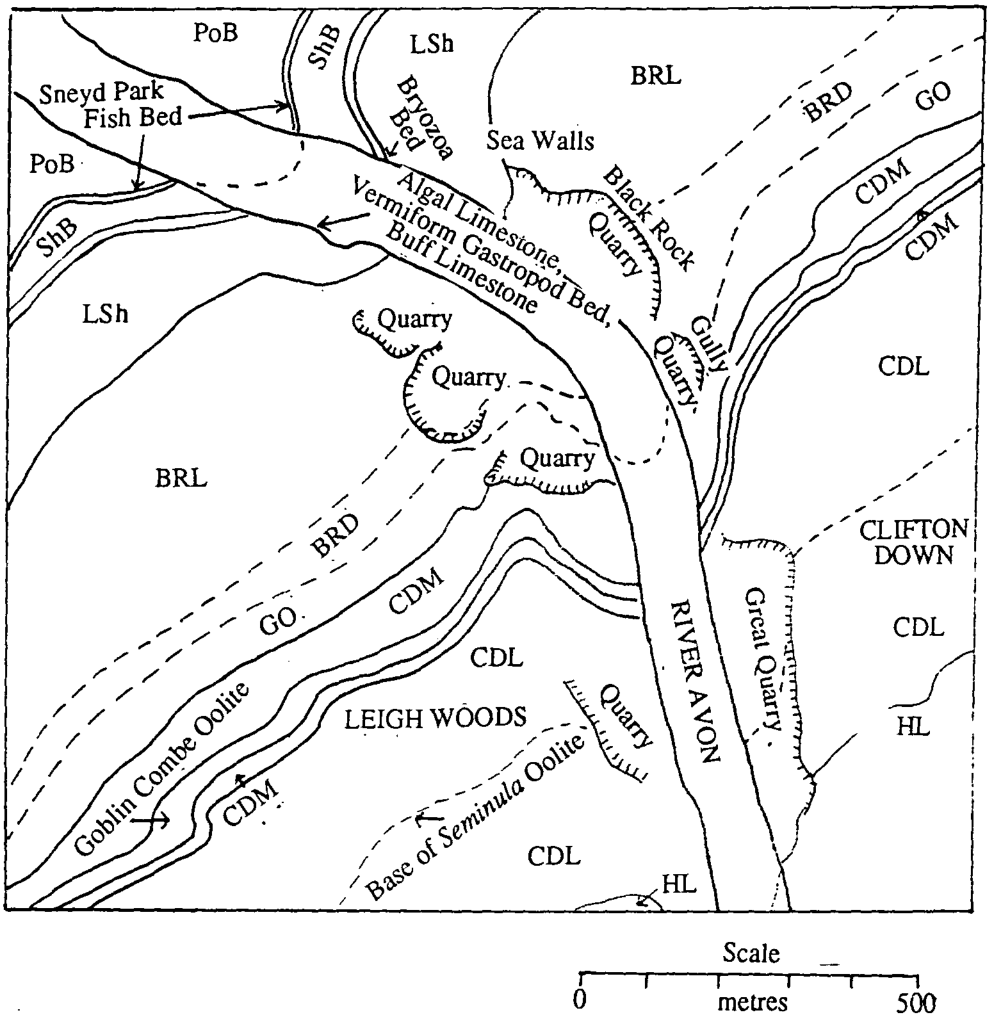
GRID REFERENCE : ST 556 746
AGE : Courceyan

The Avon Gorge is a deep natural cutting through Lower Carboniferous rocks which were formed south of the Bristol Channel area. There is a fairly complete succession of 800m of Dinantian rocks, from the Courceyan Shirehampton beds to the Brigantian Upper Cromhall Sandstone, though there are some unconformities present.

The top of the Shirehampton beds are reported to be marked by a "Bryozoa Bed". A search was therefore made to try to locate this horizon, navigating the Avon mudflat foreshore; red Devonian sandstones can be seen to be succeeded by more buff-coloured rocks, and an algal limestone and a "corallite" limestone were found in the lowermost beds (fig. 6.3). However, no horizon identifiable as a Bryozoa Bed was recorded.

At ST 556 746, though, a buff-weathering limestone, probably within the Lower Limestone Shales (Courceyan) and measuring approximately 30cm thick, yielded some rhabdomesids and fenestellids. The following taxa were recorded :

Rhabdomeson rhombifera
Fenestella cf. *plebeia*
Trepostome, indet. (very poorly preserved)



AGE	ABBR.	FORMATION
Asbian	HL	Hotwells Limestone
Holkerian/Arundian	CDL	Clifton Down Limestone
Arundian	CDM	Clifton Down Mudstone
Arundian	GO	Gully Oolite
Chadian	BRD	Black Rock Dolomite
Chadian	BRL	Black Rock Limestone
Courceyan	LSh	Lower Limestone Shale
Courceyan	ShB	Shirehampton Beds
Upper Devonian	PoB	Portishead Beds

Fig. 6.3. Geology of the Avon Gorge

Additional components of the fauna included some crinoid columnals, and a few ostracods.

The underlying "corallite" limestone was actually identified (C.T. Scrutton, personal communication) as being composed of erect vermiform gastropods. Burchette and Riding (1977) noted similar beds in the Lower Limestone Shales of South Wales and the Forest of Dean. They inferred that such gastropods lived in quiet-water, schizohaline intertidal or subtidal areas. Additionally, in these localities, the vermiform biostromal limestones overlay algal intertidal limestones, indicating a prograding succession. Thus, the succeeding bryozoan-bearing limestone probably represents slightly deeper, more normal marine nearshore conditions.

Succeeding limestones belonging to the Black Rock Limestone (Chadian) and the Clifton Down Limestone (Holkerian) were examined in quarries on the south side of the gorge. However, the quarries are now all very overgrown, and both the quarry faces and the weathering scree are covered in lichens. When fossils were found, they were predominantly brachiopods, with chonetids, spiriferids and productids being recorded, in addition to some corals, but no bryozoans were found.

Fenestella cf. *plebeia*

Parameters for the specimen of *Fenestella* found in the Avon Gorge are given in the following table :

	Fenestella plebeia						
	AG4			**Bancroft**		**Tavener-Smith**	
	n	**σ**	**x**	**x**	**t-TEST**	**x**	**t-TEST**
BW	9	0.0183	0.287	0.30	0.0401	0.292	0.6698
AD	10	0.0092	0.136	0.11	0.0000	0.111	0.0000
ID	13	0.0061	0.227	0.26	0.0000	0.260	0.0021
FL	6	0.1383	1.003	1.02	0.7689	1.166	0.0169
FW	8	0.0608	0.493	0.60	0.0000	0.641	0.0000
DW	7	0.0203	0.139	0.16	0.0049	0.174	0.0243
				TOTAL	0.1356	TOTAL	0.1189

Specimen AG4 (Plate 10, fig. j.) is a moderately well-preserved proximal portion of a *Fenestella* colony.

Branches are moderately stout (0.29mm) and frequently bifurcating, giving an open meshwork. A poorly developed sinuous median ridge is present, and branch sides slope away very steeply from this ridge. No obvious nodes were seen.

Ridge sinuosity is due to the very large apertures, placed flush on the branch surfaces; the median ridge weaves between the overlapping rows of alternately-placed apertures. Apertures are circular, measuring 0.14mm in diameter, and they are very closely-spaced (ID=0.23mm). Peristomal rims occur as very faint elevations surrounding each sunken aperture. There are four to five apertures per fenestrule.

Bifurcations are very frequent, giving a rapidly-diverging meshwork. Bifurcations have a high-angle tuning-fork appearance, and when two adjacent branches diverge at the same time, the newly-formed branches are not connected by dissepiments, but are adjoined directly together in a pattern similar to that seen in the fenestellid precursors, the Phyloporinidae. A single aperture is placed in the angle of the fork, but is set some way back from the branch margin.

Dissepiments do occur, and are moderately thick (0.14mm). They are slightly depressed beneath obverse surface branch crests, and flare moderately at branch margins. Weathered colony portions revealed that they are strongly striated on the reverse surface.

Fenestrules are elongate, averaging 1.00mm in length, but only 0.49mm in width. However, both lengths and widths can be quite variable. In outline, fenestrules are sub-rectangular.

The fact that the colony fragment is a proximal portion makes the specimen difficult to identify. High-angle bifurcations, with a single aperture in the angle of the fork, and four to five apertures per fenestrule suggests that AG4 may be referable to *Fenestella plebeia.* The thick branches and moderately-long fenestrules augment this diagnosis, but t-test data shows apertures to be larger and more closely-spaced than normal, and fenestrules to be narrower. Narrow fenestrules may be accounted for by the frequency of branching, and large apertures to diagenetic enlargement, but close aperture spacing is difficult to explain. However, of all the species of *Fenestella* compared, *F. plebeia* provided the best fit, so AG4 is tentatively assigned to this species.

Rhabdomeson rhombifera

Several small, poorly-preserved fragments of this species were found (fig. 6.6a), the largest fragment measuring only 2.5mm in length.

Colonies form moderately-slender (0.50-0.62mm) cylindrical zooecia, around which rhombically-arranged autozooecia occur. Autozooecial apertures vary in shape from sub-oval (measuring 0.16mm in length, and 0.09mm in width) to elongate sub-diagonal (measuring 0.24mm in length, and 0.10mm in width). They are quite closely-spaced, and longitudinal interwall thicknesses vary from 0.20-0.30mm, with transverse thicknesses ranging from 0.06-0.12mm.

Walls are ornamented by small stylets which surround the vestibular regions of the apertures; large, single stylets are not developed (cf. *Rhabdomeson gracilis*). Exilazooecia are absent.

Broken fragments revealed that the autozooids are budded from around a central axial cylinder, diagnostic of the genus *Rhabdomeson.*

Autozooecial aperture variation, slender cylindrical colonies, and small peristomal stylets all suggest that the specimens are referable to the species *Rhabdomeson rhombifera.* Additionally, though the match is not perfect, parameters do fall within the cited ranged of Bancroft (1984).

Stackpole Quay

GRID REFERENCE : SR 994 960
AGE : Courceyan

At Stackpole Quay, 7.5km south of Pembroke, a passage from red fluviatile Devonian rocks to marine Carboniferous limestones is displayed. The Upper Devonian sandstones are succeeded by some striped red beds, a limestone with a fauna of freshwater bivalves and then a crinoidal limestone before a series of dark grey fissile shales, the Carboniferous Lower Limestone Shales, are developed. Some brachiopods, and quite a few orthoconic nautiloids, also occur in the earlier limestones, and the shales frequently yield a fauna of orthoconic nautiloids, crinoids, and some goniatites. One limestone contains an abundant goniatite fauna.

Bryozoans were not found in these earlier limestones, despite conditions of deposition being fully marine, and do not occur until about 5m below the base of the first thick grey limestone; at this horizon, a nodular limestone is developed, and this yielded some poorly-preserved fenestellid bryozoans, and one *Fenestella* fragment was found in the underlying shales.

Succeeding limestones can be rather fossiliferous, one such crinoidal limestone bearing an abundance of the cryptostome *Rhombopora similis*, and another band (found on a later visit to Stackpole, when it was revealed by cliff fall) is extremely rich in bryozoans, and can be described as a Bryozoa Bed. However, despite the great abundance of bryozoan colony fragments, only the following taxa were recorded :

Fenestella multispinosa
Rhombopora similis
Trepostome, indet.

Many fragments were rather large, suggesting little transport of the colonies; however, no colony origins were found, suggesting some post mortem current activity. The material may well have formed originally on a bryozoan mound, with the presence of some crinoids, but the high degree of intercolonial variation suggests that the abnormal abundance cannot be attributed to rapid colonisation by asexual colony fragmentation, unlike some American communities of *Archimedes* (McKinney, 1983; McKinney & Jackson, 1989).

Fenestella multispinosa

Parameters of this species are as follows :

	Fenestella multispinosa						
	SQBB-5			Bancroft		Tavener-Smith	
	n	σ	x	x	t-TEST	x	t-TEST
BW	8	0.0260	0.275	0.24	0.0027	0.250	0.0160
AD	12	0.0072	0.093	0.09	0.1257	0.096	0.6202
ID	13	0.0324	0.243	0.26	0.0130	0.250	0.4011
FL	10	0.0764	0.727	0.65	0.0001	0.633	0.0003
FW	11	0.0526	0.493	0.49	0.8375	0.499	0.7121
DW	12	0.0076	0.121	0.13	0.2331	0.116	0.4249
IND	13	0.0522	0.378	0.35	0.0356	0.358	0.4185
				TOTAL	0.1782	TOTAL	0.3704

Fenestella multispinosa is very abundant in the Stackpole Quay Bryozoa Bed. The colony meshwork can have rather variable dimensions, but all colonies have the same arrangement of sub-parallel branches forming a rigid meshwork.

Branches are moderately-thick (0.28mm), and have a broad median ridge which bears large oval nodes with very variable spacing (IND=0.32-0.46mm). Branch sides slope quite steeply away from the ridge. The reverse surfaces of branches are relatively flat, and are ornamented by longitudinal striations.

Apertures are set just beneath the median ridge. They are moderately small and circular, averaging 0.09mm in diameter. When well-preserved, they have moderately-thick peristomes, but they do not project into the fenestrules. Unlike *Fenestella frutex*, aperture position is not stabilised against dissepiment growth, and there are three to four apertures per fenestrule.

Branch bifurcations are fairly frequent, and have a low-angle tuning-fork pattern, with branches thickening for several fenestrule lengths before bifurcation. Occasionally, a single aperture is set in the angle of the fork, but more usually, in specimens from this locality, a third row of apertures is developed for up to several fenestrule lengths prior to bifurcation. The extra third row of apertures may be flanked by two median ridges.

Dissepiments are moderately thin (0.12mm) in their centres, but flare quite markedly at the branch junctions. They are markedly depressed beneath crests on obverse branch surfaces, but are only slightly depressed beneath crests on reverse surfaces.

Fenestrules are fairly long, measuring between 0.65-0.80mm, and averaging 0.73mm in specimen $SQ^{BB}5$, but fenestrule length is rather variable even within colonies. They are moderately broad, averaging 0.49mm in width. The shape of the fenestrules varies from sub-rectangular to sub-oval.

Partial silicification reveals the internal structure of the zooecial chambers (fig. 6.6b). Chambers have hemi-hexagonal bases, measuring 0.24mm in length, and 0.14mm in width. They curve upward into funnel-shaped necks opening onto the obverse branch surfaces.

The relatively-small, moderately-spaced apertures, with three to four per fenestrule, and the rigid meshwork with a third row of apertures developed prior to branch bifurcation are features diagnostic of *Fenestella multispinosa*. Analysis of the parameters shows an excellent match with specimens of *Fenestella multispinosa* as described by Bancroft (1984) and Tavener-Smith (1973a); however, the Stackpole Quay material does have longer fenestrules than average, but the extended length still lies within tolerable t-test comparison limits.

Rhombopora similis

Specimens probably referable to this taxon (redescribed in the Tears Point section, this chapter) were found in both Bryozoa Bands; colonies can occur in some abundance. However, silicification has destroyed much of the finer detail.

Colonies form cylindrical zoaria with rhombically-arranged autozooecia and very thin interzooecial walls. Colony diameters range from 0.60-1.00mm, but are usually about 0.70mm. Branching is not infrequent, with wide bifurcation angles giving a dendritic colony. Branches are straight to slightly curved.

Recrystallization has obscured zooecial boundaries, thus making it impossible to obtain accurate measurements. However, certain estimates could be made. Autozooecial apertures are oval to sub-diagonal, depending on the degree of weathering of the specimen; apertures are quite large, measuring 0.22mm in length, and 0.12mm in width. In the vestibular region, the proximal side is steeply inclined, while the distal side slopes quite gently.

Interapertural walls are very thin between diagonally-adjacent zooids, averaging 0.05mm. They form a series of diagonal ridges running around the colony, with angles of 30°-40° between the rows. Longitudinal walls are approximately 0.20mm in length and 0.10mm in width. A single large stylet is usually developed in the centre of these walls, but smaller stylets on the lateral walls were not observed.

Exilazooecia are absent.

Transverse broken colonies revealed that the chambers are budded from the centre of the colony; the absence of a central axial cylinder thus indicates that the specimens are referable to the genus *Rhombopora* rather than *Rhabdomeson.*

The thin walls, sub-diagonal shape of the apertures, and the occurrence of a single large stylet on longitudinal walls indicate that the material belongs to *Rhombopora similis*; though colony parameters are slightly smaller than average compared to the Tears Point representatives, they closely match those of *Rhombopora similis* from Three Cliffs Bay.

Three Cliffs Bay

GRID REFERENCE : SS 535 880
AGE : Courceyan

At Three Cliffs Bay, a succession of fossiliferous, relatively undolomitised Courceyan Z1 limestones occurs. In the basal succession, 1.6m of sediment was

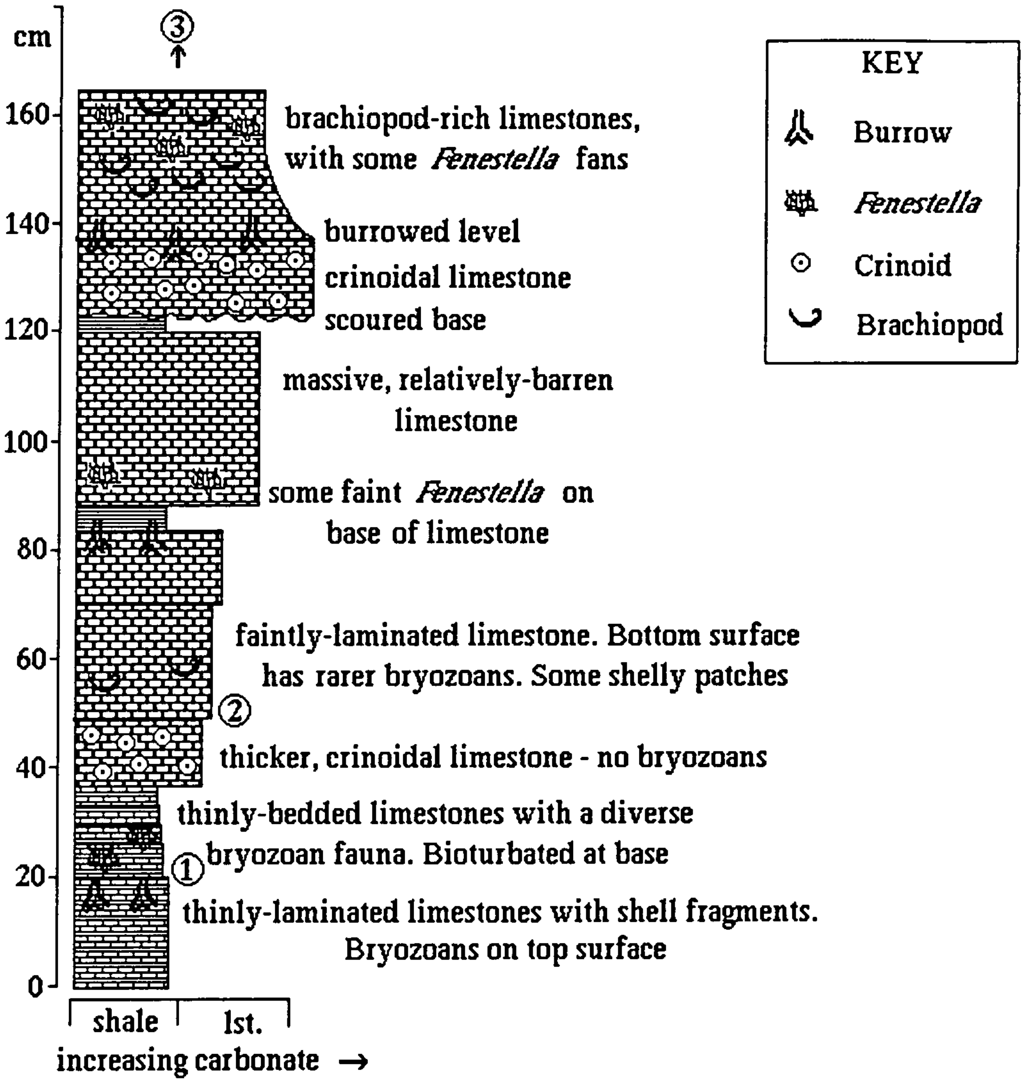


Fig. 6.4. Graphic log of the basal Courceyan limestones in Three Cliffs Bay.

logged, noting facies and faunal changes, and a moderately diverse bryozoan fauna was recovered. The log is reproduced in fig. 6.4.

The fauna was observed to change up the succession, and the differences are believed to be due to the different current strengths associated with the various facies. The bryozoan fauna recovered is discussed in the following pages, and the differences between the sample sites are considered.

Though bryozoans are rather abundant, problems arise with species identification, since the colonies are invariably recrystallised. The original positions of the apertures can be inferred, but detailed branch morphology and thickness, for instance, cannot be gauged accurately. Certain species, however, are distinctive enough to be identified from even small recrystallised colony fragments, and the following taxa were recognised in the succession :

Rhombopora similis
Fenestella bicellulata
Fenestella multispinosa
Fenestella plebeia
Polypora dendroides
Stenodiscus? (Trepostomata)

Rhombopora similis

This taxon is moderately abundant in the Three Cliffs Bay limestones. Colonies form cylindrical, dendritically-branching structures of variable width, ranging from 1.00 to 1.60mm. Branches are straight or slightly curved. Branching is quite frequent, with high angles of divergence giving a dendritic habit to the colony. A specimen on sample TCB^{3}5 shows budding from a broad basal disk, with frequent branching giving a dendritic colony.

A series of closely-spaced, sub-diamond apertures are arranged in a very regular rhombic pattern around the colony. On unweathered portions, the apertures are rounded and shallow out in the distal part of the vestibule. The vestibular region is tear-drop shaped. Apertures are approximately 0.22mm in length and 0.14mm in width. There are four to five apertures in a 2mm line in the longitudinal direction.

Interzooecial walls are relatively thin in the diagonal direction, and form a series of diagonal ridges running around the colony. Longitudinally, they measure 0.16mm by 0.07mm. At the end of the longitudinal walls, there is usually a large but poorly-developed stylet; smaller stylets are absent.

Internal structures have been inferred from broken colony portions, where weathering has naturally enhanced the zooecial chamber detail, and from an acetate peel of specimen TCB^{1}2 (fig. 6.7b). Zooids are budded from a central zone, rather than a central rod, indicating that the specimens belong to the genus *Rhombopora* rather than *Rhabdomeson.*

The lack of exilazooecia, coupled with the thin interaperture walls, suggests that the Three Cliffs Bay specimens be assigned to the species *Rhombopora similis* Phillips. However, though the parameters measured are larger than those of *Rhombopora incrassata*, another species known to occur in South Wales, they are generally smaller than the parameters recorded from specimens of *Rhombopora similis* from Tears Point. It is considered that the Three Cliffs Bay specimens are variants of *Rhombopora similis* Phillips, rather than a sub-species, since other species of *Rhombopora* can be rather variable.

Fenestella bicellulata

Representatives of this species are recognised by the very tight meshwork with small fenestrules.

Branches appear to be rather thin (approximately 0.20mm in width) and have a fairly straight central carina; nodes were not obvious. Branch surfaces slope away moderately steeply from the carina. Rather large apertures are present (though those on some specimens such as TCB^{1}3 (Plate 10, fig. f.) have probably been enlarged by erosion) which are very closely spaced (interapertural distance approx. 0.18mm). Apertures indent the fenestrules, and there are, on average, two apertures per fenestrule. On reverse surfaces, branches are well-rounded, and ornamented by strong longitudinal striations.

Bifurcations are not infrequent, and have a low-angle tuning fork pattern, with branches expanding in width for several fenestrule lengths prior to bifurcating. an additional aperture may occur in the angle of the fork.

Dissepiments are variable in thickness, but much of this variation is due to weathering; relatively unweathered dissepiments are approximately 0.08mm in width. They are well-depressed beneath branch obverse surfaces, and moderately depressed beneath reverse surfaces. In their centres, dissepiments are straight-sided, but flare quite considerably at their junctions with the branches.

Fenestrules are small, measuring between 0.34 and 0.40mm in length, and 0.30 to 0.40mm in width. They are well-rounded, and are sub-oval in outline.

The small fenestrules and parallel meshwork show this form to belong to *Fenestella bicellulata.* Thin branches with fenestrule-indenting apertures provide additional diagnostic characteristics. The ranges of the parameters match very closely those cited by Bancroft (1984) for the species.

Fenestella multispinosa

This form can be variable in appearance, on account of secondary calcification, but the species is recognised by its moderately stout, sub-parallel branched meshwork, with three to four apertures per fenestrule.

The best preserved specimen of *Fenestella multispinosa* was found on sample TCB^{3}4; this small colony fragment had not recrystallised, and was only partially weathered.

Branches are moderately thick (approx. 0.25mm in width) and have a broad, raised, straight median ridge running along their crests. Nodes were observed on one specimen (TCB^{1}5) and are very large (0.14mm in length), raised, oval in outline, and placed approximately 0.36mm apart. Branch surfaces slope quite steeply away from the ridge. Apertures are large and closely spaced. They average 0.12mm in diameter, but have probably been partially eroded, since peristomes were not apparent. Apertures are spaced approximately 0.23mm apart. On the reverse surfaces, branches are rather flat and are ornamented by prominent longitudinal striations.

Branch bifurcations are moderately common, and have a low-angle tuning-fork pattern, with a single aperture placed in the angle of the fork. The branching pattern is rapidly absorbed into the normal meshwork spacings. Specimen TCB^{1}5 is interesting in that a third row of apertures is developed before bifurcation, with three to four apertures in the row (fig. 6.7a). The median ridge splits in two, and flanks the incipient row.

Dissepiments are moderately thick and short. On secondarily calcified colonies, they may be over 0.20mm thick, but on TCB^{3}4 they average 0.12mm. Dissepiments are well-depressed beneath branch crests on the obverse surface, but on the reverse surface they are flush with the branches, or even raised above that level. They flare quite noticeably at branch margins. In contrast to the branches, dissepiment surfaces are rounded and are not particularly strongly striated.

Fenestrules are of moderate size, being of order 0.50 to 0.60mm in length, and 0.40 to 0.50mm in width. They have well-rounded tips, and are more ellipsoidal than sub-rectangular in outline, though specimen TCB^{3}4, which is not secondarily-calcified, does have sub-rectangular fenestrules.

The steep-sided branches with three apertures per fenestrule, the apertures not being regularly-placed with respect to the dissepiment position (cf. *Fenestella frutex*) and the development of a third row of apertures prior to branch bifurcation all point to the material belonging to the species *Fenestella multispinosa*. The zoarial parameters fall within the ranges cited by Bancroft for *Fenestella multispinosa*, but also match the variation of *F. frutex*. Thus, without taking a large number of measurements from the poorly-preserved specimens (with a consequently large error range), it is not possible on morphometrical features alone to assign the material to a species. However, the features cited above firmly suggest that the specimens do belong to *Fenestella multispinosa.*

Fenestella plebeia

This form is rather scarce, but a few fragments were found, recognised by broad, rather open fenestruled meshworks, with five apertures per fenestrule.

Branches are moderately thick (approx. 0.32mm) and are slightly sinuous in the proximal portions of the colony; one distal fragment was found, and the branches were more sub-parallel. A low median ridge runs down the centre of the branches on the obverse surfaces, but no nodes are preserved. Sides slope away quite gently, giving a rounded appearance to the obverse surfaces. Circular apertures are set flush on the branch sides; recrystallisation has destroyed any evidence of peristomes around the apertures. Apertures are set approximately 0.25mm apart, and have diameters in the order of 0.12mm, but diameters may be less than this. There are five apertures per fenestrule. Reverse surfaces were not observed.

Bifurcations occur in a high-angle tuning-fork pattern, with branches separating quite widely in a short distance within the meshwork. A single aperture is placed in the angle of the fork.

Dissepiments are moderately-thick (0.15 to 0.20mm) but of variable morphology; they may be short or long depending on the degree of branch divergence. Dissepiments are moderately well depressed beneath obverse surface branch crests. They can flare quite markedly at branch junctions.

Fenestrules are elongate (0.85 to 1.10mm in length) and broad (widths approximately 0.60mm). They have well-rounded tips and lateral margins, and may be coffin-shaped, sub-rectangular, or sub-oval, depending on the degree of dissepiment flaring.

Both the zoarial features (broad fenestrules, an open meshwork, and five apertures per fenestrule) and the morphometric parameters tally with the ranges cited by Bancroft (1984) for *Fenestella plebeia.*

Polypora dendroides

Only one colony fragment of this distinctive species was found (TCB^{1}9).

Branches are very broad (0.60 to 0.70mm) and rounded. There are three to four rows of apertures on each branch. Apertures are oval in outline, measuring approximately 0.20mm in diameter, and are quite widely separated, being about 0.32mm apart. There are four to five apertures per fenestrule. They are arranged in a quincunx pattern, and the calcitic fabric of the branch skeleton weaves between the apertures. Both nodes and a central ridge are absent.

Branch bifurcations have a high-angle tuning-fork pattern, and branches may thicken up to 0.90mm before bifurcation. Up to five aperture rows may develop, reducing to three on each branch after bifurcation.

Dissepiments are very broad (0.20 to 0.38mm), well-rounded, and only slightly depressed beneath branch crests on the obverse surface. They flare quite noticeably at their junctions with the branches.

Fenestrule parameters are difficult to gauge from the small fragment found, but are rather open and probably in the order of 0.90 to 1.10mm in length, and 1.00 to 1.10mm in width.

The frequent bifurcations, broad dissepiments and apertures, and squat fenestrules bracket this specimen as *Polypora dendroides*. McCoy (1844) first described this species, and the Three Cliffs Bay specimen matches well with his description, save for McCoy citing the dissepiments as being rather thin. However, as Miller (1962) observed, some of McCoy's material is referable to the thin-dissepimented *Polypora verrucosa*, and subsequent work by Tavener-Smith (1973a) and Bancroft (1984) has shown that the dissepiments are rather broad, and the Three Cliffs Bay specimen falls within their ranges.

Stenodiscus ?

Only one trepostome fragment (on specimen TCB^{3}4), tentatively assigned to the genus *Stenodiscus*, was found in the Three Cliffs Bay limestones.

The colony is cylindrical in shape, tapering slightly at one end, and averaging about 1.60mm in diameter. Autozooecial apertures are irregularly arranged around the colony, and are very closely spaced, with eight to nine occurring in a 2mm line. They are sub-polygonal in outline, and range from 0.20 to 0.24mm in diameter longitudinally, and transversely measure 0.12 to 0.14mm. Exozone walls are quite thin (0.03 to 0.05mm) and have large stylets at wall junctions, with a single row of smaller stylets between; in total, there may be up to fifteen stylets around each aperture. The stylet rows give a hexagonal appearance to the apertures.

Internally, recrystallization has destroyed much of the structure, and diagnostic features such as diaphragms and ring septa cannot be seen; however, the thickening of endozone walls into the exozone, coupled with the irregular aperture arrangement, indicate that the specimen is a trepostome.

From the external zoarial parameters it is not possible to assign the specimen to any one of the trepostome species measured by Bancroft (1984); however, the morphology of the colony, including the small closely-spaced apertures, is similar to material from Mewslade Bay, which can be demonstrated to belong to the genus *Stenodiscus*.

Fenestellid colony morphologies

Many of the fragments of *Fenestella*, most noticeably those of *Fenestella multispinosa*, are proximal portions, indicating the initial branching patterns. There appears to be quite a lot of variation, even within a single species. The following morphologies were recorded :

a. Conical colonies Colonies bud from a broad basal plate, and form a sharply-rising conical meshwork. Initial conical angles are fairly small (approximately 0.30°) as seen on specimen TCB^{1}8, but appear to spread out giving a broader cone. Apertures open on the inside of the cone; this is an important observation, since Cumings (1904) and Tavener-Smith (1969) noted that in the genus *Fenestella*, the apertures opened on the outside of the cone, while in *Polypora* they opened on the inside. Tavener-Smith thus inferred that the median carina (which is not developed in *Polypora*) therefore formed as an upfold from the basal plate. Specimen TCB^{1}12 clearly has apertures which open in the inside of the cone, with only two rows on each branch, and is strongly carinate, suggesting that the growth of the median carina is not simply an upfold from the basal plate. Further, carinate acanthocladiids such as *Septopora*, also have apertures developed on the inside of the cone.

The preserved portion of the basal disc is usually relatively small. A colony on specimen TCB^{3}8 shows budding from a hemi-cylindrical disc, measuring 1.4mm by 0.7mm, and divergence from this disc is at a high conical angle.

b. Planar fan-shaped colonies These are rarer, but one is present on TCB^{1}7. Like the conical colonies, budding takes place from a hemi-cylindrical basal disc, but the disc is rather broad, and the resultant branches expand into a planar fan, rather than curving round into a cone.

c. Sheet-like colonies One specimen on TCB^{1}10 has a 2cm-broad colony fragment in which the meshwork is foliaceous, being neither planar, nor closing into a cone. From the visible reverse surface, several thick (diameter approx. 0.80mm) *Palaeocoryne*-type spines are developed which supported the foliaceous meshwork.

The curving of the basal disc may sometimes form a sheath-like cylinder, similar to those seen on the fenestellids from Tears Point. The sheath on a fan-shaped colony on sample TCB^{3}8 has a diameter of 1.6mm, which is of a similar magnitude to the Tears Point examples. Most probably the bryozoan larvae settled on the stems of soft-tissued plants, and the basal disc wrapped around the stem for support as the colony developed. The abundance of curved basal discs suggests that the substrate was fairly soft, preventing growth of bryozoans directly from the sea bed, but attachment was facilitated by the presence of stemmed plants.

The variation in morphology of the proximal portions of a single species, *Fenestella multispinosa*, shows the flexibility of the bryozoan colony plan. Further, the variation highlights the fact that gross colony morphology cannot always be used as a taxonomically important characteristic.

Bryozoan distributions in Three Cliffs Bay

The bryozoan distributions within the succession, at the horizons indicated in figure 6.4, are discussed in the following paragraphs.

Level 1 A very diverse fauna is preserved in the thinly-bedded limestones. Bryozoans, in fact, are the dominant macrofauna. The following Bryozoa taxa were recorded, listed in order of decreasing abundance :

Fenestella multispinosa
Fenestella bicellulata
Fenestella plebeia
Rhombopora similis
Polypora dendroides
Trepostome? - indeterminate fragment

Fenestella multispinosa is by far the most dominant bryozoan, and many colony origins were found. The basal cones of the origins point downward, suggesting that the fauna is actually buried *in situ*. Some post-mortem disturbance may have taken place fragmenting some fronds.

Level 2 Bryozoans are much rarer in this facies, which is dominated by disarticulated crinoid columnals. Some small fragments of distal colony portions belonging to *Fenestella multispinosa* were found, in addition to broken chonetid and productid brachiopod shells. From the state of preservation, it is apparent that the fauna has been extensively affected by currents, and may have formed in a nearer-shore, more energetic environment than the Level 1 fauna. Scouring on the bases of some of the crinoidal limestones suggests that they may be storm-dominated accumulations.

Level 3 This level occurs about three metres up the succession from Level 2, overlying a series of regularly-bedded crinoid- and brachiopod-rich limestones.

Level 3 is a limestone surface with muddier pockets. The following were found, listed in order of decreasing abundance :

Rhombopora similis
Fenestella multispinosa
Stenodiscus?

In the muddy patches, *Rhombopora similis* is very common, with large, dendritic colonies. However, the crinoidal limestones, though containing fewer bryozoans, do contain several colony origins of *Fenestella multispinosa*, suggesting a minimal transport distance.

Further up the succession, the limestones become thicker, and crinoidal bands less common, though they may form horizons up to 40cm thick. Bryozoans become rarer, as the environment presumably became more energetic, and when they do occur they are predominantly represented by *Rhombopora similis*, though a few fenestellid fragments were found.

Rhombopora similis and *Fenestella multispinosa*, which are both relatively stout-colonied bryozoans, appear to be the best adapted to life in the more energetic environments, as witnessed by their occurrence in the uppermost limestones, and the crinoidal limestones of Level 2 respectively. However, *Rhombopora similis*, though being able to withstand a moderately energetic setting, appears to flourish best in the quieter shale-accumulating areas, where it can become very abundant; indeed, work by Bancroft (1984) showed that, in general, rhabdomesid bryozoans are commonest in deeper-shelf shale sequences.

Tears Point

GRID REFERENCE : SS 408 871
AGE : Courceyan

Topmost Courceyan beds (C_1) of the Tears Point Limestone (George *et al.*, 1976) are well exposed on the foreshore of Tears Point, near Rhossilli. The beds are represented by a thick succession of relatively thinly-bedded, dark-grey, slightly argillaceous crinoid-dominated limestones; shale partitions between the limestone posts are not common. The sequence dips fairly gently (about 15°) to the northeast, and exposure to the sea has weathered many fossils proud of the bedding planes.

The fauna is rather abundant, and, in addition to the crinoid columnals, chonetids, productids, and spiriferids number amongst the brachiopod taxa, together with many zaphrentid corals. Many bedding planes, though, are dominated by the remains of bryozoans, and the Tears Point Limestone supports a very diverse bryozoan fauna. The following taxa were noted:

Rhombopora similis
Rhombopora incrassata
Fenestella bicellulata
Fenestella frutex
Fenestella multispinosa
Fenestella plebeia
Ignotifenestella sp.
Polypora verrucosa
Penniretepora flexicarinata
Fistulipora incrustans

Higher up the sequence, the limestones become less argillaceous and more thickly-bedded. Additionally, the fauna becomes less diverse, and though bryozoans still occur, they are rarer, with only the following taxa being recognised:

Rhombopora similis
Fenestella plebeia
Fistulipora incrustans

Passing into the Caswell Bay Oolite, the beds redden, and faunal diversity drops; only crinoid remains were found, with some rarer corals, indicating the dominance of higher-energy water currents.

Environmentally, the beds from the Tears Point Limestone to the Caswell Bay Oolite represent a fairly long-lived carbonate platform. The disarticulation of many crinoid columnals, coupled with abrasion of some bryozoan remains, suggests some limited current activity, but the fauna in virtually *in situ*. The scarcity of encrusting bryozoans, coupled with the lack of trepostomes, further suggests that suitable substrates for attachment were not common, implying a rather soft, lime-mud sea floor; this is actually the favoured environment of chonetid brachiopods. The presence of soft-tissued plants is inferred from cylindrical calcite sheaths secreted by some fenestellids, a response as the colony grew around an encumbrance, and one specimen of *Fenestella* possessed a small, curved basal disc, which had similarly wrapped around a soft-tissued cylindrical stem. It is possible that the plants provided suitable mediums on which bryozoans could attach, as is seen in some Maastrichtian seagrass assemblages (Voigt, 1981). The soft nature of the substrata is further suggested by the abundance of supporting spines developed on the reverse surfaces of several fenestellid colonies. Spinose productids, though, are rare, and settlement on brachiopod spines does not seem to have been a preferred mode of life for the bryozoans of the Tears Point Limestone, in contrast to other Carboniferous soft-sediment assemblages (Billing, 1991).

Fenestella bicellulata

Parameters of the specimens of *F. bicellulata* from Tears Point are given below:

	Fenestella bicellulata				
	Gower			Bancroft	PROBABILITY
	n	σ	x	x	t-TEST
BW	12	0.0131	0.227	0.18	0.0000
AD	9	0.0074	0.071	0.07	0.7840
ID	6	0.0107	0.212	0.18	0.0000
FL	14	0.0269	0.424	0.42	0.7776
FW	12	0.0435	0.391	0.36	0.0079
DW	16	0.0207	0.082	0.08	0.6736
IND	7	0.0146	0.149	0.20	0.0000
				TOTAL	0.3204

Only two fragments of this species were found, both on specimen TP28 (fig. 6.8a). The species is characterised by its very small fenestrules.

Branches are rather slender (0.23mm wide), and have a broad median ridge running down the obverse surface. The ridge is ornamented by a series of very closely-spaced, relatively large, prominent nodes. Branch surfaces slope quite steeply away from the median ridge. Reverse surfaces are quite rounded, and are ornamented by strong longitudinal striations.

Apertures abut the median ridge, but despite being small (0.07mm in diameter), they have relatively thick, complete peristomes which project quite significantly into the fenestrules. They are placed about one aperture's diameter apart, with two apertures per fenestrule. An aperture is placed additionally in the fork of branch bifurcations. The material has slightly recrystallized, but the dentate apertures seen on some specimens by Bancroft from elsewhere were not observed on the Tears Point material.

Dissepiments are very thin, and are equally depressed beneath obverse surface and reverse surface branch crests. They are rather bar-like in their central portions, but flare quite considerably at branch junctions.

Fenestrules are square to oblong, and are rather small, measuring 0.42mm by 0.36mm. They have rather rounded corners, due to dissepiment flaring.

The small fenestrules with two apertures per fenestrule indicate that this species belongs to *Fenestella bicellulata*. Additionally, there is a good statistical match with the parameters cited by Bancroft for the species, though branch widths and aperture spacings are greater than average, while nodes are more closely spaced.

Fenestella frutex

Parameters for this species are as follows :

	Fenestella frutex					Tavener-	
	Gower			Bancroft	PROBABILITY	Smith	PROBABILITY
	n	σ	x	x	t-TEST	x	t-TEST
BW	17	0.0140	0.237	0.24	0.5937	0.254	0.0001
AD	7	0.0064	0.091	0.09	0.8091	0.083	0.0725
ID	10	0.0160	0.212	0.22	0.1191	0.201	0.0171
FL	22	0.0210	0.585	0.58	0.5792	0.556	0.0007
FW	20	0.0501	0.405	0.44	0.0051	0.461	0.0001
DW	22	0.0133	0.093	0.11	0.0001	0.150	0.0000
IND	5	0.0367	0.216	0.34	0.0000	0.236	0.0735
ZB1	10	0.0148	0.220	0.21	0.0058		
ZB2	10	0.0070	0.109	0.11	0.5021		
				TOTAL	0.2905	TOTAL	0.0234

Several fragments referable to *Fenestella frutex* McCoy were found, the largest measuring 8mm by 12mm, and coming from the distal portions of the colonies.

Branches are moderately thin (0.24mm) and sub-parallel (Plate 10, fig. g.), forming a rather tight meshwork. Obverse surfaces have a thin, straight carina, which bears faint but elevated oval nodes. Surfaces slope fairly steeply away from the carina. Branch reverse surfaces are well-rounded, and ornamented by longitudinal striations, which seem to be obscured by secondary calcification. Branching is not frequent in the distal colony portions observed, but occurs in a low-angle tuning-fork pattern, with an aperture placed in the centre of the fork.

Recrystallization of specimen TP13 (fig. 6.8c) has obscured some of the apertures, but they are still quite prominent and set low down on the branches. They are circular in outline, and have moderately-thick, complete peristomes which are thicker on the fenestrule side and actually project into the fenestrules. There are three to four apertures per fenestrule. Apertures are quite closely-spaced, and one is usually set at a branch/dissepiment junction.

Dissepiments are quite thin in their centres, but flare considerably towards the branches. They are moderately well-depressed beneath branch crests on obverse surfaces, but are almost flush with those on the reverse. In addition, they appear to be strongly striated on the obverse surfaces, which highlights the flaring, but are smoother on the reverse.

Fenestrules are well-rounded at their tips, but have straight, sometimes indented, sides. They are fairly small, averaging 0.59mm by 0.41mm, but the fenestrule gap is slightly wider than the branches.

Internally, zooecial chamber bases are hemi-hexagonal, and measure 0.22mm in length, and 0.11mm in width.

Fenestella frutex is recognised by its moderately small fenestrules, moderately narrow, steeply-sloping branches bearing a thin median carina with closely-spaced nodes, and apertures which project slightly into the fenestrules. Statistically, there is a good match with the measurements of Bancroft, except for nodes being more closely-spaced than average. Interestingly, comparisons with the parameters cited by Tavener-Smith (1973a) for *Fenestella frutex* from Carrick Lough gave rather low t-test probability scores.

Fenestella multispinosa

This species was more common in the limestones of Tears Point than *Fenestella frutex*. Fragments tended to be larger than *F. frutex*, but distal fragments were predominant, showing a similar sub-parallel branched meshwork. Colonies appear to have been planar fans.

Specimen TP23 (fig. 6.8b; Plate 10, fig. h.) shows the best-preserved example. Branches are moderately-thick (0.27mm), and have a well-defined median ridge, which has a thin carinal trace along its crest. It is ornamented by a series of quite large, well-rounded, closely-spaced nodes.

Branch surfaces slope steeply away from the carina. Apertures abut the carina, and are quite prominent. They have moderately-thin, complete peristomes, but do not project into the fenestrules. They are quite closely-spaced, and there are four apertures per fenestrule; unlike *F. frutex*, there is not the same tendency for an aperture to occur regularly at a branch/dissepiment junction.

Branch reverse surfaces are well-rounded with longitudinal striations. They may also be covered in a series of randomly-arranged nodes. Branching occurs in a low-angle tuning-fork pattern, with one aperture being placed in the angle of the fork. No development of a third row of apertures was noted, a feature which can occur in the species (Bancroft, 1984; Ulrich, 1890; Miller, 1961; Tavener-Smith, 1973a).

Dissepiments are moderately well-depressed beneath the obverse surfaces, but are flush with the reverse surfaces. They are ornamented by faint striations, and on the obverse surfaces have poorly-defined median ridges.

Fenestrules are quite well-rounded, and on obverse surfaces may take on an oval outline. The fenestrule gap is slightly wider than the branch width, and fenestrules are moderately small, measuring on average 0.69mm by 0.47mm.

Internally, zooecial chambers have hemi-hexagonal bases, and measure 0.21mm by 0.14mm.

	Fenestella multispinosa					Tavener-	
	Gower			Bancroft	PROBABILITY	Smith	PROBABILITY
	n	σ	x	x	t-TEST	x	t-TEST
BW	27	0.0213	0.276	0.24	0.0000	0.250	0.0002
AD	20	0.0086	0.086	0.09	0.0394	0.096	0.0456
ID	24	0.0199	0.233	0.26	0.0000	0.250	0.0018
FL	31	0.0393	0.688	0.65	0.0001	0.633	0.0001
FW	32	0.0411	0.474	0.49	0.0950	0.499	0.0270
DW	26	0.0102	0.127	0.13	0.5659	0.116	0.0190
IND	22	0.0124	0.198	0.35	0.0000	0.358	0.0000
ZB1	6	0.0138	0.207				
ZB2	5	0.0367	0.144				
				TOTAL	0.1001	TOTAL	0.0134

Fenestella multispinosa is recognised by its moderately-small fenestrules (which are larger than those of *Fenestella frutex*), and moderately-stout branches, bearing a broad median ridge and apertures which do not abut into the fenestrules. A comparison of the parameters for the Tears Point specimens showed rather low correlations with Bancroft's averages for the species, but still obtaining an overall probability score of 0.1001; Tavener-Smith's measurements resulted in an even lower score of 0.0134. Most significantly, branches on the Tears Point material were thicker, and fenestrules longer than average, with apertures being more closely-spaced; it is possible that the stouter meshwork may be an adaptation to the higher energy environment of the Tears Point limestones, when comparing the species with the shale-collected material of Bancroft and Tavener-Smith.

Fenestella plebeia

Parameters of the Tears Point specimens of *F. plebeia* are given below :

	Fenestella plebeia			Bancroft, 1984			Tavener-Smith, 1973		
	TP 24				Probabilities			Probabilities	
	n	σ	x	x	t-TEST	t-DIV	x	t-TEST	t-DIV
BW	12	0.0257	0.337	0.30	0.0000	0.2475	0.292	0.0003	0.1167
AD	12	0.0144	0.122	0.11	0.0042	0.3192	0.111	0.0129	0.0978
ID	12	0.0128	0.292	0.26	0.0000	0.2631	0.260	0.0045	0.1524
FL	12	0.0378	1.129	1.02	0.0049	0.3133	1.166	0.3856	0.0774
FW	12	0.0723	0.632	0.60	0.0891	0.0350	0.641	0.7062	0.0789
DW	12	0.0150	0.209	0.16	0.0000	0.0000	0.174	0.0040	0.1946
				TOTAL	0.0164	0.1963	TOTAL	0.1856	0.1196

Colony fragments of *Fenestella plebeia* are very common in the limestones of Tears Point. The meshwork, though quite variable in appearance, is fairly open, with sub-parallel straight branches, and generally with regularly-spaced dissepiments.

Branches are rather stout (0.34mm in width), and have a prominent median ridge. TP21 (Plate 10, fig. i), the best-preserved example, did not show carinal nodes along the ridges, but TP24 (Plate 10, fig. j.), a secondary calcified proximal colony fragment, had fairly prominent circular nodes, placed 0.39mm apart. On the secondarily-calcified colony, branch surfaces are gently curved, but TP21 has quite steep-sloping sides. On the reverse surfaces, colonies have flat-backed branches which are ornamented by coarse longitudinal striations.

Apertures are set fairly low on the branches, and are quite large (0.11-0.12mm). They are circular, and have complete thin peristomes. Apertures are flush with the branches, and do not project into the fenestrules. They are moderately widely spaced (0.29-0.33mm), and there are four per fenestrule.

Branches thicken towards bifurcations, which occur in a high-angle tuning-fork pattern with an aperture being placed in the angle of the fork.

Dissepiments are moderately-depressed beneath the crests of obverse branch surfaces, but are virtually flush on the reverse surfaces. Width can be variable, depending on the degree of secondary calcification (Plate 11, figs. a. and b.), but dissepiments are usually moderately thick, measuring between 0.16mm and 0.20mm in their centres, and gently flaring into the branches; dissepiments from non secondarily-calcified portions have a more bar-like appearance. Dissepiments are ornamented by rather faint striations, which parallel the flaring.

Fenestrules are fairly elongate (FL=1.02-1.16mm, FW=0.63-0.64mm) and vary in shape from sub-rectangular to "coffin" shaped (widening in their centres). They are wider than the branches in proximal portions, but the same width in distal fragments.

Internally, zooecial chamber bases (based on a partially-eroded reverse surface from a colony on specimen TP25) are hemi-hexagonal, and measure approximately 0.28mm in length and 0.16mm in width.

The specimens from Tears Point are clearly referable to *Fenestella plebeia*, being characterised by broad fenestrules, with sub-parallel , steep-sided branches, bearing four non-protruding apertures per fenestrule. However, t-test probability scores with Bancroft's averages for the species give very low correlations, since all the parameters for TP21 are larger than usual. Interestingly, the division probability scores show much higher correlations, showing that though the zoarial parameters are larger in the Tears Point material, they are uniformly larger, implying that the specimens are "scaled-up" versions of *Fenestella plebeia.*

The Tears Point specimens include two additionally interesting colonies of *Fenestella plebeia.* Specimen TP28 includes a proximal portion of a colony, showing secondary thickening near the base, and the development of supporting spines from the reverse surface (Plate 11, fig. d.; see also the "Palaeocorynid" spine, Plate 11, fig. c.). However, the basal disc area was not visible. Another *Fenestella* proximal portion was found, on specimen TP25 (fig. 6.8d), which shows a series of branches developing from a small, curved basal disc; however, it was not possible to identify this small fragment to species level. Also on specimen TP28, a fragment of *Fenestella plebeia* shows the development of a calcareous cylindrical sheath, approximately 0.90mm in diameter (Plate 11, fig. f). Shulga-Nesterenko (1951) illustrated similar structures in Carboniferous fenestellids from the Russian platform. It is most likely that they represent colony growth around immovable, cylindrical soft-tissued organisms; plant stems could have provided such an obstruction.

Ignotifenestella ? sp.

The table on the following page outlines the parameters of this taxon from Tears Point :

	Ignotifenestella			*Fenestella plebeia*			
	TP 13 & 28			TP 21	Prob.	Bancroft	Prob.
	n	σ	x	x	t-TEST	x	t-TEST
BW	20	0.0190	0.302	0.337	0.0003	0.30	0.6663
FL	21	0.0640	0.826	1.129	0.0000	1.02	0.0000
FW	21	0.0421	0.510	0.632	0.0000	0.60	0.0000
DW	21	0.0232	0.164	0.209	0.0000	0.16	0.4454
CD	21	0.0105	0.076				
				TOTAL	0.0001	TOTAL	0.2779

Several fragments which are probably referable to the Russian fenestrate genus *Ignotifenestella* Morozova (1974) were found in the Tears Point limestones. *Ignotifenestella* differs from *Fenestella* Meek, in possessing regularly-placed cyclozooecia on the reverse surface, and between the obverse surface autozooecial apertures. Only reverse surface fragments were found in this locality. The largest fragment was on specimen TP28, and shows a slightly-curved, fan-shaped colony fragment, measuring approximately 2.5cm by 3cm; another fragment from the same specimen showed spines projecting from the reverse surface of the colony (fig. 6.9b; Plate 11, fig. d.). Specimen TP13 (fig. 6.9a; Plate 11, fig. i.) has been partially eroded, illustrating the striated reverse surface, and the prominent cyclozooecia.

Branches are moderately-thick (0.30mm), and are sub-parallel, forming fairly rigid meshworks, with little bifurcation. They are ornamented by strong longitudinal striations. Branch surfaces are fairly flat. When bifurcations do occur, branching takes place in a low-angle tuning-fork pattern; bifurcations may disrupt the fenestrule shape for two fenestrules distance.

Dissepiments are fairly regularly-placed, and are flush with branch crests, occasionally raised above this level. They flare quite noticeably towards the branches, and are quite thick (0.16mm). Occasionally, dissepiments may be ornamented by striations, but more usually they are smooth.

Fenestrules are moderately large, measuring 0.82mm in length, and 0.51mm in width. In outline, they are sub-oval to sub-rectangular in shape, having rounded sides and ends.

Acetate peels (Plate 11, figs. j. to m.) revealed that autozooecial chamber bases are hemi-hexagonal in shape, and average 0.23-0.24mm in length, and 0.14-0.15mm in width.

Cyclozooecia are commonly developed, and are very regularly-placed, occurring in pairs on the distal sides of the dissepiment-branch junctions. They face into the next fenestrule, but are not always exactly opposite in position on the dissepiment. Sometimes, a single cyclozooecium may be developed, and some dissepiments appear to lack cyclozooecia in any form. Cyclozooecia are round in outline, approximately 0.08mm in diameter, and sometimes possessing very thin, complete peristomes. They are actually quite shallow, and a series of acetate peels from a fragment from specimen TP13 showed that the cyclozooecia are budded as lateral offshoots from the autozooids, developing at the initial dissepiment-branch junction, and growing towards the distal reverse surface. Additionally, there do not appear to be any cyclozooecia developed between the autozooids on the obverse surface. The exact function of the cyclozooecia is not known.

In zoarial form, the species of *Ignotifenestella* found in Tears Point looks similar to *Fenestella plebeia*, but fenestrules are smaller and more rounded, and branch surfaces are more strongly striated. The presence of regularly-paired cyclozooecia on the reverse surface dissepiments suggests an affinity with the genus *Ignotifenestella*,as first described by Morozova (1974), though she pointed out similar structures in *Fenestella* in her 1973 paper. The importance of polymorphic zooids at generic level has been reinforced by Bancroft (1986). However, *Ignotifenestella* also has cyclozooecia between the autozooids on the obverse surfaces, and the serial sections, together with eroded colony fragments, failed to reveal any obverse surface cyclozooecia. Thus, the forms from Tears Point. while not representing the genus *Fenestella*, can be assigned only tentatively to the closest genus, *Ignotifenestella*.

Polypora verrucosa

Fragments of this taxon are quite common in the limestones of Tears Point. Colonies are characterised by very broad branches (0.62mm), with widely-spaced, relatively-thin dissepiments. Only the reverse surfaces of colonies were observed.

Branch surfaces are well-rounded and ornamented by very fine longitudinal striations. Bifurcations are infrequent, and occur in a very low-angle tuning fork pattern, with branches thickening for several fenestrule lengths before bifurcation (Plate 11, fig. g.).

Dissepiments are relatively thin (0.27mm) and well-depressed beneath branch crests on the reverse surfaces. They are rather bar-like, flaring only a little towards their junction with the branches. Dissepiments also have an ornament of very faint striations, but this is less obvious than the striations on the branches.

Fenestrules are elongate, measuring approximately 2.32mm by 1.12mm, and are sub-rectangular in outline.

A ground section of specimen TP10 (Plate 11, fig. h.) showed some detail of aperture arrangement. Apertures are placed in a quincunx pattern in four rows on each branch. Autozooecia have stretched hexagonal bases in the centre two rows, and hemi-hexagonal bases at branch flanks. Shallower sections revealed a series of sinuous striations, probably visible on obverse surfaces, weaving between the apertures.

	Polypora verrucosa			Bancroft		Tavener-Smith	
	Tears Point				Prob.		Prob.
	n	σ	x	x	t-TEST	x	t-TEST
BW	14	0.0593	0.622	0.63	0.8350	0.630	0.6779
ID	9	0.0231	0.387	0.44	0.0081	0.385	0.8333
FL	11	0.2999	2.316	3.93	0.0000	4.135	0.0000
FW	12	0.1767	1.115	1.60	0.0013	1.755	0.0000
DW	20	0.0586	0.269	0.25	0.6037	0.287	0.2696
ZB1	10	0.0164	0.329				
ZB2	8	0.0087	0.210				
				TOTAL	0.2896	TOTAL	0.3562

The material is assigned to the species *Polypora verrucosa* on account of the four rows of autozooecia on each branch, rounded branch surfaces with thin dissepiments, and the elongate fenestrules. T-test comparisons with data from Bancroft (1984) and Tavener-Smith (1973a) for their specimens of *Polypora verrucosa* gave rather good correlations, despite the fenestrules being much smaller than usual for the species.

Penniretepora flexicarinata

Specimens of the genus *Penniretepora* are noticeably rare in the Tears Point limestones. Only five small fragments were recorded, the largest measuring 1cm in length. Most showed the obverse surfaces, but lateral branches were usually worn away, giving them an appearance similar to the acanthocladiid *Diploporaria*.

Branches are quite broad (0.50mm) and slightly curved. There is a prominent tripartite median carina, which is gently sinuous (Plate 12, fig. b.). Small nodes are quite widely-spaced along the central carina (IND=0.38mm), and nodes are irregularly-placed on the lateral carinae. Sinuous striations also weave between the apertures. Obverse surfaces slope gently away from the carinae; reverse surfaces are fairly flat, and are ornamented by strong longitudinal striations.

Apertures are quite prominent, and have thin, complete peristomes. They are elongate oval in outline, and are quite large (0.14mm in diameter). Apertures are flush on the branches, and do not project into the fenestrules. There are two to three apertures per lateral branch spacing; usually, one aperture occurs at the main branch/lateral junctions, and a third between the laterals.

Most lateral branches have been broken off, but those preserved were approximately 0.30mm in width. They are alternately offset along the mainstem, from which they diverge at angles of 70°-80°, and flare only slightly at their junctions with the mainstem. No preserved portions were long enough to show aperture development.

	Penniretepora flexicarinata			
	Tears Point			**Bancroft**
	n	**σ**	**x**	**range**
BW	**5**	**0.0265**	**0.504**	**0.32 - 0.53**
LBW	**2**	**0.0200**	**0.300**	**0.18 - 0.28**
AD	**20**	**0.0131**	**0.143**	**0.10 - 0.15**
ID	**24**	**0.0344**	**0.339**	**0.35 - 0.49**
LBS	**13**	**0.0499**	**0.704**	**0.68 - 0.91**
IND	**4**	**0.0218**	**0.375**	**0.30 - 0.77**

The tripartite carina identifies the specimens from Tears Point as *Penniretepora flexicarinata*, but the flat mainstem reverse surfaces are an additional pointer to the species. Additionally, zoarial parameters fall within the ranges cited by Bancroft from his studies of *Penniretepora flexicarinata*, though the apertures are slightly more closely-spaced than is usual.

Fistulipora incrustans

Only three specimens of the cystoporate *Fistulipora incrustans* were found, displaying various growth habits. The species is identified by widely-spaced circular apertures with prominent peristomes. Between the irregularly-arranged apertures are an abundance of vesicles.

Apertures are approximately 0.38mm in diameter, and are widely-spaced, with three to four apertures in a 2mm line. The peristomes extend completely around the apertures, but may be slightly raised into a poorly-developed lunarium for a third of the circumference.

Vesicles are small (average diameter is 0.12-0.15mm) and polygonal in outline. They constitute the walls between the autozooecial apertures.

Three different growth habits were observed: specimen $TP^{U}3$ (Plate 12, fig. h.) is a thin (0.80mm), well-preserved, flat sheet-like colony fragment, approximately $1cm^2$; a flattened dendritic cylindrical colony is present on TP28, approximately 2.5cm in length; and specimen TP12 (Plate 10, fig. l.) is a poorly-preserved circular colony, 2.5mm in diameter, encrusting the reverse surface of a *Fenestella plebeia* colony. However, the widely-spaced autozooecia, lacking prominent lunules, and separated by vesicular interwall material indicate that all the colonies belong to the species *Fistulipora incrustans*.

Rhombopora

The genus *Rhombopora* is moderately abundant in the Tears Point fauna. Two distinct species are present, and the well-preserved nature of this material has prompted a revision of the genus. *Rhombopora similis* (Phillips, 1841) has thin interapertural walls with a single large stylet on the lateral walls, and *Rhombopora incrassata* Ulrich, 1890, has wide interapertural walls with three or four stylets. Additionally, material tentatively assigned to *Rhombopora similis* by Bancroft (1984) is now believed to be referable to the new species *Rhombopora bancrofti*. The genus is undergoing review (Boardman *et al.*, 1983), and the taxon described as *R. incrassata* may prove to belong to *Saffordotaxis* Bassler, 1952.

Systematic descriptions of British species of *Rhombopora*

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order CRYPTOSTOMATA Vine, 1884
Suborder RHABDOMESONINA Astrova & Morozova, 1956
Family RHOMBOPORIDAE Simpson, 1895
Genus RHOMBOPORA Meek, 1872

Diagnosis (Bancroft, 1984) : "Rhabdomesid with slender, erect, ramose cylindrical dichotomous zoaria. Autozooecia are regularly budded from a quite well-defined linear axial region in a low spiral manner. Basal diaphragms are uncommon. Autozooecial apertures are large oval to round, quite closely-spaced and arranged in a rhombic pattern. Exilazooecia are rare. Stylets are abundant and structurally diverse."

Type species : *Rhombopora lepidodendroides* Meek, 1872

Stratigraphical range : Devonian to Permian

Parameters for the two species from Tears Point are given below, with the values cited by Bancroft for *Rhabdomeson* non *similis*.

	Tears Point, Gower						Bancroft, 1984
	Rhombopora incrassata			*Rhombopora similis*			*Rhombopora "similis"*
	x	s	n	x	s	n	x
ZD	0.600 - 1.360		4	1.560		1	0.63 - 1.53
AD1	0.177	0.0143	21	0.286	0.0225	12	0.23 - 0.34 av. 0.27
AD2	0.115	0.0168	21	0.183	0.0121	11	0.16 - 0.23 av. 0.20
IWT1	0.318	0.0538	21	0.232	0.0360	13	0.21 - 0.30 av. 0.25
IWT2	0.126	0.0199	21	0.136	0.0185	12	0.08 - 0.14 av. 0.11
Z2	4 - 6		5	3 - 4		5	4 - 6

Rhombopora similis (Phillips, 1841)

Plate 10, figs. d. and e.; Fig. 6.10, a. and b.; Fig. 6.7b.

1841 *Millepora similis* Phillips, p.21, Pl. 9, fig. 32.

Material : TP1, TP28, Tears Point Limestone (Upper Courceyan), Tears Point, Gower, South Wales (SS 408 871).

Other Occurrences : Courceyan strata in Cannington Park, North Devon, and Upper Devonian strata in Hope, near Torquay (Phillips, 1841). Lower Limestone Shales (Lower Courceyan), Stackpole Quay, Pembroke, South Wales. Shipway Limestone (Middle Courceyan), Three Cliffs Bay, Gower, South Wales.

Emended Diagnosis : *Rhombopora* with a moderately stout, cylindrical zoarium bearing very regularly rhombically-arranged, diamond-shaped autozooecial apertures. Interzooecial walls are thin, and form raised, diagonally-intersecting ridges around the zoarium. A single large stylet is placed centro-proximally on lateral interzooecial walls. Exilazooecia are absent.

Description : The width of colonies in this species can be rather variable, with the colony diameter ranging from 0.80mm to 1.56mm.

Autozooecia are arranged in a very regular rhombic pattern. Apertures are sub-diagonal in the vestibular region, deepening to an elliptical outline at the proximal superior hemiseptum (fig. 6.10b). The apertures are large, averaging 0.29mm in length, and 0.18mm in width.

Interapertural walls are very thin between diagonally-adjacent autozooecial apertures, and thus form well-defined diagonal ridges, with an angle of approximately 70° between the walls. Walls are thicker between laterally-adjacent apertures, measuring 0.23mm by 0.14mm. These lateral walls bear a single large stylet, oval in outline and projecting only a short distance above the zoarium. The stylet may grow centrally on the wall, or in a distal position.

Branching was not observed on the relatively small fragments collected, and exilazooecia are absent.

Acetate peels of TP27 and TP^U1 (fig. 6.7a) revealed that autozooids are budded annularly (cross-sections show a symmetrical budding pattern) from a flattened central zone. Chambers are initially rhombic, becoming pyriform in outline. A thicker exozone is developed in the outer half of the colony, composed of laminar skeletal material. The exozone is punctuated by darker cores of the large type "A" stylets.

Discussion : The specimens from Tears Point are referable to *Rhombopora similis* as originally drawn by Phillips (1841), which he assigned to the genus *Millepora* believing it to be a coral. Though he did not provide a formal description of the species, Phillips' drawings clearly show the diagonal shape of the apertures, and thin, diagonally-intersecting interzooecial walls, which are very distinctive in the Tears Point material. Bancroft (1984) described a species of *Rhombopora* from Brigantian and Arnsbergian strata in Northern England and Scotland, characterised by rounded apertures and abundant exilazooecia. He tentatively assigned the species to *Rhombopora similis*, basing his diagnosis on material from the Vine collection in the Natural History Museum, and the Young collection in the Glasgow Art Gallery and Museum, where specimens were labelled *Ceriopora similis* or *Rhombopora similis*.

Vine did not figure his specimens of *Rhombopora*, but he referred to rounded apertures and several stylets on the interzooecial walls. Thus, the material described by Vine and by Bancroft is rather different to *Rhombopora* from Tears Point. The original material of Phillips has been lost, but it is clear from his illustrations, poor in quality though they may be, that the Tears Point material is referable to his original species. Further, Phillips' specimens came from Devonian strata at Hope, near Torquay, and Lower Carboniferous strata at Cannington Park, North Devon; thus, the Courceyan age and location for the Tears Point material are more in keeping with the stratigraphical and geographical ranges of Phillips' *Rhombopora similis.*

Externally, the specimens from Tears Point look very similar to *Rhombopora gracilis*, with diagonal apertures and a single, large stylet. However, the autozooecial apertures of *Rhombopora similis* are much larger than those of *Rhabdomeson gracilis*, and the acetate peels revealed that the axial rod characteristic of the genus *Rhabdomeson* is absent.

Though the Tears Point specimens are morphologically distinct from Bancroft's material, the zooarial parameters are in close agreement. However, the abundance of exilazooecia, and the rounded outline of the apertures, suggest that the material of Vine, Young, and Bancroft should be reassigned to a new species, *Rhombopora bancrofti.* The name *Rhombopora similis* should thus be reserved for forms with thin interzooecial walls, bearing a single large stylet, having sub-diagonal autozooecial apertures, and lacking exilazooecia.

Rhombopora incrassata Ulrich, 1890
Plate 3, figs. b. and c.; Plate 6, figs. a. and b.;Plate 10, figs. b. and c.;
Fig. 6.11, a. and b.

1890 *Rhombopora incrassata* Ulrich, p.652, Pl. 70, figs. 12 to 12d.
1984 *Rhombopora* non *similis* (Phillips, 1841) Bancroft, p.99, Pl. 19, figs. c., d. and e.; Pl. 20, fig. a.

Material : TP23, Tears Point Limestone (Upper Courceyan), Tears Point, Gower, South Wales (SS 408 871).
Other Occurrences : Keokuk Group (Chadian), King's Mountain and Button Mould Knob, near Louisville, Kentucky, North America (Ulrich, 1890). Charlestown Main Limestone (Brigantian), Pathhead, East Fife, Scotland. Ironscars Limestone (Pendleian), Sugar Sands Bay, Howick, Northumberland. Cefn Mawr limestone (Brigantian), Hendre Quarry and Bryn Mawr Quarry, Clwyd, North Wales. Bishop's Quarry Beds (Brigantian), Great Orme, Llandudno, North Wales. ?Shales above the Main Limestone (Arnsbergian), Hurst, near Richmond, North Yorkshire.

Emended diagnosis : *Rhombopora* with a moderately stout cylindrical zoarium, comprising small,oval, rhombically-arranged autozooecial apertures. Interzooecial walls are thick, and are ornamented by prominent stylets, a large oval stylet being placed at wall junctions, and smaller stylets lying in a single (occasionally double) row between them. The vestibular region of the apertures is deeply set, and the hemiseptum extends almost all the way around this region. Exilazooecia are rare to absent.

Description : The width of the colony can be variable, ranging from 0.60mm to 1.36mm. Colonies are cylindrical, and the largest fragment recovered measured 12mm; no branching was observed. Exilazooecia are absent.

Autozooecia are arranged in a fairly regular rhombic pattern. Apertures are oval in outline, but in the vestibular region are more hexagonal. A proximal superior hemiseptum is developed quite shallowly within this vestibular region. The hemiseptum extends almost all the way around the apertures (fig. 6.11b). Apertures are quite small, measuring 0.18mm by 0.12mm.

Interapertural walls are rather thick, both between diagonally-adjacent zooids, and between transversely-opposite zooids. Walls therefore run in a zigzag pattern around the colony (cf. *Rhombopora similis* (Phillips 1841)). The lateral walls measure 0.32mm by 0.13mm. At the proximal and distal ends, a large oval stylet is developed, and smaller stylets occur between them; the smaller stylets are also less clearly developed along the diagonal walls.

The internal structure was inferred from a broken portion of a well-preserved colony on specimen TP13 (fig. 6.11a). A thicker exozone is developed in the outer half of the colony. Zooecial chambers bud annularly from a central zone, initially diagonal but becoming rounded in outline in the exozone. Apertures diverge at an angle of about 20°, bending more sharply towards the colony surface only in the outermost section.

Discussion : *Rhombopora incrassata* Ulrich, 1890, is characterised by thick, hexagonal interapertural walls, ornamented by abundant stylets, and having small, rounded apertures. Exilazooecia are notably absent. The material from Gower matches closely with Ulrich's description of *R. incrassata* from Louisville, Kentucky. Ulrich described a robust colony (1.2 - 1.8mm in width) with small apertures (AD1=0.17mm, AD2=0.09mm) separated by thick, stylet-bearing walls. He recorded five apertures diagonally in a 5mm line, which compares with six in a 5mm line for the Tears Point specimens. His illustration of a shallow tangential section revealed almost completely encircling hemisepta. The Keokuk (Chadian) age for his specimens is stratigraphically close to the Upper Courceyan age of the material from Tears Point, though forms believed to be referable to *R. incrassata* are illustrated by Bancroft (1984) in Arnsbergian strata.

Apertures are significantly smaller than those of other British Carboniferous species of *Rhombopora* (*Rhombopora radialis* Owen 1966, AD1=0.20-0.25mm, AD2=0.12-0.15mm, *Rhombopora* non *similis* Bancroft, 1984, AD1=0.23-0.34mm, AD2=0.16-0.23mm, *Rhombopora similis* Phillips, 1841, AD1=0.29mm, AD2=0.18mm). Both *R. radialis* and *R. similis* lack exilazooecia, but differ from *R. incrassata* in stylet types; *R. radialis* does not bear stylets, and *R. similis* has a single large type "A" stylet on the walls. Bancroft's illustrations of *R.* non *similis* illustrate rather variable morphologies; most specimens are referable to *R. bancrofti* sp. nov., and despite many forms having exilazooecia, one variety (ABRH.3R.5. Plate 19, fig. c.) seems to lack exilazooecia, and has rows of small type "C" stylets surrounding the apertures. This variety is most probably referable to *Rhombopora incrassata*, but Bancroft's material is now unobtainable, and the parameters for this variety cannot be compared with those of *R. incrassata.*

Rhombopora bancrofti sp. nov.

Plate 3, fig. a.; Plate 10, fig. a.

1881 *Ceriopora* non *similis* (Phillips, 1841) Vine, p.338.
1885 *Rhombopora* non *similis?* (Phillips) Vine, p.93.
1889 *Rhombopora* non *similis?* (Phillips) Vine, p.198.
1984 *Rhombopora* non *similis* (Phillips) Bancroft, p.99, Pl. 19,
figs. a. and b.(right)

Holotype : HML29, Shales above the Main Limestone (Arnsbergian), Hurst, near Richmond, North Yorkshire (NZ 044 023).
Paratypes : HML27-28, from the same horizon and locality as holotype.
Other Occurrences : Hosie Limestone, Lower Limestone Group (Brigantian), Hairmyres, Scotland (Bancroft, 1984). Dun Limestone (Asbian), Hilton Bay, near Lamberton, Northumberland. Sandbanks Limestone (Brigantian), Lady's Hole, Beadnell, Northumberland. Cefn Mawr Limestone (Brigantian), Bryn Mawr Quarry, Clwyd, North Wales. Oystermouth Beds (Brigantian), Black Lias Quarry, Oystermouth, South Wales.

Diagnosis : *Rhombopora* with large, circular apertures arranged in a rhombic pattern. Interzooecial walls are moderately-thin, and may be ornamented by a variety of stylets, which occupy variable positions. Exilazooecia are very common, and may occur singly or in clusters on the colony.

Derivation of name : The species is named after Adrian J. Bancroft, who produced detailed descriptions of material referable to this species.

Zoarial Parameters :

Rhombopora bancrofti			
	x	σ	n
ZD	0.953	0.0854	9
AD1	0.257	0.0259	29
AD2	0.194	0.0243	24
IWT1	0.295	0.0820	24
IWT2	0.162	0.0548	25
ED	0.073	0.0303	23
Z2	3 - 5		

Description : Colonies are cylindrical, and variable in diameter, but are moderately slender, ranging from 0.90mm to 1.00mm in width.

Autozooecia are arranged in a rhombic pattern, but this pattern is often disrupted by the growth of exilazooecia. Apertures are almost circular in outline, and are rather large (AD1=0.26mm, AD2=0.19mm). They may be surrounded by a poorly-defined rim, which occasionally has its inner margin ornamented by small stylets.

Interapertural walls are thin in the direction between diagonally-adjacent apertures, but, because of the circular outline of the apertures, they are moderately-thick in a proximal-distal direction, averaging 0.30mm by 0.16mm; however, these thicknesses can be very variable. Walls may be ornamented by small stylets, giving a beaded appearance, though more usually stylets are irregularly developed; sometimes large stylets occur at wall junctions, or around exilazooecia.

Exilazooecia are common, but are randomly arranged on the colony; occasionally, there may be a tendency for a single exilazooecium to grow on the longitudinal interaperture wall. Exilazooecia sometimes cluster in threes or fours on the walls. They are very variable in size and shape, ranging from circular apertures to lobate ovals, and with diameters ranging from 0.04mm to 0.14mm.

The internal structure of the colonies has yet to be determined.

Discussion : *Rhombopora bancrofti* differs from described forms of *Rhombopora* in possessing large, circular, approximately rhombically-arranged apertures, and an abundance of exilazooecia.

Bancroft (1984) described rhabdomesids from the Brigantian of the Midland Valley, and the Arnsbergian of Richmond. He tentatively assigned all the specimens to *Rhombopora similis*, but reassessment of Phillips' 1841 identification shows that Bancroft's material is not actually referable to this species. Similarly, the descriptions of Vine (1881; 1885; 1889) describe specimens of *Rhombopora* possessing large, rounded apertures, in clear contrast to the diamond-shaped apertures of *R. similis*; thus, the material of Vine is most probably referable to *R. bancrofti.*

Some of the figures of Bancroft (1984) illustrate specimens here assigned to *Rhombopora incrassata*, but others (namely HM D.110, Plate 19, figs. a. and b., from the John Young collection in the Hunterian Museum, and labelled *Rhombopora (Ceriopora) similis*) are here assigned to *R. bancrofti* sp. nov.. In addition, three specimens from Hurst, Richmond, which Bancroft labelled *Rhombopora similis*, have been studied and reassigned to *R. bancrofti*; measurements cited in the table are taken from these specimens.

Mewslade Bay

GRID REFERENCE : SS 419 872
AGE : Holkerian

At Mewslade Bay, a succession of well-bedded grey limestones of S2 Holkerian age are exposed. The limestones are mainly crinoidal, but one bedding plane revealed a richer fauna, including both tabulate and rugose corals, chonetid brachiopods, echinoid spines, trilobite tails, and the bryozoan, *Fenestella multispinosa.* Other bedding planes yielded sprawling trepostomes and one unidentifiable rhabdomesid.

Several of the fenestellid fan fragments are quite large, but the general abrased nature of the fossils suggests that some transportation of the remains had taken place, probably from an area of the shelf with a high diversity fauna.

Fenestella multispinosa

The only specimens of the genus *Fenestella* found in Mewslade Bay belong to *Fenestella multispinosa.* The colony meshworks can be rather variable in appearance, but branches are always sub-parallel, with moderately large fenestrules.

Parameters for specimens belonging to this species are given in the following table :

	Fenestella multispinosa						
	MB7			Bancroft		Tavener-Smith	
	n	σ	x	x	t-TEST	x	t-TEST
BW	12	0.0128	0.262	0.24	0.0122	0.250	0.1046
AD	12	0.0085	0.113	0.09	0.0000	0.096	0.0102
ID	12	0.0099	0.252	0.26	0.0389	0.250	0.6444
FL	12	0.0272	0.706	0.65	0.0000	0.633	0.0001
FW	12	0.0272	0.481	0.49	0.4382	0.499	0.1370
DW	12	0.0085	0.153	0.13	0.0032	0.116	0.0000
IND	12	0.0263	0.305	0.35	0.0001	0.358	0.0270
				TOTAL	0.0704	TOTAL	0.1319

Branches are moderately thick (0.22 - 0.32mm, depending on the extent of secondary calcification). They are sub-parallel, and form a fairly rigidly-defined meshwork. On obverse surfaces, a prominent median ridge is present, bearing oval nodes placed approximately 0.31mm apart. Branch surfaces slope away fairly steeply from the median ridge. On the obverse surfaces, branches are flatter, and are ornamented by longitudinal striations; with secondary calcification, the surfaces become more rounded and the ornament is obscured.

Branch bifurcations are infrequent, and have the low-angle tuning fork pattern, resulting in little disruption to the sub-parallel nature of the meshwork. Branches may increase in thickness over four fenestrule lengths prior to bifurcation, and reach thicknesses of 0.70mm. On obverse surfaces, an aperture is placed in the angle of the fork; no incipient third aperture row was observed, but only one specimen (MB7) showed a well-preserved obverse surface.

Apertures appear to be rather large (approx. 0.11mm) and circular in outline; however, this diameter is probably greater than normal due to weathering, since some chambers have been filled with sparry calcite, and have been weathered proud of the branch surfaces. Apertures are moderately closely-spaced, with an interaperture distance of approx. 0.25mm, and there are three apertures per fenestrule. Aperture position is not stabilised with dissepiment position (cf. *Fenestella frutex*), and they do not indent the fenestrules.

Dissepiments are moderately thick, though the thickness can be variable, ranging from 0.14mm to 0.22mm. On obverse surfaces, they bear a small median ridge, which joins up with the ridges of the branches, but are slightly depressed beneath this level. Dissepiments flare quite markedly at branch junctions. On reverse surfaces, they are flush to elevated above the branch surfaces. They are only faintly striated.

Fenestrules can be variable in length, ranging from 0.65 to 0.75mm, but are usually between 0.48 and 0.50mm in width. They can vary from sub-rectangular to sub-oval in outline, attaining the latter shape when the colony is extensively secondarily-calcified.

Internally, broken colony portions showed the zooecial chamber bases to be hemi-hexagonal in shape.

The rigidly-constrained meshwork with moderate-sized fenestrules, coupled with steeply-sloping obverse branch surfaces and three apertures per fenestrule indicate that the specimens belong to the species *Fenestella multispinosa*, matching well with Ulrich's 1890 description. Additionally, specimens fall within the ranges cited by Bancroft (1984) and Tavener-Smith (1973a) for the species. However, statistical comparisons of the best preserved Mewslade Bay specimen, MB7, with Bancroft's data yielded rather low probability scores, but slightly higher scores with Tavener-Smith's material. The most noticeable discrepancies are in aperture diameter (which is diagenetically-larger in MB7) and fenestrule length. MB7 does actually have larger fenestrules than average for the Mewslade Bay population, but still lies just within the colony ranges cited by Bancroft and Tavener-Smith.

Stenodiscus tumida?

A few fragments of a broad, compressed cylindrical trepostome were found in Mewslade Bay. Colonies up to 5cm in length were noted, averaging 3mm in width. Some branching occurs, with high-angle bifurcations.

Apertures are rounded to oval in outline, and are quite sunk beneath thick interaperture walls. They are irregularly arranged, and vary in size, but usually occur between 0.18mm and 0.20mm in diameter. Spacing can be variable, with between five and seven complete apertures in a 2mm line.

Interaperture walls can be variable in thickness, from 0.08mm to 0.16mm, but usually lie in the range 0.13 - 0.14mm. They are quite well-rounded, and a ridge may run along the wall crests; this can give a more polygonal outline to the apertures.

Stylets are not pronounced, but moderately large stylets may grow at interaperture wall junctions.

Exilazooecia are commonly developed, and are irregularly scattered as individuals around the colony. Aperture diameter is variable, ranging from 0.07mm to 0.12mm.

An acetate peel of MB2 revealed that the colony has a sharply-defined, relatively narrow exozone, with skeletal laminae deflecting orally into stylet cores in the centre of the interaperture walls. Ring septa are absent, but some complete basal diaphragms were observed in the lower portions of the zooids; this observation, combined with the sporadic distribution of the exilazooecia, suggests that the material is referable to the trepostome genus *Stenodiscus*. The zoarial parameters mainly fall within the ranges cited by Bancroft for the species *Stenodiscus tumida*, but the apertures are noticeably smaller. However, the thick exozones of other species of *Stenodiscus*, described by Lee (1912) as *Stenopora*, distinguish them from the thin endozoned material of Mewslade Bay; thus, the material is tentatively assigned to the species *Stenodiscus tumida.*

Red Chamber

GRID REFERENCE : SS 422 868
AGE : Holkerian

The strata at Red Chamber are laterally-equivalent to the S2 Holkerian thin-bedded limestones at Mewslade Bay, from which they are separated by approximately 1km. The material for this study was collected from a very fossiliferous bedding surface and, as at Mewslade Bay, bryozoans are very abundant, occurring together with rugose and tabulate corals, chonetid brachiopods and trilobites. Despite the poor preservation of the material, it was noticed that the bryozoan fauna is more diverse than that at Mewslade Bay, and the following taxa were recorded :

Fenestella plebeia
Fenestella multispinosa
Stenodiscus tumida
Fistulipora incrustans
Ptylopora cf. *pluma*
Rhabdomesid - one poorly-preserved fragment

Fenestella multispinosa and *Stenodiscus* are similar to their Mewslade Bay equivalents. The additional taxa are described in the following pages.

Fenestella plebeia

In the Red Chamber strata, *Fenestella plebeia* is actually dominant over *Fenestella multispinosa* and is distinguished by its broader fenestrules and four to five apertures per fenestrule.

Branches are quite thick (0.32mm) and have a prominent median ridge running down the centre of the obverse surface branches. Nodes had not been preserved.

Branch surfaces slope away moderately steeply. On the reverse surfaces, branches are ornamented by strong longitudinal striations.

Bifurcations are frequent in the initial portions of the colony (as seen on specimen RC12), and occur in a high-angle tuning-fork pattern, with a single aperture placed in the angle of the fork. In the more distal portions, bifurcations are rarer, and branches become sub-parallel.

Apertures are circular and moderately large (aperture diameter approx. 0.11mm). They are set low down on the branches, and have faint peristomes but do not indent the fenestrules. Apertures lie approximately 0.25mm apart.

Dissepiments are variable in length, depending on the extent of branching of the meshwork . They are also variable in thickness, ranging from 0.12mm to 0.16mm. Dissepiments are moderately depressed beneath the crests of the obverse surface branches, but less depressed on the reverse surfaces. They are poorly-striated.

Fenestrules are usually rather open, and vary in length from 0.85mm to 1.30mm, averaging about 1.00mm. Likewise, widths can be very variable, especially in the proximal portions, ranging from 0.40mm to 0.65mm; in the distal portions of colonies, widths of about 0.60mm are more normal. Fenestrules vary in shape from sub-rectangular to elongate oval, depending on dissepiment flaring and fenestrule width.

The parameters and external characteristics match fairly closely with *Fenestella plebeia* McCoy, as described by Bancroft (1984). The species, though, is rather variable in the Red Chamber strata, and a larger sample may have shown distinct morphological groupings. However, it is more likely that most of the variation in the specimens from this locality can be attributed to the astogenic portion of the colony which the particular fragment represents. Shrubsole (1879) also noted the great variability of *Fenestella plebeia*, with different morphologies occurring depending upon the portion of the colony studied. Though gross morphology may vary, the autozooecial parameters (aperture diameter, interaperture distance, aperture position) remain much the same, suggesting that just a single species is being represented.

Ptylopora cf. *pluma*

Only one fragment of this acanthocladid was found (specimen RC13). The genus *Ptylopora* is very distinctive, with a stout mainstem giving rise to regularly-spaced lateral branches (diverging at angles of approx. 45°), connected by dissepiments.

Parameters for the Red Chamber specimen are as follows :

	Ptylopora pluma	
	RC 13	Bancroft
	x	x
MS:BW	0.50	0.56 - 2.80
LBW	0.30	0.34 / 0.27 - 0.43
FL	0.75	1.06 / 0.80 - 1.30
FW	0.48 - 0.60	0.65 / 0.48 - 0.83
DW	0.14 - 0.16	0.22 / 0.16 - 0.31

The mainstem is straight and well-rounded, and is covered by longitudinal striations on the reverse surface. It is approximately 0.50mm in diameter, though it tapers slightly in the distal direction.

Lateral branches are well-depressed beneath the crest of the mainstem, and do not flare at their junctions with the stem. They are quite stout (approx. 0.30mm) and have well-rounded reverse surfaces with longitudinal striations. Only one set of laterals was preserved, and thus staggering of laterals on opposite sides of the mainstem was not observable.

Dissepiments are moderately well-depressed beneath the lateral branch crests. They are quite stout (0.14 - 0.16mm) and bar-like, flaring only slightly at their junctions with the laterals. They are faintly striated.

Fenestrules are moderately large, averaging 0.75mm in length, and 0.48mm to 0.60mm in width. They are sub-rectangular in outline.

Bancroft (1984) recorded only one species of *Ptylopora* from Britain, namely *Ptylopora pluma.* Zoarially, the descriptions match with those given by Bancroft, but McCoy's (1884) descriptions discuss only the obverse surfaces. Parametrically, the specimen from Red Chamber falls at the lowest ranges for *Ptylopora pluma* cited by Bancroft, and also shows a close comparison with a specimen of *Ptylopora* recorded in the Brigantian strata of Black Lias Quarry.

Fistulipora incrustans

One sheet-like colony was found (specimen RC14), approximately 1.8mm in thickness, and comprising two layers of autozooecia, one encrusting an older layer. The fragment is fairly large, measuring 1.5cm^2. Despite being recrystallized and weathered, it can be assigned to the Cystoporata on account of the interzooecial walls, which are composed of polygonal vesicular skeletal material. Further, the specimen belongs to the species *Fistulipora incrustans* since it possesses large (0.30 - 0.40mm diameter), widely-separated (3 - 4 apertures in a 2mm line) apertures which lack large lunaria. However, interaperture walls are thicker than those described by Bancroft (1984) for the species, measuring approximately 0.20mm (compared with Bancroft's average of 0.09mm). Aperture-free monticules are developed quite frequently over the colony surface. Monticules are up to 1mm in diameter, and may be slightly elevated above the colony surface.

Black Lias Quarry

GRID REFERENCE : SS 615 884
AGE : Brigantian

The best exposures of the Brigantian (D_3) Oystermouth Beds (Upper Limestone Shales) can be found in Black Lias Quarry, just north of Oystermouth. A series of black, muddy, northward-dipping limestones and shales are exposed in a disused quarry, now employed as a "Pay-and-Display" car park (35p for one hour!). A field sketch of the succession has been made (fig. 6.5), and five distinct facies were noted.

At the base of the quarry, a grey, coarse, oolitic limestone occurs, and this appears to be barren. The oolite is overlain by a prominent shaly bedding plane, which has a very rich brachiopod and bivalve fauna (as listed in Owen and Rhodes, 1960), but no bryozoans were observed. Above the shale, there is a more massive shelly limestone, which is dominated by the brachiopods *Schellwienella* and *Syringothyris*, which are virtually intact, and some remarkable, large stenoporid bryozoans, belonging to the species *Stenodiscus tumida*. Material from this facies was actually collected from fallen blocks, rather than from the cliff face.

At the top south end of the quarry, and overlying the shelly limestone, are a black, shaly micritic limestone, capped by a buff-weathering limestone with a more restricted fauna. The micrite yielded some well-preserved bryozoans, which dominated the fauna, including *Polypora*, *Fenestella*, *Rhombopora*, *Penniretepora*, and *Ptylopora*. The buff-weathering limestone was more massive, and yielded only a few fossils, but *Fenestella plebeia* and *Penniretepora flexicarinata* were found.

Environmentally, the changes from the oolitic limestone to the buff-weathering limestone are interpreted as representing deepening water, with a fairly abrupt change between the oolite and the first shale. This abrupt change is probably due to terrigenous input diluting carbonate production in association with basin subsidence. By the level of the micrite, the succession represents a moderately deep shelf

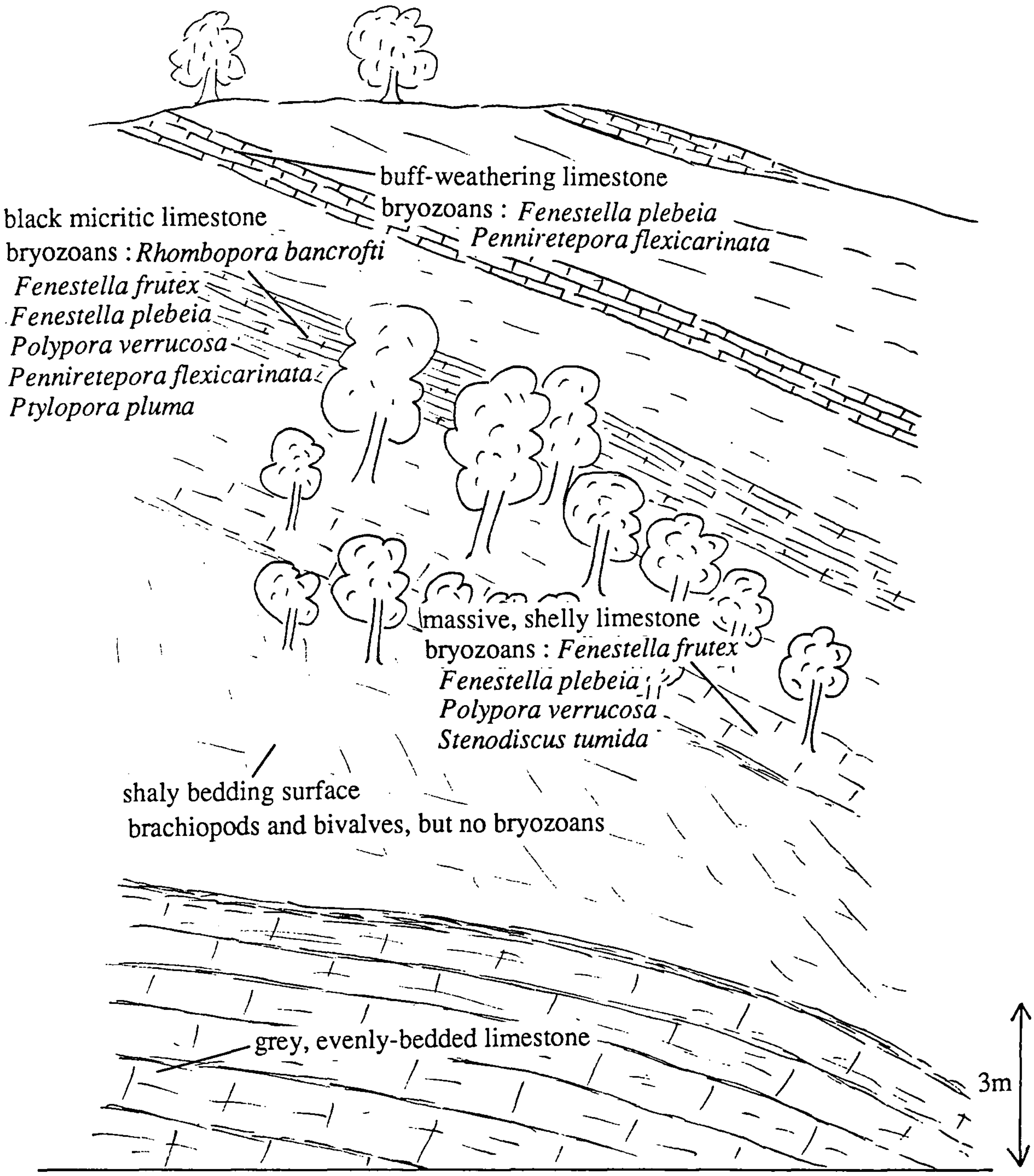


Fig. 6.5. Fieldsketch of Black Lias Quarry

environment, mud-dominated, and has many elements in common with the Mud Community of Ramsbottom (1978).

a. Shelly Limestone fauna

Stenodiscus tumida

Large colonies of the trepostome *Stenodiscus tumida* are very common in the shelly limestone facies, and are up to 5mm in diameter and 35mm in length. They are invariably broken lengthwise, revealing little of the external morphology, but showing the internal structure of curved autozooecial chambers and a thin exozone. Colonies are cylindrical, but curve slightly. The material is assigned to the genus *Stenodiscus* since imperforate basal diaphragms can be seen in the exozone region of many zooecial chambers. There are about three to four per chamber, and this frequency is consistent with the species *Stenodiscus tumida* (Phillips) as recorded by Bancroft (1984).

Chambers curve round from an almost recumbent position in the central zone, becoming gently recurved, and bending sharply in the last 0.4mm of the exozone to be perpendicular to the colony growth direction (Plate 12, fig. f.).

The exozone is very sharply defined as a white calcite band, about 0.4mm thick, around the edge of the colony (Plate 12, fig. d.). Smaller stylets appear to be developed within this zone, and stylets also occur; the stylets have 0.03mm diameter cores, perpendicular to the edge of the colony, and with skeletal laminae curving upwards into the zone.

Acetate peels from samples BLQ20 (Plate 12, fig. g.) and BLQ21 (Plate 12, fig. e.) show some extra detail that could not be seen from the broken specimens; the laminar nature of the well-defined exozone is shown rather clearly in BLQ21, with strong oral flexure towards the core of the stylets. However, neither peel showed the basal diaphragms as clearly as could be seen on the broken colony surfaces.

Polypora verrucosa

Several small fragments referable to the fenestrate *Polypora verrucosa* were found, one showing a broken reverse surface which revealed the four rows of autozooecial apertures which are characteristic of the species. Apertures appear to be circular, measuring 0.12mm in diameter, and are relatively widely-spaced (ID = 0.30mm) in the typical quincunx pattern of the genus.

Fenestrules are large and open, sub-rectangular in outline, and measuring 2.10mm by 1.50mm. Dissepiments are relatively thin, being 0.20mm in diameter, flaring slightly towards the branch margins. All surfaces are striated, with parallel longitudinal striations on the reverse branch surfaces and dissepiments, and sinuous striations on the obverse branch surfaces.

The parameters are smaller than the averages of Bancroft, but are similar to those of better-preserved specimens of *Polypora verrucosa* from the black micrite.

Fenestella plebeia

A few colony fragments of this species were noted in the shelly limestone facies, showing the reverse surface detail. The material is characterised by an open meshwork with strongly-striated, broad (0.30mm) branches, and moderately-broad (0.20mm) dissepiments, which flare very slightly at the branch margins. The colony often branches, with broad "tuning-fork" bifurcations, with the resulting branches rapidly incorporated into the normal meshwork spacing.

In places on a specimen on sample BLQ21, the compressed colony of *Fenestella plebeia* is a composite mould, and there are indications of the autozooecial apertures. Apertures are circular, and spaced approximately 0.28mm apart.

Fenestrules are sub-rectangular, and measure approximately 1.05mm by 0.60mm. These parameters give a good match with the material described by Bancroft, and also with other specimens from the black micrite and the buff-limestone.

Fenestella frutex

Fragments of *Fenestella frutex* were the most abundant fenestellid remains in the shelly limestone facies. Most specimens have been flattened, so have greater branch widths than normal. Branches are sub-parallel, forming a fairly tight meshwork. Reverse surfaces are fairly flat, and have prominent longitudinal striations, which can also be seen on the dissepiments. Bifurcations, when present, occur in a low-angle "tuning-fork" pattern, in contrast to that of *Fenestella plebeia.*

On the obverse surfaces, seen best on a specimen from sample BLQ20, branches appear to slope away quite steeply from a well-defined, thin median carina, along which a series of very closely-spaced, small oval nodes occurs. Apertures are placed towards the branch margins, with three per fenestrule. They are circular, and have thin, complete peristomes, jutting slightly into the fenestrules.

Dissepiments are moderately-depressed beneath the obverse surface branch crests, but are almost flush on the reverse surfaces. They flare gently into the branch margins, but are relatively narrow in their centres. Fenestrules are sub-rectangular in outline, having rounded corners because of dissepiment flaring. They are approximately 0.55mm long by 0.50mm wide. Parameters for BLQ20 are as follows:

Fenestella frutex							
	BLQ 20			**Bancroft**		**Tavener-Smith**	
	n	**σ**	**x**	**x**	**t-TEST**	**x**	**t-TEST**
BW	7	0.0336	0.291	0.24	0.0000	0.254	0.0002
AD	10	0.0137	0.079	0.09	0.0097	0.084	0.3855
ID	10	0.0176	0.221	0.22	0.8508	0.201	0.0002
FL	10	0.0756	0.558	0.58	0.2361	0.556	0.9202
FW	6	0.0670	0.493	0.44	0.0101	0.461	0.1230
DW	7	0.0368	0.151	0.11	0.0001	0.150	0.9217
IND	9	0.0137	0.208	0.34	0.0000	0.236	0.0000
				TOTAL	0.1581	**TOTAL**	0.3358

The sub-parallel branches, with striated reverse surfaces, and three circular apertures per fenestrule point to this material belonging to the species *Fenestella frutex* McCoy. However, branches and dissepiments are broader than those recorded by Bancroft for the species (probably due to diagenetic compaction), and nodes are much more closely-spaced. Thus, t-test correlations with Bancroft's averages, while giving the highest scores for any species of *Fenestella*, returned relatively low probability scores for the comparison with *Fenestella frutex.*

Interestingly, the parameters matched very closely with those recorded by Tavener-Smith for specimens of *Fenestella frutex* from the Calp Shales of County Fermanagh, and very high probability comparisons were recorded. This is in contrast to the analysis of specimens of the species from the black micrite, which showed much greater affinities with the Bancroft averages. It is possible that the diverse shale fauna from Carrick Lough is more comparable with the shelly facies within the Black Lias than the faunally-sparse micrite.

b. Black Micrite Fauna

Rhombopora bancrofti

Only one specimen belonging to this cryptostome species was found in Black Lias Quarry (BLQ15, Plate 10, fig. a.). It is a moderately-poorly preserved cylindrical colony, approximately 0.64mm in diameter, and characterised by large, rounded, rhombically-arranged autozooecial apertures. These apertures are broadly oval in shape, measuring 0.22mm by 0.15mm, but are not absolutely regularly-arranged; hence there is much variation in the longitudinal inter-aperture wall thickness. Occasionally, the walls bear circular exilazooecia of small-diameter (about 0.07mm). Exilazooecia distribution is rather sporadic.

Most stylets which may have been present appear to have been eroded away, but a low-angle light revealed part of the colony where two moderately-large oval nodes occur in the centre of an interaperture wall.

Rhombopora bancrofti				
	BLQ15			Bancroft
	n	σ	x	x
ZD	1		0.640	0.89
AD1	6	0.0243	0.223	0.27
AD2	5	0.0098	0.148	0.20
IWT1	5	0.0950	0.256	0.25
IWT2	5	0.0240	0.092	0.11
ED	3	0.0094	0.067	0.04 - 0.13
Z2			4 - 5	4.28

The specimen is assigned to the species *Rhombopora bancrofti* on the basis of the large, circular, rhombically-arranged autozooecial apertures, and the presence of exilazooecia. In addition, the zoarial parameters tally with those of Bancroft (1984) for *Rhombopora bancrofti* sp. nov. non *similis*, but apertures are actually slightly smaller than usual. Similarly, there is a moderate match with the remeasured specimens from the Arnsbergian strata of Hurst (described in the *Rhombopora bancrofti* systematics section), but the Black Lias Quarry specimen also has smaller apertures.

Fenestella frutex

Two colonies belonging to the species *Fenestella frutex* were found in the micrite. Specimen BLQ14 is rather poorly-preserved, but BLQ6 is well-preserved, and broken portions of the branches revealed the internal zooecial chambers; descriptions are based on this latter specimen.

Branches are moderately-thin (0.22mm), sub-parallel, and form a fairly tight meshwork. They are ornamented on the reverse surfaces by strong, widely-spaced longitudinal striations. Reverse branch surfaces are well-rounded. Branching is not infrequent, and bifurcations are of a low angle "tuning-fork" type, with thickening up to 0.38mm before splitting.

Dissepiments are moderately slender (0.10mm) and moderately well-depressed beneath reverse surface branch crests. They have a bar-like appearance, with very little flaring towards the branch margins. Faint longitudinal striations run along the dissepiments. Fenestrules are rectangular, and are fairly open, measuring 0.61mm by 0.43mm.

The broken portions of branches reveal the internal structure; zooecial chamber bases are hemi-hexagonal in shape, and measure 0.22mm by 0.10mm.

	Fenestella frutex					***Fenestella. multispinosa***	
	BLQ 6			**Bancroft**		**Bancroft**	
	n	**σ**	**x**	**x**	**t-TEST**	**x**	**t-TEST**
BW	**12**	**0.0142**	**0.220**	**0.24**	**0.0036**	**0.24**	**0.0230**
FL	**12**	**0.0370**	**0.610**	**0.58**	**0.0261**	**0.65**	**0.0029**
FW	**12**	**0.0412**	**0.433**	**0.44**	**0.5907**	**0.49**	**0.0001**
DW	**12**	**0.0144**	**0.095**	**0.11**	**0.0082**	**0.13**	**0.0001**
ZB1	**12**	**0.0144**	**0.215**	**0.21**	**0.1301**		
ZB2	**12**	**0.0101**	**0.103**	**0.11**	**0.0006**		
				TOTAL	**0.1581**	**TOTAL**	**0.0065**

The two species *Fenestella frutex* and *Fenestella multispinosa* can be rather difficult to distinguish, especially from the reverse surfaces. The depressed dissepiments, coupled with the strong longitudinal striations would point to BLQ6 being *Fenestella frutex.* Some branches have faint node-like structures running along the branch centres; this feature was recorded by Bancroft on some specimens of *Fenestella frutex.*

The t-test analysis of the data shows that the material is referable to *Fenestella frutex* rather than *Fenestella multispinosa*, despite BLQ6 having a larger fenestrule length than average. The match with Bancroft's data is rather good, considering the low standard deviations associated with that data; t-test correlations using the total intra-colonial coefficients of variation from his data, rather than the inter-colonial parameters, give marginally-higher scores, with a total probability of 0.1544.

Fenestella plebeia

The most abundant species of *Fenestella* from this horizon appears to be referable to *Fenestella plebeia.* Six colony fragments were recovered, in variable states of preservation, but BLQ18 had the best preserved specimen on it, showing part of the obverse surface.

Parameters are as follows :

Fenestella plebeia							
	BLQ 18			Bancroft		Tavener-Smith	
	n	σ	x	x	t-TEST	x	t-TEST
BW	12	0.0435	0.287	0.30	0.1276	0.292	0.7075
ID	3	0.0340	0.287	0.26	0.0425	0.260	0.2399
FL	12	0.1040	0.915	1.02	0.0129	1.166	0.0000
FW	12	0.0619	0.572	0.60	0.1123	0.641	0.0042
DW	7	0.0256	0.186	0.16	0.0013	0.174	0.4407
				TOTAL	0.0593	TOTAL	0.2785

Colonies appear to have rather thin meshworks, but this is due to partial burial of the meshworks in the rock matrix. The measurements given for BLQ18 are close approximations to the true parameters, since the measurements were made on exposed broken branch tips.

Colonies form planar, fan-shaped structures, and have a more irregular aspect than is usual for the species. Branches are moderately-thick, and are sub-triangular in cross-section; a transverse breakage through BLQ18 (fig. 6.12a) shows that the branch sides slope steeply away from a broad median ridge, with dissepiments well-depressed beneath the branch crests. The reverse surfaces are gently rounded, and thus dissepiments are virtually flush with these surfaces.

Reverse surfaces of branches are ornamented by longitudinal striations, but in secondarily-calcified specimens such as BLQ18, the striae are obscured, and surfaces are smooth. Despite wide angles of branch divergence, branches tend to remain sub-parallel, with frequent "tuning-fork" bifurcations.

Dissepiments are moderately-thick and bar-like; there is little flaring at their junctions with branches. They, like the branches, are ornamented by longitudinal striations. Fenestrules have a rectangular shape and appear rather open, but measurements show them to actually be slightly smaller than average.

The steep-sided nature of the obverse branch surfaces, being slightly rounded on the reverse, and their sub-parallel orientation point to the specimens belonging to the species *Fenestella plebeia.* However, most of the parameters are slightly smaller than average, except the inter-aperture distances (based on only three measurements) and dissepiment widths. Hence, t-test correlations with Bancroft's averages gave relatively-low probability scores, but matched very well with *Fenestella plebeia* from Tavener-Smith's Carrick Lough material.

Polypora verrucosa

Several specimens referable to *Polypora verrucosa* were found, the best-preserved being a planar, fan-shaped colony, 2cm long and extending up to 1.5cm across (BLQ13). The fragment shows the impression of the reverse surface, and, in places, the obverse surface of the branches. Towards the proximal end of the colony, some flattened "rhizoid" spines are developed, presumably to help the colony remain upright.

Polypora verrucosa					PROBABILITY SCORES	
	BLQ 13			Bancroft		
	n	σ	x	x	t-TEST	t-DIV
BW	12	0.0655	0.670	0.63	0.3095	0.1150
AD	12	0.0202	0.135	0.13	0.3354	0.1260
ID	12	0.0480	0.410	0.44	0.2766	0.0449
FL	12	0.1854	2.353	3.93	0.0000	0.0000
FW	12	0.2175	1.317	1.60	0.0599	0.4358
DW	12	0.0469	0.200	0.25	0.2139	0.3167
				TOTAL	0.1992	0.1731

Branches are moderately-thick for the genus *Polypora,* being approximately 0.67mm in diameter; they have probably been compressed during diagenesis. The impressions of the reverse surfaces show that they were ornamented by closely-spaced longitudinal striations. On the obverse surfaces, there are three to four rows of apertures, expanding to six before branch bifurcation, arranged in a quincunx pattern, and with six per fenestrule.

Apertures are circular to slightly oval, and appear to have fairly thick, complete peristomes. A series of sinusoidal, longitudinal ridges weave between the apertures.

Branches frequently bifurcate, thickening up to 3.6mm before splitting, but expanding to this width in only one fenestrule length. New branches are rapidly incorporated into the normal open meshwork pattern.

Dissepiments are relatively thin for the genus (0.20mm) and are typically "bar-like" in appearance, flaring only occasionally at the branch/dissepiment boundaries. They are ornamented by longitudinal striations, which flare into those on the branches.

Fenestrules are typically rectangular, and are long and broad, measuring 2.35mm by 1.32mm.

The four rows of apertures on each branch, the thin dissepiments, and the peristomes with striations weaving around them, point to this specimen being referable to *Polypora verrucosa.* Additionally, there is a very good probability match from the t-test with Bancroft's averages for the species; only the fenestrule length scored low, and this parameter was rather smaller than usual. Similarly, relatively high division-test results show that the relative ratios of the Black Lias Quarry specimen and the Bancroft material are similar.

Interestingly, relatively low probability scores resulted from comparing BLQ13 with Tavener-Smith's Carrick Lough material of the same species, resulting in a total probability of only 0.0200. There is little doubt, however, that the specimens are referable to *Polypora verrucosa.*

Penniretepora flexicarinata

Parameters for the specimens of this acanthocladiid are given below :

	Penniretepora flexicarinata			
	BLQ 12			Bancroft
	n	σ	x	x
BW	1		0.36 - 0.50	0.32 - 0.53
1:2 LBW	9	0.0442	0.253	0.18 - 0.28 (0.25)
2:1 LBW	1		0.44	0.24 - 0.46
LBS	9	0.0358	0.702	0.68 - 0.91 (0.81)

Several specimens of *Penniretepora* were found, showing the reverse surface detail. Colonies are fragmented, but a moderately-thick, relatively flat-surfaced mainstem has quite widely-spaced 1:2 lateral branches, diverging at angles of approximately 70°. Laterals are offset in a slightly staggered pattern on opposite sides of the primary branch. They are more slender than the primary branch, but their original length could not be determined; the maximum observed length was 1mm for 1:2 branches, and 1.3mm for a 2:1 lateral branch. There is a slight flaring at the branch boundaries.

The reverse surfaces of both primary and lateral branches are ornamented by broad, longitudinal striations which are pustulose in nature. These striations, coupled with the flat reverse surface and the zoarial parameters, indicate that the specimens belong to the species *Penniretepora flexicarinata*, despite the distinctive obverse surface being shown only on one poorly preserved specimen. This specimen, BLQ1 (fig. 6.12b), shows a rather flattened obverse surface with circular apertures (0.11mm in diameter and spaced at 0.38mm) and a median carina, with an indication of additional faint carinae running between the apertures; this is a very characteristic feature of the species *Penniretepora flexicarinata*.

Ptylopora? pluma

Parameters of the specimen are given in the following table :

Ptylopora pluma		
	BLQ17	Bancroft
	x	x
MS:BW	0.50	0.56 - 2.80
LBW	0.30	0.34 / 0.27 - 0.43
FL	0.80 - 0.90	1.06 / 0.80 - 1.30
FW	0.60 - 0.80	0.65 / 0.48 - 0.83
DW	0.12 - 0.26	0.22 / 0.16 - 0.31

Specimen BLQ17 (Plate 12, fig. c.) shows the proximal end of a fenestellid colony, with the reverse surface uppermost, and comprises a thick (0.50mm) central branch developing from a slightly curved basal disk. Offset lateral branches (0.30mm) are developed, diverging at an angle of 60° to 70°. Several of these branches are connected by well-depressed, bar-like dissepiments. The fenestrules, calculated from the initial growth stages, should be rectangular, and measure 0.80mm - 0.90mm by 0.60mm - 0.80mm.

The mainstem is ornamented by broad longitudinal striations, which are seen more faintly on the lateral branches, which are quite well-depressed beneath the level of the mainstem.

Though this specimen could be the initial growth stages of a *Fenestella*, the prominence of a mainstem, with laterals connected by dissepiments, points to it being a *Ptylopora*. The parameters are slightly smaller than those of Bancroft for the only recorded British species *Ptylopora pluma*, most noticeably in the fenestrule measurements. These parameters, though, would probably have been slightly different from a more distal portion of the colony, and specimen BLQ17 may well belong to the species *Ptylopora pluma*.

c. Buff-Coloured Limestone Fauna

Fenestella plebeia

One large, but poorly-preserved fragment of a fenestellid fan was found in this facies. The specimen shows the obverse surface, but appears to have been compressed. There is a prominent central ridge, which is flanked by two rows of circular (AD approx. 0.11mm), moderately well-spaced (ID approx. 0.25mm), thin-peristomed apertures, which do not project into the fenestrules, but are flush on the branches. There are five apertures per fenestrule.

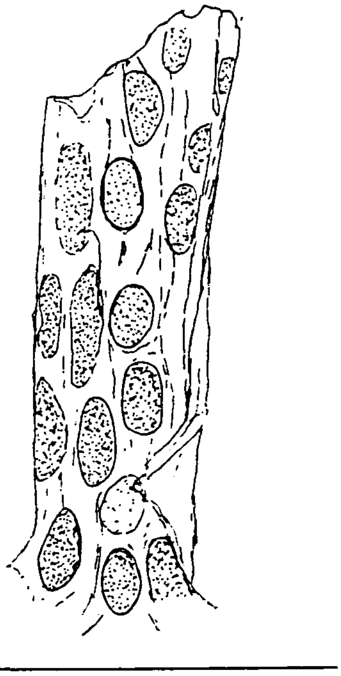
The flattened branch width is approximately 0.37mm, and branches are sub-parallel. The fenestrules are rather broad, measuring 1.25mm by 0.70mm. Dissepiments are somewhat obscured, but appear moderately-thick, measuring 0.16mm in diameter.

These parameters, tied with the zoarial descriptions, match well with those of *Fenestella plebeia* as described by Bancroft.

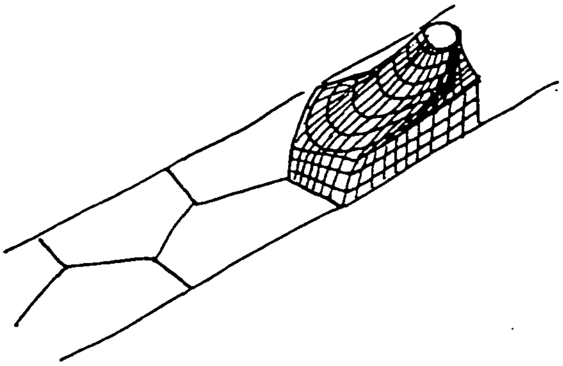
Penniretepora flexicarinata

Two fragments of this species were found in the buff-coloured facies (Specimen BLQ8, Plate 12, fig. a.). They appear very similar to those from the black micrite horizon. Both colonies show reverse surfaces, comprising a broad, flat-surfaced mainstem about 0.38mm in width, with short lateral branches diverging at angles of 80°. These laterals have a staggered offset on either side of the primary branch, and are approximately 0.24mm wide. All branches are ornamented by longitudinal striations.

Zoarial parameters and the flat nature of the reverse surfaces indicate that the specimens can be assigned to *Penniretepora flexicarinata*.

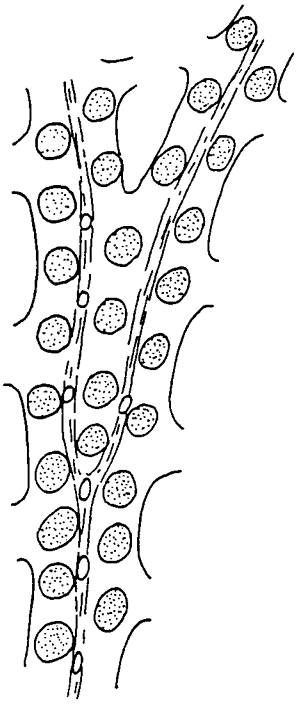


a. *Rhabdomeson rhombifera* colony surface AG1

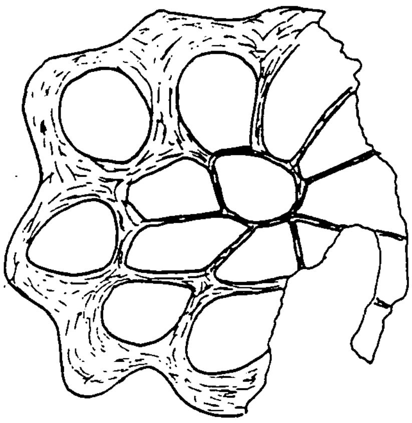


b. Schematic contouring of *Fenestella* zooid chamber,
based on broken specimens from the Stackpole Quay bryozoan band

Fig. 6.6. Bryozoans from the Avon Gorge and Stackpole Quay

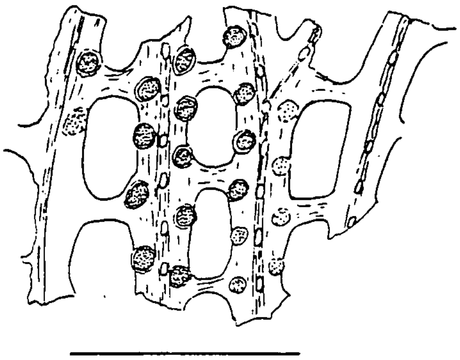


a. *Fenestella multispinosa* obverse surface. TCB¹5

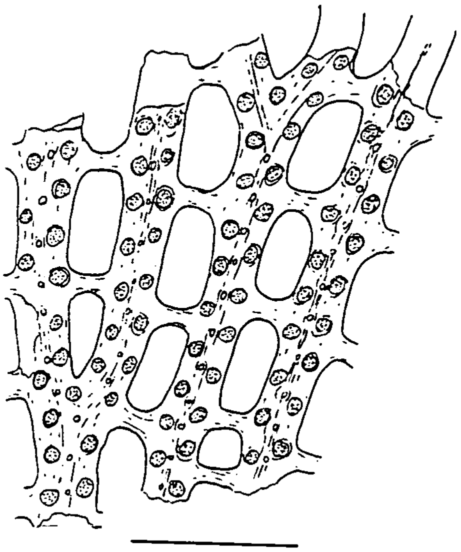


b. *Rhombopora similis* transverse acetate peel TCB¹2

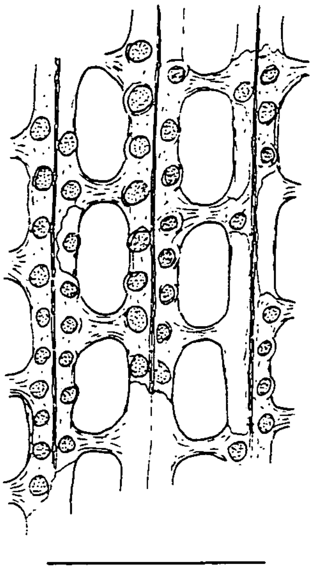
Fig. 6.7. Bryozoans from Three Cliffs Bay



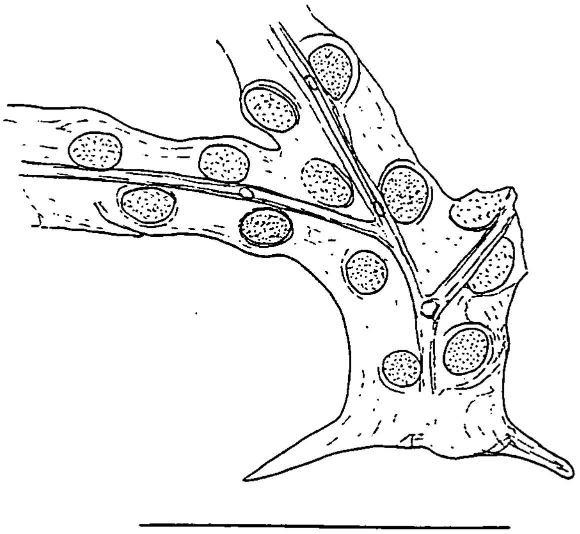
a. *Fenestella bicellulata* obverse surface TP28



b. *Fenestella multispinosa* obverse surface TP23

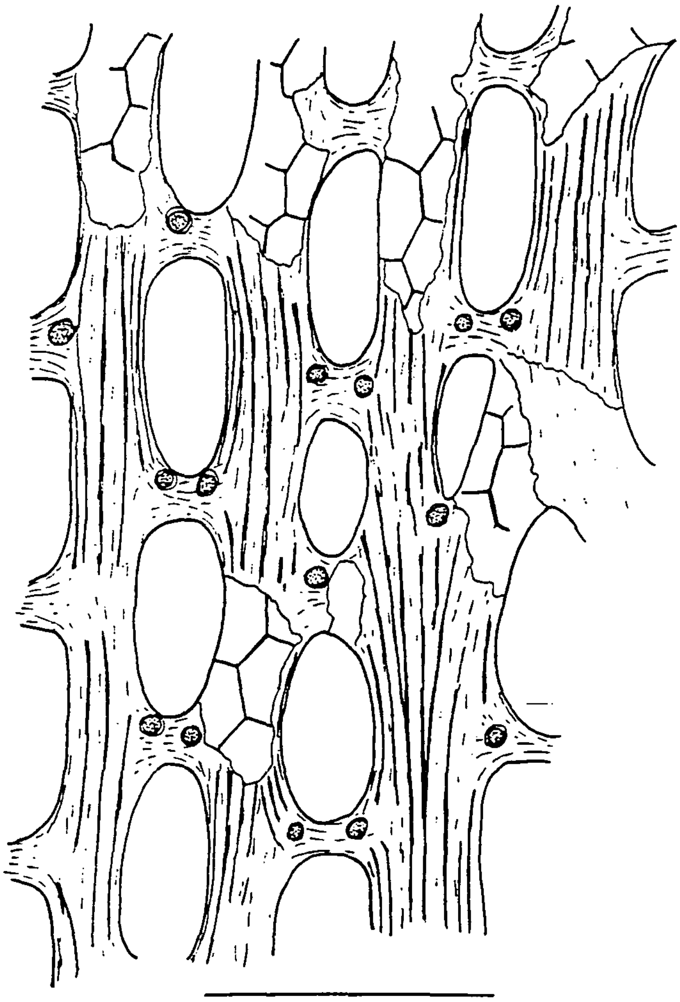


c. *Fenestella frutex* obverse surface TP13

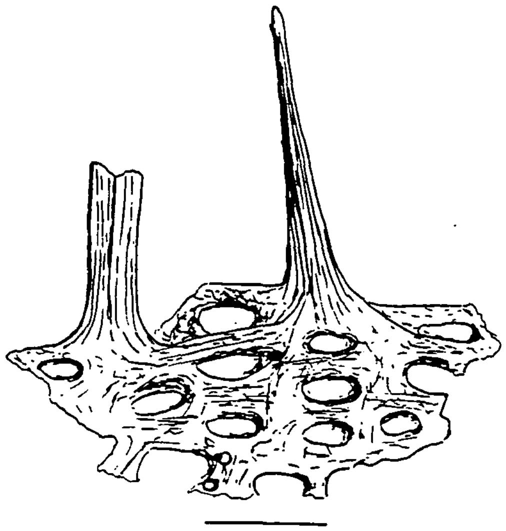


d. *Fenestella* colony origin TP25

Fig. 6.8. Bryozoans from Tears Point

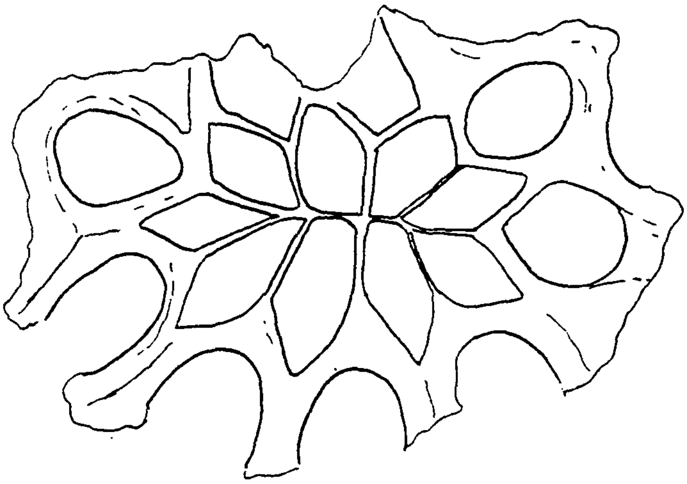


a. Partially broken reverse surface TP13

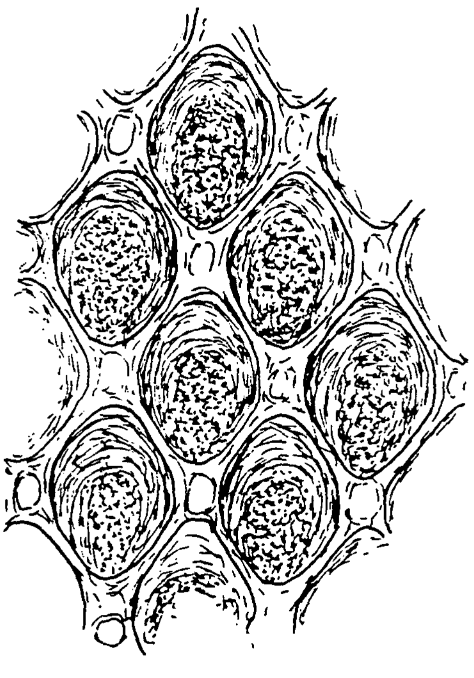


b. Reverse surface with spine development TP28

Fig. 6.9. *Ignotifenestella?* from Tears Point

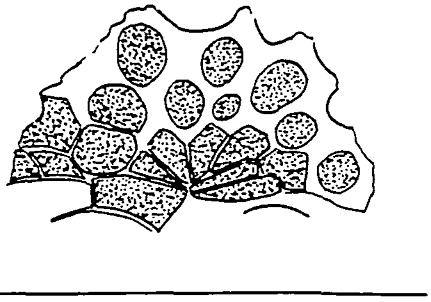


a. Transverse acetate peel TP1

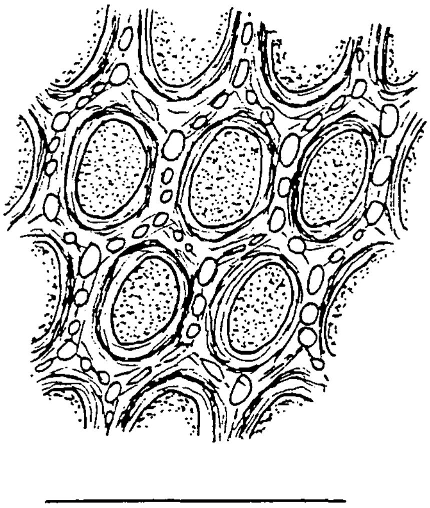


b. Surface detail TP1

Fig. 6.10. *Rhombopora similis* from Tears Point

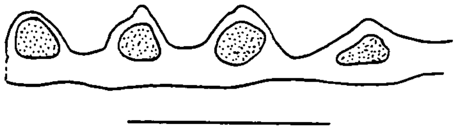


a. Broken colony section TP13

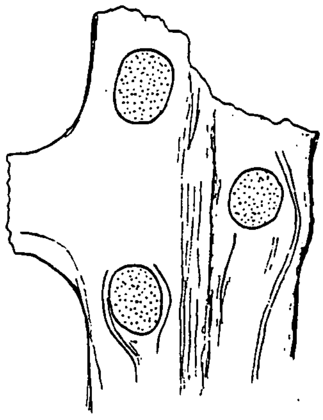


b. Surface detail TP13

Fig. 6.11. *Rhombopora incrassata* from Tears Point



a. Transverse view of broken colony of *Fenestella plebeia* showing depression of dissepiments BLQ18



b. *Penniretepora flexicarinata* obverse surface BLQ1

Fig. 6.12. Bryozoans from Black Lias Quarry

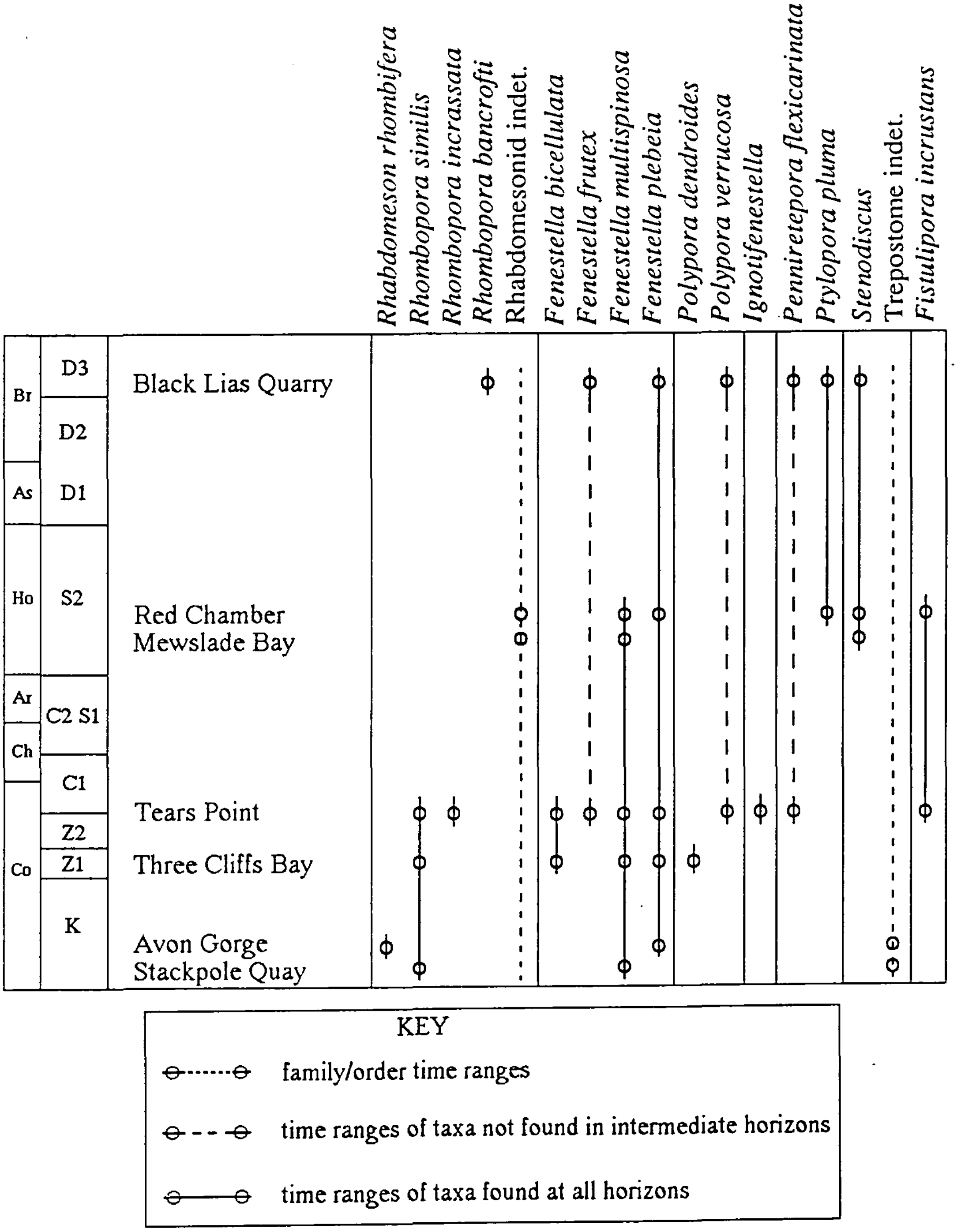


Fig. 6.13. Stratigraphical ranges of bryozoans from South Wales and Avon

Distribution of Bryozoans in South Wales and Avon

Figure 6.13 shows the occurrence of the bryozoan taxa found in South Wales and the Avon Gorge during the fieldwork for this project.

Marine conditions are believed to have been fully developed throughout the whole of the Dinantian in South Wales, though the onset of a marine environment is documented in the lowermost Courceyan strata at Stackpole Quay. Here, within a few tens of metres of marine sediment, a band with an abundance of bryozoan material is recorded; a bryozoan band is also reported at the base of the marine sequences in the Courceyan of the Avon Gorge, though this was not located in this study.

Though bryozoans can be very common in the lower Courceyan, the species present are not particularly diverse; there is a slight increase in species diversity during the Z1 horizon (recorded at Three Cliffs Bay), and maximum diversity is attained in the uppermost Courceyan strata at Tears Point, where ten distinct species have been recorded. The acanthocladiid *Ptylopora pluma* has also been collected at this locality, but was not identified during the fieldwork. There are actually many similarities between the fauna of Tears Point, and the fauna of similarly-aged Courceyan Z1 - C1 rocks from Hook Head, County Wexford, Southern Ireland. The Hook Head peninsula has a series of relatively thinly-bedded grey, slightly argillaceous limestones, as at Tears Point, and a very diverse bryozoan fauna has been recorded. The preservation of the bryozoans, as white calcitic colonies weathering proud of the grey rock matrix, is also strikingly similar. Bancroft (1984) visited Hook Head, but concluded that the material was too poorly-preserved to identify to species level; this is in contrast to Dresser (1960) who, as part of an M.Sc. thesis, described the bryozoan fauna at Hook Head. Dresser identified 34 species, including 17 which were cited as new species. However, many of the fenestellid identifications are based on features such as sharpness of the carinal ridge and presence of carinal nodes; these features are greatly affected by the degree of weathering of a specimen. The following taxa, though, are known to occur with some degree of certainty, and they are compared with the faunal list from Tears Point :

HOOK HEAD	TEARS POINT
Rhombopora sp.	*Rhombopora similis*
	Rhombopora incrassata
Fenestella bicellulata	*Fenestella bicellulata*
Fenestella frutex	*Fenestella frutex*
	Fenestella multispinosa
Fenestella hemispherica	
	Fenestella plebeia
	Ignotifenestella sp.
Polypora dendroides	
Polypora verrucosa	*Polypora verrucosa*
Penniretepora pulcherrima	
Penniretepora flexicarinata	*Penniretepora flexicarinata*
Penniretepora elegans	
Diploporaria sp.	
Icthyorachis newenhami	
Ptylopora pluma	*(Ptylopora pluma)*
Tabulipora sp.	
Fistulipora incrustans	*Fistulipora incrustans*

There is a strong faunal similarity between the two areas, but Tears Point has fewer acanthocladiids than Hook Head. It is thus interesting to note that adjacent areas of similar age, and similar facies do actually appear to contain similar bryozoan faunas.

Chadian and Arundian strata were examined at Caswell Bay (grid reference SS 594 874). Dolomitic limestones and crinoidal limestones are developed, and though they supported a quite diverse coral and brachiopod fauna, conditions were probably too turbulent for bryozoans to thrive.

During the Holkerian, there appears to be a slight drop in diversity (compared with the richly-fossiliferous Tears Point strata) most probably as a result of higher energy conditions prevailing over the area, as witnessed by the development of crinoidal and oolitic limestones. In horizons where the beds are less massive, bryozoans can be quite common; thin-dissepimented fenestellids, such as *Fenestella frutex* and *Polypora verrucosa* are absent at this level, but stouter forms such as *Fenestella multispinosa* were able to survive and proliferate at this time. The trepostome genus *Stenodiscus* made its first appearance in Wales during the Holkerian, though some unidentifiable trepostomes were found in Courceyan strata. The Upper Holkerian is represented on the Gower Peninsula by a series of thick crinoidal and coralline limestones, and despite much searching at Overton Cliffs (grid reference SS 455 848) no bryozoans were recorded.

Beds of Asbian age were seen in the Craig-y-Dinas quarry in the Pont-Nedd Fechan district in the Vale of Neath, but the massive limestones failed to yield any bryozoans. Upper Namurian marine bands were also searched in the same region, but again no bryozoans were found.

Upper Brigantian rocks were studied in Black Lias Quarry, where a variety of different facies are developed. The bryozoan fauna is actually quite diverse, and the micritic community in Black Lias Quarry has many bryozoan species in common with the highly diverse Tears Point fauna, comprising *Rhombopora* (though Black Lias Quarry yielded *Rhombopora bancrofti*, usually found in the North of England), a variety of fenestellids, including *Fenestella frutex* and *F. plebeia*, *Polypora verrucosa*, and the acanthocladiids *Penniretepora flexicarinata* and *Ptylopora pluma*. Though the micrite is slightly muddier than that at Tears Point, both these facies represent sub-wave base calcareous sediment accumulations, and support similar bryozoan communities, despite a difference in age of about thirty million years.

The changes in the bryozoan faunas in South Wales and South West England seem to be associated with changes in facies development. Over the Dinantian, there is little evidence for new species evolving in the region, though *Rhombopora similis* is exclusively recorded in South Wales and South West England. In the Upper Courceyan, several taxa make their last Welsh appearance, and several more make their first. A slightly less pronounced faunal turnover occurs in the Lower Holkerian. However, these apparent extinctions are only local in their extent; *Fenestella bicellulata*, for example, is not found in South Wales in rocks younger than the Courceyan, but in the Pennines region of England, it has been reported in rocks as young as the Arnsbergian.

Of the fifteen taxa recorded in the region, four appear in rocks from Courceyan to Brigantian age. Only one taxon, *Fenestella plebeia*, appears at all the levels from which bryozoans were collected; this is in keeping with the very wide time range known to exist within Britain for this species.

CHAPTER 7 : THE NORTHUMBERLAND COAST

Stratigraphy and Palaeogeographical Setting

The Northumberland Coast provides a good section through the Upper Dinantian and Lower Silesian rocks of the Tweed Basin. The area lies to the southeast of the Southern Uplands Massif, which separates it structurally from the Midland Valley of Scotland; Grayson and Oldham (1987), though, following on from the work of George *et al.* (1976) showed that the eastern end of the Southern Uplands Massif provided no obstacle between the Midland Valley and the Northumberland Trough. Sedimentation was dominated by a large fluvial system situated to the northeast, flowing from Laurasia (as illustrated in Leeder, 1987), and the Southern Uplands Massif provided little clastic input (Wilson, 1989). Within this setting, though there are episodes of marine incursions, with the production of some relatively thin limestones and marine shales during the Asbian to Arnsbergian stages.

The Carboniferous stratigraphy is outlined in figure 7.1 (though the formations are not drawn to an exact scale), which also indicates the localities from which bryozoans were recovered during fieldwork. The Great, Cushat, and the Upper and Lower Foxton Limestones were examined, but no bryozoans were found at these exposures. The thicknesses of the formations (from Johnson, 1980) is given below :

Longhoughton Grits	over 100m
Upper Limestone Group	220m
Lower Limestone Group	375m
Scremerston Coal Group	275m
Fell Sandstone Group	250m
Cementstone Group	430m

Carboniferous sedimentation in the region succeeds a series of redbeds of Old Red Sandstone facies (though of possible lowermost Carboniferous age) with the development of the Cementstone Group. This is a series of shales and impure limestone bands with the development of algal bands at Burnmouth, though they are more marine elsewhere in the Northumberland Basin (Johnson, 1980). Deltaic sandstones dominate the Fell Sandstone Group and the Scremerston Coal Group, and it is not until the Lower Limestone Group is reached that marine horizons are demonstrably developed.

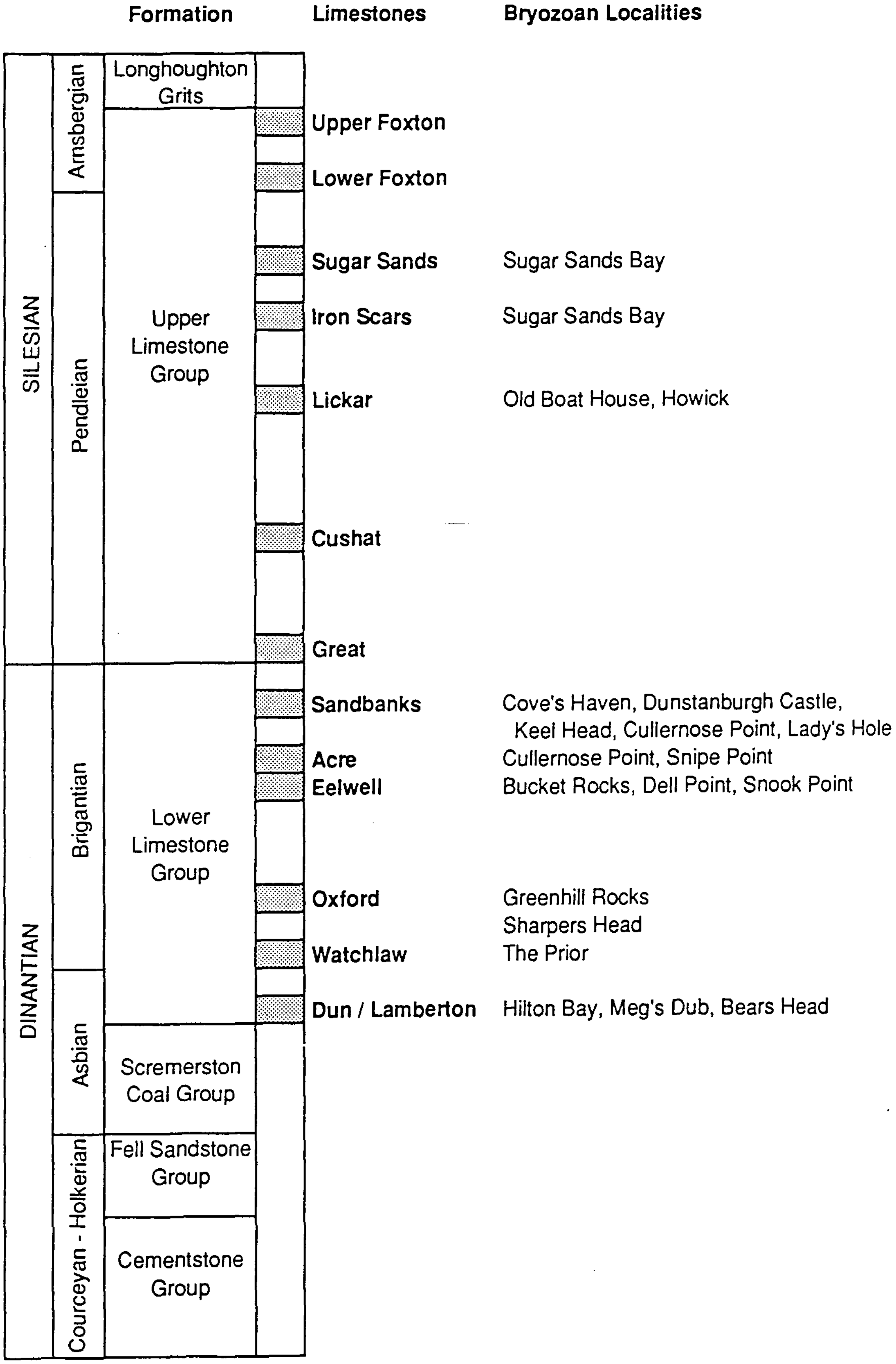


Fig. 7.1. Stratigraphy of the Northumberland Coast

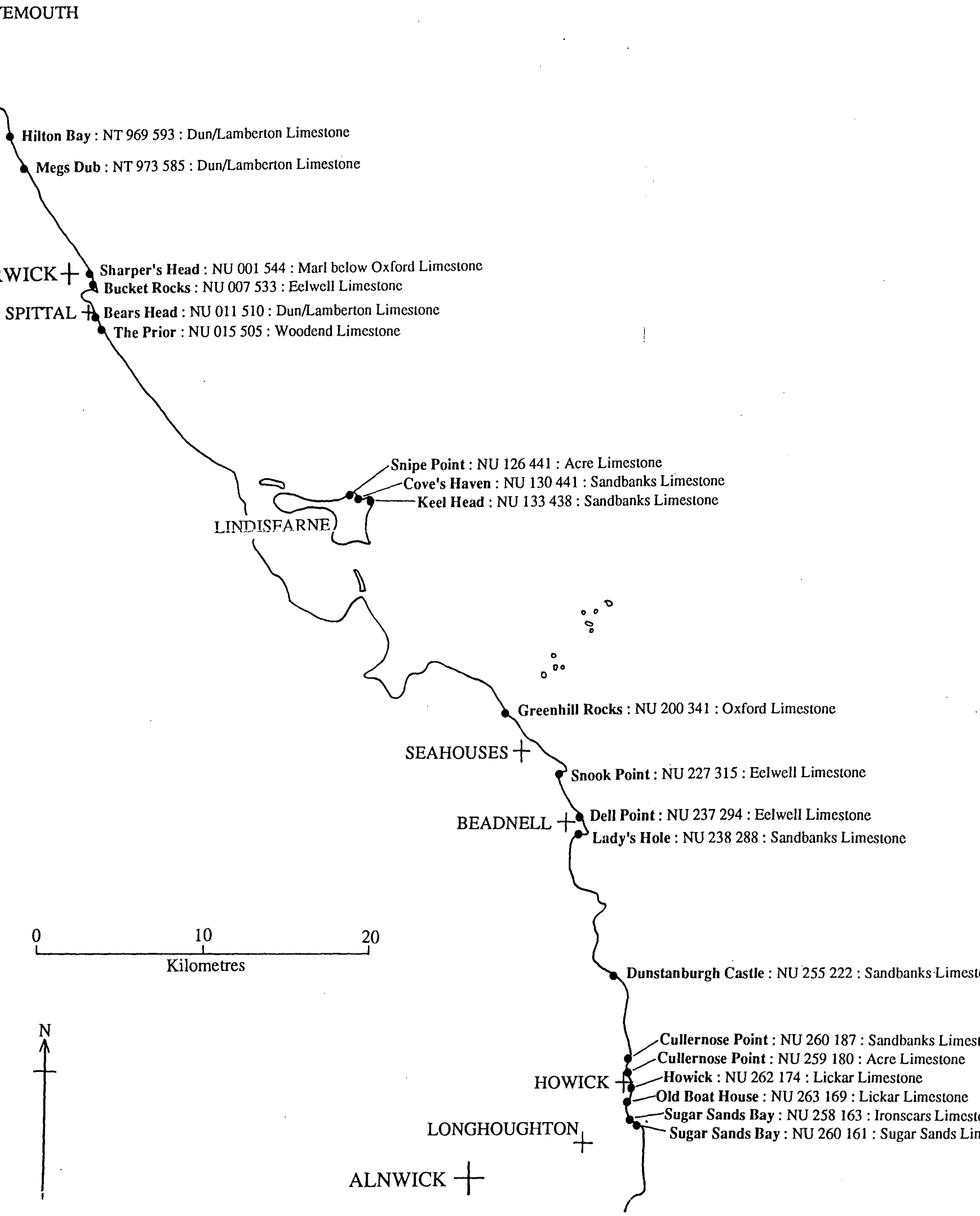


Fig. 7.2. Bryozoan localities on the Northumberland Coast

Bryozoan-bearing localities are illustrated on the map of the Northumberland Coast (fig. 7.2). The area from Burnmouth, a few kilometres south of Eyemouth, to Longhoughton Steel, with the appearance of the Longhoughton Grits, was examined. An outline of the bryozoan faunas found at the major marine horizons is given in the following pages, with some discussion of the environmental settings. Unusual or noteworthy bryozoans are described in more detail, but most of the taxa present are similar in appearance to those discussed in the sections on Fife, Arran, and South Wales, where the taxonomic criteria used in their identification has been documented.

A selection of the bryozoans collected from the Northumberland Coast are illustrated in Plates 3 to 5.

Dun / Lamberton Limestone

The Dun Limestone (Asbian) is the oldest bryozoan-bearing limestone encountered in the Carboniferous rocks of the Northumberland Coast. North of the Scottish border it is a relatively thin band, with shale partitions separating it from the sandwiching deltaic sandstones. It is buff-coloured, but south of the border, where it is known as the Lamberton Limestone, the horizon is somewhat thicker (up to two metres), and reddened. Colonies of the rugose coral *Siphonodendron* are rather abundant, and these large "thickets" suggest that the fauna is probably *in situ.* The bryozoans, though, tend to be rather fragmented. and at Hilton Bay occur within the thickets, suggesting some current activity.

The limestone was studied *in situ* at Hilton Bay, and fallen blocks were found in Meg's Dub. In the blocks from Meg's Dub, the coral thickets were seen to occur in the lower levels of the limestone, and bryozoan-bearing horizons were found 20cm above the top of the coral bands. At Bears Head, near Spittal, the limestone grades into a darker, more shaly level, in which bryozoans are an abundant and dominant constituent of the fauna. The abundance of thin-branched bryozoans such as *Diploporaria*, *Sulcoretepora*, and *Penniretepora flexicarinata* suggests a possible deepening of the environment to depths below storm wave base, and the increase in clastics could reflect a reduction in carbonate production.

Hilton Bay : NT 969 593

Rhabdomeson rhombifera
Rhombopora bancrofti (Plate 3, fig. a.)
Fenestella frutex
Fenestella plebeia?
Penniretepora pulcherrima
Trepostome - probably *Tabulipora*

Meg's Dub : NT 973 585

Fenestella frutex
Fenestella multispinosa
Fenestella plebeia
Trepostome - *Tabulipora?*
Fistulipora incrustans
Sulcoretepora parallela

Bears Head : NU 011 510

Rhabdomeson rhombifera
Hyphasmopora buskii
Fenestella multispinosa
Fenestella plebeia (Plate 3, fig. n.)
Penniretepora flexicarinata (Plate 4, figs. h. and i.)
Diploporaria marginalis

One noteworthy point from the fauna is the occurrence of the rhabdomesid *Hyphasmopora buskii* (Plate 3, figs. e. and f.). This form was described initially by Etheridge Jun. (1875), and is characterised by an abundance of small exilazooecia surrounding the rhombically-arranged autozooecial apertures, with the exilazooecia additionally concentrating on one preferred surface. The zooids bud from an axial zone, rather than from an axial cylinder.

Woodend Limestone

The Woodend Limestone (Brigantian), or Watchlaw Limestone,is separated from the Lamberton Limestone by a series of cross-bedded deltaic sandstones. It was only studied at "The Prior" along the Spittal section; here it is approximately two metres thick, and is a highly fossiliferous, rather muddy limestone, again dominated by *Siphonodendron* colonies. Only one bryozoan fragment was found, a rather poorly-preserved example of a probable *Fenestella frutex.*

The Prior : NU 015 505

Fenestella frutex?

Oxford Limestone (underlying marl)

At Sharper's Head, a fairly thick (two metres) band of soft green-grey marl is exposed in the cliffs. The marl contains very abundant *Siphonodendron* corals, and some crinoid remains. A sample of the marl was collected, and washed and sieved back in the laboratory; much searching yielded one specimen of *Rhabdomeson rhombifera* and a few fragments of the acanthocladiid *Penniretepora pulcherrima* (Plate 4, fig. j.). Though the bryozoans could have lived amongst the thickets, the fragmentation and scarcity of the specimens suggests that they were swept into the area.

Sharper's Head : NU 001 544

Rhabdomeson rhombifera
Penniretepora pulcherrima

Oxford Limestone

The Oxford Limestone (Brigantian) was seen *in situ* at Greenhill Rocks. Here, it comprises a horizon approximately 3.5m in thickness, made up of several posts separated by shaly partings. The different posts have varying lithologies, from polished micritic levels to sparry blocky limestones, and one shaly, fissile limestone. A fauna of rugose corals is supported, with dielasmid and *Syringothyris* brachiopods and an abundance of crinoid material. The shaly limestone yielded a moderately diverse fauna of bryozoans, though they are actually rather scarce and fairly fragmented, suggesting a certain degree of transportation. Interestingly, this horizon also yielded an abundance of *Tetrataxis* and other foraminifera.

Greenhill Rocks : NU 200 341

Rhabdomeson rhombifera
Fenestella multispinosa
Fenestella plebeia
Penniretepora flexicarinata
Diploporaria marginalis (Plate 4, fig. 1.)
Trepostome indet.

Eelwell Limestone

The Eelwell Limestone (Brigantian) is a fairly widespread deposit, and is rather thick, measuring up to seven metres in the Berwick district. It is usually divided into several posts, separated by thin shales, but the limestone itself is a fairly massive grey, hard biomicrite. At Ladies Skerrs the limestone was seen to contain abundant spiriferids and plant remains (suggesting a proximity to a shoreline) but no bryozoans. The interbedded shales yielded plant fragments but no marine fossils, suggesting the possibility of emergence, but no palaeokarstic surfaces or desiccation features were found. Two bryozoans were found in a fallen block at Bucket Rocks. Similarly, occurrences of the Eelwell Limestone along the Spittal section, and at the Tumblers near Sea Houses failed to yield any bryozoans.

The more southerly outcrops of the limestone, however, contained quite an abundance of bryozoans; both Dell Point near Beadnell, and Snook Point near Sea Houses had similar bryozoan faunas, with the most diverse components occurring in the upper, buff-coloured levels. However, a study of the bryozoan faunas from the different posts failed to reveal any consistent changes within the bryozoans through the limestones. The bed overlying the limestones at both Dell Point and Snook Point is worthy of mention; it is a relatively thin dark-grey, calcareous mudstone, packed with the brachiopods *Eomarginifera* and *Spirifer*. The persistence of this horizon over a distance of at least three kilometres suggests that it could be a storm deposit.

Bucket Rocks : NU 007 533

Rhabdomeson gracilis
Tabulipora?

Dell Point : NU 237 294

Hyphasmopora buskii
Fenestella multispinosa
Fenestella tuberculo-carinata
Fenestella plebeia
Penniretepora flexicarinata
Synocladia sp.
Tabulipora sp. (Plate 5, fig. h.)
Sulcoretepora parallela (Plate 5, fig. o.)

Snook Point : NU 227 315

Lower Post
Rhabdomeson gracilis
Fenestella bicellulata
Fenestella multispinosa
Fenestella plebeia
Polypora verrucosa (Plate 4, fig. e.)
Septopora carbonaria
Trepostome indet.
Fistulipora incrustans (Plate 5, fig. n.)

Lower-Middle Post
Rhabdomeson gracilis
Fenestella multispinosa
Penniretepora sp.
Tabulipora urii

Middle Post

Rhabdomeson gracilis
Fenestella bicellulata (Plate 3, fig. g.)
Fenestella frutex
Fenestella multispinosa
Fenestella plebeia
Penniretepora flexicarinata
Sulcoretepora parallela

Top Shales

Rhabdomeson gracilis
Fenestella bicellulata
Fenestella frutex (Plate 3, fig. h.)
Fenestella multispinosa
Penniretepora spinosa (Plate 4, fig. g.)
Trepostome indet.

The Eelwell Limestone marks the first entry of the acanthocladiid *Septopora carbonaria* in the Carboniferous of Northumberland. An additional occurrence of interest is one fragment referred to the allied genus *Synocladia*; the specimen, DP11 (Plate 5, fig. a.), is characterised by a fairly thick mainstem from which a few laterals diverge, the stem bearing three rows of apertures. The genus *Synocladia* is very rare in the British Carboniferous; one specimen has been reported from the Brigantian of the Midland Valley (Kirkby, 1880), though most of the material referred to as *Synocladia* (for example, Etheridge, 1873a; Young & Young, 1878) has subsequently been shown to belong to the genus *Septopora* (Bancroft, 1987).

One specimen of *Fenestella multispinosa* (SP^{T}8) is noteworthy in showing the meshwork growing around an obstructing brachiopod spine, with the partial development of an enclosing sheath, similar to those seen in the fenestellids of Tears Point in South Wales. Another specimen of this species (Plate 3, fig. i) was seen to have a defensive palaeocorynid spine developing from the meshwork.

The good preservation of the material in the Eelwell Limestone enabled a thin section of the trepostomes to be taken; SP6 (Plate 5, figs. f. & g.) was shown to belong to the species *Tabulipora urii* on account of possessing a fairly wide endozone region, and with six ring septa occurring in the endozone region of each zooecial chamber.

Acre Limestone

The Acre Limestone (Brigantian) is a rather thick unit, measuring approximately 5.5m in Northumberland. The limestone itself is crinoidal, though there are several shaly partings within the main unit. Outcrops of this horizon at Spittal, Snipe Point on Lindisfarne, at Beadnell, and at Cullernose Point all failed to yield any bryozoans within the limestone unit itself; however, the shaly partition within the unit at Snipe Point yielded a diverse, if not abundant bryozoan fauna. Fragmentation of the colonies suggests some degree of transport of the deposit, whose bryozoans are typically representative of moderately tranquil water conditions.

Though the Acre Limestone near Cullernose Point failed to yield any bryozoans, the overlying, iron-stained shales supported a very abundant fauna in which bryozoans are by far the commonest constituent. Trilobites, *Schellwienella* brachiopods, bivalve fragments and some crinoid remains make up the remainder of the macrofaunal population. Delicate fenestellid fans and branching *Rhabdomeson* colonies are preserved, indicating that the fauna must be *in situ*, since these delicate constituents would have been fragmented with transportation. Replacement by iron minerals has destroyed much of the detail of these bryozoans, but many of the colonies are distinctive enough to be identified to specific level. The thin branches of the *Fenestella* colonies indicates that the assemblage lived in tranquil water environments, though no direct indication on the depth of the assemblage can be gauged. However, the occurrence of *Schellwienella* listed in Ramsbottom (1978) seems to be limited to relatively shallow water settings.

Cullernose Point : NU 259 180

Rhabdomeson gracilis
Fenestella frutex
Fenestella plebeia
Fenestella polyporata (Plate 3, fig. m.)
Penniretepora spinosa
Penniretepora flexicarinata
Sulcoretepora parallela

Snipe Point : NU 126 441

Rhabdomeson rhombifera
Fenestella multispinosa
Fenestella plebeia
Polypora verrucosa
Diploporaria marginalis (Plate 4, fig. k.)
Trepostome indet.
Dyscritella miliaria (Plate 5, figs. k. and l.)

Sandbanks Limestone

The Sandbanks Limestone (Brigantian) is a rather thick unit in Northumberland, with reported thicknesses varying from 7m to 11m (Fowler, 1926; Carruthers *et al.*, 1927). It is divided into several posts separated by shaly partings. The limestone usually supports only a sparse fauna, but in places it can contain an abundance of fossil fragments.

On the island of Lindisfarne, the Sandbanks Limestone was encountered at Cove's Haven and at Keel Head. The base of the Sandbanks at Cove's Haven is marked by a calcareous shale which is crowded with bioclastic remains, crinoid columnals, echinoid spines, brachiopod débris, and bryozoan fragments constitute much of the fauna. The extensive faunal fragmentation suggests that this horizon has been subjected to some current activity. A few fragmentary bryozoans were collected from the main part of the Sandbanks Limestone at Keel Head; though poorly-preserved, their parameters suggested that they are fragments of *Fenestella multispinosa.*

Examples of the Sandbanks Limestone baked by doleritic intrusions were seen near Dunstanburgh Castle and at Cullernose Point. Rhabdomesids dominated the bryozoans in both localities, though some fenestellid fragments were found. At Cullernose Point, the fauna was concentrated in "pockets" on the bedding planes, implying a degree of current sorting of the material.

The most diverse fauna within the Sandbanks Limestone was found at Lady's Hole on the Beadnell section, from the shale partings. As in the other localities, the fauna is fragmented and dominated by rhabdomesids; however, three species of rhabdomesid were identified, together with other bryozoan remains and many brachiopod fragments. The abundance of rhabdomesids suggests that the original fauna lived in a tranquil water setting.

Cove's Haven : NU 130 438

Fenestella plebeia
Trepostome indet.

Keel Head : NU 133 438

Fenestella multispinosa

Dunstanburgh Castle : NU 255 222

Rhabdomeson gracilis
Fenestella multispinosa

Cullernose Point : NU 260 187

Rhabdomeson gracilis
Fenestella multispinosa
Fenestella plebeia

Lady's Hole : NU 238 288

Rhabdomeson gracilis
Rhabdomeson rhombifera
Rhombopora bancrofti
Rhombopora incrassata
Polyfenestella fenestelliformis
Trepostome indet.
Sulcoretepora parallela

Some of the specimens of *Rhabdomeson gracilis* from Dunstanburgh Castle are rather unusual. Though they possess the axial cylinder characteristic of the genus, and parameters consistent with the species *R. gracilis*, they sometimes have small stylets around the autozooecial apertures in addition to the large stylet that is invariably present at the distal end of the aperture (a single-stylet bearing variety is illustrated in Plate 3, fig. d.). Additionally, specimens of the species *Rhombopora* *incrassata* (Plate 3, figs. b. and c.) are present; these forms also have small stylets on the interaperture walls, but have much larger apertures than *Rhabdomeson gracilis*.

An unusual bryozoan from Lady's Hole is a fenestellid referable to the genus *Polyfenestella* (Bancroft, 1986a); the specimen (LH4; Plate 4, fig. f.) is the reverse surface of a rather open meshwork. The branches bear randomly-arranged type B-zooecia (Bancroft, 1986a) which are small (0.08mm in diameter), circular, and apparently sealed by a calcite plate. The reverse branches are ornamented by longitudinal striations. *Polyfenestella* is distinguished from *Ignotifenestella* (as found at Tears Point, South Wales) in having randomly-arranged cyclozooecia, and from the acanthocladiid *Septopora* in possessing sterile dissepiments. The obverse surface of the dissepiments could not be seen on specimen LH4, but the widths (0.18 - 0.28mm) are consistent with dissepiment widths recorded by Bancroft, compared with lateral branch thicknesses of up to 0.34mm for *Septopora*, recorded in Bancroft (1987a). Further, flaring at the branch junctions and lack of "chevroning" of the structures suggests they are dissepiments rather than laterals. Fenestrule lengths of 0.90 - 1.60mm and widths of 0.60 - 0.90mm agree with the parameters of Bancroft for *Polyfenestella fenestelliformis* (Young, 1881).

Lickar Limestone

The Lickar Limestone (Pendleian) is a relatively thin unit, measuring 1.35m at Howick, comprising a 25cm-thick limestone, and a series of dark, fossiliferous shales. The marine horizon actually overlies a seat earth, with the first bryozoans occurring in lenses approximately 25cm above this horizon. The succession at Howick is shown in the accompanying graphic log. Bryozoans were mainly recovered from the shales underlying the Lickar Limestone, but one specimen of *Septopora* was found in the reddened limestone itself, and some fenestellids were recovered from the limestone at the Old Boat House. The bryozoans in the shale are mainly poorly-preserved, since iron precipitation has altered them; however, they are still distinctive enough to be identified to species level, and stouter bryozoans such as *Dyscritella* are actually quite well-preserved. Many large sheets of *Fenestella* are present, and the limited fragmentation suggests that the deposit is more-or-less *in situ*.

The occurrence of the shales and limestone over a seat earth suggests that the Lickar Limestone formed in relatively shallow water after the drowning of a deltaic system, or a cessation in terrigenous input; this is supported by the high mica content in the shales, which suggests proximity to a terrestrial source, rather than a deep shelf setting. Marine influence seems to have gradually declined over the area, marked by the onset of ironstone nodule formation as a prelude to delta progradation.

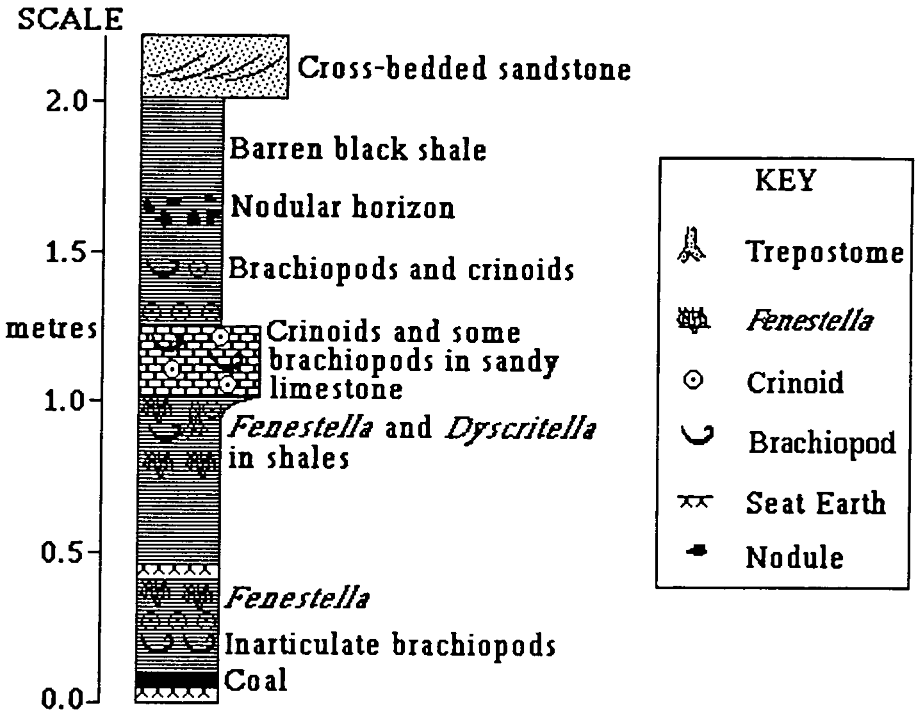


Fig. 7.3. Graphic log of the Lickar Limestone at Howick

Old Boat House : NU 263 169

Fenestella plebeia
Septopora carbonaria (Plate 5, fig. b.)

Howick : NU 262 174

Rhabdomeson gracilis
Fenestella multispinosa
Fenestella plebeia
Septopora carbonaria
Trepostome indet.
Dyscritella sp.

Ironscars Limestone

The Ironscars Limestone (Pendleian) was studied in Sugar Sands Bay, between Howick and Longhoughton. The limestone itself is relatively thin, measuring only

40cm in thickness, and is rather micaceous, suggesting some terrigenous input into the area. A very diverse bryozoan fauna was collected from the weathering bedding planes, with fifteen distinct taxa being recognised. The high diversity, and the observation that many large, relatively uncrushed sheet-like fenestellid fans are preserved, suggests that the fauna was buried *in situ.* Additional components of the fauna include trilobites, goniatites, productid and *Brachythyris* brachiopods, and crinoidal débris. The bryozoans are usually poorly-preserved, but a few satisfactory acetate peels were made of some specimens. In places, the bryozoans have been selectively preserved in pyrite, which though destroying the detailed morphology does give a reasonable mould of the colony.

The shales overlying the Ironscars Limestone also contain some bryozoans, which can be moderately-well preserved, and are associated with the inarticulate brachiopod *Orbiculoidea.*

Sugar Sands Bay : NU 258 163

Main Limestone

Rhabdomeson gracilis
Rhombopora incrassata
Hyphasmopora buskii
Fenestella frutex?
Fenestella multispinosa (Plate 3, fig. j.)
Fenestella tuberculo-carinata (Plate 3, figs. k. and l.)
Fenestella plebeia
Polypora hexagonaria
Penniretepora sp.
Septopora carbonaria
Tabulipora sp.
Stenodiscus tumida (Plate 5, figs. i. and j.)
Dyscritella sp.
Fistulipora incrustans
Eridopora cf. *beilensis*

Overlying Shales

Fenestella frutex
Fenestella multispinosa
Fenestella tuberculo-carinata
Septopora carbonaria

The Ironscars Limestone provides the only recorded occurrence of the fenestellid *Polypora hexagonaria* sp. nov.. This taxon is discussed in more detail at the end of this section.

Another noteworthy taxon recorded at this horizon is the cystoporate *Eridopora* cf. *beilensis* (Plate 5, fig. m.). This rare North American bryozoan is characterised by the hood-like lunaria which partially cover the autozooecial apertures, and has occurrences at Ashfell Edge and Hurst (Bancroft, 1984; 1986f) and possibly in the Midland Valley and North Wales (this study). The relatively small autozooecial apertures distinguish this taxon from the other species of *Eridopora* recorded in Britain, *Eridopora macrostomata.*

Several fragments of the acanthocladiid *Septopora carbonaria* were collected (Plate 5, figs. c. to e.); one specimen is particularly important since it shows a cone-shaped colony, which possesses apertures opening on the inside of the cone (Plate 5, fig. e.). This is in contrast to most colonies of the genus *Fenestella* (Cumings, 1904; Tavener-Smith, 1969) and many other fenestellidae in which the apertures open on the outside of the cone. However, though this distinction may be of taxonomic importance, a fauna of *Fenestella multispinosa* from Three Cliffs Bay in South Wales (this study) showed some colonies with apertures developed on the inside of the cone (the implication of this arrangement of feeding autozooids is discussed in Chapter 13). Thus, disposition of apertures cannot be used confidently for even specific level taxonomic distinctions.

One specimen of the rhabdomesid *Hyphasmopora* was found which was encrusted by another rhabdomesid, *Rhombopora incrassata.* Thus, there is some indication of competition for suitable substrates for larval settlement and attachment. Though brachiopod spines are a common component in the fauna, no encrusted spines were observed, in contrast to a similarly diverse fauna from Redesdale (Billing, 1991). However, a trepostome-encrusted crinoid stem was discovered. The stem was clearly encrusted after death and disarticulation of the crinoid, since only one side was encrusted, the trepostome overlaps onto the surrounding sediment, and the bryozoan sheet extends over and around a broken tip of the stem.

Systematic Palaeontology of *Polypora hexagonaria* sp. nov.

Classification :

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order FENESTRATA Elias & Condra, 1957
Family POLYPORIDAE Vine, 1883
Genus POLYPORA McCoy, 1844

Diagnosis (Emended by Bancroft, 1985a) : "Polyporid with zoaria forming planar, foliaceous or conical reticulate expansions of branches connected by sterile dissepiments. Branches bear three or more rows of autozooecia; obverse surfaces are non-carinate, usually smooth or with low longitudinal ridges separating rows of autozooecial apertures and may bear nodes. Reverse surfaces may be smooth, granular, longitudinally striated or pustulose. Ovicells and secondary nanozooecia may occur."

Type species : *Polypora dendroides* McCoy, 1844
Stratigraphical range : Ordovician to Permian

Polypora hexagonaria sp. nov.
Plate 4, figs. a. to d. ; Figs. 7.4 and 7.5

Holotype : SSB10 (Plate 4, fig. c.; Fig. 7.4b), Ironscars Limestone (Upper Pendleian), Sugar Sands Bay, near Howick, Northumberland (NU 258 163).
Paratype : SSB13 (Plate 4, fig. a.), from the same horizon and locality as the holotype.
Other Material : Several fragments from the same horizon and locality as the holotype. Specimens SSB1 to SSB21. Colony fragments in varying states of preservation of which SSB12, SSB14b, SSB15 and SSB21 show obverse surface detail. Specimens SSB16 to SSB18 are oblique tangential sections through the meshwork.

Diagnosis : *Polypora* with a very high-angle (flattened) conical zoarium. Branches are straight to regularly sinuous, and are robust. In distal portions of the colony, branch sinuosity is very regular, and the alternate disposition of the dissepiments gives the meshwork a hexagonal appearance. Obverse surfaces are gently rounded, and nodes are absent. Autozooecial apertures are of moderate diameter, circular, and are closely spaced, arranged in quincunx, in four to six longitudinal rows. Dissepiments are stout, virtually flush with the crests of branches on both the obverse and reverse surfaces, and flare very little at the branch junctions. Fenestrules are moderately large, and are sub-rectangular to sub-hexagonal in outline.

Derivation of name : The species is named on account of the development of a hexagonal meshwork in distal portions of the colony.

Zoarial parameters :

Polypora hexagonaria					
	N	n	σ	range	x
BW	9	78	0.0858	0.604 - 0.913	0.728
AD	2	34	0.0090	0.140 - 0.158	0.149
ID	5	84	0.0127	0.261 - 0.294	0.276
FL	12	116	0.0872	1.700 - 2.038	1.891
FW	13	129	0.1316	1.130 - 1.640	1.336
DW	9	89	0.0653	0.440 - 0.651	0.530

Description : The exact shape of the zoarium is uncertain; several large fragments have been found, the largest single fragment measuring 15mm by 15mm, indicating little curvature of the meshwork, and low angles of branch divergence. A compressed and slightly scattered series of broken colony fragments on specimen SSB21 indicate that the colony may have a very high-angle conical zoarium, with a radius of at least 55mm. Apertures open on the inside of the cone, as is found in all species of *Polypora* so far described.

Branches are very broad, averaging 0.73mm in width, and are straight to gently sinuous. In the distal portions of the colony, the sinuosity may become very regular, and dissepiments placed on alternate bends in the branches; this disposition gives the meshwork a hexagonal appearance, and is shown very clearly on specimen SSB13 (Plate 4, fig. a.). Obverse branch surfaces are gently curved, but the lateral margins curve away quite sharply. Reverse surfaces are usually smooth, though weathered patches on specimens SSB11 and SSB14a revealed a series of closely-spaced, prominent longitudinal striations on a flat branch surface. The reverse surfaces are usually secondarily calcified, which not only obscures the striations but also elevates the crests of the branches into a broad ridge from which the lateral branch margins slope away at a fairly steep angle. Branch cross sections may therefore vary from flattened oval to sub-triangular, depending on the extent of secondary calcification.

Apertures are moderately large, circular in outline, and with possible faint peristomes (seen only on specimen SSB10; fig. 7.4b). They are arranged in quincunx (fig. 7.4a), as is common in the genus *Polypora*, in four to six longitudinal rows on the obverse surface of each branch (see fig 7.5),and there are six to seven apertures per fenestrule. Apertures are closely spaced, and alternate rows actually overlap slightly. The rows are separated by fairly prominent, slightly raised striations (see fig. 7.4b, and fig. 7.5) which, because of the close spacing of alternate rows, weave sinuously between the apertures. Before branch bifurcation, up to ten rows of apertures may develop, and the branch width increase to 1.3mm. Bifurcations have a high-angle "tuning fork" shape, with the branches increasing in width for up to two fenestrule lengths prior to bifurcation.

Dissepiments are variable in length, but are comparatively short and stout, slightly less thick than the branches. They are slightly depressed or flush with the crests of branches on both the obverse and reverse branch surfaces. Dissepiments are well-rounded on the obverse surfaces, and, like the branches, vary from being flat to crested on the reverse surfaces. Before secondary calcification, dissepiments are ornamented by faint striations. They flare very little at their junctions with the branches, and are thus bar-like.

Fenestrules are moderately large, and range from sub-rectangular to sub-hexagonal in outline. They are relatively squat, having a length only one-and-a-half to two times their width; the width is equal to, or slightly less than, the width of the branches.

Zooecial chamber bases are initially rhombic, becoming hexagonal, in the centre of branches (see Plate 4, fig. d.), and lateral chambers have a hemi-hexagonal shape.

Discussion : Six species of *Polypora* have previously been identified from the Carboniferous of Britain: *P. dendroides* McCoy, 1844; *P. verrucosa* McCoy, 1844; *P. marginata* McCoy 1844; *P. tuberculata* Prout, 1859; *P. stenostoma* Tavener-Smith, 1971; *P. binodus* Bancroft, 1985a. *P. hexagonaria* is distinct from these forms, and, additionally, does not compare with any of the species of *Polypora* described by Ulrich (1890). Comparisons with five of these species (no parametric data is available for *P. tuberculata*) using the t-test analysis are as follows :

		t-test Scores						
SOURCE	*Polypora*	BW	AD	ID	FL	FW	DW	Av.
Bancroft, '84	*P. dendroides*	0.2493	0.0039	0.0000	0.5484	0.1079	0.0060	0.1526
Tavener-Smith, '73	*P. dendroides*	0.0365	?	0.0000	0.0001	0.0617	0.3193	0.0835
Bancroft, '84	*P. verrucosa*	0.0879	0.0116	0.0000	0.0000	0.0245	0.0001	0.0207
Tavener-Smith, '73	*P. verrucosa*	0.0012	0.0004	0.0000	0.0000	0.0000	0.0000	0.0003
Bancroft, '84	*P. marginata*	0.1268	0.0007	0.0445	0.0001	0.0052	0.0004	0.0296
Bancroft, '85a	*P. binodus*	0.0034	0.0222	0.0023	0.0000	0.0000	0.0000	0.0046
Tavener-Smith, '71	*P. stenostoma*	0.0000	0.0000	0.0545	0.6025	0.0000	0.0000	0.1095

Of these five species, the meshwork of *P. dendroides*, as measured by Bancroft (1984) has a relatively close comparison with *P. hexagonaria.* However, *P. hexagonaria* has smaller apertures, which are additionally more closely-spaced. *P. dendroides* is a rather distinctive species, characterised by a planar, fan-shaped colony with frequently-bifurcating branches, and only three to four rows of apertures on each branch. Apertures are also surrounded by 15 to 16 small pustules (Miller, 1963; Bancroft, 1984) which thin sections have shown to be absent in *P. hexagonaria.* Further, *P. dendroides* has rhombic central autozooecial chamber bases, in common with many species of *Polypora* (Bancroft, 1984) whereas those of *P. hexagonaria* become hexagonal after an initial rhombic stage (Plate 4, fig. d.).

The zoarial form of *P. hexagonaria,* a very high-angle conical colony, is similar to that of *P. binodus.* In all other respects, though, the two species are very different, *P. binodus* having smaller meshwork parameters, larger apertures, and a double row of nodes.

Polypora tuberculata has some resemblance to *P. hexagonaria* in bearing striations between the apertures, having fenestrules twice as long as they are wide, and possessing non-flaring, slightly depressed dissepiments. However, branches are illustrated as being rather rounded (Prout, 1859), they bear a central row of nodes, and the fenestrules are smaller, averaging 0.83mm in width. Further, *P. tuberculata* has only five apertures per fenestrule (*P. hexagonaria* has six to seven) which have thin, raised peristomes.

Polypora verrucosa, like *P. hexagonaria,* has sinuous striations between longitudinal aperture rows (Tavener-Smith, 1973a), but has much longer fenestrules, thin dissepiments, and only four rows of apertures per branch. The absence of central nodes on the obverse surface is a further character which *P. verrucosa* shares with *P. hexagonaria.* Miller (1963) cited lack of nodes to query the placing of *P. verrucosa* within the genus *Polypora,* in the same way that fenestellids lacking nodes are placed in the genus *Levifenestella* Miller, 1961, rather than *Fenestella.* However, the importance of branch nodes for taxonomic distinction is questionable (Tavener-Smith, 1973a, p.482; Bancroft, 1984, p.241) since nodal disposition can be very variable. Bancroft (1985) erected the species *P. binodus* for a specimen which possessed two rows of nodes. However, Prout (1859) described the nodes on *P. tuberculata* and noted that in some places nodes were absent on a branch, and in other places a double row of nodes developed. Thus, the lack of nodes on *P. hexagonaria* should not preclude the species from being placed within the genus *Polypora.*

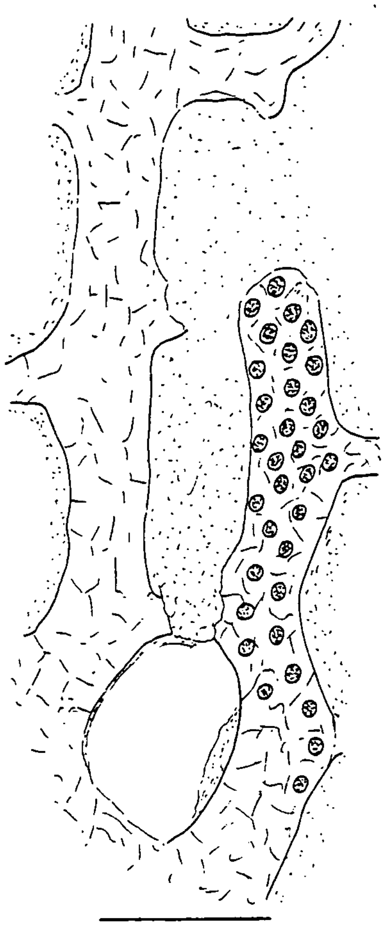
Sugar Sands Limestone

The Sugar Sands Limestone (Pendleian) was the youngest limestone encountered on the Northumberland Coast which contained a bryozoan fauna. The limestone is quite thick (approximately three metres), and divided into several posts. Though bryozoans are not common in this horizon, fenestrates and one trepostome were found in this dark-grey, micritic, bioclastic limestone. Large productids are common, and much of the bioclastic débris is composed of brachiopod spines.

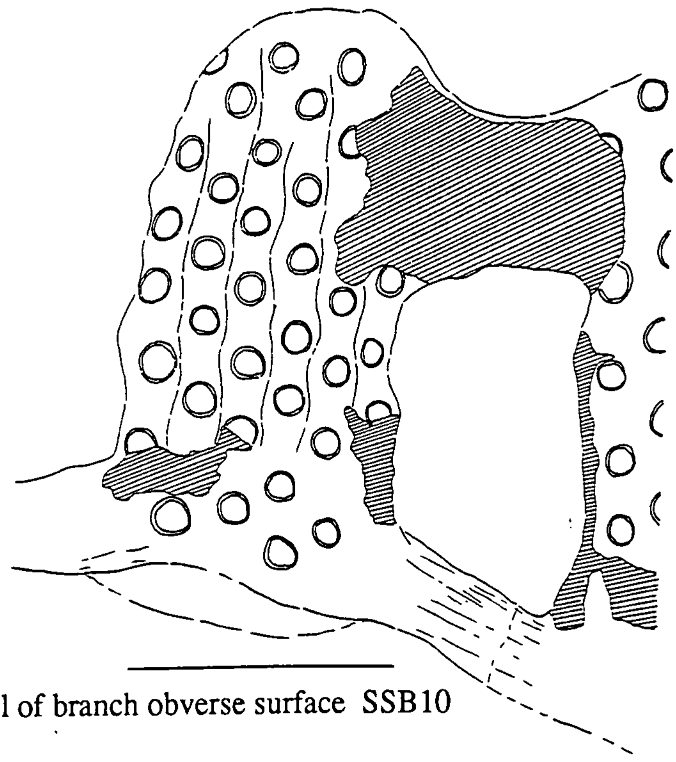
Sugar Sands Bay : NU 260 161

Fenestella frutex
Fenestella plebeia
Septopora?
Trepostome indet.

The specimen of a possible *Septopora* is a moderately-large colony fragment showing the reverse surface. Though the colony at first glance has the appearance of *Fenestella,* and there are no obvious cyclozooecia, there is some "chevroning" of the dissepiment-like structures, suggesting that they are zooid-bearing lateral branches. This is augmented by the observation that the meshwork branches out not by branch bifurcation (as in *Fenestella*), but by fusion of the lateral branches to give a new main branch. These features are very typical of the acanthocladiids, and suggest that specimen SSL1 is actually a *Septopora.*

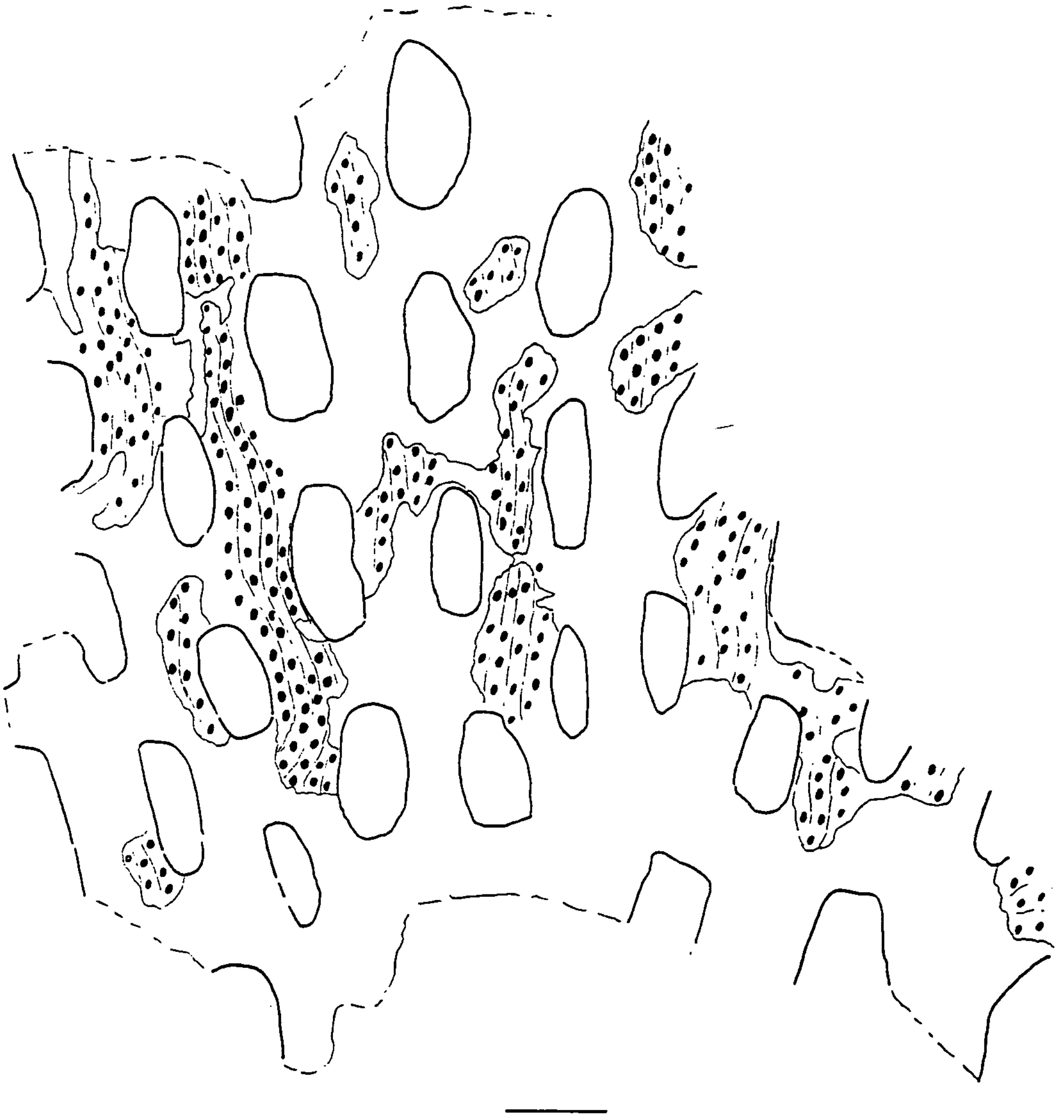


a. Shallow tangential section SSB16



b. Detail of branch obverse surface SSB10

Fig. 7.4. *Polypora hexagonaria* from the Ironscars Limestone



Weathered obverse surface of mid-proximal colony fragment SSB12

Fig. 7.5. *Polypora hexagonaria* from the Ironscars Limestone

Distribution of Bryozoans from the Northumberland Coast

The bryozoan fauna from Northumberland is actually quite diverse, with 26 distinct taxa being recorded. However, excessive weathering of several limestone horizons means that some may have an under-representative bryozoan association; the Woodend Limestone, for instance, has only one species described from it. An additional problem in drawing up true diversity range charts is that local facies variation may have a bearing on the fauna recorded; the Eelwell Limestone has a much more diverse fauna in the southern outcrops than in the northern ones.

The oldest Carboniferous bryozoans from the Northumberland Coast are found in the Dun Limestone, of Asbian age. Though this is the first appearance, the fauna is moderately diverse, with twelve taxa being located at this horizon.

A diversity peak is seen in the Middle Brigantian, with fifteen taxa in the Eelwell Limestone. The Middle Brigantian Sandbanks, Acre and Eelwell Limestones seem to mark an episode of faunal turnover; eleven species have their last appearances, and ten have their first, though six of these have appearances limited to this stage. The turnover is only of local extent, since of the eleven species which disappear, ten of them are known to have ranges into the British Arnsbergian elsewhere. The six species limited to the Middle Brigantian include the elongate-fenestruled, quiet-water dwelling forms *Fenestella polyporata, Polyfenestella fenestelliformis, Polypora verrucosa,* and the delicate-colonied forms *Fenestella bicellulata* and *Penniretepora spinosa.* It is possible that this period of time represents the deepest-water facies of the area, though non-marine plant-bearing levels were found within the northern outcrops of the Eelwell Limestone.

A final diversity peak occurs in the Middle Pendleian Ironscars Limestone, where again fifteen bryozoan taxa are recorded. Though the fauna is preserved *in situ* it is probably representative of a shallower-water assemblage than the Middle Brigantian levels, since not only are large mica flecks found (indicating proximity to source), but the delicate-colonied fenestrates and acanthocladiids are absent. However, the stouter rhabdomesids and trepostomes are rather abundant, and a thick-branched taxon, *Polypora hexagonaria* is also found.

Of the 26 species recorded from the Northumberland coast, only six occur throughout in rocks of Asbian, Brigantian, and Pendleian age. As is seen in other areas, especially in South Wales, the most ubiquitous species are *Fenestella multispinosa* and *Fenestella plebeia,* though *Rhabdomeson gracilis* has a constant occurrence from its appearance in the Brigantian, and *Fenestella frutex* is moderately widespread.

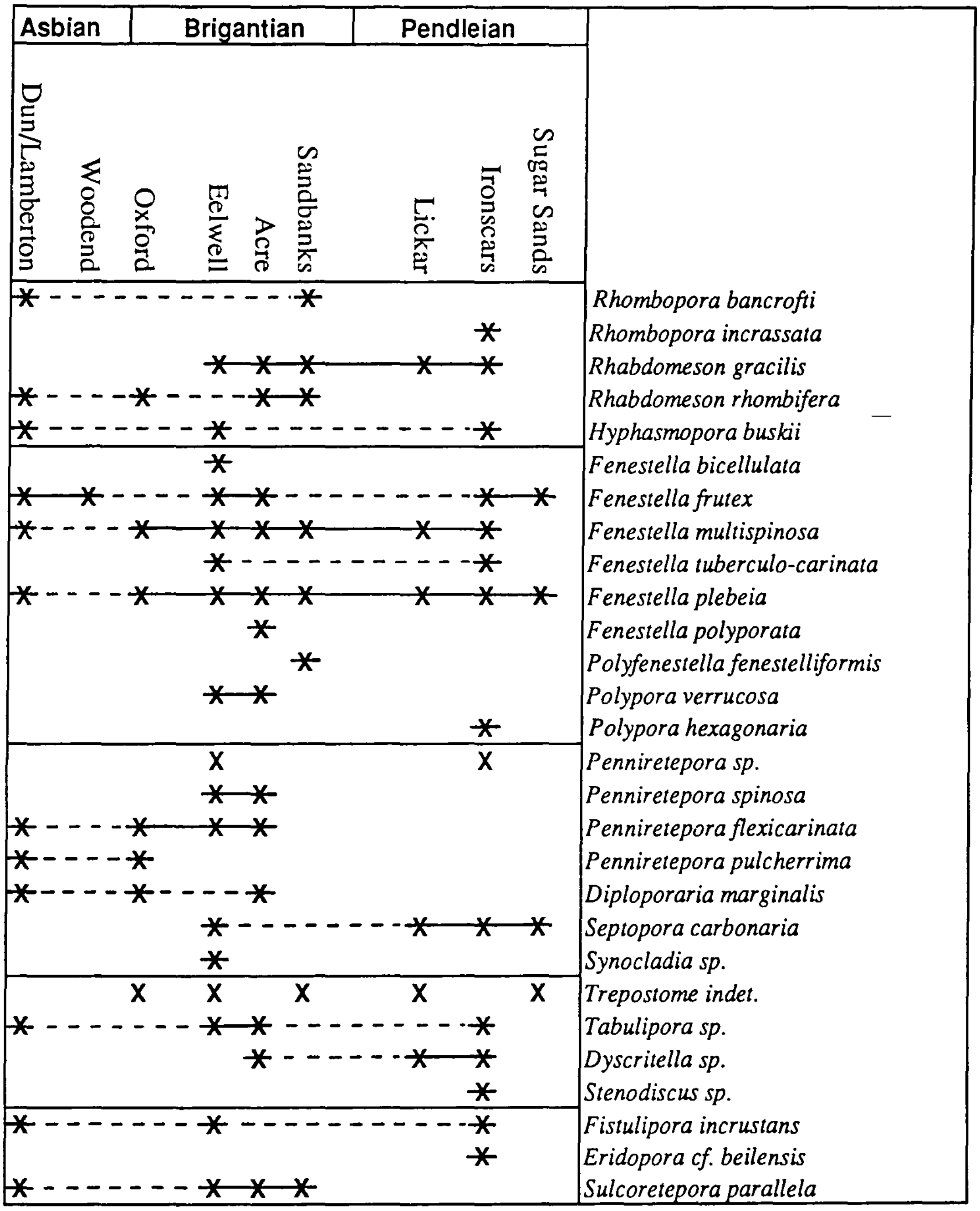
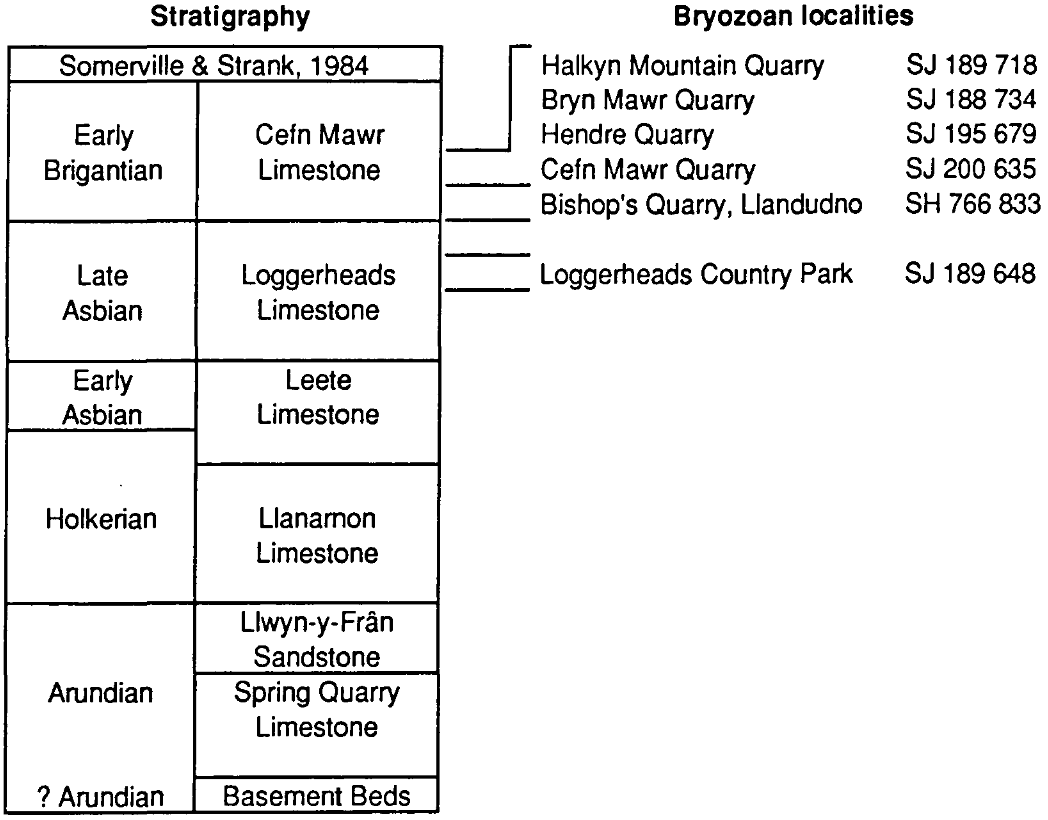


Fig. 7.6. Stratigraphical ranges of bryozoans from the Northumberland Coast

CHAPTER 8 : NORTH WALES

Stratigraphy and Palaeogeographical Setting

The outcrops of Carboniferous strata in North Wales formed on a shelf area bordering the northern flank of St. George's Land (see fig. 1.4). There appears to have been very little terrigenous run-off into the area, and thick, relatively-pure limestones were able to develop on the carbonate-platform, above a sequence of conglomeratic and sandy Basement Beds. Marine sedimentation was originally thought to have commenced in the Asbian (George *et al.*, 1976), but Somerville and Strank (1984) discovered Arundian and Holkerian micro- and macro-fossils in the former Leete Limestone (Somerville, 1979a). The revised stratigraphy of Somerville and Strank (1984) is given in fig. 8.1, with the stratigraphical positions of the localities visited during the fieldwork for this project :



Stratigraphy

Somerville & Strank, 1984	
Early Brigantian	Cefn Mawr Limestone
Late Asbian	Loggerheads Limestone
Early Asbian	Leete Limestone
Holkerian	Llanamon Limestone
Arundian	Llwyn-y-Frân Sandstone
	Spring Quarry Limestone
? Arundian	Basement Beds

Bryozoan localities

Halkyn Mountain Quarry	SJ 189 718
Bryn Mawr Quarry	SJ 188 734
Hendre Quarry	SJ 195 679
Cefn Mawr Quarry	SJ 200 635
Bishop's Quarry, Llandudno	SH 766 833
Loggerheads Country Park	SJ 189 648

Fig. 8.1. Stratigraphy of North Wales

Somerville and Strank (*ibid.*) believe that the Arundian-Holkerian transgression was confined to an embayment bounded by reactivated faults running along the Menai Straits (the Dinorwic Fault) and through the Bala district (the Bryneglwys Fault). A later Asbian transgression marked the onset of wider-spread marine conditions across the North Wales area. Relative sea level was not constant, and Somerville (1979a, b and c) has recognised transgressive/regressive cycles within the Asbian and Brigantian carbonates. Several of these cycles appear to have been emergent, as indicated by the development of palaeosols and palaeokarstic surfaces. However, very little siliciclastic sediment was introduced into the basin, and most of the carbonates in North Wales were deposited in rather shallow, clear water. A representative cycle, redrawn from Somerville (1979a) is shown below:

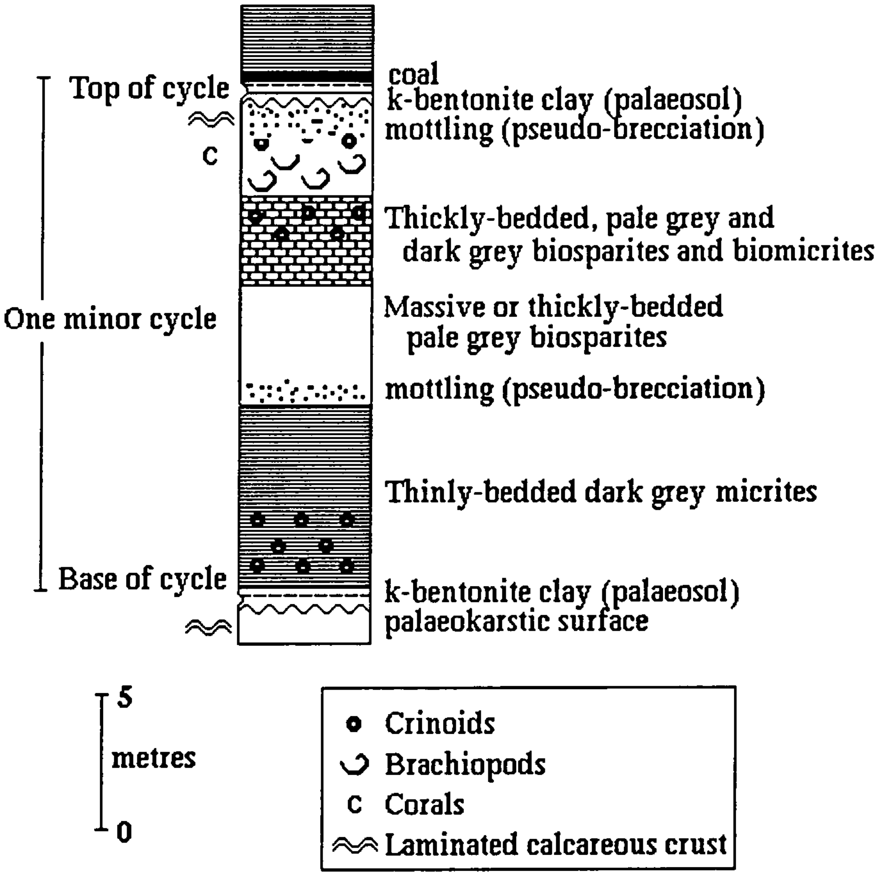


Fig. 8.2. Lower Carboniferous sedimentary cycle

The facies and associated bryozoan faunas from Hendre Quarry and Cefn Mawr Quarry, where the sequences have been logged by Somerville (1979a), can be analysed in terms of their relative palaeodepths, inferred from this cyclicity.

Somerville and Strank, basing their maps on Anderton *et al.* (1979), illustrate the North Wales region as lying in a partially enclosed basin within the southern Laurasian continental shelf, extending eastward to the Craven Basin, northward to the Isle of Man, and westward to central Ireland. Dinantian outcrops are primarily confined to the shallow margins of this basin. The good marine communications

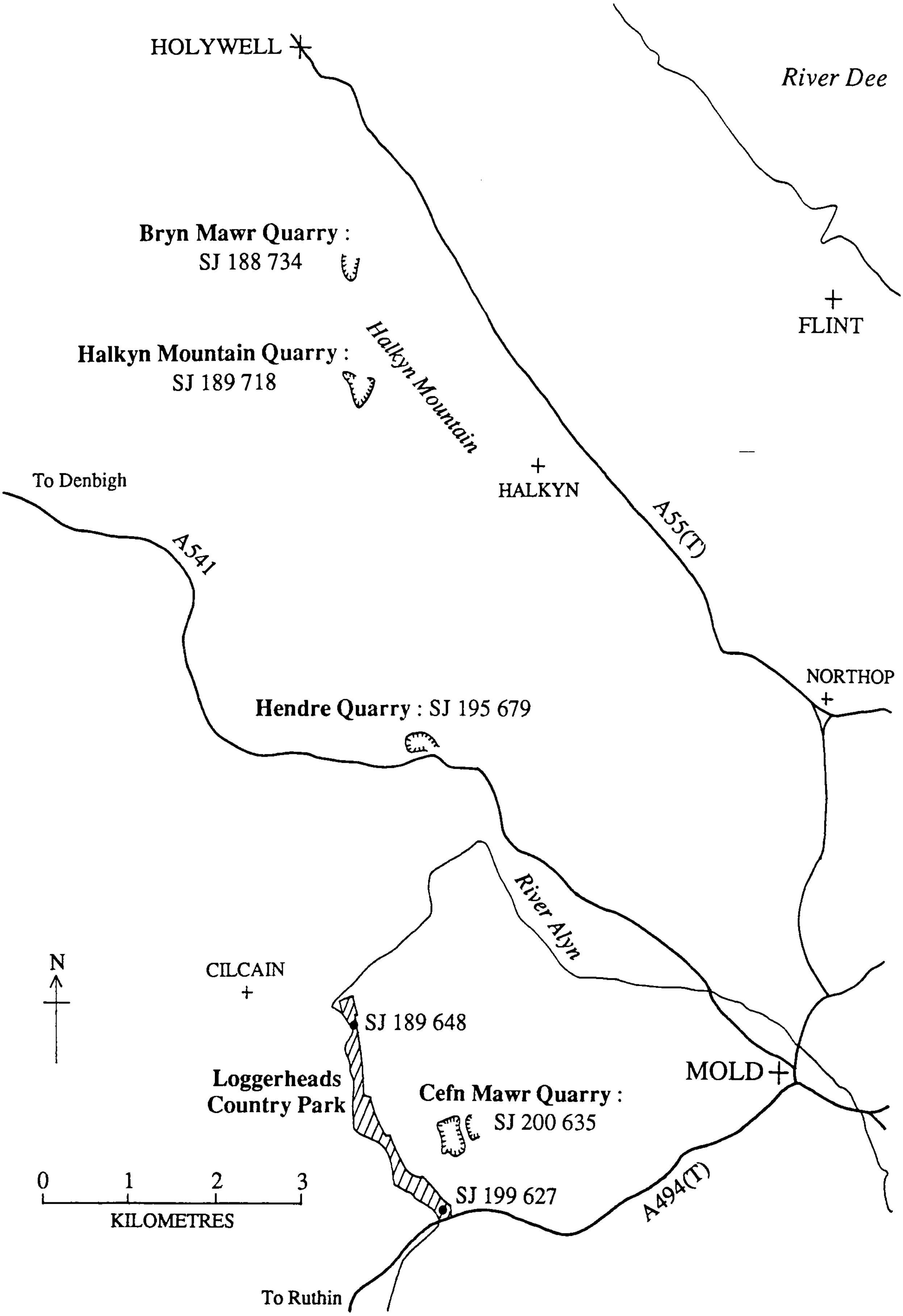


Fig. 8.3. Bryozoan localities in North Wales

Loggerheads	Bishop's Quarry	Cefn Mawr Quarry	Hendre Quarry	Bryn Mawr Quarry	Halkyn Quarry	
				x		*Rhombopora bancrofti*
	x		x	x		*Rhombopora incrassata*
			x	x	x	*Rhabdomeson gracilis*
	x					*Rhabdomeson rhombifera*
			x	x		*Fenestella bicellulata*
	x		x	x		*Fenestella frutex*
x			x	x	x	*Fenestella multispinosa*
	x	x	x	x	x	*Fenestella plebeia*
	x	x		x	x	*Fenestella polyporata*
x						*Hemitrypa hibernica*
			x	x		*Polypora verrucosa*
	x		x	x		*Polypora dendroides*
			x	x		*Penniretepora spinosa*
	x		x	x	x	*Penniretepora flexicarinata*
		x			x	*Penniretepora pulcherrima*
	x					*Penniretepora laxa*
	x			x		*Penniretepora cf. grandis*
	x					*Diploporaria marginalis*
		x				*Septopora cf. carbonaria*
		x		x		*Baculopora*
		x	x	x		*Tabulipora sp. indet.*
			x	x		*Tabulipora urii*
x		x				*Stenodiscus tumida*
		x	x	x		*Fistulipora incrustans*
		x				*Eridopora beilensis*
Asbian	Brigantian					

Fig. 8.4. Bryozoan occurrences in North Wales

between North Wales, the Pennines region, and Central Ireland may account for the high degree of faunal similarity between the three areas, discussed in the Distribution chapter.

Despite their scarcity in published literature relating to the area, bryozoans are actually fairly abundant in North Wales. A bryozoan build-up, possibly analogous to the Waulsortian mud mounds, has been recorded from the Llandudno area (R.A.H. Nichols, 1965; Bancroft *et al.* 1988; Wyse-Jackson *et al.* 1991), and a three-phase ecological succession has been established, representing the topographical increase of the mound into more energetic environments. Such a build-up has not been recorded in the platform carbonates encountered in the quarries visited during this study; these mudmounds are recorded in several localities within the Asbian strata of North Wales (Bancroft *et al.*, 1988, fig. 8.), but are restricted to the distal edges of the shelf margins, at the boundary with the deeper Irish Sea basinal deposits.

The localities in the Clwydian mountain range which have been visited during fieldwork for this study are shown in fig. 8.3. An additional visit was made to the Brigantian rocks of Bishop's Quarry on the Great Orme, Llandudno. A diverse bryozoan fauna was recorded, with some twenty three species occurring (summarised in fig. 8.4), in a variety of shallow-water carbonate facies. Representative bryozoans from North Wales are illustrated in Plates 6 to 9.

The lithofacies for each locality are discussed in the following pages, with a list of the associated bryozoans and a discussion of the more important aspects of the fauna.

Loggerheads Country Park

Grid reference : SJ 200 635 (bottom) to SJ 189 648 (top)

Loggerheads Country Park is set along a prominent escarpment of the Upper Asbian Loggerheads Limestone (formerly the Middle White Limestone), cut by the River Alyn. The limestone sequence comprises a series of thick, poorly-bedded, pale grey biosparites, and at Loggerheads reaches its maximum thickness of 170m (Somerville & Strank, 1984). Though the units are massive, Somerville & Strank recorded the presence of six widespread cyclothem emergence horizons within the Loggerheads Limestone; these cyclothem units have also been recorded in the Asbian limestones of Llangollen (Somerville, 1979b; 1979c). The presence of emergence horizons, combined with the lithologies of cross-bedded crinoidal biosparrudites, and well-sorted biopelsparites (Somerville & Strank, 1984), suggests that the limestones formed in relatively shallow, nearshore waters in a moderately high energy environment.

The macrofauna is actually rather sparse, but at the far end of the park (grid reference SJ 189 648), towards the top of the unit, large strophomenid brachiopods are quite common, especially the chonetid *Davidsonia llangollensis* and the productid *Linoprotonia hemisphærica.* Corals, though rare, do occur, and Somerville (1979a) cites *Dibunophyllum bourtonense*, and *Lithostrotion junceum*, amongst others. Similarly, though bryozoans are rare, they are present, and the following forms were recorded :

Fenestella multispinosa
Hemitrypa hibernica
Stenodiscus sp.

Of these, the trepostome *Stenodiscus* is the commonest, occurring in the lowermost levels of the Loggerheads Limestone (grid reference SJ 199 627). The species is recognised by a cylindrical, moderately broad colony form (up to 1mm in diameter). Apertures are small (0.08mm in diameter) and quite widely-spaced, and exilazooecia are rare. Most diagnostically, acetate peels (LLG1, Plate 9, figs. f. and g.) revealed that imperforate diaphragms are present in the relatively narrow exozone, a feature characteristic of *Stenodiscus.* The small apertures, narrow exozone and scarcity of exilazooecia suggest that the material is not referable to *Stenodiscus tumida* as described by Bancroft (1984), but a comparison with the material and additional species described by Lee (1912) would be needed before making a new species.

A fairly large fragment of the fenestellid *Hemitrypa hibernica* was also found (LLG2, Plate 8, fig. h.); the fragment was of the distinctive hexagonal mesh which is formed as a protective shield above the obverse surface of the colony fronds (Bancroft, 1986e; Cole, 1893; Miller, 1962b). The fragment appears to have belonged to a planar colony, rather than a low-angle conical colony. This distinction supports the observation of Bancroft (1986e) that the planar colonies of *Hemitrypa hibernica* are commonest in shallow-water, higher-energy limestones.

Bishop's Quarry, Llandudno

Grid reference : SH 766 833

Bishop's Quarry was excavated on the summit of the Great Orme's Head, Llandudno, and provides an outcrop of the Lower Brigantian Bishop's Quarry beds. The geology of the area was described in some detail by Smyth (1925), and George *et*

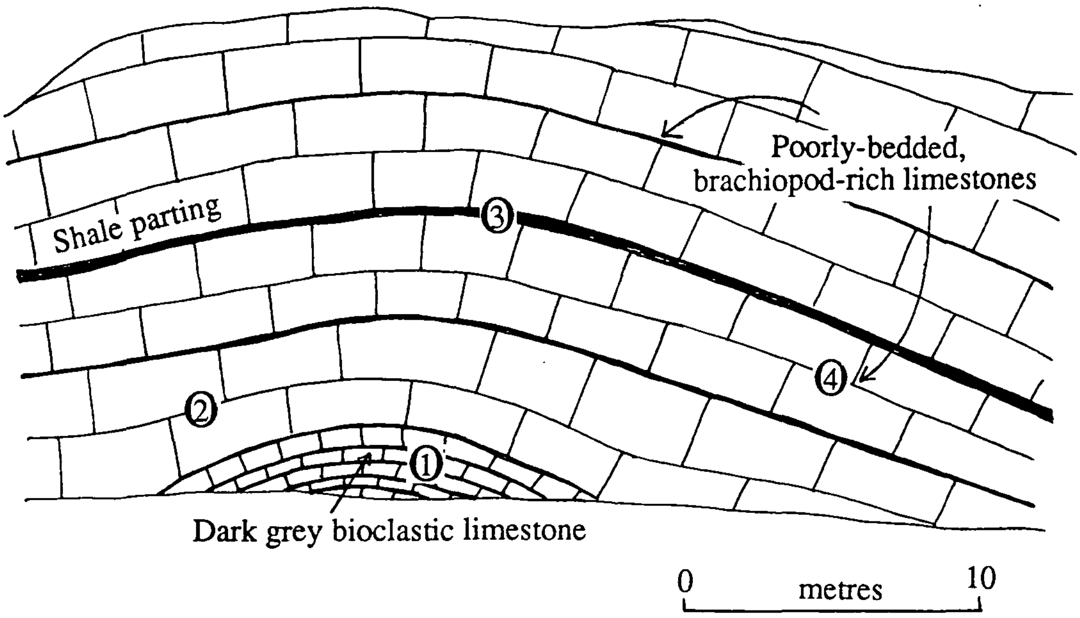


Fig. 8.5. Fieldsketch of Bishop's Quarry

al. (1976) placed the Asbian/Brigantian boundary some ten metres below the base of the Bishop's Quarry Beds.

The Bishop's Quarry Beds comprise a series of dark grey limestones with several thin shale bands, and the succession as seen in the quarry is shown in figure 8.5. Bryozoans were collected from four facies within the succession:

Level 1 : LLD^1

This facies is exposed at the base of the quarry and comprises a dark grey, bioclastic, micritic limestone, characterised by the presence of pearly, beautifully-preserved productid shells. Additionally, some trilobite remains were found, and several bryozoans were recorded:

Rhabdomeson rhombifera
Fenestella plebeia
Fenestella polyporata
Polypora dendroides?
Penniretepora flexicarinata
Penniretepora laxa
Penniretepora cf. *grandis*

Several species of the genus *Penniretepora* were found, and though poorly preserved, they have been assigned to various species from parametrical comparisons with the data of Bancroft (1984). Two rarer forms, which are provisionally identified as being present, include *P. laxa* (LLD^{1}5, Plate 6, fig. g.) and *P.* cf. *grandis* (LLD^{1}4, Plate 6, fig. h.). Better preservation may have allowed for a more confident species assignment of the acanthocladiids. The specimen of *Rhabdomeson rhombifera* (LLD^{1}1, Plate 6, figs. c. and d.) was actually exceptionally well-preserved, and the grading of the autozooecial apertures and small stylets around the aperture rims characterised this species; there is, in fact, no observable difference between this Brigantian specimen, and Bancroft's Arnsbergian material from Yorkshire.

The diversity of slender acanthocladiids, and the presence of the long-fenestruled fenestrate *Fenestella polyporata* all support the notion of the micrite forming in a very quiet-energy environment. Though there has been some fragmentation of the specimens, there is little to suggest any significant current activity at this level.

Level 2 : LLD^2

The facies at level 2 consists of a poorly-bedded white-grey limestone with some brachiopods and crinoids. Bryozoans are rather rare, and only one fenestellid was found:

Fenestella plebeia

The stout meshwork of *Fenestella plebeia* probably enabled it to survive in higher energy environments than the acanthocladiids.

Level 3 : LLD³

Level 3 is represented by a shale parting between the poorer-bedded limestones. The shale is very friable and dark green-grey in colour. As at Level 1, some brachiopods and trilobites were found, together with the fragmentary bryozoans listed below:

Fenestella frutex
Fenestella polyporata?
Penniretepora flexicarinata
Diploporaria marginalis

Of these, *Penniretepora flexicarinata* is the most abundant species recorded.

Level 4 : LLD⁴

This level comprises a band rich in gigantoproductid brachiopods, whose flattened and fragmented shells actually comprise about 80% of the rock. However, two bryozoan species were recorded:

Rhombopora incrassata
Fenestella plebeia

These bryozoans, unlike those from Levels 1 and 3, are stout-colonied, and presumably were better adapted for surviving in more turbulent conditions. The large size of the fragments of the fenestellid meshwork, coupled with the preservation of dendritic branching within the rhabdomesid colony suggest that the bryozoans have not actually been transported any great distance, and may well have co-existed with the productid brachiopods.

Cefn Mawr Quarry

Grid reference : SJ 200 635

The top levels of this quarry, exposed in Cefn Mawr Old Quarry, provide an exposure of the middle levels of the Cefn Mawr Limestone. The strata consist of a series of thin limestones, varying from white, bioclastic strophomenid-dominated sparites to micritic coral-dominated levels. These levels belong to cycle six of Somerville (1979a). The following bryozoans were recovered:

Fenestella plebeia
Fenestella polyporata
Penniretepora sp. indet.
Penniretepora pulcherrima
Septopora cf. *carbonaria*
Baculopora?
Tabulipora sp.
Stenodiscus? sp.
Fistulipora incrustans
Eridopora beilensis

Many of the *Lithostrotion* coral colonies in the micritic horizon, and several *Dibunophyllum* colonies, have been encrusted by bryozoans; *Tabulipora* and *Fistulipora* (see specimen CMQ1, Plate 9, fig. h.) are the commonest encrusters, and these species were also found encrusting strophomenid valves. Additionally, the cystoporate *Eridopora beilensis* was found encrusting *Lithostrotion.* Fenestellids also occur in the more micritic, quieter-water deposits, and an excellently-preserved low-angled conical colony of *Fenestella polyporata* was found (specimen CMQ3, Plate 7, fig.h.).

Bryozoans are rarer in the strophomenid-rich biosparites, but included several fragmented fronds of *Fenestella*, the rare stick-like acanthocladiid *Baculopora*, and fragments of cylindrical colonies of *Stenodiscus.* Of importance is the occurrence of the fenestrate acanthocladiid *Septopora*; this particular specimen (CMQ2, Plate 8, fig. i.) shows a reverse surface, which is very similar in appearance and dimensions to *Fenestella plebeia.* However, a broken portion of the colony revealed that the "dissepiments" actually bear zooecia, and are therefore the lateral branches of an acanthocladiid. The very regular arrangement of the lateral branches is most noticeable, and is better developed than in any other reported specimen of *Septopora carbonaria* from the British Carboniferous.

Hendre Quarry

Grid reference : SJ 195 679

The workings at Hendre Quarry provide an extensive section through the Cefn Mawr Limestone, and the base of the group, with its disconformable contact with the underlying Asbian Loggerheads Limestone (there is an emergence horizon with a prominent palaeokarstic surface, as reported in Somerville and Strank, 1984) is exposed in the bottom of the quarry. Most of the bryozoans were collected from the

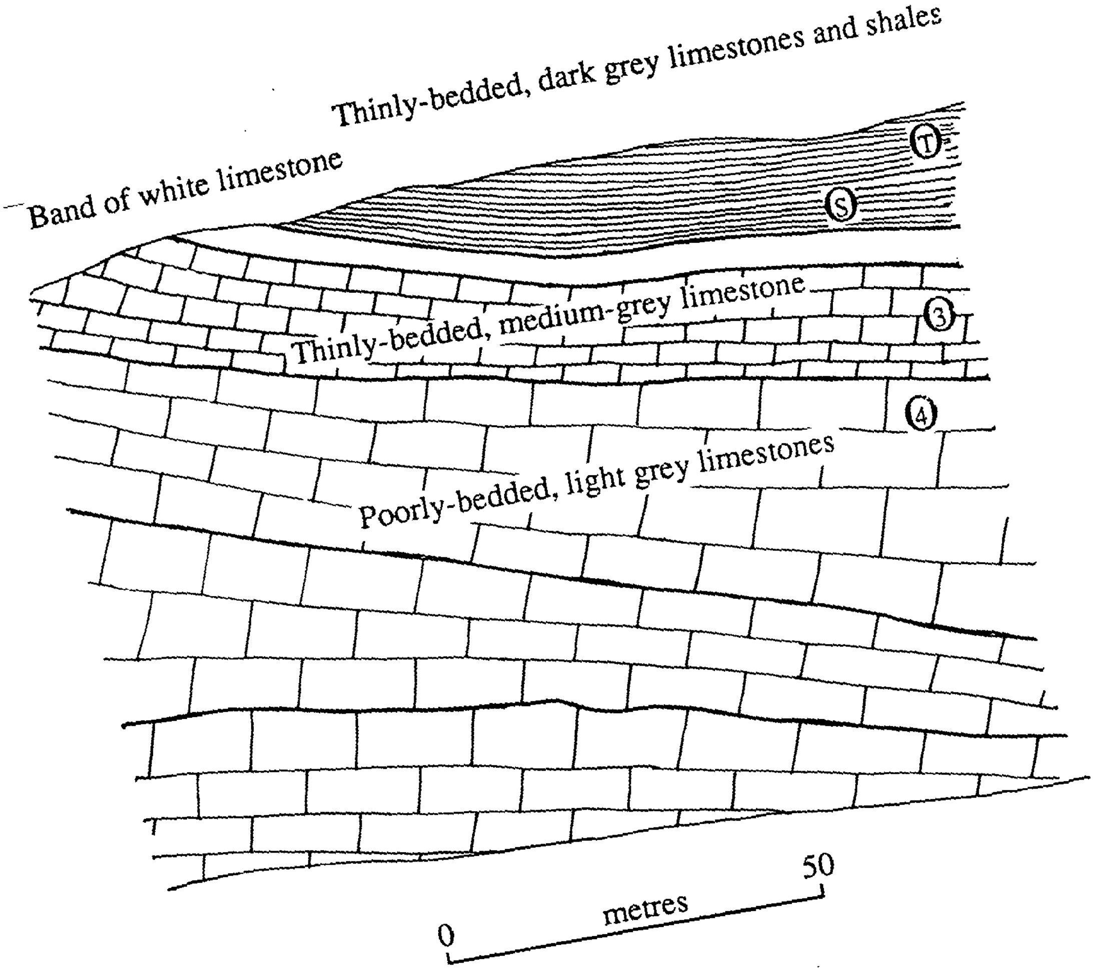


Fig. 8.6. Fieldsketch of Hendre Quarry

upper levels; the position of the collection horizons is shown on fig. 8.6. The thicker biosparite limestones (poorly-bedded, light grey limestones) were examined, but failed to yield any bryozoans. However, an abundant and diverse fauna was obtained from the following horizons:

Top levels : HQ^T

Cycle 8: thinly-bedded, grey biomicrites, weathering to a buff colour.

Rhabdomeson gracilis
Rhombopora incrassata
Fenestella bicellulata
Fenestella frutex
Fenestella plebeia
Polypora dendroides
Polypora verrucosa
Penniretepora flexicarinata
Tabulipora sp.
Fistulipora incrustans

Shales : HQ^S

Cycle 8: base of cycle, dark-grey, friable, slightly micaceous shales.

Fenestella bicellulata
Fenestella frutex
Fenestella cf. *plebeia*
Penniretepora spinosa
Penniretepora flexicarinata

Level 3 : HQ^3

Cycle 7: Thinly-bedded, light grey biomicrites.

Rhabdomeson gracilis
Rhombopora incrassata
Fenestella frutex
Fenestella multispinosa
Fenestella plebeia
Penniretepora flexicarinata
Tabulipora urii
Tabulipora sp. indet.
Fistulipora incrustans
Eridopora beilensis

Level 4 : HQ^4

Cycle 6: Friable calcareous shale horizon towards the base of the cycle.

Rhabdomeson gracilis
Rhombopora incrassata
Fenestella bicellulata
Fenestella multispinosa
Fenestella plebeia
Tabulipora sp.
Fistulipora incrustans

Two distinct bryozoan facies are present; the quiet-water shales (HQ^S and HQ^4) and the slightly higher energy micrites (HQ^T and HQ^3). The shales have a less diverse fauna than the micrites, and are dominated by slender-branched bryozoans such as *Fenestella bicellulata*, and HQ^S has a moderate abundance of the thin-branched acanthocladiid *Penniretepora spinosa.* The calcareous shales of HQ^4 may actually have been formed in a slightly higher energy environment than those of HQ^S, since no species of *Penniretepora* were found; however, the thicker-branched *Penniretepora flexicarinata* does occur quite commonly in the micritic levels. Similarly, the trepostome *Tabulipora* and the cystoporate *Fistulipora* , both of which needed a more solid substrate over which to encrust in their early growth stages, are absent from the muddy environment represented by HQ^S, but occur in the other three facies.

The micritic levels (HQ^T and HQ^3) have similar bryozoan faunas, differing mainly with the occurrence of two species of *Polypora* in the topmost micrite (*Polypora dendroides*, specimen HQ^{T}17, is illustrated on Plate 8, fig. f.). Of interest is a specimen of *Fenestella* (HQ^{T}5, Plate 8, fig. d.) which shows a colony origin initiating from a curved basal sheath which had probably wrapped around a soft-tissued plant (?) stem of 0.9mm diameter. Encrusting specimens of *Tabulipora* are also quite abundant, some growing on brachiopod shells (HQ^{T}1, Plate 9. fig. a.) and one encrusting around a gastropod shell (HQ^{3}1.1, Plate 9. fig. e.). Other encrusters include *Eridopora beilensis* and *Fistulipora incrustans*, the latter being observed, in some cases, to overgrow chaetetid sclerosponges (specimen HQ^{3}2, Plate 9. fig. j.).

A large frond of *Fenestella multispinosa* was found on an earlier visit to the quarry in March, 1982 with the Liverpool Geological Society. The specimen (HQ1, Plate 7, figs. c. and d.) is rather beautiful, being mottled in shades of brown by iron staining, but is most noticeable for the large size of the fragment, measuring 6cm by 3cm, and the hexagonal appearance of the meshwork. Such a hexagonal aspect is common in the species *Fenestella tuberculo-carinata*, commonest in Scotland and Northern England, but the parameters of the specimen are actually consistent with *Fenestella* *multispinosa*; further, a broken portion of the colony (Plate 7, fig. d.) revealed that there are three apertures per fenestrule (*F. tuberculo-carinata* has four). Thus, with secondary calcification of the fronds *Fenestella multispinosa* and *Fenestella tuberculo-carinata* may develop similar meshworks, differing only in the size of the fenestrules.

Bryn Mawr Quarry

Grid reference : SJ 188 734

Like Hendre Quarry, the workings at the disused Bryn Mawr Quarry on Halkyn Mountain expose strata within the Cefn Mawr Limestone. Bryozoans were collected from several facies on two visits to the quarry, and are listed in ascending stratigraphical order:

Bottom Levels : BMQ^B (approx. 10m in thickness)

Hard cherty limestones, dark brown in colour, interbedded with a few shale units. Fossils are not abundant, and in addition to the bryozoans listed below, a few chonetid brachiopods, some solitary rugose corals, and several crinoid ossicles were found.

Rhabdomeson gracilis
Rhombopora bancrofti?
Rhombopora incrassata?
Fenestella plebeia
Fenestella polyporata
Penniretepora flexicarinata
Baculopora sp.

Middle Levels : BMQ^M (approx. 8m in thickness)

Two alternating lithologies occur in the middle portions of the quarry.

a. Bioclastic, light grey limestone facies, with many crinoid columnals :

Fenestella bicellulata
Fenestella multispinosa
Fenestella plebeia
Polypora verrucosa
Tabulipora sp.
Fistulipora incrustans

b. Shaly, dark grey facies, yielding strophomenid brachiopods :

Fenestella multispinosa
Fenestella plebeia
Penniretepora grandis?
Tabulipora sp.
Fistulipora incrustans

Top Levels : BMQ^T (approx. 5m in thickness)

Pale coloured bioclastic limestones, dominated by strophomenid brachiopods. Chaetetid sclerosponges up to 25cm in diameter are present, sometimes encrusted by bryozoans. The bioclastic limestone is overlain by alternating black shales and dark-grey, ironstained limestones, which bear a sparse fauna, with some brachiopods in the limestones. Above these shales, a fossiliferous dark biomicrite occurs.

Rhabdomeson gracilis
Fenestella plebeia
Polypora dendroides
Tabulipora sp.
Fistulipora incrustans

Dark Biomicrites : BMQ^D

A buff-weathering, dark grey micrite, with some crinoids, but dominated by a well-preserved bryozoan fauna, in which *Penniretepora flexicarinata* is very common. This unit is overlain by 30cm of mudstones with some representatives of *Penniretepora*, 60cm of a sparsely-crinoidal limestone, and a thin bryozoan-bearing shale.

Rhabdomeson gracilis
Fenestella frutex
Fenestella plebeia
Penniretepora flexicarinata

Thin Shales : BMQ^S

Black, irregularly-cleaved shales, occurring in a thin, wavy band, which is only a couple of centimetres thick. This is the Halkyn Shale, present in many museums around Britain, which has been collected since it preserves a fine fauna of flattened fenestellid fronds. A specimen (BMQ^{S}1), showing the typical preservation of the colonies, is illustrated in Plate 8, fig. a. The thin shale band is overlain by 8 metres of sugary-looking crinoidal limestone. Most of the specimens were actually collected from fallen blocks.

Rhabdomeson gracilis
Fenestella plebeia
Fenestella polyporata
Penniretepora spinosa?
Penniretepora flexicarinata

Limestones : BMQ^L

Rubbly-weathering, poorly-bedded brown limestones, rich in corals and large crinoid stems, many of which are still articulated for up to 30cm of their length. This horizon was collected from loose blocks, and may correspond with the bioclastic limestones of BMQ^T.

Rhabdomeson gracilis
Fenestella multispinosa
Fenestella plebeia
Polypora cf. *dendroides*
Polypora verrucosa
Penniretepora flexicarinata
Tabulipora urii
Fistulipora incrustans

The bryozoans of the Bryn Mawr Quarry are quite diverse in their abundances. Following a similar pattern to the faunas from Hendre Quarry, the more delicately-branched bryozoans (especially *Fenestella polyporata* and most specimens of *Penniretepora*) are limited in their occurrence to the dark shaly facies, while the stouter-meshworked *Polypora* is commonest in the higher-energy limestones. *Fenestella plebeia* seems to show very little facies-dependency, and occurs in all the environments represented in Bryn Mawr Quarry.

Bryozoans of note include the occurrence of *?Rhombopora bancrofti*, poorly-preserved, but possessing large, rounded apertures and sporadic exilazooecia. This taxon is more common in the Viséan of Northumberland. Some representatives of the acanthocladiid genus *Baculopora* were found, identified by large rounded apertures, arranged in several rows on the branch obverse surface, but lacking apertures on the reverse surface, which is ornamented by longitudinal striations.

The trepostome *Tabulipora urii* was positively identified from this locality; good preservation had allowed sections to be made of some cylindrical colonies, which were found encrusting around an assemblage of broken crinoid stems. An acetate peel of specimen BMQ^{L}2.1 (Plate 9, figs. b. and c.) showed a moderately wide exozone, and zooecial chambers bearing an average of five ring septa per chamber.

A beautiful specimen of *Penniretepora flexicarinata* was recovered from the dark micrite (BMQ^{D}2, Plate 6, fig. k.), illustrating the development of 2:1 lateral branches, which bear smaller 2:2 laterals. Such a delicate colony plan could only have remained stable in waters with minimal bottom current activity, and the fauna is almost certainly buried *in situ.*

Several colony origins of fenestellid colonies were found in various facies in Bryn Mawr Quarry. The Limestones (BMQ^{L}) yielded two specimens of *Fenestella plebeia* which had very different colony origins; BMQ^{L}3 (Plate 8, fig. b.) developed a fan-shaped colony from a narrow cylindrical sheath, which may have wrapped around a brachiopod spine: BMQ^{L}4 (Plate 8, fig. c.) developed a high-angle colony, strengthened by extensive secondary calcification of the proximal portions of the colony. An origin of *Fenestella frutex* (BMQ^{D}1, Plate 8, fig. e.) was found in the dark micrites, and may have encrusted a brachiopod spine; this mode of life was seen in a poorly-preserved specimen of *Fistulipora* from the limestones (BMQ^{L}7), in which the spine was seen to be still attached to the pedicle valve of the productid.

Halkyn Mountain Quarry (Northern Aggregates)

Grid reference : SJ 189 718

This quarry was visited in the summer of 1988, and has undergone dramatic excavations since an earlier visit in 1984; the top spoilheaps have been removed, and it was from these tips that an exceptionally well-preserved bryozoan fauna had been recovered from the dark grey micrites. The following species have been identified from amongst some of the fossils collected on the amateur 1984 visit:

Rhabdomeson gracilis
Fenestella multispinosa
Fenestella plebeia
Fenestella polyporata
Penniretepora flexicarinata
Penniretepora pulcherrima

The specimens of *Penniretepora* are very detailed in their preservation (see specimen HMQ5, Plate 6, figs. i. and j.), and *Penniretepora pulcherrima* is readily identified from the pustulose reverse surface. A bedding surface crowded with branching colonies of *Rhabdomeson gracilis* (HMQ4, Plate 6, fig. f.) was also found; the large size of the colony fragments suggests little post-mortem transportation had taken place, and the colonies may have been washed into a bryozoan build-up, similar to the modern *Flustra* banks found along British shorelines.

CHAPTER 9 : CLITHEROE

The Clitheroe area of Lancashire is noted for the development of Waulsortian-type reefs (Miller & Grayson, 1970; Grayson, 1981; Lees & Miller, 1985; Donovan, 1989). Though such sub-photic zone reefs in the Dinantian strata of Belgium are characterised by mud mounds dominated by fenestrate bryozoans, Lees *et. al.* (1985) showed that such formations are depth-dependant, and four stages of Waulsortian reef formation can be identified. In the English Dinantian, stage one is usually absent, and the reefs start formation from the second stage, in which sheet fenestellids are rarer, and the fauna more diverse, including hyalosteliid sponges. Lees and Miller (1985) inferred that the fragmentation of the fenestellids was due to an influx of grazing taxa onto the reef, rather than a change in the energy levels of the environment.

Two quarries in the Chadian strata of the Clitheroe district were studied, during the 1989 Palaeontological Association Fieldtrip :

Coplow Quarry. Grid reference SD 751 432. *gemmulifera 2* zone
Salthill Quarry. Grid reference SD 756 425. *castroliobole* zone
The zones are those cited by Donovan (1989).

Both the quarries comprise Waulsortian carbonate build-ups, predominantly within the third and fourth stages of development (Lees & Miller, 1985). Though the fauna is more diverse in these phases, bryozoans are rarer than in the "classic" stage one of the Waulsortian reefs.

The sediments in Coplow Quarry comprise thinly-bedded limestones, and calcareous shales in the lower portion of the quarry. These Coplow Bank Beds (Miller & Grayson, 1970) have yielded many brachiopods and crinoid material (including calyxes) and *Fenestella, Polypora* and *Penniretepora* have been reported to occur (Miller & Grayson, 1970). During fieldwork for this project, fenestellid fragments were extracted in some abundance from the shales, but were inevitably found to be quite poorly-preserved. However, some moulds of obverse surface fragments were recovered, showing five apertures per fenestrule and a well-defined median ridge; the moderately large length of the fenestrules(approx. 0.95mm), and the wide bifurcation patterns provide additional features which point to the fragments belonging to the species *Fenestella plebeia.*

A specimen in the Natural History Museum (PD 5486) from Coplow Quarry is labelled *Fenestella* cf. *hemispherica*; a few fragments were recovered which showed very strong striations on the reverse surface. Their branches are parallel, with few bifurcations, and the fenestrules are rather rectangular, measuring approximately

0.75-0.77mm by 0.45-0.50mm. Thus, the fragments may be referable to *Fenestella hemispherica*, based on a comparison with material cited by Tavener-Smith (1973a) from Asbian strata. However, the colony form cannot be deduced (the classic shape of this species was likened by McCoy, 1844, to a tea cup), and the dissepiments appear to be flush with the reverse surfaces, rather than depressed beneath them.

In the upper part of the quarry, thin limestones are more common, and are predominantly crinoidal. However, a few bryozoan fragments were found, including some parallel-branched specimens of *Fenestella plebeia*, and one broad-branched, lax-fenestruled colony of *Minilya oculata*, characterised by nodes placed on alternate sides of the median carina. One very large sheet of *Fenestella plebeia* was found, measuring 10cm by 10cm. Lees and Miller (1985) report that sheet fenestrates may be found in phase four of a Waulsortian reef, but are commonly encrusted; the specimen found in Coplow Quarry did actually have some colonies of the cystopore *Fistulipora* on the reverse surface of the frond, together with one specimen of an unidentifiable trepostome.

Point three of Grayson (1981) was visited in Salthill Quarry. This is a rather weathered, rubbly crinoidal limestone face, from which many crinoid calyxes have been recovered. Many crinoid stems are encrusted by the corals *Cladochonus* and *Emmonsia* (Grayson, 1981), but no encrusting bryozoans were found. However, a few small fragments of a fenestellid (probably *Fenestella plebeia*) were found on small blocks of the limestone, and one specimen of *Minilya oculata* was discovered. This is a rather rare fenestrate, having previously been recorded only in Ireland (McCoy, 1844; Tavener-Smith, 1973a).

Minilya oculata

The specimen CSQ1 (fig. 9.1), assigned to *Minilya oculata* (McCoy, 1844), is a moderately well-preserved colony fragment, showing the obverse surface detail, and weathered in parts to reveal the internal structure. The colony fragment measures approximately 1.5 x 1.3 cm, and has a tightly-spaced meshwork with closely-spaced, rather broad branches and thinner dissepiments.

When well-preserved, branches are seen to be relatively straight, broad (0.30-0.44mm) and have steep-sloping sides. When branching occurs, a typical "tuning fork" pattern develops, with the dividing branch thickening only within about 0.5mm of bifurcation. The newly-formed branches likewise quickly spread out, and run parallel to the meshwork, with normal branch spacing developed within one fenestrule's distance. One aperture is usually placed in the angle of the fork.

There is a broad median ridge on some branches, but others have a sharp, sinuous carina instead. Both structures bear the biserial rows of nodes which are diagnostic of the genus *Minilya*. Nodes are regularly placed, occurring diagonally between apertures. The nodes themselves are fairly small, elongate oval structures, which have a core of glassy-grey calcite, so when they are slightly eroded they stand out as small black dots. The median ridge is also ornamented by a concentration of longitudinal striae, which occur less obviously all over the surface of the branches. It is probable that the sharp carina represents the unabraded state of the specimen, and flattens out into a striated median ridge on weathering.

Dissepiments are relatively short and narrow (0.12-0.18mm), flaring considerably towards the branches. They are rather sunken beneath the branch crests, and are also covered by striae which run parallel to their flared margins and onto the branch surface where they curve round and run parallel to the median ridge.The flaring of the dissepiments gives the fenestrules a rounded appearance.

Apertures are large and prominent (0.11-0.14mm) and are round to slightly oval, being elongated in a direction at right angles to the median ridge. Poorly-developed apertural rims are present, which may occasionally abut into the fenestrules, but more usually apertures are flush with the branch margins. Towards the dissepiments, apertures may be placed further from the median ridge than those in the centre of the fenestrules. Apertures are rather widely-spaced (0.28-0.34mm), being more than their own diameter apart.

In one broken part of the colony, it could be seen that the zooecial bases are hemi-hexagonal in shape, while another broken portion revealed that the basal surface is strongly striated.

The zoarial parameters are shown in the following table:

Minilya oculata						
	Salthill Quarry, Clitheroe			Carrick Lough	PROBABILITY SCORES	
	n	σ	x	x	T-FEN	T.FEN.DIV
BW	27	0.0213	0.379	0.367	0.0311	0.0334
AD	25	0.0095	0.118	0.111	0.0294	0.0558
ID	26	0.0175	0.318	0.315	0.5000	0.2039
FL	25	0.0744	1.096	1.222	0.0000	0.1008
FW	25	0.1026	0.696	0.780	0.0023	0.1124
DW	26	0.0241	0.147	0.196	0.0000	0.0001
IND	28	0.0194	0.328	0.328	1.0000	0.1003
					TOTAL	0.0867

Minilya oculata is a rare species, previously being recorded only in Ireland and the Upper Carboniferous of Samarskaia Luka in the Urals (Nikiforova, 1933). McCoy (1844) gave the first description of the species, calling it *Fenestella oculata* and noting its occurrence in Waterford, Eire, in probable Tournasian rocks. Miller (1961) redescribed the species, and erected a paratype from McCoy's material. Though he noticed the sinuous carina, he did not place taxonomic importance on the biserial nodes, despite endorsing, earlier in the paper, the validity of Crockford's genus *Minilya* for fenestellids with two rows of nodes. Tavener-Smith, in finding specimens from the silicified Asbian limestones of Carrick Lough in County Fermanagh, Northern Ireland, found that his material was conspecific with *Fenestella oculata* McCoy, and since two rows of nodes were present, assigned the species to the genus *Minilya*.

The specimen from Salthill corresponds very well with the average parameters published by Tavener-Smith for *Minilya oculata*. Branch width, aperture diameter, inter-apertural distance, and internodal distance all correspond very closely. However, the values of fenestrule width, fenestrule length, and dissepiment width are all much lower than Tavener-Smith's material. These parameters do, though, fall in the very minimum values of Tavener-Smith's colony means.

Measurements given by Miller on the paratype are rather ambiguous. From the quoted micrometric formula, the fenestrule length (derived from number of dissepiments in a 10mm line) is 0.75-1.25mm, yet he cites actual fenestrule length ranges of only 0.60-0.75mm. Presumably, Miller did not measure fenestrule lengths from dissepiment midpoints, but from dissepiment edges. Even adding on the dissepiment widths to his figures still only gives ranges for the lengths of 0.84-0.99mm, which are far below the corresponding lengths of either this study or Tavener-Smith's work. Both Miller's micrometric formula and cited fenestrule width measurements, though, give a range of 0.69-0.86mm for this parameter, which match the fenestrule widths of Tavener-Smith and the Salthill Quarry specimen.

The similarities and discrepancies with Tavener-Smith's material are shown by the t-test results, which are included in the table of parameters for *Minilya oculata*. Fenestrule length and dissepiment width both score 0.0000, while fenestrule width rates only 0.0014. T.FEN.DIV gives better all-round probability correlations with Tavener-Smith's material, having an overall probability score of 0.1030, but dissepiment width still scores 0.0000. McCoy's original description of *Fenestella oculata* states "dissepiments less than one-fourth the thickness of the interstices". Thus, the thinner dissepiments of the Salthill form are closer to the original species than the Carrick Lough material.

The median ridge and nodes are much clearer on the Salthill Quarry specimen than on either the photograph of McCoy's paratype, or on the silicified material of Carrick Lough. The Chadian age of the Salthill specimen could correspond with the Tournasian date tentatively assigned by Miller to McCoy's Waterford material. However, to hypothesize contemporaneous occurrences would imply a rather broad distribution pattern for this species, and this has yet to be recorded. The specimen of *Minilya oculata* from Salthill was found in a high-energy crinoidal limestone forming the flank of a reef knoll. Bryozoans are usually rather rare in crinoidal limestones, so it is possible that *Minilya oculata* was somehow specialised for living in these areas. However, until more specimens are discovered, it will be very difficult to deduce the environmental preferences of this species.

The similarity between *Minilya oculata* and *Fenestella plebeia* was remarked upon by Miller; he cited differences in the zooecial aperture distribution, and carinal nodes, as distinguishing characteristics. Using the t-test, a comparison of the parameters of the Salthill specimen CSQ1 and Bancroft's measurements for *Fenestella plebeia* gave an overall probability of only 0.0038 (cf. 0.2233 when specimen CSQ1 is compared with Tavener-Smith's *Minilya oculata*), thus clearly distinguishing the two species as being different.

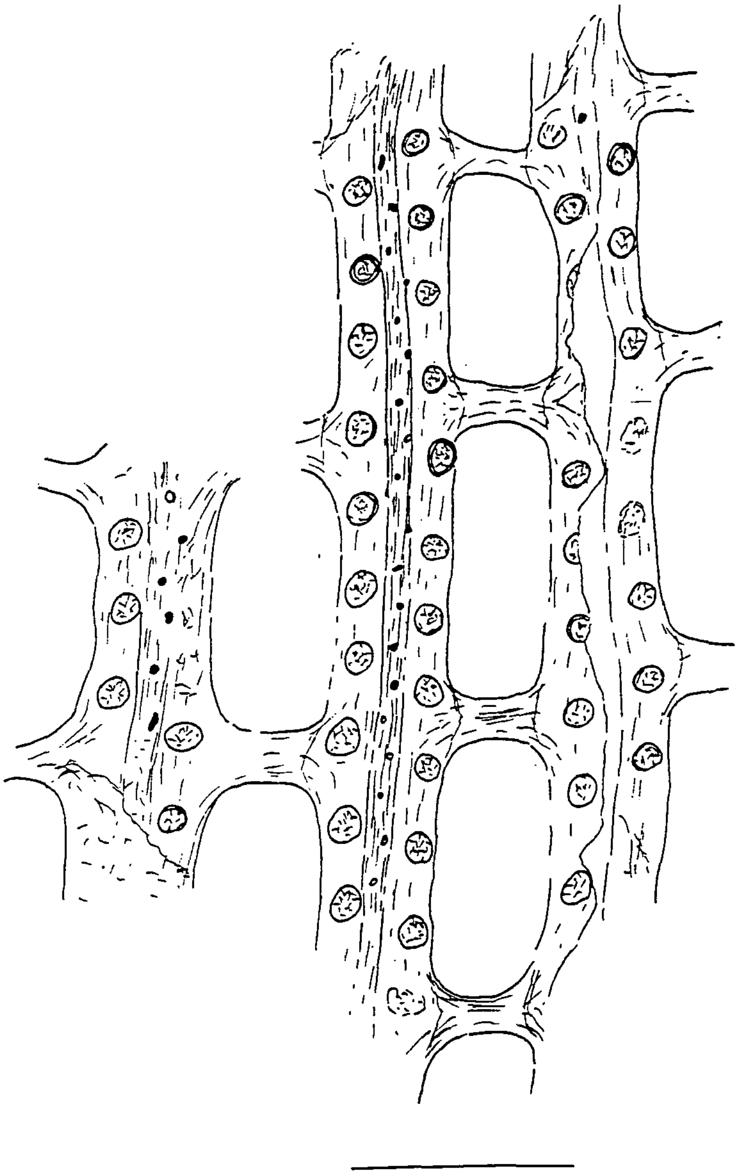


Fig. 9.1. *Minilya oculata* from Salthill Quarry CSQ1

CHAPTER 10 : REDESDALE

GRID REFERENCE : NY 8936 8290

"The Steel" quarry in Redesdale, Northumberland exposes workings of the Redesdale Ironstone, an iron-rich biomicrite. Both the ironstone and the associated shales support a very diverse fauna, including spinose productid brachiopods, edmondiid bivalves, crinoids, fish and orthoconic nautiloids. Smith (1910) listed the fauna from the Redesdale Ironstone Shale, and viewed the assemblage as being typical of a shallow-water bivalve-dominated community; however, the association is believed here to be more typical of a lower reef-slope brachiopod community.

Bancroft (1984) produced a list of the bryozoans found in the quarry. Bryozoans are actually very abundant, and a diverse, if slightly fragmented, bryozoan fauna is preserved. A faunal list based on collection for this thesis is presented below :

- Cryptostomata
  - *Rhabdomeson rhombifera*
- Fenestrata : fenestellidae
  - *Fenestella bicellulata*
  - *Fenestella* cf. *ivanovi*
  - *Fenestella frutex*
  - *Fenestella multispinosa*
  - *Fenestella plebeia*
  - *Fenestella polyporata*
- Fenestrata : acanthocladiidae
  - *Penniretepora flexicarinata*
  - *Diploporaria marginalis*
  - *Septopora carbonaria*
- Trepostomata
  - *Tabulipora* cf. *howsii*
  - *Stenodiscus tumida*
- Cystoporata
  - *Fistulipora incrustans*
  - *Sulcoretepora parallela*

Apart from the excellent preservation of much of the material, the bryozoans are noteworthy for their inferred mode of life; many colony origins are preserved, showing attachment around productid brachiopod spines. This lifestyle is inferred

(Billing, 1991) to represent an adaptation for colonisation of a substrate too muddy for direct larval settlement. Though crinoid stems were presumably available for settlement, only one specimen of *Tabulipora* was observed encrusting a stem, and some specimens of *Fistulipora* were seen encrusting brachiopod shells. However, brachiopod spines could have been settled in preference, since they would have elevated colonies into areas of faster current flow above the boundary layer.

The fauna is discussed in more detail in Billing (1991); a copy of this paper is enclosed in the end-pocket of this thesis.

CHAPTER 11 : STANHOPE

GRID REFERENCE : PARSON BYERS QUARRY : NY 993 375
ASHES QUARRY EAST : NZ 001 397

Both Parson Byers Quarry and Ashes Quarry East provide exposures of the Great Limestone and the overlying shales. The Great Limestone is of lowermost Pendleian age, the base of the stage being considered to correspond to the base of the Limestone.

The Great Limestone is a rather thick (approximately 10m), relatively poorly-bedded carbonate, comprising three biostrome units (Johnson, 1958):

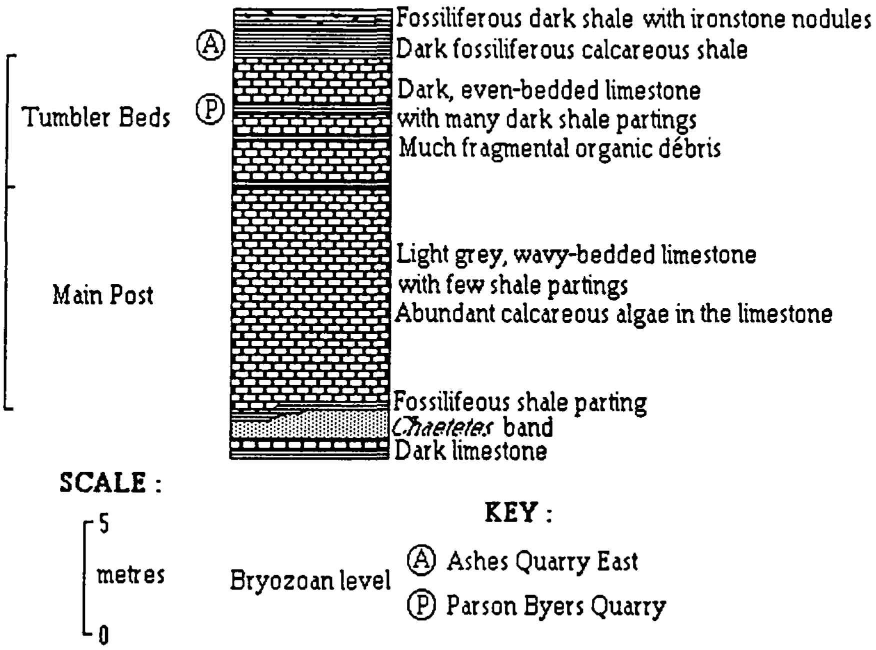


Fig. 11.1. Section through the Great Limestone (based on Johnson, 1958)

Though no bryozoans were found in the main post of the Great Limestone in Parson Byers Quarry, the overlying Tumbler Beds there contained a quite diverse fauna of bryozoans. The Tumbler Beds probably represent an increase in clastic sedimentation into the area, resulting in a dilution of the pure carbonate mud. The bryozoans were collected from the interbedded shales; disarticulation of the accompanying crinoid stems and fragmentation of most of the bryozoans suggests that some disturbance of the material had occurred. However, some moderately large fragments of the usually delicate cystoporate *Goniocladia* were found, implying that any transportation of the material had not carried the bryozoans very far. The following bryozoans were recorded:

Cryptostomata
- *Rhombopora bancrofti*

Fenestrata : fenestellidae
- *Fenestella bicellulata*
- *Fenestella frutex*
- *Fenestella multispinosa*
- *Fenestella plebeia*

Fenestrata : acanthocladiidae
- *Penniretepora flexicarinata*

Trepostomata
- *Tabulipora* sp.

Cystoporata
- *Fistulipora incrustans*
- *Goniocladia cellulifera*

At Ashes Quarry East, the calcareous shales overlying the Tumbler Beds were examined. A fairly diverse fauna was recorded (White, 1990) including small brachiopods, gastropods, ostracods, trilobites, crinoids and echinoids, in addition to a fragmented bryozoan fauna :

Cryptostomata
- *Rhabdomeson gracilis*

Fenestrata : fenestellidae
- *Fenestella bicellulata*
- *Fenestella plebeia*

Trepostomata
- *Tabulipora minima?*

Cystoporata
- *Fistulipora incrustans*
- *Sulcoretepora parallela*

The faunas are interesting in that the branching cystoporates *Goniocladia* and *Sulcoretepora* are moderately abundant. These bryozoans (Bancroft, 1984) appear to be restricted to mudstone facies formed in tranquil environments, in association with brachiopods and some crinoids.

PART III : BRYOZOAN DISTRIBUTIONS

CHAPTER 12 : BRITISH CARBONIFEROUS BRYOZOAN DISTRIBUTION PATTERNS

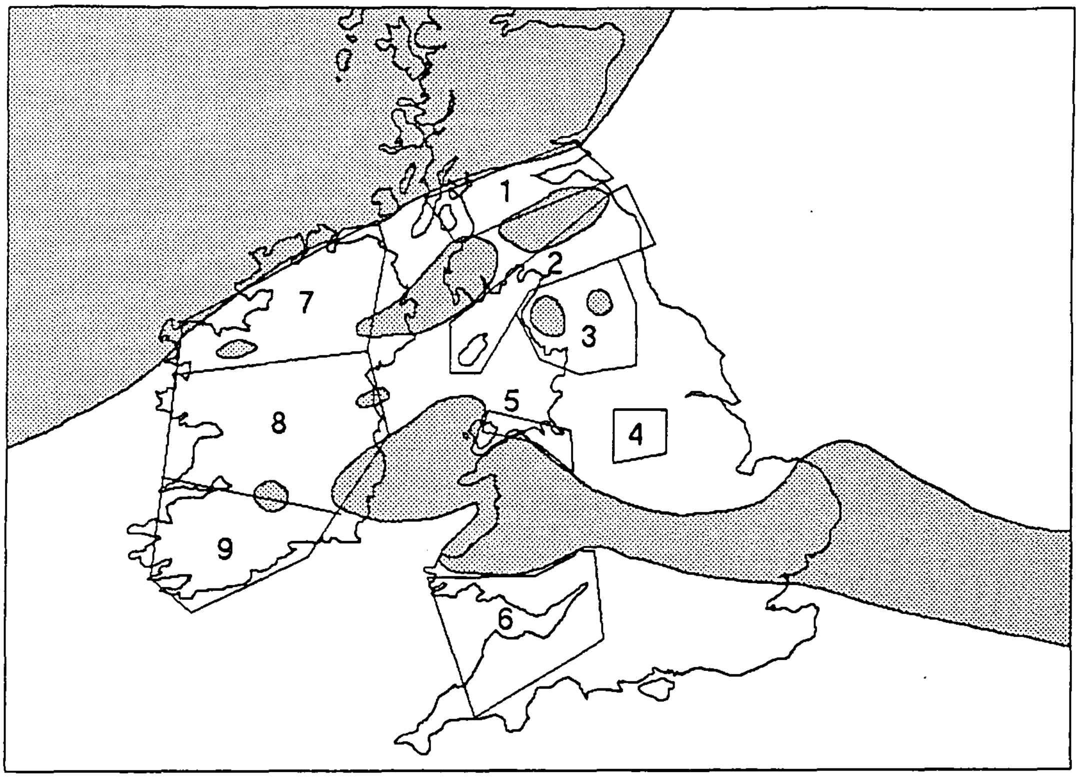
Background

Distribution patterns for any taxon are subject to several conditions; the data has to be stratigraphically constrained, geographically accurate, and devoid of collection bias. In practice, these requirements are very rarely met, since a study of every outcrop of a particular horizon would require many years of meticulous examination. Therefore, any conclusions on biogeographical patterns can be assumed to be only a first order approximation. These constraints hold true in this particular study; there are almost certainly many gaps, and much more could be gleaned from a continued study of areas which have had to been omitted for lack of time. An analysis of the Derbyshire fauna, for instance, would most certainly have filled in conspicuous gaps in the data. However, though the dataset may be limited, there is still enough detail to begin to analyse the British Carboniferous bryozoan distribution patterns.

An aim of the study was to determine the similarity of the faunas from different areas within the British Isles. Similarity/dissimilarity studies are constrained by the uniformity of detail relating to each area under scrutiny; for instance, there are two large publications on the bryozoans of Carrick Lough (Asbian), County Fermanagh (Tavener-Smith, 1974; Olaloye, 1977), yet very little is known about the bryozoans of Central Ireland. Thus, in this study, the Asbian of Northern Ireland may be considered to be over-represented, while other areas in Britain are undoubtedly under-represented.

Despite these constraints, it has been possible to calculate coefficients of similarity between nine geographically-distinct areas. The British Isles have been divided into the following regions, based on inferred Carboniferous palaeogeographies (fig. 12.1):

1. The Midland Valley of Scotland (Fife to Arran)
2. The Northumberland Basin (Northumberland, Dumfries, and the Isle of Man)
3. Pennines and Cumbria (including South Durham and Yorkshire)
4. Derbyshire
5. North Wales
6. South Wales, Avon and Devon
7. North Ireland
8. Central Ireland
9. South Ireland



Key to Zones

1. The Midland Valley
2. Northumberland Region
3. Pennines and Cumbria
4. Derbyshire
5. North Wales
6. South Wales, Avon, and Devon
7. North Ireland
8. Central Ireland
9. South Ireland

Fig. 12.1. Zones defined for biogeographical analysis

The boundaries of these areas run parallel to the ancient shorelines of Laurasia, and in some cases may seem to be arbitrary. However, while plotting up the data there has been little doubt about which area the information should be placed; thus, from a practical point of view, the regions appear to be satisfactorily-defined. Redefinition of the areas may have provided different results, but the regions appointed for this project seem to have yielded internally-consistent similarity coefficients.

Two coefficients of similarity have been used in this study, though many comparative coefficients are available (see Newton, 1990, for a review):

The Simpson Coefficient can be defined as

$$\text{Simpson Coefficient} = \frac{S_c}{T_s}$$

where

S_c = Number of species in common between two populations

T_s = Number of species in the smaller population

The Jaccard Coefficient can be defined as

$$\text{Jaccard Coefficient} = \frac{S_c}{T_1 + T_2 - S_c}$$

where

T_1 = Total number of species in one population

T_2 = Total number of species in other population

Of the two coefficients, Simpson Coefficient is quicker to calculate, and is less affected by over-sampling in one of the areas, since the number of species recorded in the larger population is not included in the calculation of the coefficient. Indeed, Simpson Coefficients of faunal similarity tend to be larger than the Jaccard Coefficients. Jaccard Coefficients, though, can give a truer representation of dissimilarity between a large fauna and a much smaller fauna. The smaller fauna may contain only the relatively pandemic taxa, and so would give anomalously high Simpson Coefficients; Jaccard Coefficients would consider the larger number of taxa absent from the smaller site, but present in the larger sample, hence giving a more realistic indicator of faunal dissimilarity.

Some problems do arise with the Jaccard Coefficient when applying it to areas in which one of the populations is rather small, which will be the case if one area is under-represented. In such a case, even if the smaller population contains all the faunal constituents of the larger area, the Jaccard Coefficient may still be relatively low :

If $S_c = T_1$ (with T_1 as the smaller population) then

$$\text{Jaccard Coefficient} = \frac{T_1}{T_1 + T_2 - T_1}$$

$$\text{Thus, Jaccard Coefficient} = \frac{T_1}{T_2}$$

Even though the Simpson Coefficient would give a correlation of 1.000 in the above instance, the Jaccard Coefficient will only be equal to 1.000 if the number of taxa recorded in the two localities is exactly the same. In this study, for instance, a comparison of the fauna from North Ireland (with 59 bryozoan species) and Central Ireland (with only 11 recorded species) could not yield a Jaccard Coefficient greater than 0.186. However, the apparent observation that 48 species recorded in North Ireland are absent in Central Ireland could be construed as a significant difference between the two areas. Most probably, further study on the Central Ireland faunas would yield many more taxa which are represented in the North Ireland region.

At generic level, Bambach (1990) cites Simpson Coefficients up to 0.93 and Jaccard Coefficients of up to 0.70 for adjacent provinces. In this study, coefficients over 0.65 and 0.40 for the Simpson and Jaccard methods respectively, represent close similarity at specific level, but, for the reasons outlined above, it is not possible to cite absolute cutoff values for the coefficients. However, the following values give a guide to the Simpson Coefficient comparisons for correlation at specific level:

over 0.65 = high correlation
0.50-0.65 = moderate correlation
less than 0.50 = low correlation

For the Jaccard Coefficients, cutoff values are less easy to define, since the coefficient scale is more compressed, and is more affected by under-representation of faunas. However, the following values seem reasonable in most instances:

over 0.40 = high correlation
0.25-0.40 = moderate correlation
less than 0.25 = low correlation

These values were determined from the distribution data presented here, and are referable only to this study; cutoff values will depend on the quality of the source data, and the lack of bias over the area studied. Here, there is undoubtedly an under-representation of bryozoan data for all the areas, but since the distribution coefficients are internally consistent, these values may be regarded as good approximations for the available data set. Further, it is not the absolute values of the coefficients which is important, but the relative values of coefficients from different areas at the same time.

The analysis of distributions by similarity coefficients (phenetic biogeography) has several advantages over the alternative method of cladistic biogeography, which links geographical areas of species occurrence into hierarchical groups (reviewed in Newton, 1990). Not only do cladistical approaches limit the number of fossil groups and areas that can be analysed (Jablonski *et al.*, 1985), but widespread taxa, which are actually more abundant than endemic taxa, are only incorporated with some difficulty into such schemes. Thus, phenetic biogeographical methods remain the easiest approach to the analysis of the faunal similarities of geographical zones.

Faunal comparisons between areas were calculated at two levels; species correlations using the Simpson Coefficient for separate Dinantian and Lower Silesian stages (Courceyan to Arnsbergian), and correlations at both specific and generic levels with the Simpson and Jaccard Coefficients for the Dinantian to Lower Silesian as one time unit. The Dinantian to Lower Silesian time unit is rather long, being about 35-40 million years in length. However, Bambach (1990), in his study on Late Palaeozoic Marine Provinciality, points out that the larger the time scale used, the less likely a taxon is to remain endemic to just one region. Thus, there is less chance of showing regional differences over such a large time scale, compared to comparisons at stage level. Balanced against this, comparisons in this study at stage level suffer from a lack of data from all the areas concerned. For instance, only 27 species of bryozoan are recorded from three areas (out of nine) in the Courceyan. Only the Asbian has data from all nine areas of study, and the distribution pattern closely parallels that of the large Dinantian to lower Silesian time unit.

Figs. 12.4 and 12.14 to 12.16 show the coefficients of similarity for the nine areas outlined, at generic and specific level, calculated from the geographical and time range table (fig. 12.3) for 126 Carboniferous bryozoan species and 40 genera.

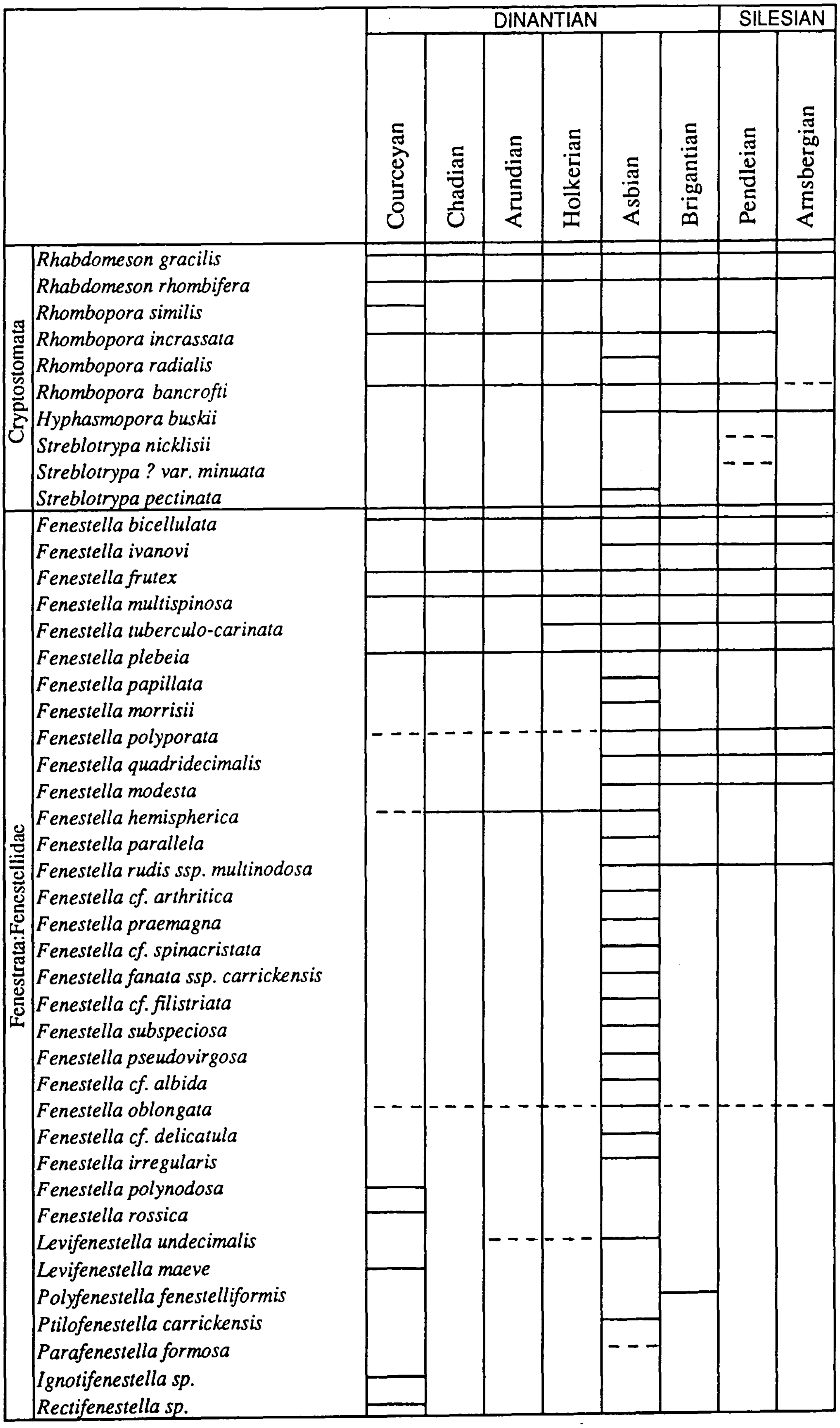


Fig. 12.2. Stratigraphical ranges of British Carboniferous Bryozoa (from data in fig. 12.3)

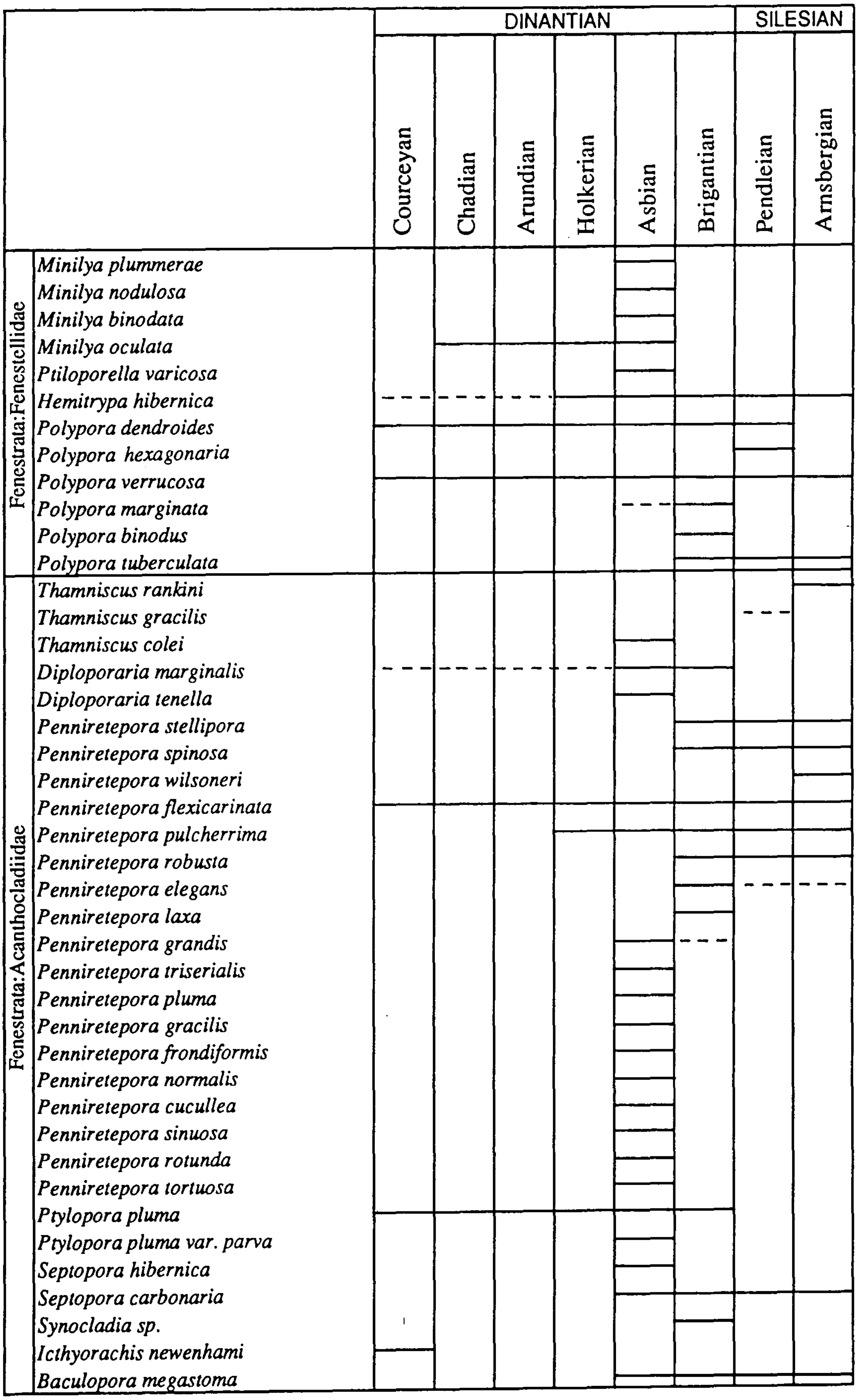


Fig. 12.2. (continued)

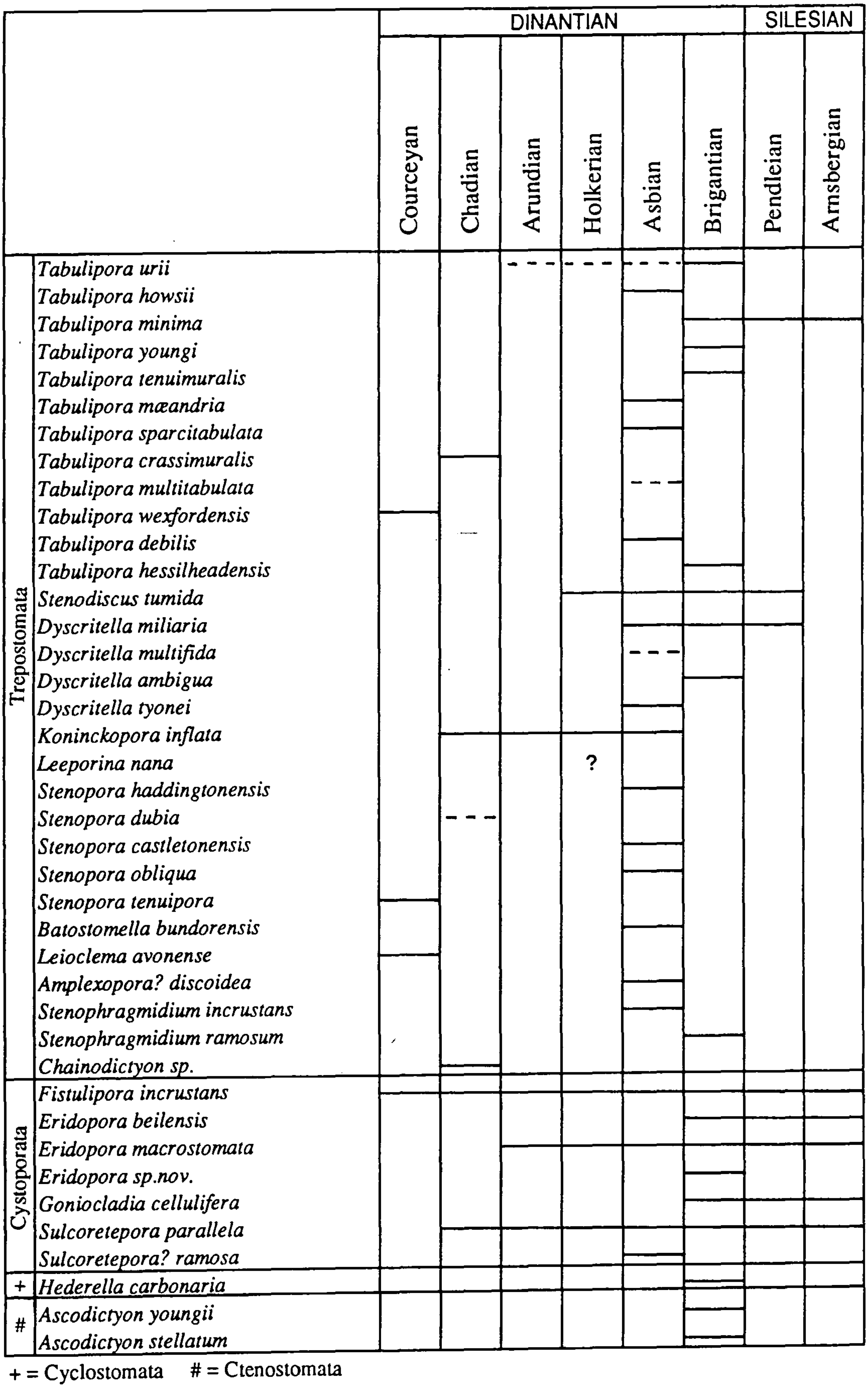


Fig. 12.2. (continued)

ZONE	1	2	3	4	5	6	7	8	9
	Midland Valley	Northumberland Dumfries & I.O.M.	Pennines & Cumbria	Derbyshire	North Wales	South Wales & Devon	Northern Ireland	Central Ireland	Southern Ireland
Rhabdomeson gracilis	As-Br	As-Pe	As-Arn	?	Br	Co?-Ho?	As	?	Co-As
Rhabdomeson rhombifera	As-Br	As-Br	Arn	?	Br	Co	As		
Rhombopora similis						Co			
Rhombopora incrassata	Br	Pe				Co			
Rhombopora radialis				As					
Rhombopora bancrofti	Br	As-Br	As-Arn		Br	Br		Co-Ho	Co
Hyphasmopora buskii		As-Pe	Arn?						
Streblotrypa nicklisii	Pe?	Pe?	Pe?						
Streblotrypa ? var. minuata	Pe?	Pe?	Pe?						
Streblotrypa pectinata				As					
Fenestella bicellulata	As-Br	As-Br	Aru-Arn	?	Br	Co	?	?	
Fenestella ivanovi		As?	Arn						
Fenestella frutex	Br	As-Pe	As-Arn		Br	Co-Br	Aru-As		Co
Fenestella multispinosa	As-Arn?	As-Pe	As-Arn	As	As-Br	Co-Ho	Ho-As	?	Co
Fenestella tuberculo-carinata	As-Arn	Br-Pe	Ho?-Arn						
Fenestella plebeia	As-Br	As-Pe	Ch-Arn	Co?As-B	Br	Co-Br	As	Co-As	Co
Fenestella papillata							As		
Fenestella morrisii	As								
Fenestella polyporata	Br	Br	As-Arn	As	Br		As		Co?, As
Fenestella quadridecimalis	Arn		Arn				As		
Fenestella modesta	?Br		?Arn	?Ar			As		
Fenestella hemispherica			?Ch				As		
Fenestella parallela							As		
Fenestella rudis ssp. multinodosa			?Arn				As		
Fenestella cf. arthritica							As		
Fenestella praemagna							As		
Fenestella fanata ssp. carrickensis							As		
Fenestella cf. spinacristata							As		
Fenestella cf. filistriata							As		
Fenestella subspeciosa							As		
Fenestella pseudovirgosa							As		
Fenestella cf. albida							As		
Fenestella oblongata			?Arn				As		?Co
Fenestella cf. delicatula				?As			As		
Fenestella irregularis							As		
Fenestella polynodosa									Co
Fenestella rossica									Co
Levifenestella undecimalis			?Aru					As	
Levifenestella maeve									Co
Polyfenestella fenestelliformis		Br							
Ptilofenestella carrickensis							As		
Parafenestella formosa							?As		
Ignotifenestella sp.						Co			
Rectifenestella sp.									Co

Fig. 12.3. Geographical distributions of British Carboniferous Bryozoa

ZONE	1	2	3	4	5	6	7	8	9
	Midland Valley	Northumberland Dumfries & I.O.M.	Pennines & Cumbria	Derbyshire	North Wales	South Wales & Devon	Northern Ireland	Central Ireland	Southern Ireland
Minilya plummerae			As				As		
Minilya nodulosa			As				As		
Minilya binodata							As		
Minilya oculata			Ch				As		
Ptiloporella varicosa							As		
Hemitrypa hibernica		As-Arn	Aru-As	As	Co?, As		Ch?-As	As?	Ho-As
Polypora dendroides	Br		Pe		Br	Co-Ch	As	Co	Co
Polypora hexagonaria		Pe							
Polypora verrucosa	Br?	Br	Br-Arn		Br	Co-Br	As	Co	?
Polypora marginata				?As			Br		
Polypora binodus	Br								
Polypora tuberculata	Br-Arn								
Thamniscus rankini	Arn								
Thamniscus gracilis			Pe?						
Thamniscus colei							As		
Diploporaria marginalis	Br-Arn?	As-Br	As-Br	?Aru	Br				?Co
Diploporaria tenella							As		
Penniretepora stellipora	Br-Arn		Arn						
Penniretepora spinosa	Br		As-Arn		Br				
Penniretepora wilsoneri	Arn								
Penniretepora flexicarinata	Br	As-Br	Br-Arn		Br	Co-Br	?As		
Penniretepora pulcherrima	Br-Arn	As	Br-Arn		Br		Ho-As		?Ho
Penniretepora robusta	Br-Arn		Br						
Penniretepora elegans	Br-Arn?		Arn?		Br				
Penniretepora laxa	Br		Br		Br				
Penniretepora grandis				?	?Br			As	?
Penniretepora triserialis				As					
Penniretepora pluma							As		
Penniretepora gracilis							As		
Penniretepora frondiformis							As		
Penniretepora normalis							As		
Penniretepora cucullea							As		
Penniretepora sinuosa							As		
Penniretepora rotunda							As		
Penniretepora tortuosa							As		
Ptylopora pluma	Br		Ch-Br	As	As-Br	Ch-Br		Co-Ch	Co-Ho
Ptylopora pluma var. parva							As		
Septopora hibernica							As		
Septopora carbonaria	Br-Arn	As-Pe			Br				
Synocladia sp.	Br	Br							
Icthyorachis newenhami									Co
Baculopora megastoma			Arn		?Br		As	?	

Fig. 12.3. (continued)

ZONE	1	2	3	4	5	6	7	8	9
	Midland Valley	Northumberland Dumfries & I.O.M.	Pennines & Cumbria	Derbyshire	North Wales	South Wales & Devon	Northern Ireland	Central Ireland	Southern Ireland
Tabulipora urii	Br	Br			Br	Br	?Aru?		
Tabulipora howsii	As	As	As		?		As		
Tabulipora minima	Br	As	Arn						
Tabulipora youngi	Br								
Tabulipora tenuimuralis			Br						
Tabulipora mæandria			As						
Tabulipora sparcitabulata	As	As				As			
Tabulipora crassimuralis						Ch			
Tabulipora multitabulata			As?						
Tabulipora wexfordensis									Co
Tabulipora debilis			As						
Tabulipora hessilheadensis	Br								
Stenodiscus tumida	As	As-Pe	As		As	Ho-Br			
Dyscritella miliaria	Br	As-Pe	As						
Dyscritella multifida								As?	
Dyscritella ambigua						Br			
Dyscritella tyonei							As		
Koninckopora inflata			As			Ch			
Leeporina nana			?						
Stenopora haddingtonensis	As								
Stenopora dubia							Ch?		
Stenopora castletonensis				As					
Stenopora obliqua		As							
Stenopora tenuipora						Co			
Batostomella bundorensis							As		
Leioclema avonense						Co			
Amplexopora? discoidea				As					
Stenophragmidium incrustans							As		
Stenophragmidium ramosum	Br								
Chainodictyon sp.				Ch					
Fistulipora incrustans	Br-Pe?	As-Pe	Ch-Arn	Aru-As	Br	Co-Ho	As	Ch-As?	Co
Eridopora beilensis	?Br	Pe	Arn		Br				
Eridopora macrostomata			Aru-Arn		?Br				
Eridopora sp.nov.	Br								
Goniocladia cellulifera	Br-Arn		Br-Arn		Br		As		
Sulcoretepora parallela	Br	As-Br	Ho-Arn	Aru?-As	Br	Ch-Ho	Aru		
Sulcoretepora? ramosa							As		
Hederella carbonaria			Br		Br?				
Ascodictyon youngii	Br								
Ascodictyon stellatum	Br								

Fig. 12.3. (continued)

Simpson Coefficient for Courceyan-Arnsbergian interval at species level

Data within this table is internally consistent, with a general pattern of more widely-separated areas having lower coefficients of similarity. Taking such a wide time interval allows for a statistically large number of species to be included in each area of comparison, with the numbers recorded ranging from 59 in North Ireland to 11 in Central Ireland. Thus, though there are undoubtedly many species which do occur in some regions but are not recorded, the samples presented here are large enough to lessen the effect of under-representation.

Within the tables the figures in light type in the top and left-hand margins indicate the total number of bryozoan species recorded in that area. Light figures in the central portion of the table record the number of species in common between the corresponding areas, and the bold numbers give the correlation coefficients. Average coefficients for each area are given in light type in the right hand column.

Plots of the coefficients for each of the areas are given in figs. 12.5 to 12.13.

COURCEYAN - ARNSBERGIAN	1 48	2 33	3 52	4 16	5 30	6 24	7 59	8 11	9 22	x
1 **Midland Valley** 48		**0.788** 26	**0.667** 32	**0.375** 6	**0.833** 25	**0.667** 16	**0.333** 16	**0.636** 7	**0.545** 12	0.606
2 **Northumberland, Dumfries, & Isle Of Man** 33	**0.788**		**0.758** 25	**0.313** 5	**0.667** 20	**0.583** 14	**0.455** 15	**0.545** 6	**0.455** 10	0.571
3 **Pennines & Cumbria** 52	**0.667**	**0.758**		**0.467** 7	**0.900** 27	**0.625** 15	**0.500** 26	**0.818** 9	**0.636** 14	0.543
4 **Derbyshire** 16	**0.375**	**0.313**	**0.467**		**0.438** 7	**0.188** 3	**0.438** 7	**0.364** 4	**0.375** 6	0.367
5 **North Wales** 30	**0.833**	**0.667**	**0.900**	**0.438**		**0.625** 15	**0.567** 17	**0.909** 10	**0.591** 13	0.691
6 **South Wales & South West England** 24	**0.667**	**0.583**	**0.625**	**0.188**	**0.625**		**0.458** 11	**0.636** 7	**0.364** 8	0.518
7 **North Ireland** 59	**0.333**	**0.455**	**0.500**	**0.438**	**0.567**	**0.458**		**0.727** 8	**0.591** 13	0.508
8 **Central Ireland** 11	**0.636**	**0.545**	**0.818**	**0.364**	**0.909**	**0.636**	**0.727**		**0.727** 8	0.670
9 **South Ireland** 22	**0.545**	**0.455**	**0.636**	**0.375**	**0.591**	**0.364**	**0.591**	**0.727**		0.536

n 36
x 0.573
s 0.177

Fig. 12.4. Simpson's coefficients at Specific Level

The Midland Valley

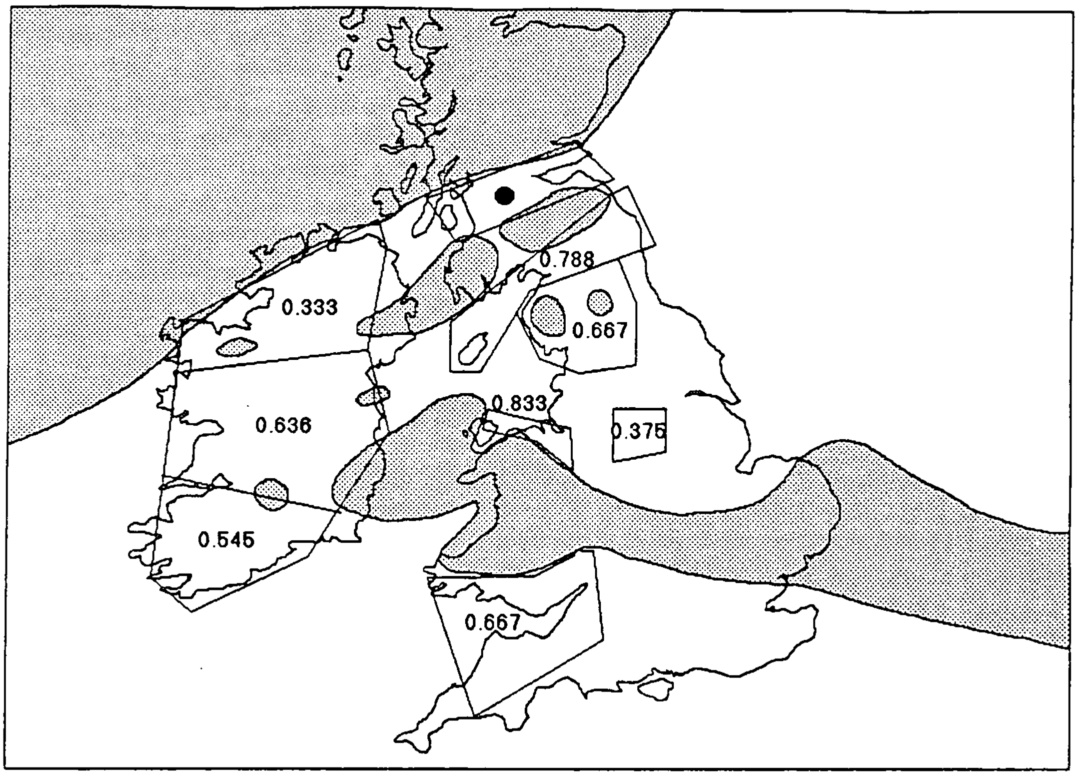


Fig. 12.5. Simpson Coefficients at specific level for the Midland Valley

The Midland Valley region shows high Simpson Coefficients with the adjacent areas of Northumberland and the Pennines region, but has a very low coefficient with North Ireland, despite being adjacent, and seemingly connected by a seaway. Moderate similarities exist with Central and Southern Ireland, and there are relatively high values when compared with South Wales. The North Wales fauna shows a very high coefficient of similarity, while comparisons with Derbyshire yield the lowest correlation score.

Northumberland, Dumfries, and the Isle Of Man

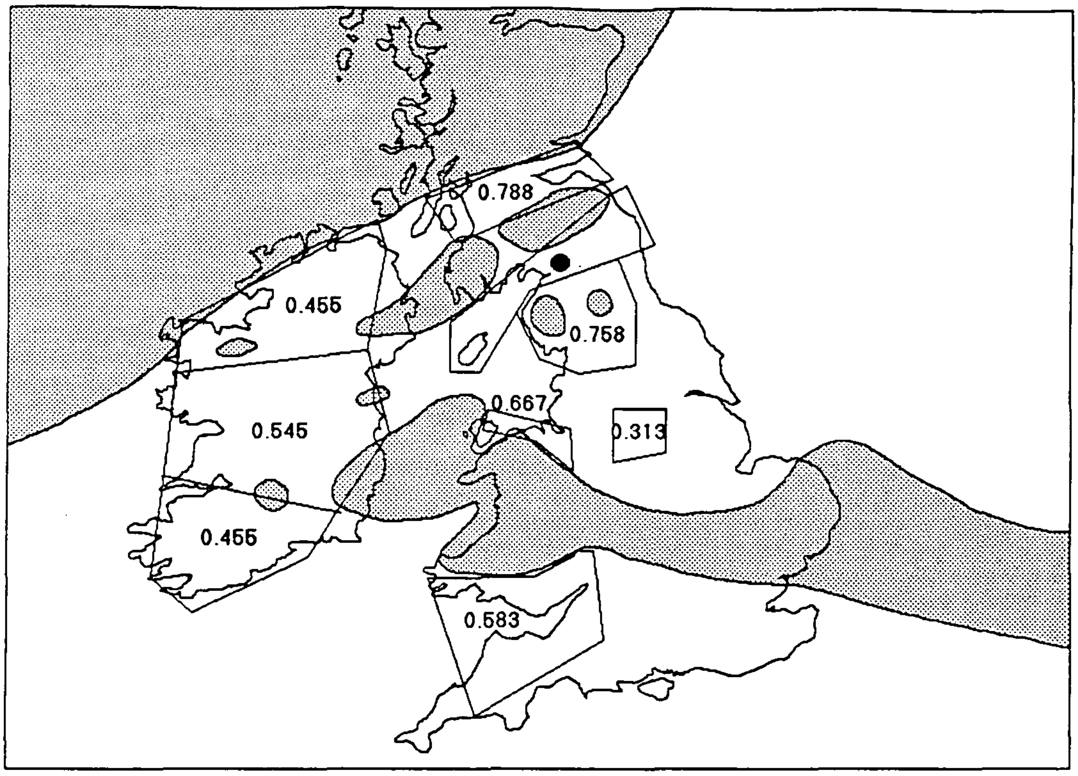


Fig. 12.6. Simpson Coefficients at specific level for the Northumberland Region

The Northumberland region has high coefficients of similarity with the adjacent regions of the Midland Valley and the Pennines. High, but slightly lower correlations also exist with North Wales, and there are moderate Simpson Coefficients of similarity with South Wales and Central Ireland. Fairly low correlations exist between Northumberland and North and South Ireland, and the lowest score occurs with Derbyshire.

Pennines Region and Cumbria

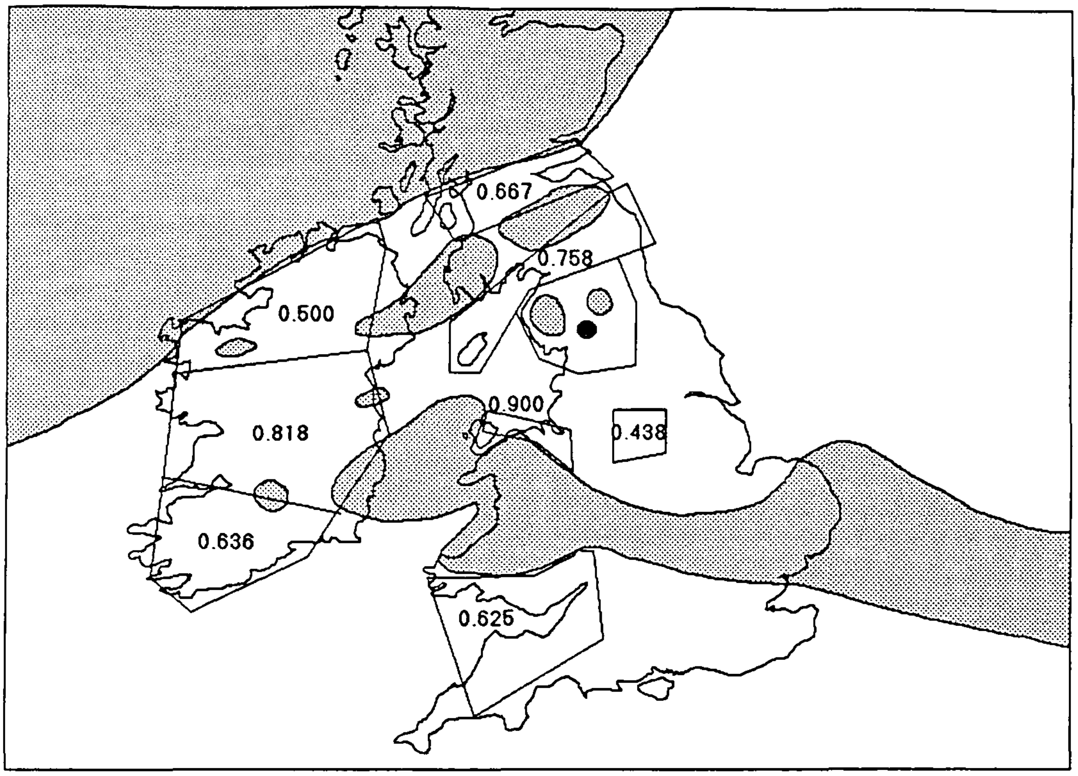


Fig. 12.7. Simpson Coefficients at specific level for the Pennines Region

The Pennines district has its highest correlations with the proximal areas of North Wales, Central Ireland, and Northumberland; of these, the North Wales score is exceptionally high, being 0.900. Lower, but still relatively high correlations also exist between the Pennines and the Midland Valley and South Ireland. Comparisons with North Ireland yielded a moderate Simpson Coefficient, but Derbyshire returned the lowest score.

Derbyshire

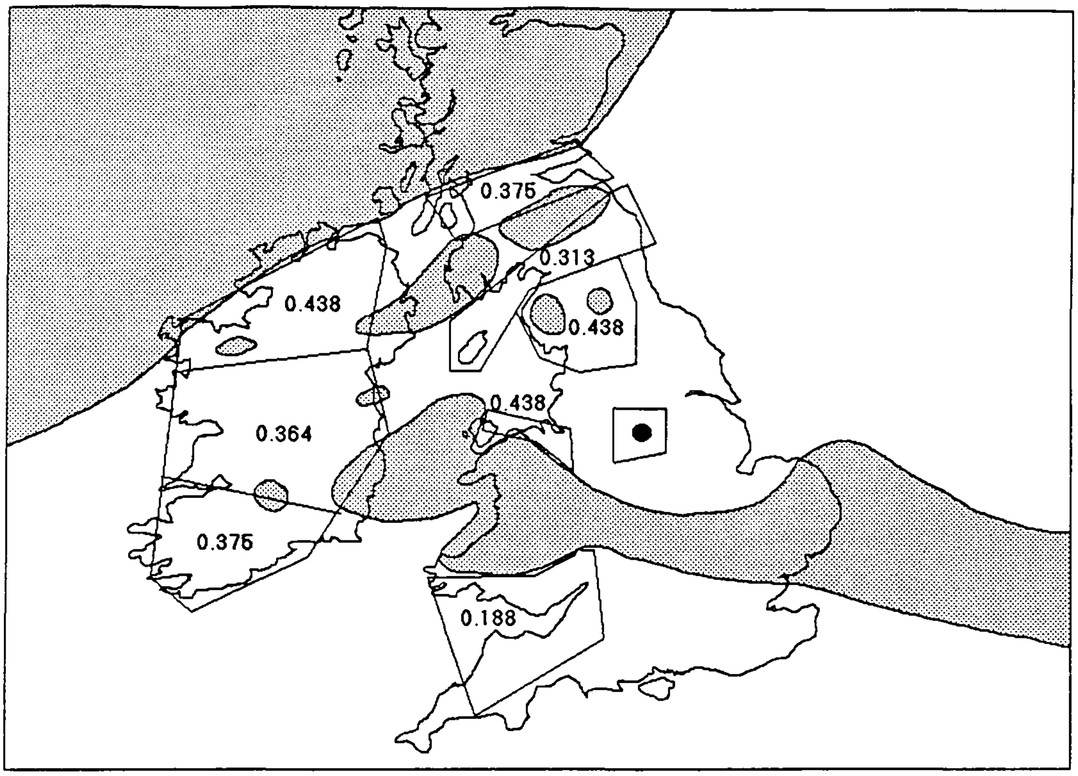


Fig. 12.8. Simpson Coefficients at specific level for Derbyshire

The Derbyshire district has very low coefficients of similarity with all the other areas; the average similarity score is only 0.367 at specific level. The highest correlations exist with the adjacent areas of North Wales and the Pennines, though North Ireland has an equally high coefficient. Lower coefficients are returned by the remaining areas, and the lowest score is that between Derbyshire and South Wales (0.188).

North Wales

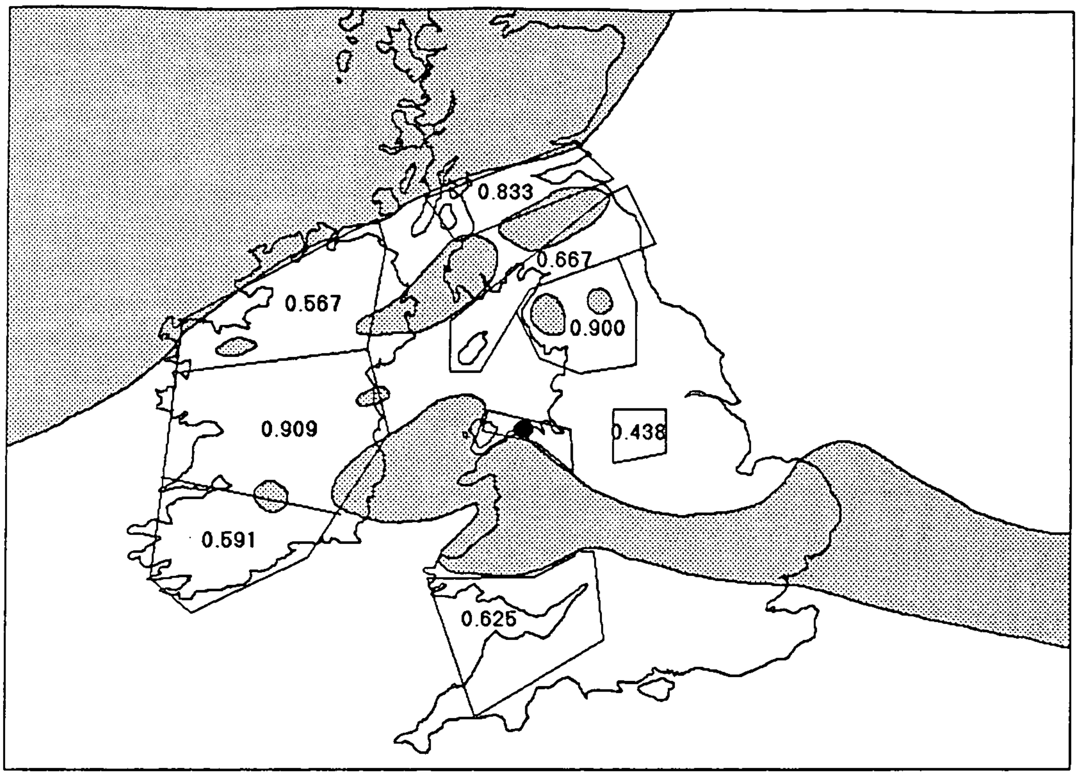


Fig. 12.9. Simpson Coefficients at specific level for North Wales

North Wales has its highest similarity coefficients with the Pennines region and Central Ireland, both being adjacent areas, and both having coefficients over 0.900. There are relatively high scores with Northumberland and South Wales, and a rather high comparison with the Midland Valley. Moderate correlations are recorded with North and South Ireland, but the lowest coefficient of similarity exists between North Wales and Derbyshire.

South Wales and South West England

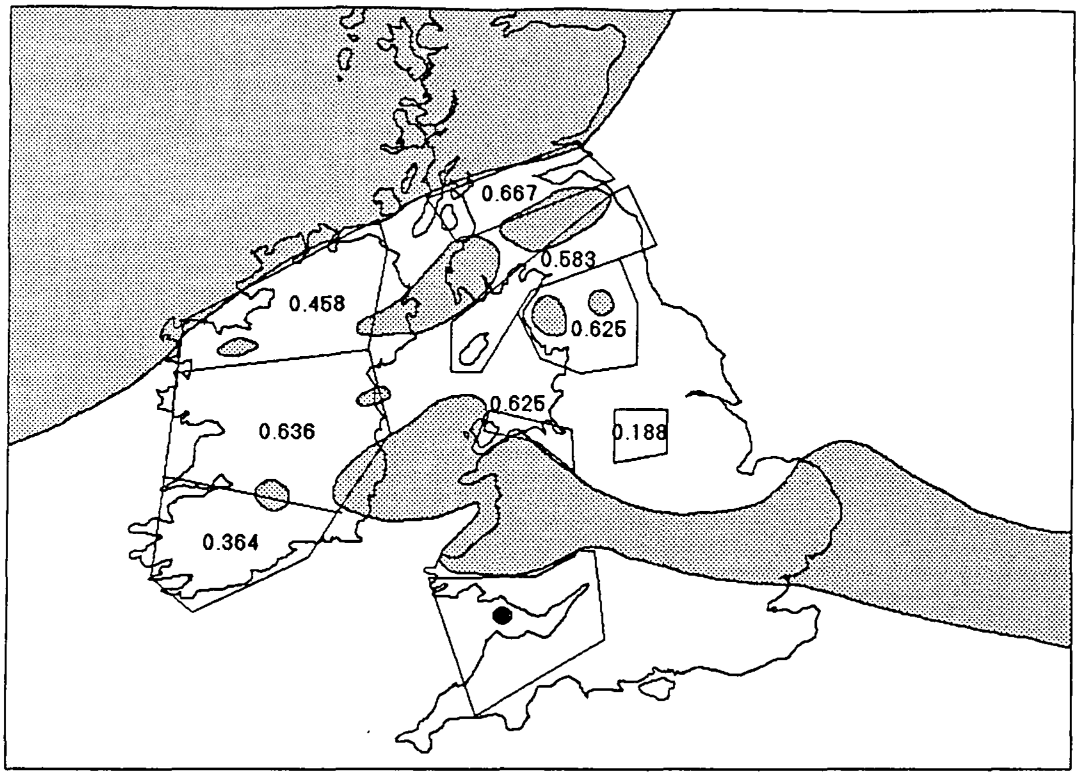


Fig. 12.10. Simpson Coefficients at specific level for the South Wales Region

This region shows an anomalous coefficient in that the highest correlation is with the Midland Valley; intervening areas, namely Northumberland, the Pennines and North Wales do return high coefficients of similarity, but not as pronounced as that of the Midland Valley. Despite its proximity, South Ireland has a low Simpson Coefficient, and the South Wales fauna shows more affinity with that from the Central Ireland region. Moderately low comparisons exist with North Ireland, and the lowest similarity score is returned by Derbyshire.

North Ireland

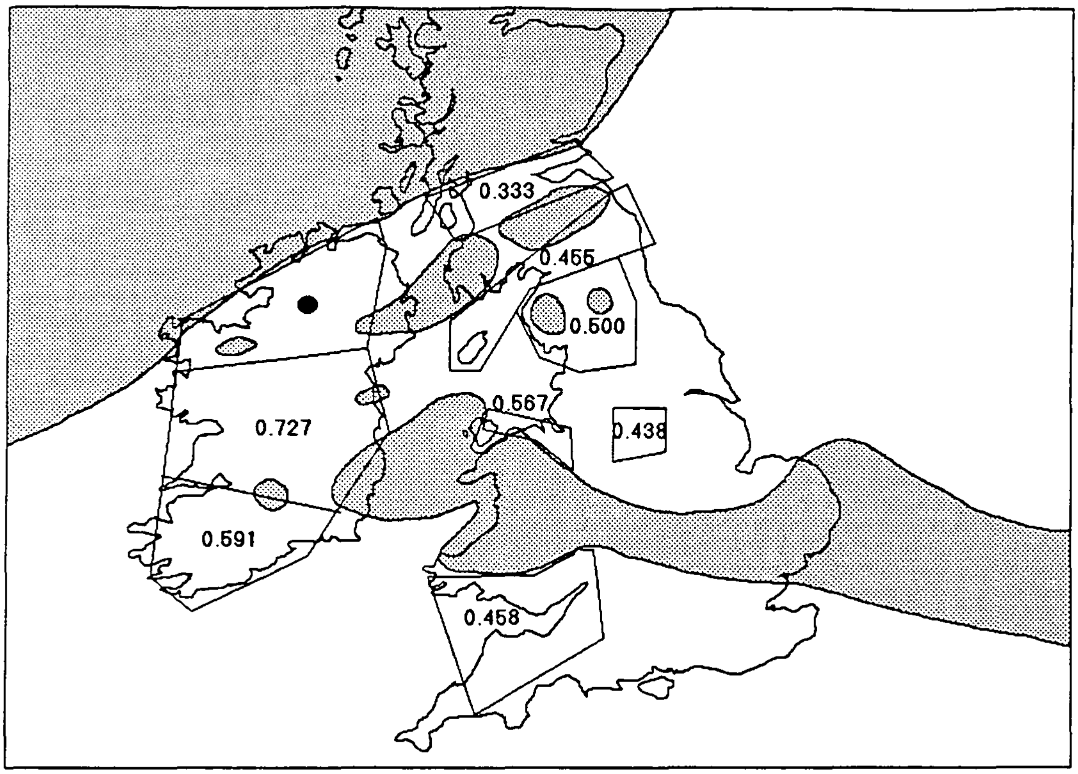


Fig. 12.11. Simpson Coefficients at specific level for North Ireland

North Ireland has its greatest similarities with the faunas of Central and Southern Ireland, the highest coefficient being shown by the adjacent area of Central Ireland. Moderate correlations exist with North Wales and the Pennines district, but moderately low scores are returned by South Wales, Northumberland and Derbyshire. The lowest comparison was actually between North Ireland and the Midland Valley.

Central Ireland

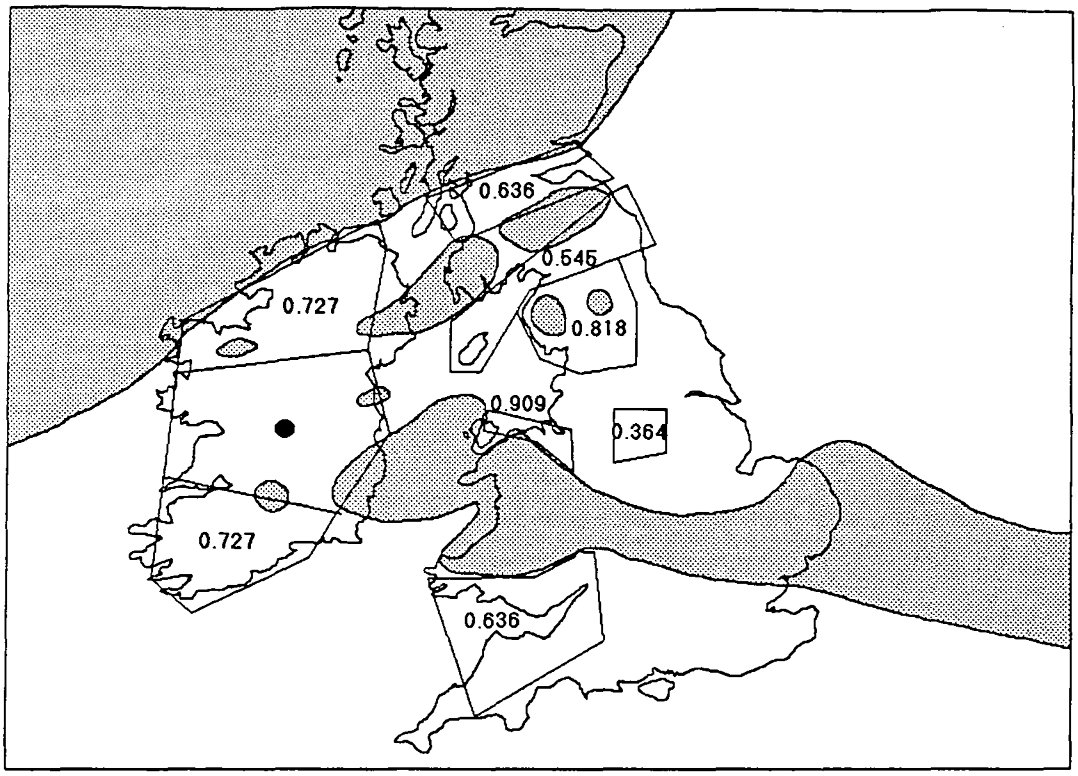


Fig. 12.12. Simpson Coefficients at specific level for Central Ireland

Central Ireland shows very high coefficients of similarity with North Wales and the Pennines region, scores being 0.909 and 0.818 respectively. Very high scores are also recorded with the other adjacent regions, North and South Ireland, which both have coefficients of 0.727. Relatively high correlations occur with South Wales and the Midland Valley, and there is a moderate score between Central Ireland and Northumberland. By far the lowest score exists with Derbyshire.

South Ireland

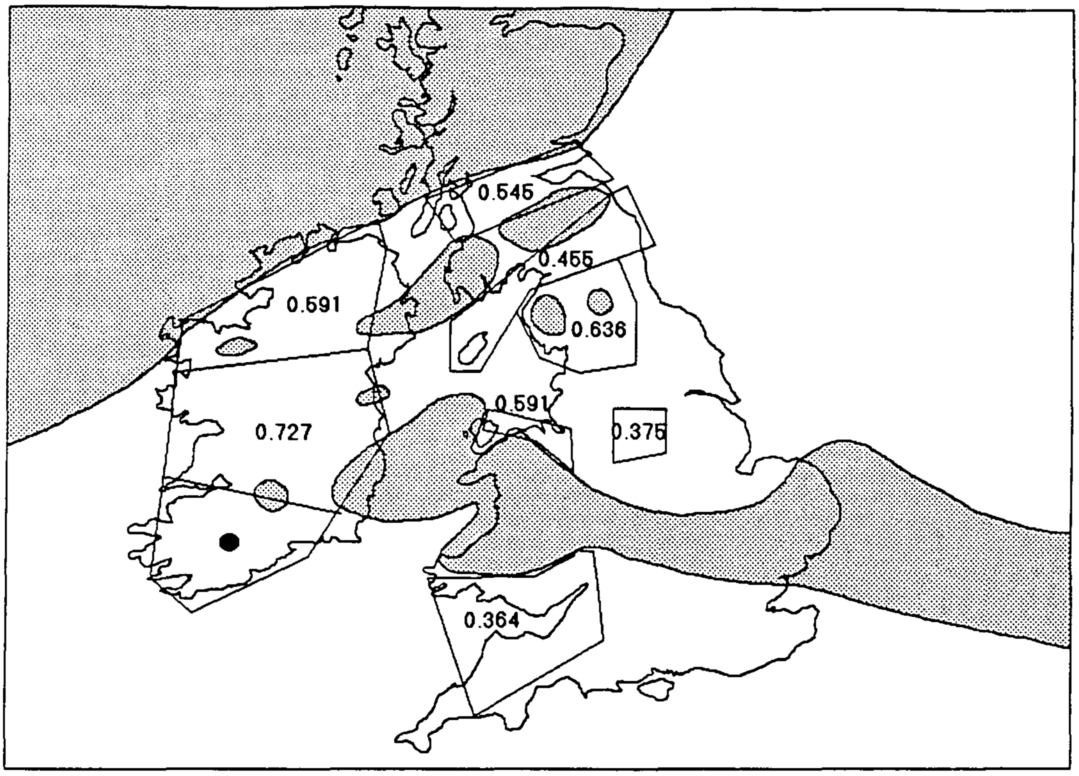


Fig. 12.13. Simpson Coefficients at specific level for South Ireland

South Ireland has its highest coefficient of similarity with Central Ireland, and a slightly lower score with the fauna of the Pennines. Moderately high scores also exist between South Ireland and North Wales and North Ireland. There is a moderate correlation with the faunas of the Midland Valley and a lower score with the Northumberland region. The lowest correlations occur with Derbyshire and, surprisingly, South Wales.

Jaccard Coefficient for Courceyan-Arnsbergian interval at species level

A similar spread to the Simpson Coefficient is found (fig. 12.14), though there are some slight differences:

The Midland Valley again has its strongest faunal affinities with Northumberland, the Pennines and North Wales, and there are lower correlations with South Wales and Derbyshire. Low scores are obtained for all the Ireland regions.

Northumberland has rather high Jaccard Coefficients when compared with the Midland Valley, the Pennines region, and North Wales, with a slightly lower correlation score for South Wales. Low correlations are recorded against Derbyshire and the Irish regions, though of these, South Ireland returned the highest coefficient.

The Pennines region scores highest in comparisons with the Midland Valley, the Northumberland region, and North Wales. There are moderate correlations with North Ireland, South Wales, and South Ireland, but in contrast to the Simpson Coefficient results, there is a relatively low score with Central Ireland. Derbyshire yielded the lowest correlation score.

Derbyshire faunas gave rather low Jaccard Coefficients with all areas. Though one of the highest correlations was with North Wales, in contrast to the Simpson Coefficient data, the highest score was with the Midland Valley. Interestingly, North Ireland yielded the second highest correlation, in accordance with the Simpson Coefficient data. Also agreeing with the Simpson Coefficient results was the observation that the lowest Derbyshire score was with South Wales.

North Wales scores most highly with the Midland Valley, Northumberland, and the Pennines region. Only a moderate score was obtained with Central Ireland, but this was actually the highest correlation for the Central Ireland region. Moderate scores also exist between North Wales and South Wales and South Ireland, but North Ireland and Derbyshire gave lower correlations.

The South Wales region has its highest correlations with North Wales and the Northumberland district. Moderate scores exist with the Midland Valley, the Pennines, and Central and South Ireland, but again there are greater affinities with the Central Ireland faunas than with those of South Ireland. The lowest correlations were returned by North Ireland and Derbyshire.

North Ireland shows greatest affinities with North Wales and the Pennines region, which yielded moderate correlations with the Simpson Coefficient. Other areas give rather low correlations, and unlike the results with the Simpson Coefficient, Central and South Ireland do not give high coefficients of similarity. The lowest correlation is with Derbyshire.

COURCEYAN - ARNSBERGIAN	1 48	2 33	3 52	4 16	5 30	6 24	7 59	8 11	9 22	x
1 Midland Valley 48		0.473 26	0.471 32	0.250 6	0.566 25	0.286 16	0.176 16	0.135 7	0.207 12	0.321
2 Northumberland, Dumfries, & Isle Of Man 33	0.473		0.417 25	0.114 5	0.465 20	0.326 14	0.195 15	0.158 6	0.222 10	0.296
3 Pennines & Cumbria 52	0.471	0.417		0.115 7	0.491 27	0.246 15	0.306 26	0.167 9	0.233 14	0.306
4 Derbyshire 16	0.250	0.114	0.115		0.179 7	0.081 3	0.103 7	0.174 4	0.188 6	0.151
5 North Wales 30	0.556	0.465	0.491	0.179		0.385 15	0.236 17	0.323 10	0.333 13	0.371
6 South Wales & South West England 24	0.286	0.326	0.246	0.081	0.385		0.153 11	0.250 7	0.211 8	0.242
7 North Ireland 59	0.176	0.195	0.306	0.103	0.236	0.153		0.129 8	0.191 13	0.186
8 Central Ireland 11	0.135	0.158	0.167	0.174	0.323	0.250	0.129		0.320 8	0.207
9 South Ireland 22	0.207	0.222	0.233	0.188	0.333	0.211	0.191	0.320		0.238

n 36
x 0.258
s 0.123

Fig. 12.14 **Jaccard coefficients at Specific Level**

Central Ireland , like North Ireland, has relatively low Jaccard Coefficients of similarity with all areas, but the highest correlations are with North Wales, South Ireland, and South Wales, in agreement with the Simpson Coefficient data, save for the lower correlation coefficient with the Pennines region. The other areas have much lower coefficients, and there is little to separate them.

South Ireland has relatively high Jaccard Coefficients with Central Ireland and North Wales. The remaining areas all have coefficients of about 0.200, though of these, the highest is the Pennines region, in a pattern similar to that of the Simpson Coefficient results, and the lowest is with Derbyshire.

The coefficient distributions using the Jaccard Coefficient are, in general, similar to those of the Simpson Coefficient. The Jaccard method, though, may be more sensitive to under-representation, as illustrated by the relatively low scores for Central Ireland, which has the lowest number of recorded bryozoan species. However, there is not a correlation between the average Jaccard Coefficient and the size of the sample; the second lowest average coefficient, in fact, was that of North Ireland, which has the largest fauna.

The Jaccard method and the Simpson method both show similar patterns regarding the average coefficients for each area. Though there is some variation in the exact order, the highest coefficients are shown by North Wales, the Midland Valley, and Northumberland, and the lowest are given by North Ireland and Derbyshire. Central Ireland is the only anomalous area, having the second highest Simpson Coefficient, but the third lowest Jaccard Coefficient; this is most probably due to under-representation, since only 11 species are recorded. Thus, there is a greater chance of high Simpson Coefficients, since only the common British forms have been noted in the region: Jaccard Coefficients, by contrast, will probably never be high, since all the other regions have significantly larger populations, thus lowering the coefficients of similarity.

Correlations at generic level

Coefficients of correlation at generic level are, in all cases, higher than the corresponding coefficients at specific level. In a natural population, this is to be expected, since for higher correlations at specific level, the following condition must hold true for both the Jaccard and the Simpson Coefficients:

$$\frac{S_c}{T_s} > \frac{G_c}{T_g}$$

where

S_c= Species in common
G_c= Genera in common
T_s= Total number of species
T_g= Total number of genera

This condition is difficult to achieve in natural populations, since it involves virtually all the species in common belonging to one or two genera, with the remaining genera represented by only one species.

Both the Jaccard Coefficients and the Simpson Coefficients show a greater degree of similarity between the areas at generic level. Not only are the coefficient values higher, as would be expected normally, but the standard deviations of the coefficients are significantly lower; at specific level, the high degree of variation was shown by standard deviations of σ=0.177 for the Simpson Coefficient, and σ=0.123 for the Jaccard Coefficient: at generic level, σ was only 0.095 and 0.085 respectively, despite much higher average coefficients. Thus, differences in the bryozoan distributions between the areas are not as obvious at generic level, and the results are also more susceptible to the smaller figures involved by grouping the species into a statistically small set of genera.

However, within these limitations the distribution patterns bear many resemblances to those seen at specific level (figs. 12.15 and 12.16). The clearest results are outlined below:

The Midland Valley has its highest correlations with Northumberland and the Pennines, but lower correlations with North Ireland, though the Jaccard Coefficient for the latter area shows a moderate similarity.

The Pennines region has its greatest affinities with North Wales, though the data for other areas is not as clear using the Simpson Coefficient.

Derbyshire has relatively low matches with all areas.

North Ireland has its best matches with North Wales, Central Ireland and the Pennines region, though the match with the Midland Valley is also rather high with the Jaccard Coefficient.

South Ireland has high matches with North Wales, the Pennines, and Central Ireland.

Though there are some regional differences, there is a relatively high degree of faunal similarity between all the areas at generic level.

COURCEYAN - ARNSBERGIAN	1 21	2 19	3 24	4 11	5 17	6 15	7 21	8 10	9 12	x
1 Midland Valley 21	▒	**0.789** 15	**0.762** 16	**0.727** 8	**0.824** 14	**0.800** 12	**0.619** 13	**0.800** 8	**0.667** 8	0.749
Northumberland, **2 Dumfries,** **19 & Isle Of Man**	**0.789**	▒	**0.789** 15	**0.727** 8	**0.765** 13	**0.738** 11	**0.558** 10	**0.800** 8	**0.667** 8	0.729
3 Pennines & Cumbria 24	**0.762**	**0.789**	▒	**0.727** 8	**0.941** 16	**0.800** 12	**0.714** 15	**1.000** 10	**0.833** 10	0.821
4 Derbyshire 11	**0.727**	**0.727**	**0.727**	▒	**0.727** 8	**0.636** 7	**0.818** 9	**0.600** 6	**0.727** 7	0.711
5 North Wales 17	**0.824**	**0.765**	**0.941**	**0.727**	▒	**0.667** 10	**0.647** 11	**0.900** 9	**0.750** 9	0.778
South Wales & **6 South West England** 15	**0.800**	**0.738**	**0.800**	**0.636**	**0.667**	▒	**0.600** 9	**0.800** 8	**0.727** 7	0.721
7 North Ireland 21	**0.619**	**0.558**	**0.714**	**0.818**	**0.647**	**0.600**	▒	**0.900** 9	**0.750** 9	0.701
8 Central Ireland 10	**0.800**	**0.800**	**1.000**	**0.600**	**0.900**	**0.800**	**0.900**	▒	**0.700** 7	0.813
9 South Ireland 12	**0.667**	**0.667**	**0.833**	**0.727**	**0.750**	**0.727**	**0.750**	**0.700**	▒	0.728

n 36
x 0.750
s 0.095

Fig. 12.15 Simpson's Coefficients at Generic Level

COURCEYAN - ARNSBERGIAN	1 21	2 19	3 24	4 11	5 17	6 15	7 21	8 10	9 12	x
1 Midland Valley 21		0.600 15	0.552 16	0.333 8	0.583 14	0.500 12	0.448 13	0.348 8	0.320 8	0.461
2 Northumberland, Dumfries, & Isle Of Man 19	0.600		0.536 15	0.364 8	0.565 13	0.478 11	0.333 10	0.381 8	0.348 8	0.451
3 Pennines & Cumbria 24	0.552	0.536		0.296 8	0.640 16	0.444 12	0.500 15	0.417 10	0.385 10	0.471
4 Derbyshire 11	0.333	0.364	0.296		0.400 8	0.368 7	0.391 9	0.400 6	0.438 7	0.374
5 North Wales 17	0.583	0.565	0.640	0.400		0.455 10	0.407 11	0.500 9	0.450 9	0.500
6 South Wales & South West England 15	0.500	0.478	0.444	0.368	0.455		0.333 9	0.471 8	0.350 7	0.425
7 North Ireland 21	0.448	0.333	0.500	0.391	0.407	0.333		0.409 9	0.375 9	0.400
8 Central Ireland 10	0.348	0.381	0.417	0.400	0.500	0.471	0.409		0.467 7	0.424
9 South Ireland 12	0.320	0.348	0.385	0.438	0.450	0.350	0.375	0.467		0.392

n 36
x 0.433
s 0.085

Fig. 12.16 Jaccard Coefficients at Generic Level

Correlations between the areas for individual stages

Simpson Coefficients were calculated at species level for all the areas over each of the stages from the Courceyan to the Arnsbergian (figs. 12.17 to 12.24). Splitting the data into such small packages has the danger of manipulating very small populations, which can yield some anomalous results, and highlights the under-representation of certain areas. The data does, though, mirror the onset of marine conditions at different times in different areas during the Carboniferous. Indeed, only the Asbian has data from all nine areas under study, and though this shows a similar pattern to the results over all the stages combined, the results from Central and South Ireland are anomalously different, showing a very low correlation with North Wales.

One interesting result is the changes in the average values of the Simpson Coefficient through the Carboniferous :

Stage	Coefficient	Data Points	Species
Courceyan	0.622	3	27
Chadian	0.217	15	19
Arundian	0.356	15	16
Holkerian	0.419	15	17
Asbian	0.484	36	85
Brigantian	0.552	21	48
Pendleian	0.500	3	33
Arnsbergian	0.179	3	35

The number of data points refers to the maximum number of coefficients which can be calculated for each stage. For example, the Chadian has data from 6 of the 9 areas, so a maximum of 15 coefficients can be calculated between these 6 areas.

The number of species refers to the total recorded from all nine areas for that particular stage.

It is clear that there is not a direct relationship between the total number of species recorded, and the Simpson Coefficient, nor with the number of data points. However, for those stages which have only 3 data points, the corresponding average coefficients cannot be considered statistically secure.

There appears to be an increase in the average Simpson Coefficient from the Chadian to the Brigantian, suggesting increased bryozoan distributions. Though this trend is inferred from only five stages, it echoes the changes in global generic level bryozoan patterns, which show an increase in both diversity and distribution during the Lower Carboniferous (Ross 1981, 1990; Ross & Ross 1985). Ross also reports a

COURCEYAN	1	2	3	4	5	6 15	7	8 5	9 18
1 Midland Valley	▨								
2 Northumberland, Dumfries, & Isle Of Man		▨							
3 Pennines & Cumbria			▨						
4 Derbyshire				▨					
5 North Wales					▨				
6 South Wales & South West England 15						▨		0.600 3	0.467 7
7 North Ireland							▨		
8 Central Ireland 5						0.600		▨	0.800 4
9 South Ireland 18						0.467		0.800	▨

n 3
x 0.622
s 0.137

Simpson's Coefficients at Specific Level

Fig. 12.17. Courceyan

CHADIAN	1	2	3 5	4 1	5	6 12	7 2	8 5	9 4
1 **Midland Valley**	▨								
2 **Northumberland, Dumfries, & Isle Of Man**		▨							
3 **Pennines & Cumbria** 5			▨	**0.000** 0		**0.600** 3	**0.000** 0	**0.600** 3	**0.500** 2
4 **Derbyshire** 1			**0.000**	▨		**0.000** 0	**0.000** 0	**0.000** 0	**0.000** 0
5 **North Wales**					▨				
6 **South Wales & South West England** 12			**0.600**	**0.000**		▨	**0.000** 0	**0.800** 4	**0.500** 2
7 **North Ireland** 2			**0.000**	**0.000**		**0.000**	▨	**0.000** 0	**0.000** 0
8 **Central Ireland** 5			**0.600**	**0.000**		**0.800**	**0.000**	▨	**0.250** 1
9 **South Ireland** 4			**0.500**	**0.000**		**0.500**	**0.000**	**0.250**	▨

n 15
x 0.217
s 0.285

Simpson's Coefficients at Specific Level

Fig. 12.18. Chadian

ARUNDIAN	1	2	3 7	4 3	5	6 9	7 3	8 4	9 2
1 Midland Valley	▨								
2 Northumberland, Dumfries, & Isle Of Man		▨							
3 Pennines & Cumbria 7			▨	0.333 1		0.429 3	0.667 2	0.500 2	0.500 1
4 Derbyshire 3			0.333	▨		0.667 2	0.333 1	0.333 1	0.000 0
5 North Wales					▨				
6 South Wales & South West England 9			0.429	0.667		▨	0.333 1	0.750 3	0.500 1
7 North Ireland 3			0.667	0.333		0.333	▨	0.000 0	0.000 0
8 Central Ireland 4			0.500	0.333		0.750	0.000	▨	0.000 0
9 South Ireland 2			0.500	0.000		0.500	0.000	0.000	▨

n 15
x 0.356
s 0.248

Simpson's Coefficients at Specific Level

Fig. 12.19. Arundian

HOLKERIAN	1	2	3 8	4 2	5	6 10	7 3	8 5	9 4
1 **Midland Valley**									
2 **Northumberland, Dumfries, & Isle Of Man**									
3 **Pennines & Cumbria** 8				1.000 2		0.500 4	0.333 1	0.400 2	0.500 2
4 **Derbyshire** 2			1.000			1.000 2	0.000 0	0.500 1	0.000 0
5 **North Wales**									
6 **South Wales & South West England** 10			0.500	1.000			0.333 1	0.800 4	0.250 1
7 **North Ireland** 3			0.333	0.000		0.333		0.000 0	0.667 2
8 **Central Ireland** 5			0.400	0.500		0.800	0.000		0.000 0
9 **South Ireland** 4			0.500	0.000		0.250	0.667	0.000	

n 15
x 0.419
s 0.331

Simpson's Coefficients at Specific Level

Fig. 12.20. Holkerian

ASBIAN	1 11	2 22	3 25	4 11	5 4	6 7	7 56	8 6	9 3
1 Midland Valley 11	▨	0.727 8	0.636 7	0.000 0	0.500 2	0.429 3	0.455 5	0.333 2	0.333 1
2 Northumberland, Dumfries, & Isle Of Man 22	0.727	▨	0.591 13	0.273 3	0.750 3	0.714 5	0.500 11	0.667 4	0.333 1
3 Pennines & Cumbria 25	0.636	0.591	▨	0.455 5	1.000 4	0.571 4	0.440 11	0.667 4	0.667 2
4 Derbyshire 11	0.000	0.273	0.455	▨	0.500 2	0.206 1	0.455 5	0.333 2	0.667 2
5 North Wales 4	0.500	0.750	1.000	0.500	▨	0.500 2	0.750 3	0.250 1	0.333 1
6 South Wales & South West England 7	0.429	0.714	0.571	0.206	0.500	▨	0.714 5	0.167 1	0.000 0
7 North Ireland 56	0.455	0.500	0.440	0.455	0.750	0.714	▨	0.500 3	0.667 2
8 Central Ireland 6	0.333	0.667	0.667	0.333	0.250	0.167	0.500	▨	0.333 1
9 South Ireland 3	0.333	0.333	0.667	0.667	0.333	0.000	0.667	0.667	▨

n 36
x 0.484
s 0.216

Simpson's Coefficients at Specific Level

Fig. 12.21. Asbian

BRIGANTIAN	1 38	2 22	3 23	4 1	5 26	6 9	7 1	8	9
1 Midland Valley 38		0.819 18	0.826 19	1.000 1	0.846 22	0.778 7	0.000 0		
2 Northumberland, Dumfries, & Isle Of Man 22	0.819		0.636 14	1.000 1	0.682 15	0.778 7	0.000 0		
3 Pennines & Cumbria 23	0.826	0.636		1.000 1	0.783 18	0.667 6	0.000 0		
4 Derbyshire 1	1.000	1.000	1.000		1.000 1	0.000 0	0.000 0		
5 North Wales 26	0.846	0.682	0.783	1.000		0.778 7	0.000 0		
6 South Wales & South West England 9	0.778	0.778	0.667	0.000	0.778		0.000 0		
7 North Ireland 1	0.000	0.000	0.000	0.000	0.000	0.000			
8 Central Ireland									
9 South Ireland									

n 21
x 0.552
s 0.403

Simpson's Coefficients at Specific Level

Fig. 12.22. Brigantian

PENDLEIAN	1 13	2 16	3 20	4	5	6	7	8	9
1 Midland Valley 13		0.462 6	0.538 7						
Northumberland, 2 Dumfries, 16 & Isle Of Man	0.462		0.500 8						
3 Pennines & Cumbria 20	0.538	0.500							
4 Derbyshire									
5 North Wales									
South Wales & 6 South West England									
7 North Ireland									
8 Central Ireland									
9 South Ireland									

n 3
x 0.500
s 0.031

Simpson's Coefficients at Specific Level

Fig. 12.23. Pendleian

ARNSBERGIAN	1 13	2 1	3 28	4	5	6	7	8	9
1 Midland Valley 13	▨	0.000 0	0.538 7						
Northumberland, **2 Dumfries,** 1 **& Isle Of Man**	0.000	▨	0.000 0						
3 Pennines & Cumbria 28	0.538	0.000	▨						
4 Derbyshire				▨					
5 North Wales					▨				
South Wales & **6 South West England**						▨			
7 North Ireland							▨		
8 Central Ireland								▨	
9 South Ireland									▨

n 3
x 0.179
s 0.253

Simpson's Coefficients at Specific Level

Fig. 12.24. Arnsbergian

decrease in bryozoan distributions during the Silesian; though such a decrease is apparently shown by the data presented here for the Pendleian and Arnsbergian, the limited amount of information makes the validity of such a result uncertain. However, there are more species and more localities involved in the Silesian data than for the anomalously high coefficients from the poorly-constrained Courceyan data.

Correlations from fieldwork material

Enough data has been collected from fieldwork during this project to present a series of Simpson and Jaccard Coefficient tabulations at specific level:

COURCEYAN - ARNSBERGIAN	1 38	2 34	5 23	6 15
1 Midland Valley 38		0.824 28	0.783 18	0.733 11
2 Northumberland, Dumfries, & Isle Of Man 34	0.824		0.870 20	0.733 11
5 North Wales 23	0.783	0.870		0.800 12
6 South Wales & South West England 15	0.733	0.733	0.800	

Fig. 12.25. Simpson Coefficients at specific level for fieldwork data

COURCEYAN - ARNSBERGIAN	1 38	2 34	5 23	6 15
1 Midland Valley 38		0.636 28	0.419 18	0.262 11
2 Northumberland, Dumfries, & Isle Of Man 34	0.636		0.541 20	0.289 11
5 North Wales 23	0.419	0.541		0.462 12
6 South Wales & South West England 15	0.262	0.289	0.462	

Fig. 12.26. Jaccard Coefficients at specific level for fieldwork data

Coefficients are, on average, higher than those from the general data collected from many sources. The Simpson Coefficient has an average value of 0.791 and that of the Jaccard 0.435 (cf. 0.573 and 0.258 respectively for the general data). This highlights the problem of species identification by several authors, which may produce endemism as a result of over-splitting of taxa by some authors working in specific field areas. The only true picture of bryozoan distributions throughout the whole of Britain would be gained by a single worker collecting and identifying faunas from all areas of Carboniferous rocks. Despite the fact that a project of this scale would involve a lifetime of study, it is interesting to note that the bryozoan distributions from the general data and from the fieldwork data give very similar results. This indicates that any regional bias produced by many different workers has little effect on the apparent patterns of distributions, but may alter the level of endemism observed.

The coefficients show a strong gradient of dissimilarity with increasing distance between areas. Each of the four areas has its highest coefficients with the neighbouring areas, and its lowest coefficient with the area which is geographically furthest from it. For example, the Midland Valley has its highest coefficient with Northumberland, a lower score with North Wales, and its lowest score with South Wales. One departure from the general data is that though the Midland Valley has a fairly high correlation with North Wales, it is not anomalously high, as is the case with the general data.

The Simpson and Jaccard Coefficients give virtually identical patterns, the only difference being that Northumberland shows a slightly greater affinity with North Wales than with the Midland Valley using the Simpson Coefficient, but this situation is reversed with the Jaccard Coefficient. Of the two methods, interestingly the Jaccard Coefficient gives a greater spread of the data, with a standard deviation of $\sigma=0.132$ (coefficient of variation = 30.34), compared with a Simpson Coefficient standard deviation of $\sigma=0.049$ (coefficient of variation = 6.19).

Species Locality Maps

For those species with well-constrained data, it has been possible to produce species distribution maps, showing the areas in which they have been recorded, and their time ranges within the nine broad regions (figs. 12.27 to 12.42). This method, more than any other, is most susceptible to limitations on the available data, but does give a visual display of the approximate distributions. With further work, it is certain that some species will be found in areas in which they are currently recorded as being absent, but it is not known how much change such discoveries would make on the broader distribution patterns.

There is much variation in the distribution ranges of different species; some species are pandemic across Britain, while others are more geographically restricted. Species distribution maps are given in the following pages, showing the reported occurrence of some of the commoner, more pandemic bryozoans.

Species such as *Fenestella plebeia* and the cystoporate *Fistulipora incrustans* have very broad temporal and geographical distributions, being found in all nine regions and both ranging through from the Courceyan to the Arnsbergian. However, such a pattern is in contrast to that of *Fenestella tuberculo-carinata* which, while being the most abundant fenestellid bryozoan in the Midland Valley, has a scant record elsewhere, with some occurrences in Northumberland and Cumbria. Another common Midland Valley bryozoan, the trepostome *Tabulipora urii*, is rarer outside Scotland, though it is more widely reported than *Fenestella tuberculo-carinata* and, in addition to the Pennines region, occurs in Wales and North Ireland. Similarly, representatives of the genus *Penniretepora* are commonest in the more northern regions (Midland Valley, North Ireland, Northumberland and the Pennines) but occur throughout all nine areas. However, the commonest species, *Penniretepora flexicarinata* does occur in South Wales, though it was found through fieldwork that it is never abundant there.

It is important to note that of the 126 species utilised in this study, over half of them (69) have been reported in only one of the nine regions; 22 of these are described in the works on Carrick Lough (Tavener-Smith, 1973a; Olaloye, 1974; Wyse-Jackson, 1988) and a further 13 from various areas by Lee (1912). This may suggest an overprint of collection/reportage bias on the data, giving artificially-discrete correlation coefficients and further studies may reveal the presence of these species in additional areas. However, a moderately-high percentage of species from North Ireland are also found exclusively in association with the Pennines region, and the coefficients of comparison support the observation that when a species is recorded in only a limited number of areas, those areas tend to be adjacent, rather than randomly spread across Britain.

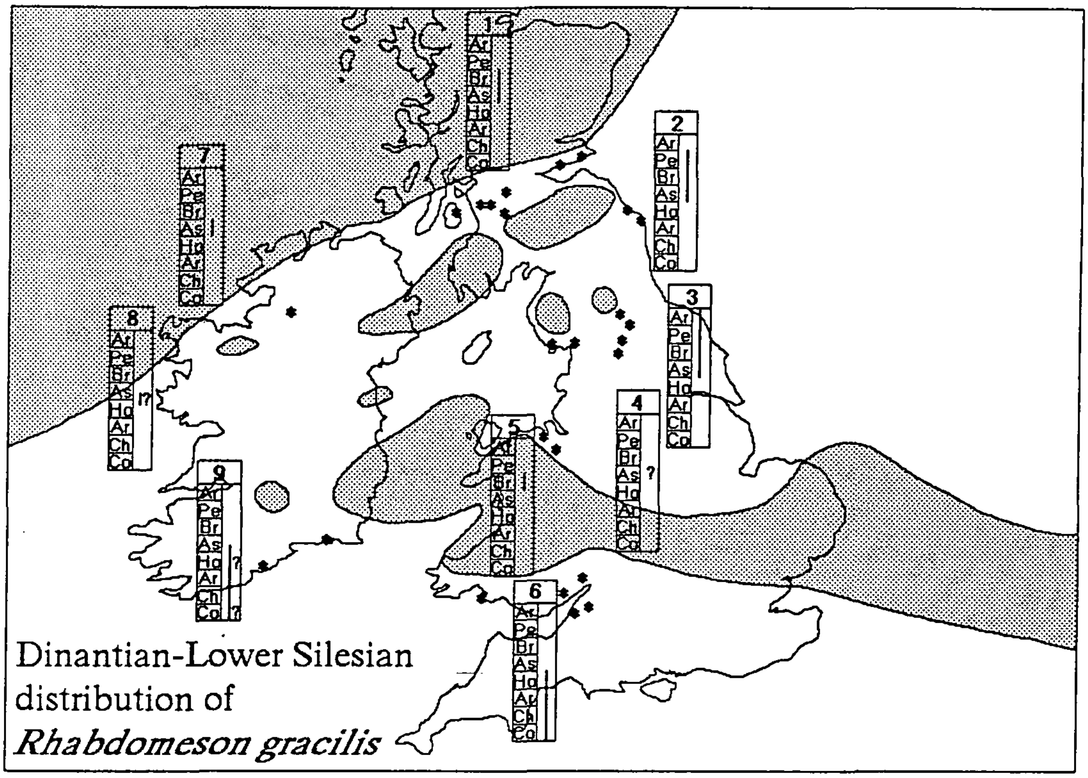


Fig. 12.27

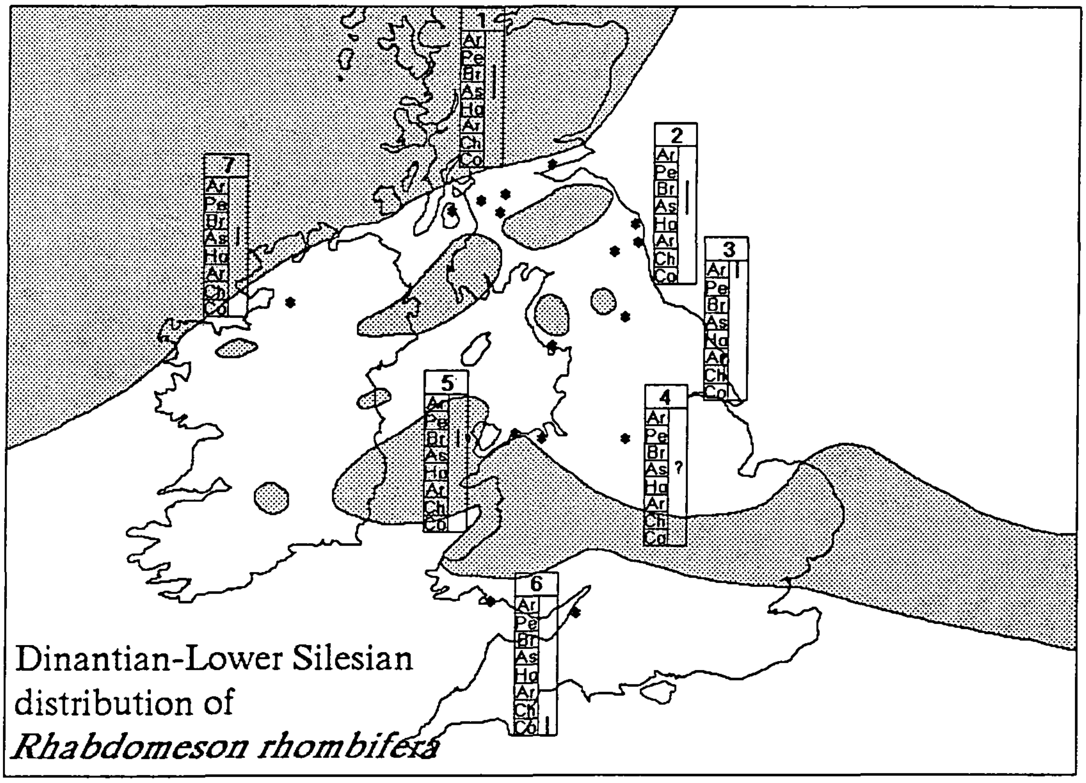


Fig. 12.28

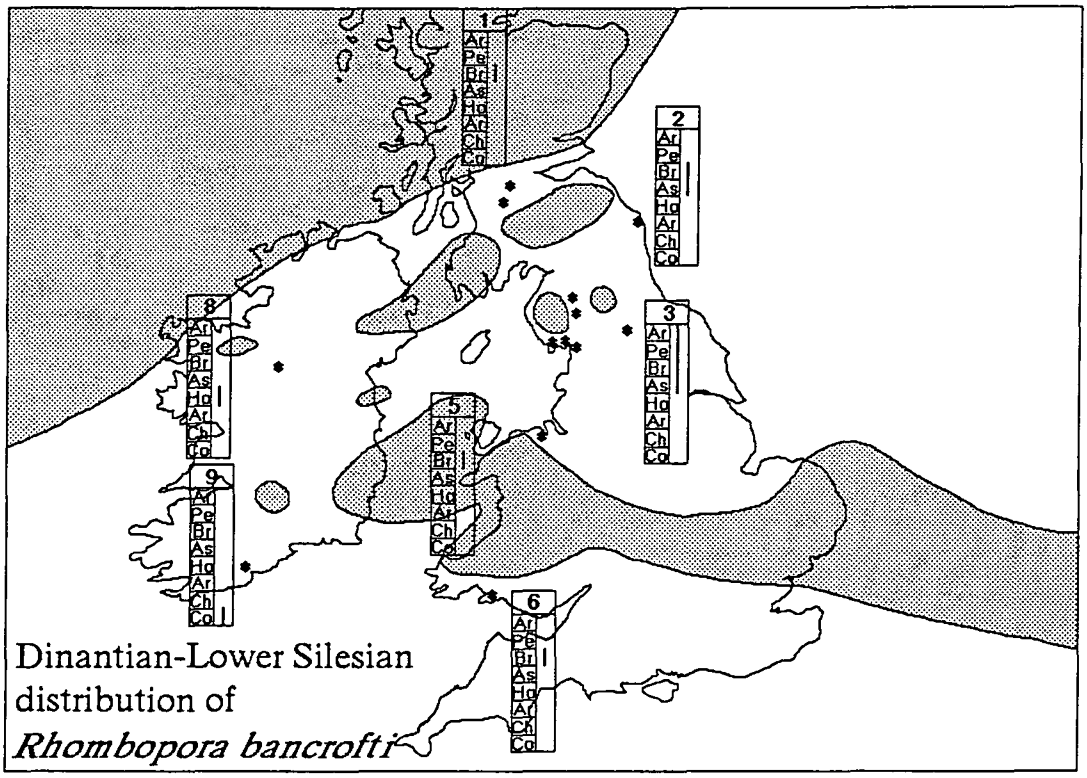


Fig. 12.29

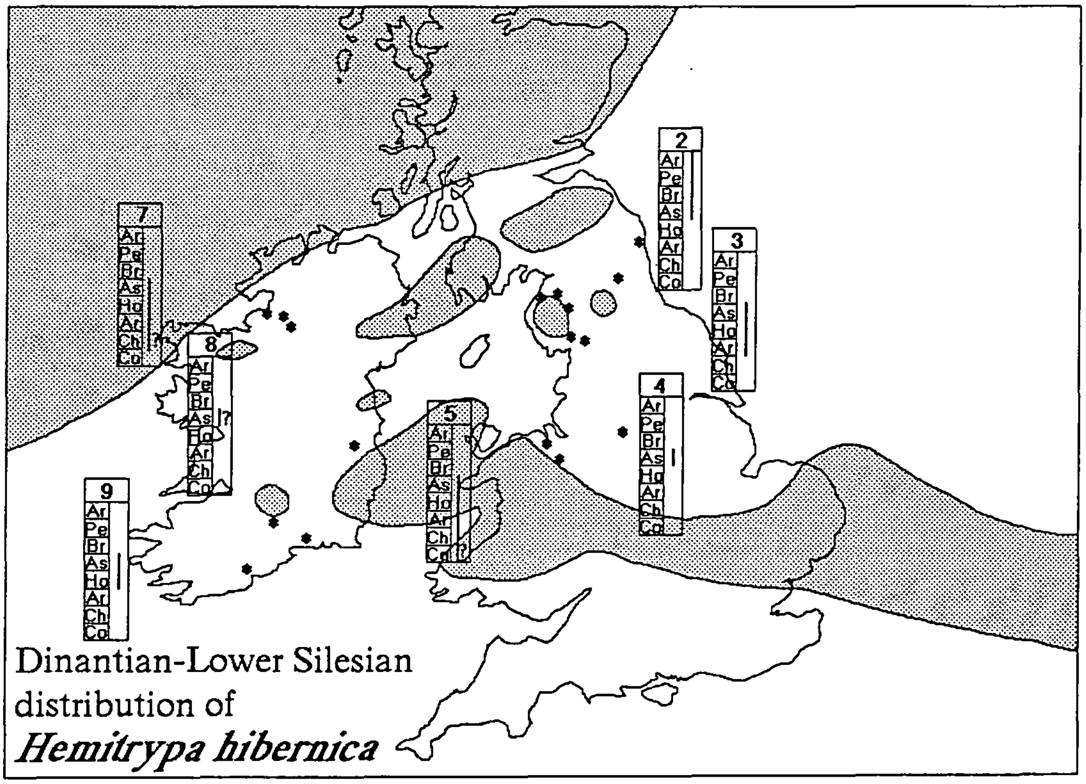


Fig. 12.30

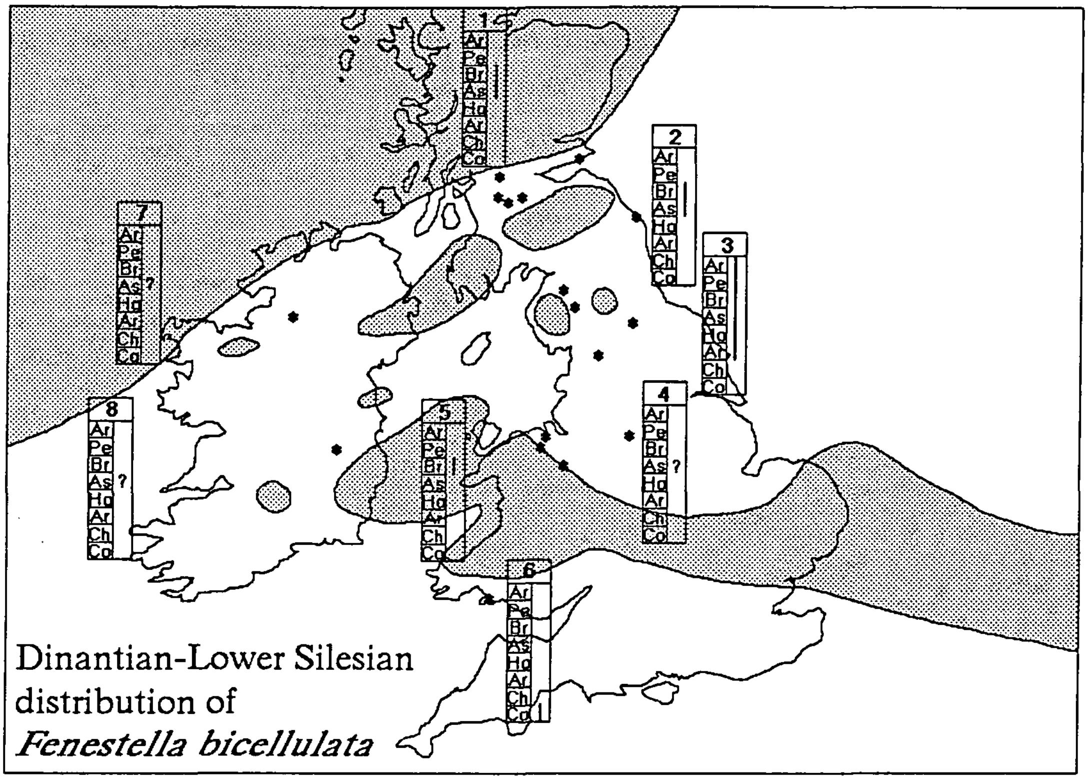


Fig. 12.31

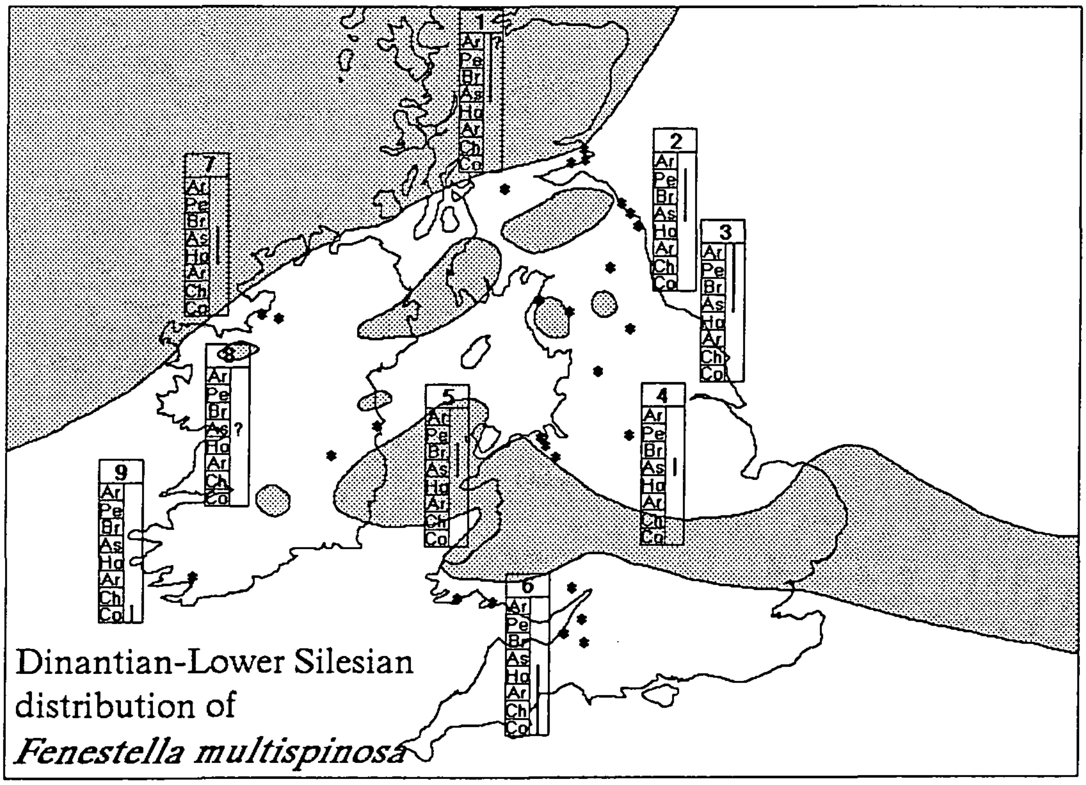
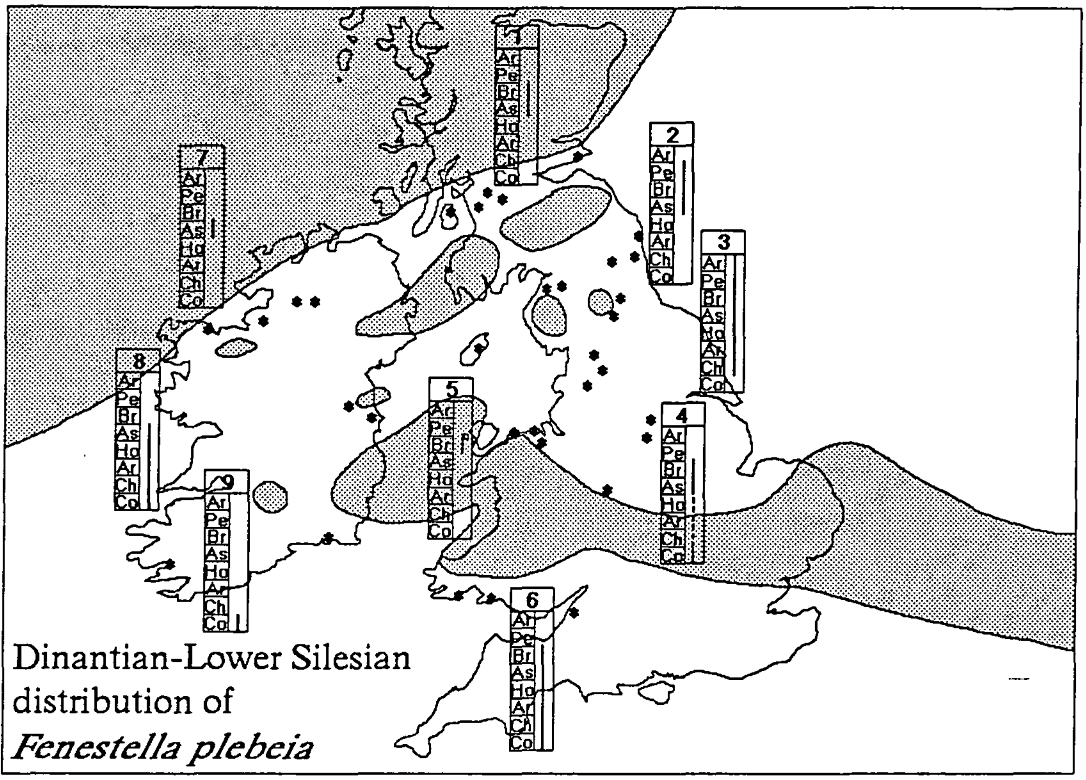
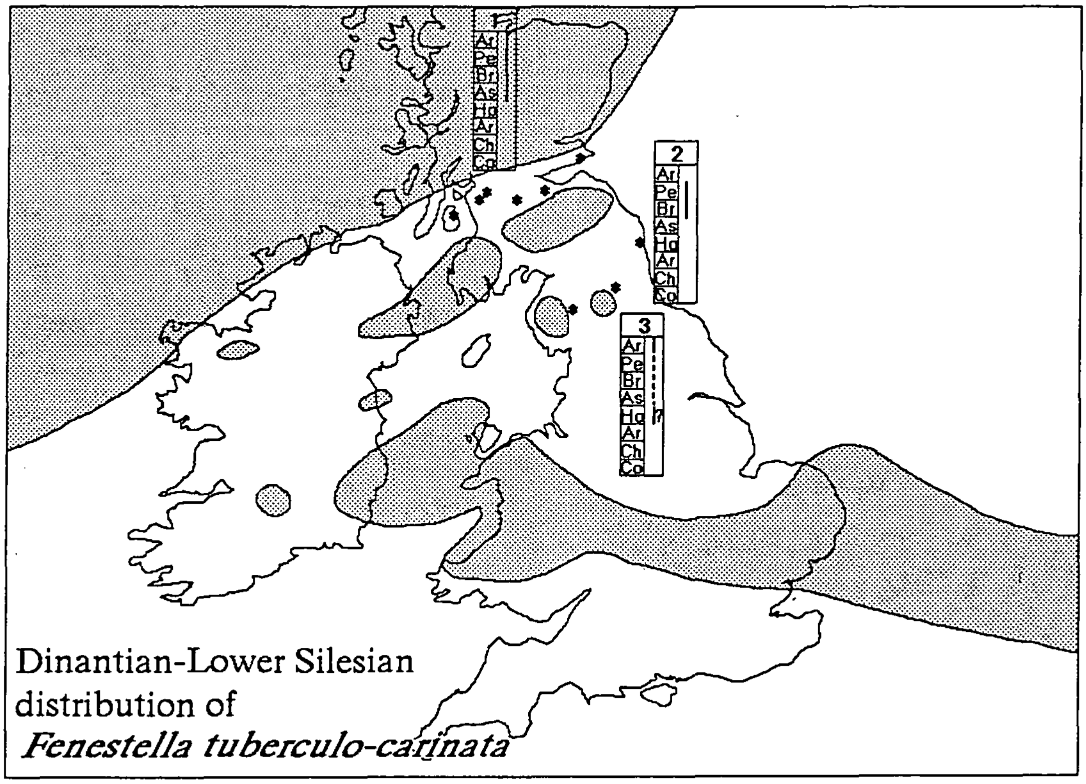


Fig. 12.32



Dinantian-Lower Silesian distribution of *Fenestella plebeia*

Fig. 12.33



Dinantian-Lower Silesian distribution of *Fenestella tuberculo-carinata*

Fig. 12.34

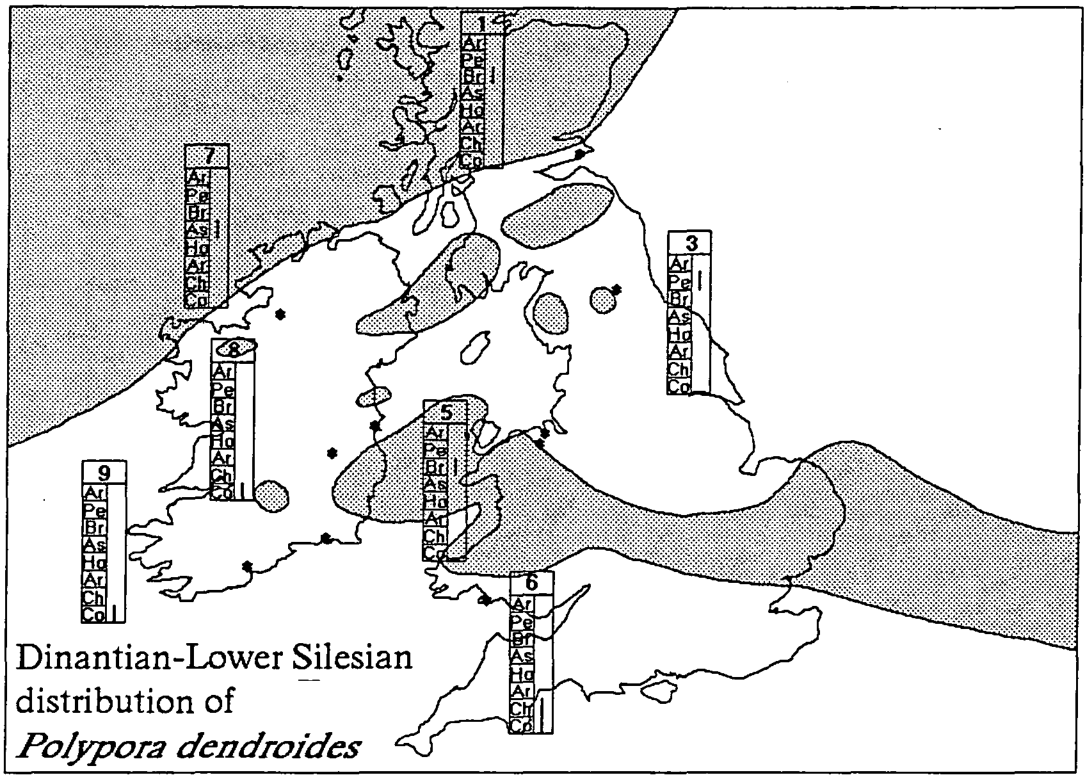


Fig. 12.35

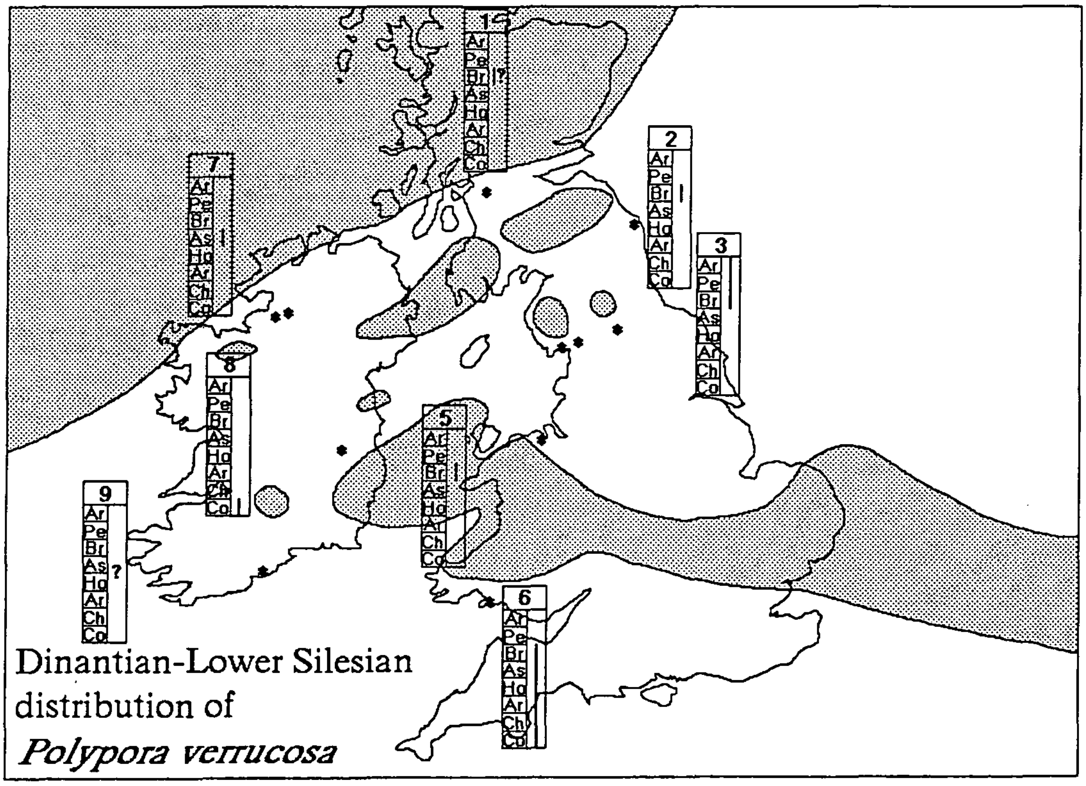
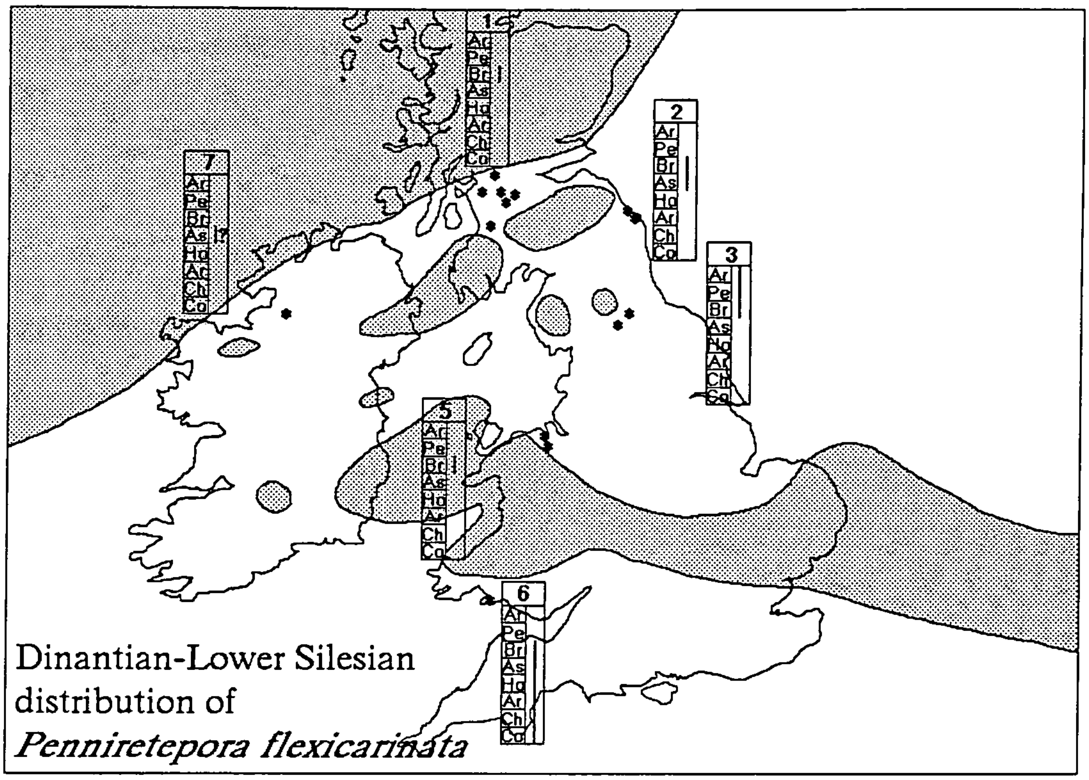
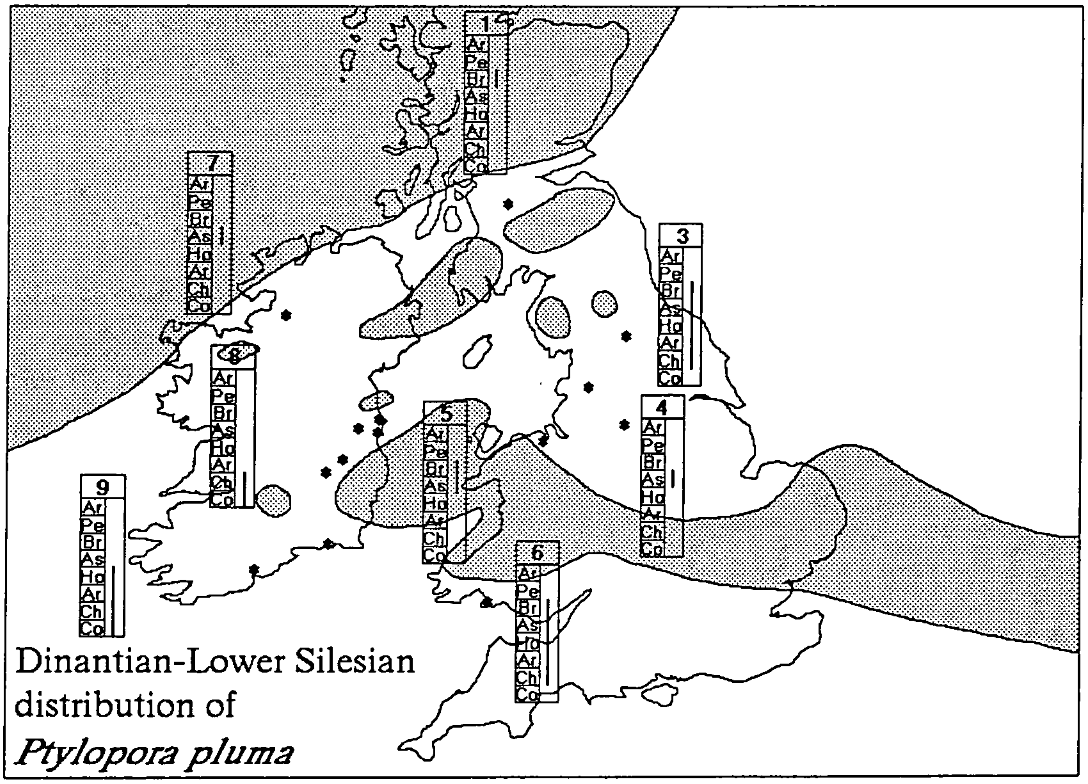


Fig. 12.36



Dinantian-Lower Silesian distribution of *Penniretepora flexicarinata*

Fig. 12.37



Dinantian-Lower Silesian distribution of *Ptylopora pluma*

Fig. 12.38

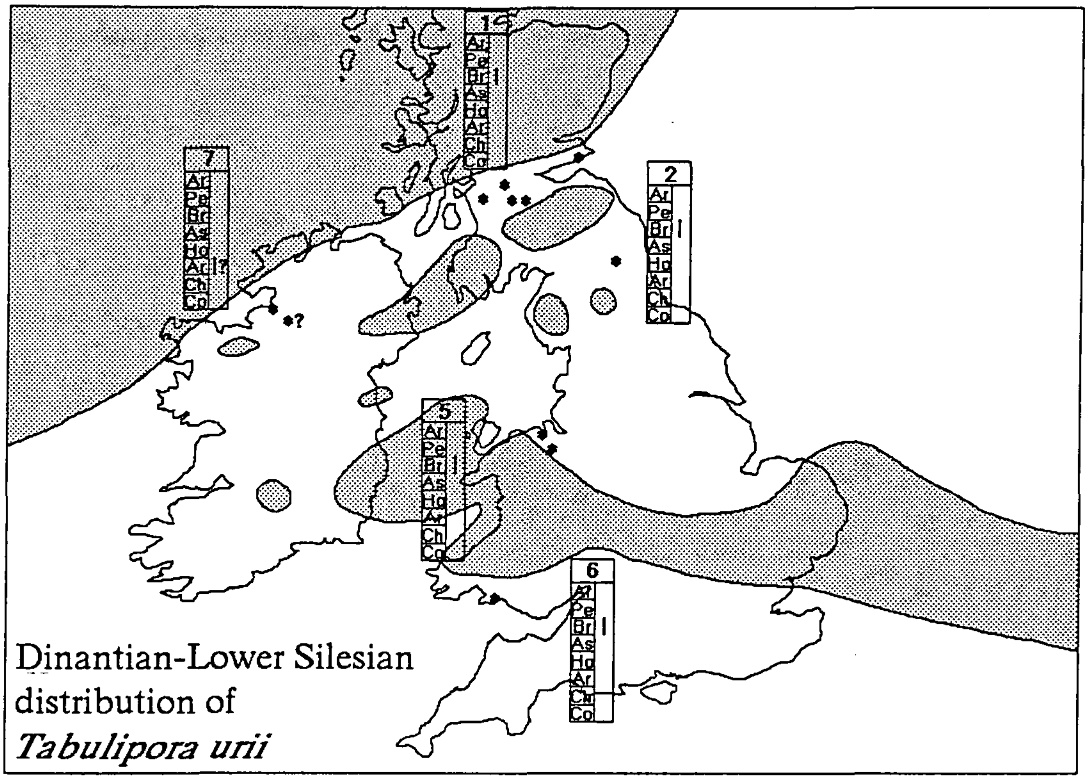


Fig. 12.39

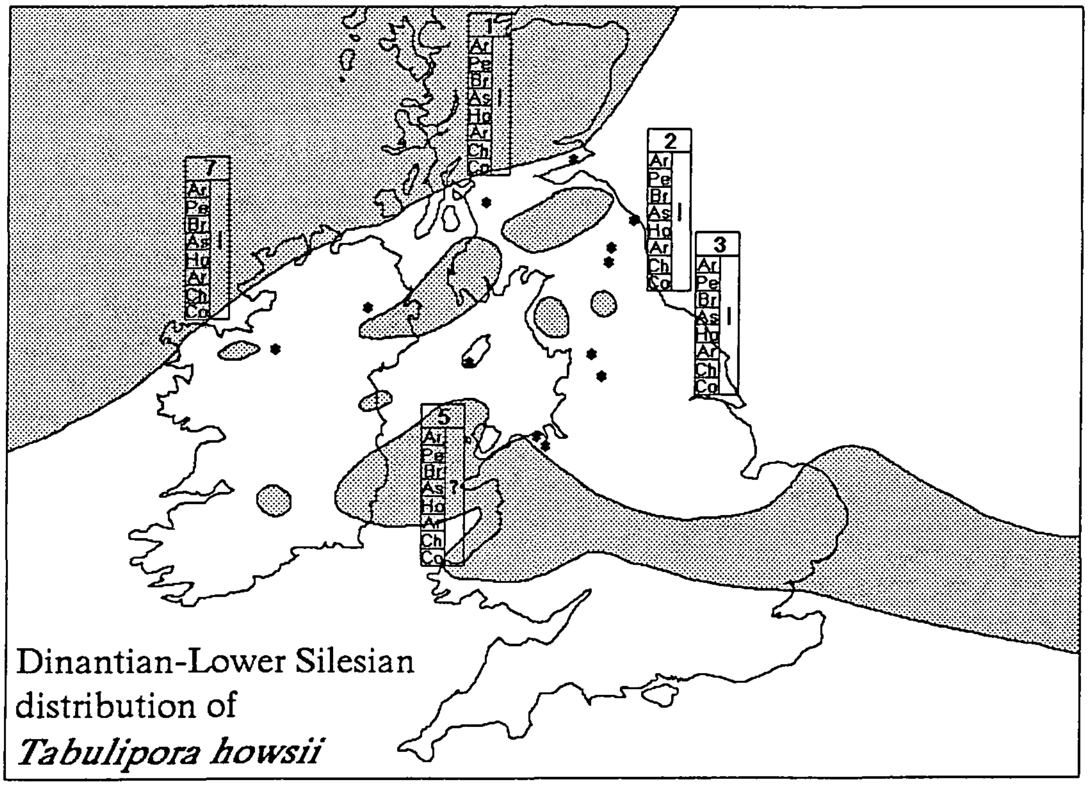
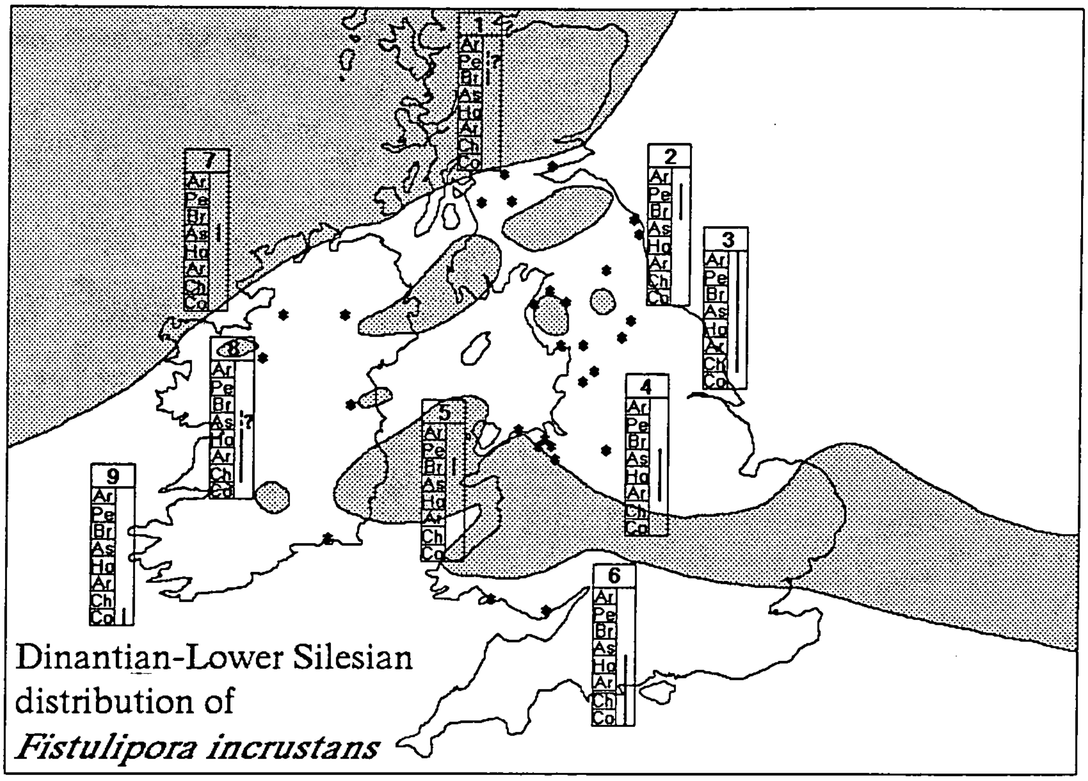
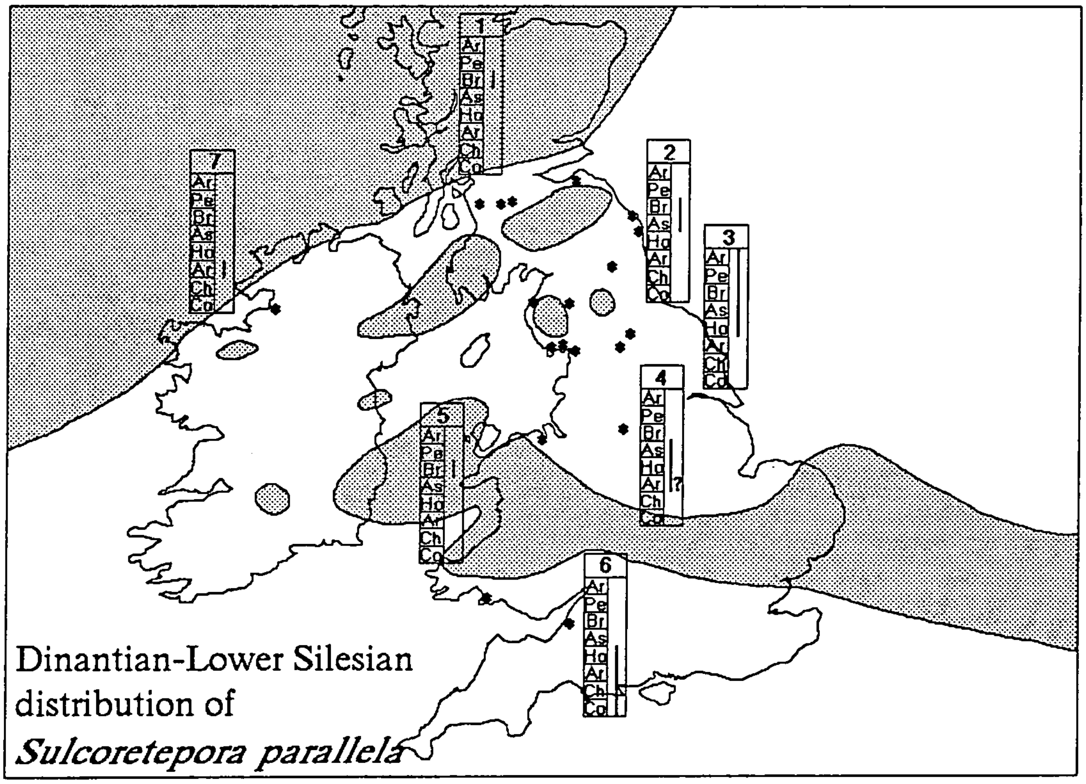


Fig. 12.40



Dinantian-Lower Silesian distribution of *Fistulipora incrustans*

Fig. 12.41



Dinantian-Lower Silesian distribution of *Sulcoretepora parallela*

Fig. 12.42

CHAPTER 13 : ANALYSIS OF BRYOZOAN DISTRIBUTION PATTERNS

Introduction

Limitations of biogeographical studies

All observable species from all the known kingdoms of life have defining population limits; there is no single species which can be found in every available habitat on the Earth. The boundaries which define the extent of a species population can have several forms: geographical features may physically prevent a species dwelling in certain areas; facies-related factors (such as sediment stability and environment energetics) may preclude colonisation of an area by an unsuitably-adapted species; physical and chemical differences, including pH variations, heavy metal concentrations, salinity, local temperature and light concentrations, will additionally disadvantage species which are not specially adapted to live in that environment. Further, distributions are markedly affected by inter-species competition; even if an environment is perfectly suitable for a particular species, a better-adapted species has a greater chance of occupying that niche, and so displacing the less-adapted one.

Though all of the above limits can normally be observed in living populations, it is very unlikely that such a complete environmental reconstruction can ever be built for fossil populations. The exact depth of deposition of marine beds is very rarely known, and the nature of current activity in an area can only be approximated. Geographical reconstructions are usually quite general, and much evidence may have been obscured by later tectonic events. Perhaps most importantly, only a small proportion of a fauna has a chance of becoming fossilised, and it is very rare indeed to glean information about the soft-bodied faunal and floral constituents, which may actually comprise a substantial percentage of a community.

These limitations must be borne in mind when analysing the results of palaeobiogeographical research. It is not possible, for instance, to visit every outcrop of Carboniferous rock in Britain, nor to turn over every stone; thus it is inevitable that there will be some gaps in the data. However, there is enough data available to address some important questions:

a. are bryozoans distributed evenly throughout the palaeogeographical extent of shelf seas around Britain, or is the distribution purely random, or is there, in fact, a definable pattern to the distributions?

b. if there is a pattern to bryozoan distributions, can biological, environmental and geographical explanations account for the patterns?

c. are particular bryozoans associated with particular facies, and thus, do similar faunas occur in similar environments from different places?

d. do Carboniferous bryozoan species have limited temporal occurrences, restricted to a few stages, or are most species relatively long-lived?

e. are there any differences between, for instance, Courceyan and Arnsbergian representatives of a species, and are there differences between geographically-separated species populations?

f. is it possible to detect the evolution of new species within Britain, and can patterns of species migration be elucidated?

The pattern of bryozoan distributions

Statistical analysis and plots of bryozoan distributions reveal that the occurrence of Carboniferous Bryozoa in Britain is certainly not uniform. However, it would be more surprising if this were the case, since that would imply that all 126 species cited in this study occurred in all the areas, with corresponding coefficients of similarity of 1.000. Further, the distributions do not appear to be random; if each species had an equal probability of occurring in all areas, then the same coefficients would be found from all nine areas, though the coefficients of similarity would be less than 1.000. For example, with a completely random bryozoan distribution, the Midland Valley of Scotland would return an identical Jaccard Coefficient from a comparison with Northumberland as with a comparison against South Ireland.

The data clearly shows neither a uniform nor a random distribution. Rather, there is a general case that zones will have high similarity coefficients with neighbouring areas, and low coefficients with more distant areas. There are several important exceptions to this rule, which will be discussed later. The implications from this result are that bryozoan faunas tend to be most similar between adjoining areas. Though this may seem to be very obvious, the fact that this hypothesis can be proven from the data indicates that enough data has been used to create valid distribution analyses.

It must be asked whether the patterns produced in the previous section could have resulted from strong collection bias. Certainly, the fauna from Carrick Lough in North Ireland has been described in far greater detail in the literature than any other area in Britain, but the large number of species recorded from this locality do not affect the Simpson Coefficient, which utilises only the number of species in the smaller population; the highest Simpson Coefficient was with the adjoining Central Ireland region, as would be expected. Moreover, the highest Jaccard Coefficient, which does actually use the total numbers of species recorded, produced the highest score with the neighbouring Pennines region, suggesting that even in this extreme case, collection bias has not unduly affected the results.

The converse of the "similar neighbours" hypothesis needs to be considered; namely, geographically-distant areas tend to have different bryozoan populations. This observation is less obvious, given that modern bryozoan species are noted for their extremely wide occurrences, with some species occurring from pole to pole (Lagaaij & Cook, 1973). Indeed, as Lagaaij and Cook reported, several authors have been surprised at the geographical range which certain species can encompass. Thus, though while the observation that neighbouring areas have similar faunas is in keeping with Lagaaij & Cook's findings, the fact that not all species occur in all zones within an area measuring only 720km by 540km does not. However, just as the coefficients of similarity show that bryozoan distributions within the nine areas are not pandemic, they are not completely exclusive, which would return coefficients of 0.000. The fauna of the Midland Valley of Scotland, for instance, is not completely endemic to that area, such that none of the bryozoans which occur there are found in the Northumberland area. The average Simpson Coefficient at species level for the nine areas is actually 0.573, which suggests that the bryozoan faunas are more similar than they are dissimilar, and at generic level, the Simpson Coefficient is much higher, being 0.750.

Distribution maps of the commoner species (figs. 12.27 to 12.42) show that some species are actually quite widely distributed throughout Britain, but those species which are not pandemic tend to occur only in adjacent areas, rather than being randomly scattered throughout the Carboniferous shelf area. Thus, the coefficients of similarity which are produced are the result of an interaction between a core of common, widely-distributed species, and a relatively large number of species which are much more restricted in their extent. If the restricted species were rare forms, then the variations in coefficients of similarity could be explained purely by collection bias; Lee (1912) redescribed the British Trepostomata, and of the twelve species of *Tabulipora* described in his paper, seven have been recorded within just a single geographical zone. It is possible that more detailed collecting may reveal these rarer species in additional areas, or a restudy may show them to be synonymous with previously-described, commoner forms; in either case, such action would result in a lower degree of faunal dissimilarity between areas. However, many of the species used in this study are not particularly rare; species such as *Fenestella tuberculo-carinata* and *Tabulipora howsii* are very common within the Midland Valley, but are only occasionally recorded outside Scotland. It is therefore necessary to search for explanations to account for the limited distribution of obviously successful species.

The relationship between bryozoan biology and their distribution patterns

Lagaaij & Cook (1973) noted that the wide distribution of modern Bryozoa was not actually in keeping with their known larval biology. The majority of modern bryozoans have brooded larvae which lack an alimentary canal, and on release from the parents' ovicells must settle within twenty four hours; thus, species with brooded larvae should have a more restricted distribution than non-brooded larvae. However, even the free-swimming (planktotrophic) larvae, which do possess a fully functional digestive system, have larval stages of only two months, whereas Thorson (1961) calculated that a larval life of 5 months is needed for a species to cross an ocean the size of the Atlantic. Further, many species possessing planktotrophic larvae do not actually have particularly wide distributions, and studies reported in McKinney & Jackson (1989) show that most of the larvae of the living *Lichenopora* actually travel only a few centimetres before settling. Additional studies by Jackson (1986) concluded that there is, in fact, no correlation with the length of larval life and the corresponding species' distributions.

It is increasingly apparent that the main mechanism of bryozoan dispersal is not by larval release, but is by rafting of colonies on uprooted plant stems, floating pumice, and kelp fronds (Cheetham, 1960 ; Jackson, 1986). Keough (1986) reported finding healthy bryozoans, some bearing embryonic larvae, on floating seagrass blades which had been torn up from their shoots by storm activity.

Palaeozoic bryozoans may have had a very different biology to their modern day counterparts. Zooid specialisation, characteristic of the modern cheilostomes, has allowed the group to adopt a wide variety of colony morphologies, but such specialisation is rarely developed in the Palaeozoic group, the stenolaemates. Most importantly, the major Cretaceous radiation of the cheilostomes has been linked to the development of brooded, non-planktotrophic larvae (Taylor, 1988). Brooding of larvae normally takes place in specialised globular calcified ovicells, formed around the orifice of the maternal zooid, though about 8% of British cheilostomes have an internal brooding method, without the development of ovicells.

Ovicells have actually been recorded in Palaeozoic stenolaemates, having evolved in an independent lineage to the Mesozoic ovicell-bearing cheilostomes. The presence of ovicells is being reported in an increasing number of taxa. Tavener-Smith (1966b) first noted inflated ovicells in the genus *Fenestella*, and ovicells were illustrated, but not recognised, by Dresser (1960) in *Fenestella frutex,* and Ulrich (1890) mentioned possible ovicells in *Fenestella multispinosa*. Within the Fenestrata, Bancroft (1986c; 1988a) has reported five different ovicell morphologies from amongst twelve genera. However, such ovicells are only rarely found, and it is inferred that the majority of stenolaemates had non-brooded, free-swimming larvae; it is important to realise, though, that the absence of ovicells does not automatically imply that the larvae were not brooded.

If rafting was the major method of bryozoan dispersal in the Carboniferous, then there should be little difference in the distribution patterns between brooding and non-brooding genera. The brooding genera identified by Bancroft are :

Acanthocladia, Fabifenestella, Fenestella, Hemitrypa, Isotrypa, Laxifenestella, Penniretepora, Polypora, Rectifenestella, Septatopora, Synocladia, Thamniscus, Utropora

Of these, certainly *Fenestella, Hemitrypa, Penniretepora, Polypora* and *Rectifenestella* have wide geographical distributions in the Carboniferous (Ross, 1981; Ross & Ross, 1990), but other fenestrates such as *Septopora* and *Ptylopora* are quite widespread, and ovicells have yet to be reported in these genera. Even within the genus *Fenestella*, not all species have been identified as having ovicells, and ovicells have not been recorded in the very widely-distributed rhabdomesids, or in the trepostomes and cystoporates. Thus, the ranges of distributions of brooding and non-brooding Carboniferous species are probably similar, though many under-studied genera may yet prove to possess brooded larvae.

Cheetham (1960) studied Tertiary bryozoan faunas, and discovered that the forms which had been able to cross the Atlantic were those cheilostomes which had an encrusting habit, or possessed chitinous attachment threads; non-encrusting dendritic, rigid colonies, and free-living forms showed little trans-Atlantic migration. Amongst the Palaeozoic Bryozoa, even the dendritic fenestellids seem to have been encrusters at some stage in their lives, the attachment anchorages including brachiopod spines (Billing, 1991) and probably plant stems (see South Wales chapter, Tears Point fauna). However, though it is fairly well-established that stenolaemates encrusted a firm object during larval settlement, it is not clear which taxa preferred to encrust shell fragments or hardgrounds, and which settled mainly on plant material. Of all the available attachment objects, lightweight plant fronds would have had the best chance of being swept considerable distances; unfortunately, such plants and algae are only rarely preserved, and only a rudimentary picture of the floral constituent of the Carboniferous seas floors can be established.

Bryozoan inter-specific competition and the effect on distribution patterns

The concept of competition amongst the Bryozoa needs to be discussed. Studies of modern bryozoan competition on stable substrata (Keough and Butler, 1983) have shown that organisms encrust about 75% of the available surfaces (in this case, pier pilings). There is much competition for space, and those organisms which are able to compete for space and regenerate colony injuries predominate; in this case, bryozoans are not the dominant encrusting taxon, since despite having a very high rate of larval recruitment, sponge and colonial ascidians are more efficient encrusters, and thus overgrow any cleared patches. The pattern of competition in areas of intermediate substratal stability (Keough, 1984; McKinney & Jackson, 1989) is rather different; bryozoans encrust exposed, widely-dispersed semi-infaunal molluscs, but less than 40% of the exposed shell surface is usually encrusted. Thus, the limiting factor on bryozoan coverage is not available encrusting space, but the isolated occurrence of suitable substrata, which constrains bryozoan encrustation since bryozoan larvae have very limited dispersal distances.

There are some advantages associated with limited larval dispersal. Concentration of populations into clusters will increase the level of larval recruitment, as illustrated in the last paragraph; individuals have a greater chance of fertilisation of eggs in larger populations. Though such a strategy may increase the chances of speciation, since short larval dispersal distances from the local bryozoan population will increase the genetic relatedness, but reduce the gene flow between isolated populations (McKinney & Jackson, 1989); however, frequent rafting of individuals should counteract this process (*ibid.*). Indeed, bryozoans which have wide geographical distributions also have greater species longevities.

The concept of inter-specific competition is less clear in erect bryozoans; during the initial stages of colony growth, such taxa have encrusting habits, perhaps with competition for encrusting space as discussed above. However, such forms rapidly adopt an erect growth habit, and are thus less prone to being over-encrusted. The advantage of encrusting growth habits was discussed by McKinney and Jackson (1990):

a. high tissue area and volume, which increase feeding and reproductive capacity per unit area of substratum

b. increased access to food in the water column

c. greater isolation from competitors, predators, and sediments on the substratum.

However, erect colonies are far less "streamlined" than flat, encrusting colonies, and are thus more prone to breakage or toppling of the colony in higher current velocities (Cheetham & Thomsen, 1981; McKinney & Jackson, 1990; Billing, 1991). Studies by Cheetham & Thomsen (1981) have further shown that almost all the species of cheilostome bryozoans in their study were resistant to breakage at high velocities in their early growth stages. However, colony strengths within the rigidly erect taxa becomes polarised as the adult growth habits are reached, with some taxa surviving currents in excess of 2 m sec^{-1}. Thus, it is inferred that colony strength is a limiting factor on the colonisation of high-energy environments by rigidly-erect bryozoans such as *Fenestella.*

Within the erect Carboniferous Bryozoa, short larval dispersal distances are augmented by frequent colony growth from asexual colony fragmentation, as documented in the genus *Archimedes* (McKinney, 1983). Fusion of erect colonies, or the growth of colonies in close proximity, can form bryozoan baffles; Stratton and Horowitz (1984) noted that several species of *Polypora* from Ohio developed supporting struts, 4 to 6mm in length, from the reverse surface of one frond, and extending towards the obverse surface of another frond. Such an arrangement of the colonies into baffles would have greatly decreased the current velocity on the obverse side (downcurrent) of the frond, with this effect being enhanced by each successive frond. Thus, downcurrent colonies could have utilised their ciliary method of nutrient extraction to greater effect, without interference from the ambient higher-velocity currents. McKinney *et al.* studied the modern erect unilaminate bryozoan *Bugula neritina* and found that individuals could increase sedimentation rates behind the colony, by drawing sediment- and organic-laden waters toward them, with the lophophore ciliary action. The inference is that banks of bryozoans in the Carboniferous may have been responsible for the accumulation of Waulsortian mud mounds, demonstrating the effectiveness of ciliary "pumping" through the meshwork.

The Effect of Carboniferous Ocean Currents

The evidence for easterly currents

Bryozoan distributions in the Carboniferous should be expected to be dominated by the prevalent ocean current systems. Whether larval swimming or rafting produced the mechanics for dispersal, bryozoan distributions reflect the main ocean current trends. Palaeo-oceanographical data for the Carboniferous of Northern Europe suggests that currents derived from the east. Ramsbottom (1978) believed that the high proportion of taxa unique to the mid-western United States was a result of its position at the extremity of the southern Laurasian shelf; newly-evolved forms would be unable to migrate into Northern Europe against a strong easterly oceanic current. Nudds & Johnson (1985) studied the first appearances of the coral genera *Lithostrotion* and *Aulina* and concluded that *Aulina* had evolved in China in the Middle Viséan and migrated, via the Russian Platform, arriving in Britain in the Arnsbergian; this pathway is indicative of an eastern-derived ocean current system. It is also interesting to note that the modern day South Equatorial current flows from east to west, but ocean current circulation patterns can be greatly affected by the configuration of the continents, and as Wilson (1989) pointed out, it may be taking uniformitarianism too far to imply a direct analogy.

Wilson (1989) carried out an extensive study of the marine macrofauna of central Scotland, and similarly concluded that many of the faunas had first appearance patterns that suggested derivation from the east. He also envisaged a Baltic "larval pool" from which various species could recolonise the Midland Valley during the episodes of marine transgressions across the area, but remained uncertain about larvae being able to travel the distance of the ocean between China and the Laurasian continent. Wilson additionally questioned the "provincialism" of many Carboniferous faunas, and pointed out that unless workers compare their specimens with representatives from collections from different parts of the world, there is a tendency to use the established taxonomy of their own country. Certainly this is true in the field of bryozoology; a prolific number of described Soviet Carboniferous bryozoans exists, but unfortunately many of the publications are printed in Russian, and it is difficult to compare the species outlined in such papers with European and American representatives. Similarly, several publications relate to the bryozoans of China, and though there are English summaries, the illustrations may be a little difficult to decipher. Examples include the work of Jingzhi *et al.* (1988) who produced a short monograph on the late Devonian and early Carboniferous bryozoans of Central Hunan; within this publication, 100 new species were erected, from 127 collected taxa, bearing little taxonomic resemblance to the European faunas. Similarly, Feng-Sheng (1987) erected a completely new Carboniferous trepostome family, the Nipponostenoporidae, with two new genera, from just three zoarial fragments. However, Feng-Sheng & Xiaoliang (1986) discussed the Carboniferous Bryozoa of Xinjiang, and many familiar European genera were described, with a close affinity to the Russian species. However, it should be pointed out that Hunan and Xianjiang are virtually at opposite ends of the Chinese Republic. A recent publication by Linhuang (1989) described the fauna from the Late Early Carboniferous of the Nan Shan range, near Mongolia. This is a very good paper dealing with the biostratigraphical, palaeobiological, palaeogeographical and systematic aspects of the fauna. At generic level, there are many similarities with the British bryozoan taxa and the following were recorded :

Rhabdomeson Rhombopora Fenestella Polypora Penniretepora Septopora Thamniscus Tabulipora Dyscritella Stenopora Fistulipora Eridopora

the American forms :

Meekopora Anisotrypa Rhombocladia Hyalotoechus Streblotrypella Heloclema Cheilotrypa Cliotrypa Callocladia Nicklesopora

the Asian genera :

Dybowskiella Fistulotrypa

and the endemic Chinese genera :

Cliocystiramus Cystiramus Qilanopora

Several of the species recorded by Linhuang from the Nan Shan range are familiar British and American forms, including *Rhabdomeson rhombifera, Fenestella multispinosa, Fenestella rudis, Fenestella tenax, Penniretepora laxa, Penniretepora elegans,* and *Eridopora macrostomata.* Thus, species such as *Fenestella multispinosa* have occurrences ranging from North America, Great Britain, Belgium, Russia, (cited in Miller, 1962) and China. Such widespread occurrences are in accordance with the Tournasian-Viséan cosmopolitan bryozoan faunas described by Ross & Ross (1990). However, many American taxa such as the very distinctive screw-stemmed acanthocladiid *Archimedes* are only rarely recorded outside of America (this taxon has been reported from the Russian platform and from Australasia); Wilson (1989) used the example of *Archimedes* to argue the case for a predominantly easterly ocean current system along the southern Laurasian shelf.

The application of current systems to British Carboniferous bryozoan distributions

If British Carboniferous bryozoan distributions are controlled exclusively by easterly current systems, then the distribution patterns should reflect the ancient palaeogeography of the British Isles. As was discussed in the Introduction, the area of Carboniferous Britain formed a series of archipelagic islands on a shallow shelf margin, which deepened off the area forming Cornubia. Can the distribution coefficients be explained by this palaeogeography? Certainly, the greatest correlations exist between those areas which lie on northeast-southwest trends; the three areas which would have been most open to the main easterly current systems, namely the Pennines region, North Wales, and Central Ireland, have by far the highest correlations with each other, when analysing the data with the Simpson Coefficient. This suggests that species which originated in the east of the Mid- European Sea had little problem being transported westwards by the predominant ocean currents.

The coefficients may show additional patterns which can be best explained by an easterly current system. A summary of the average coefficients for the nine areas under study is given in the table below, from which various graphs have been plotted:

Area	1	2	3	4	5	6	7	8	9
Number of species	48	33	52	16	30	24	59	11	22
Number of genera	21	19	24	11	17	15	21	10	12
Simpson coeff: species	0.606	0.571	0.543	0.367	0.691	0.518	0.508	0.670	0.536
Simpson coeff: genera	0.749	0.729	0.821	0.711	0.778	0.721	0.701	0.813	0.728
Jaccard coeff: species	0.321	0.296	0.306	0.151	0.371	0.242	0.186	0.207	0.238
Jaccard coeff: genera	0.461	0.451	0.471	0.374	0.500	0.425	0.400	0.424	0.392

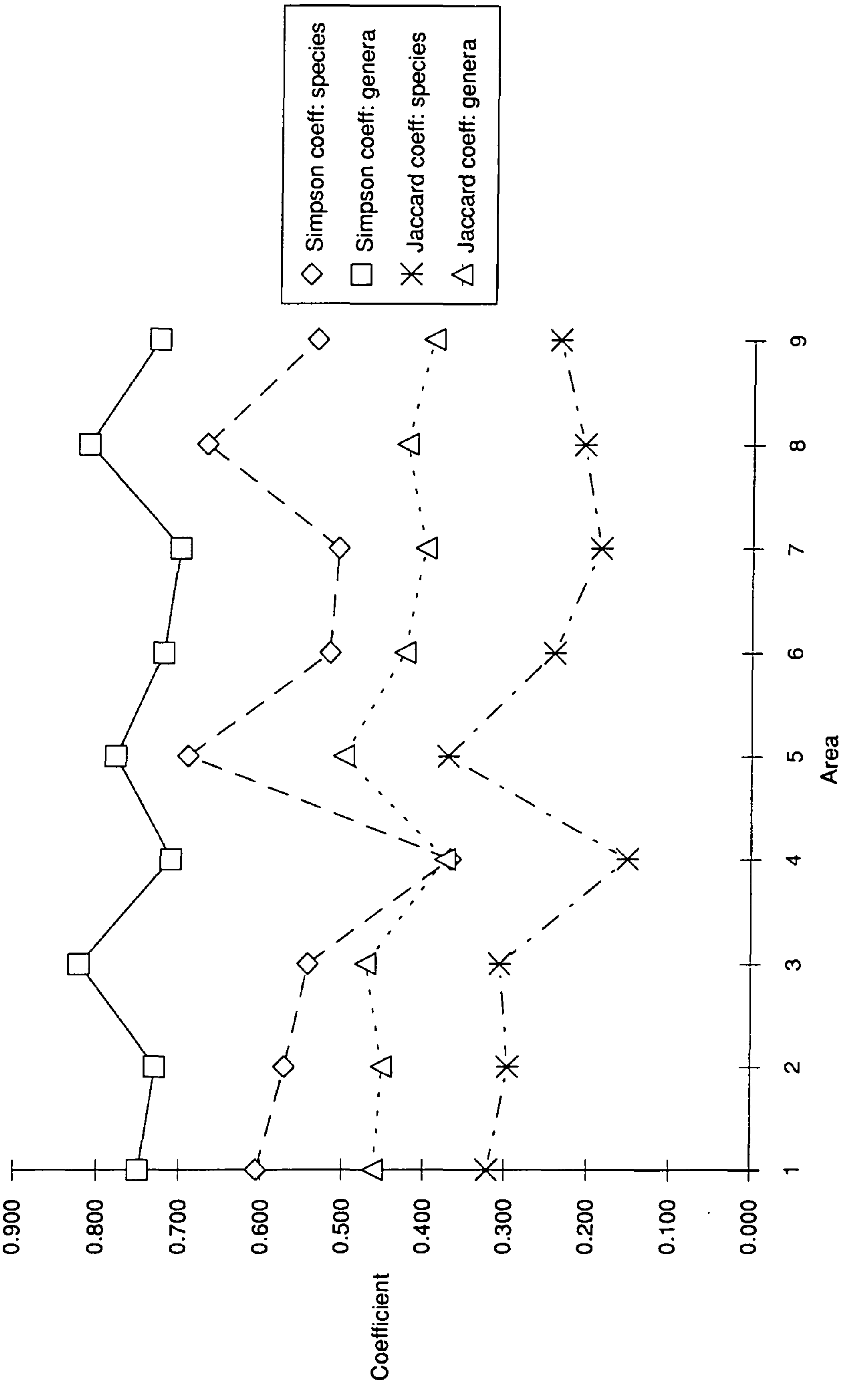


Fig. 13.1. Plots of correlation coefficients against geographical area

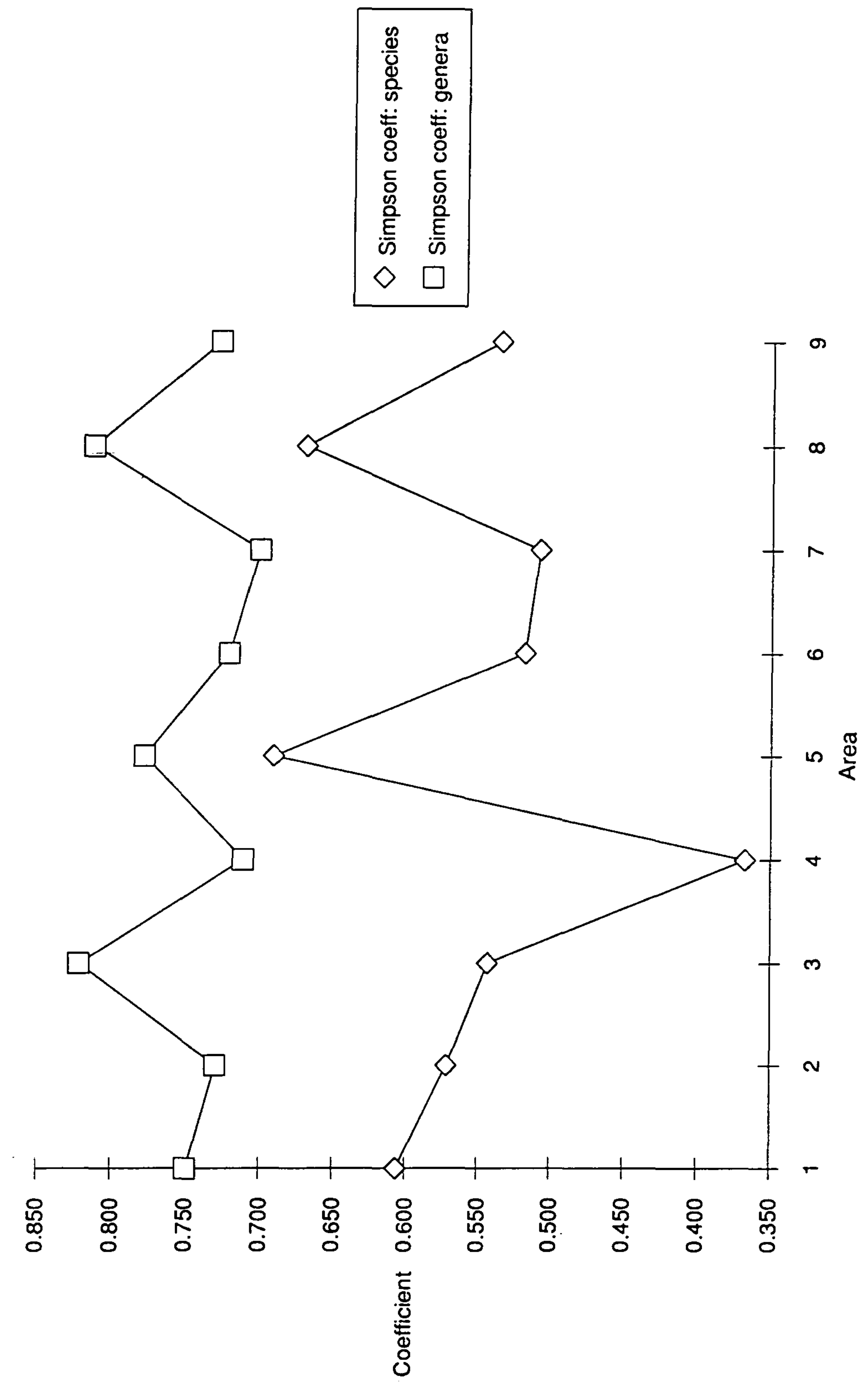


Fig. 13.2. Plots of Simpson Coefficients against geographical area

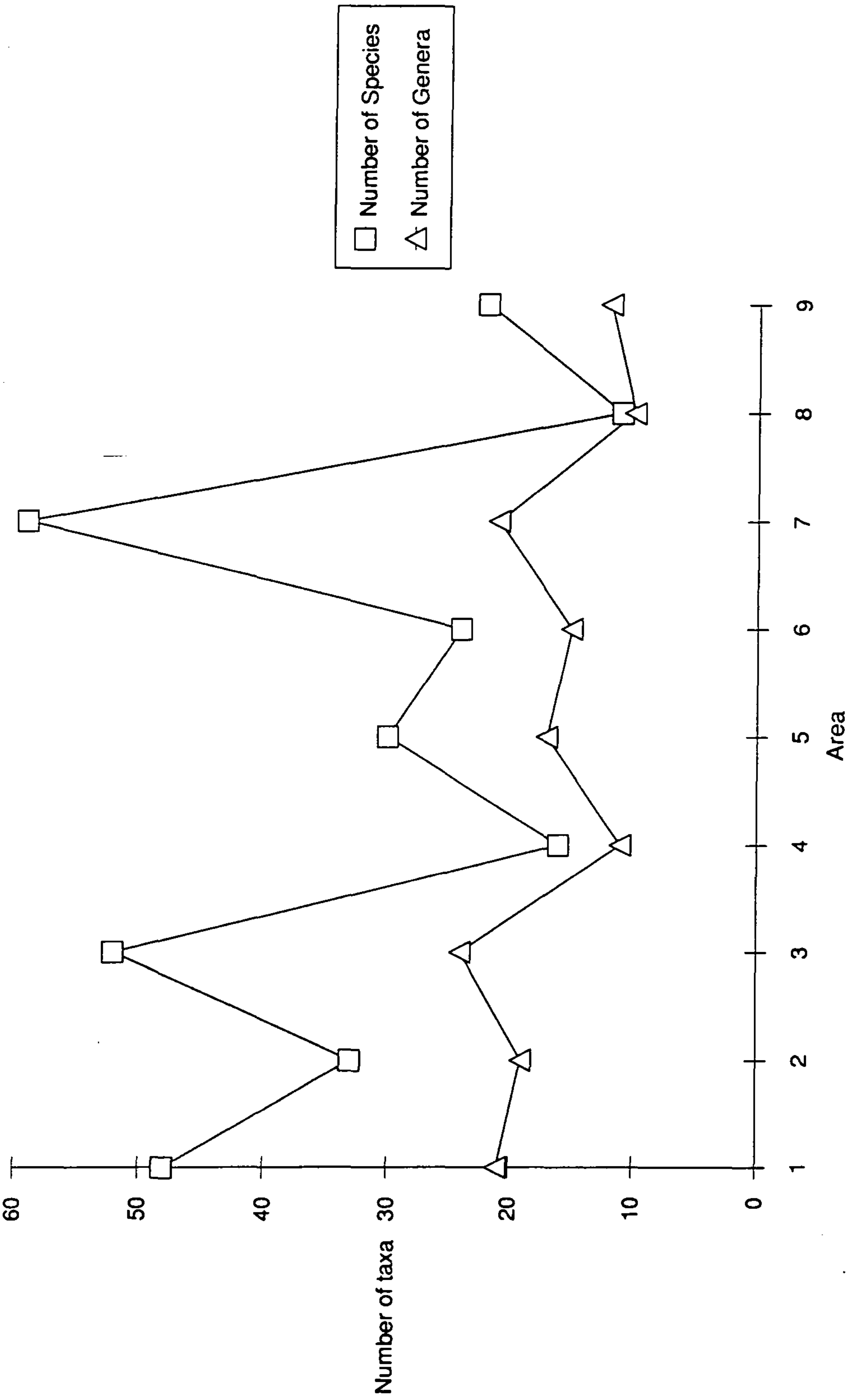


Fig. 13.3. Plots of numbers of species against geographical area

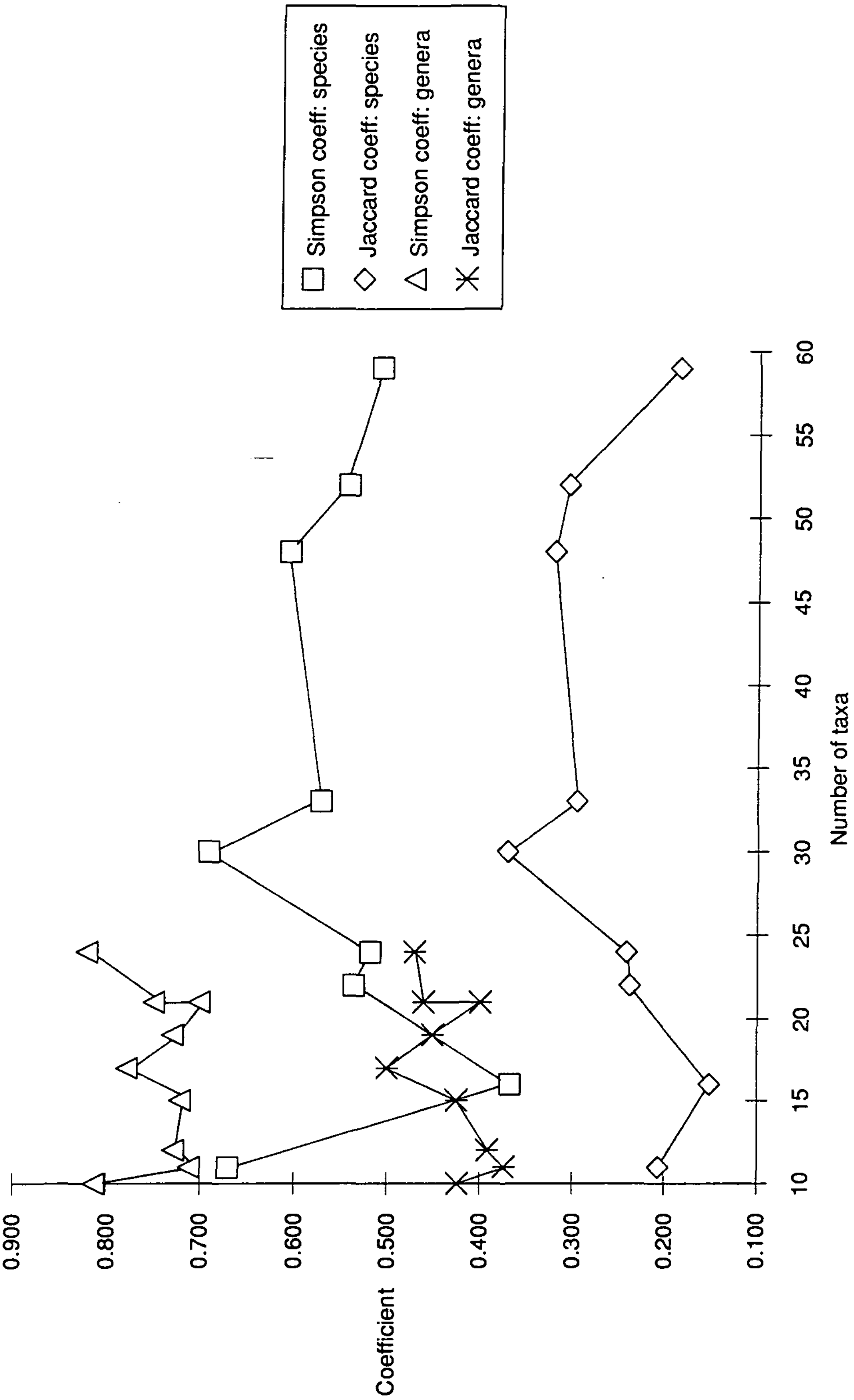


Fig. 13.4. Plots of correlation coefficients against number of taxa

Figs. 13.1 and 13.2 show plots of average coefficients against the geographical position of the areas. The areas are arranged in a very crude northeast-southwest order, and the average Simpson and Jaccard Coefficients at both specific and generic level for the respective areas is shown. Though there is a lot of variation in the data, there is a very weak northeast-southwest trend of decreasing values of the average coefficients of similarity; however, Derbyshire is anomalously low (for reasons discussed later in this chapter), while North Wales has an anomalously high set of coefficient averages. This trend could indicate that faunas in the downcurrent west side of the area are more dissimilar with neighbouring zones than faunas in the east. However, it is debatable whether Simpson and Jaccard Coefficients should show a decreasing gradient in coefficient averages. To test this hypothesis, several mathematical matrices have been constructed, analysing the trends of the average Simpson Coefficients with varying degrees of species evolution and dispersal. These are illustrated in figures 13.5 to 13.8.

Notations : **a.** Mathematical matrices : arrows («««) indicate species migration into the next area. Total number of species in each area shown in bottom row.

b. Simpson Coefficient matrices : Total number of species in each zone shown on top line. Within each cell, number of common taxa shown in top left, Simpson Coefficient in centre.

Premises : **a.** Easterly current, **b.** initial population of 10, **c.** six geographical zones, **d.** species can migrate downcurrent, but cannot migrate eastward, against the current.

Model 1 : Decrease of 1 taxon per zone, evolution of 1 new taxon per zone with a single-zone longevity.

Result = Initially low average coefficient, increasing in central areas, and then decreasing in the western areas to values lower than the initial easterly average.

Model 2 : Decrease of 1 taxon per zone, evolution of 1 new taxon per zone which is then dispersed to all succeeding westerly zones.

Result = Initially low average coefficient, increasing in central areas, then decreasing symmetrically, with a westerly coefficient average the same as the initial easterly one.

Model 3 : No decrease in taxa between zones, evolution of 1 new taxon per zone which is then dispersed to all succeeding westerly zones.

Result = Uniform average of 1.00 between all zones.

Model 4 : Decrease of 1 taxon per zone, evolution of 1 new taxon per zone, which then remains endemic within that zone.

Result = Steady decline of the average Simpson Coefficient in western areas.

Mathematical matrix

F	E	D	C	B	A	Zone
5	«« 6	«« 7	«« 8	«« 9	«« 10	
			1	«« 1		
		1	«« 1			
	1	«« 1				
1	«« 1					
1						
7	8	9	10	10	10	Total

Simpson Coefficient matrix

	A 10	B 10	C 10	D 9	E 8	F 7	Av
A		9 0.90	8 0.80	7 0.78	6 0.75	5 0.71	0.788
B	0.90		9 0.90	7 0.78	6 0.75	5 0.71	0.808
C	0.80	0.90		8 0.89	6 0.75	5 0.71	0.810
D	0.78	0.78	0.89		7 0.88	5 0.71	0.808
E	0.75	0.75	0.75	0.88		6 0.86	0.798
F	0.71	0.71	0.71	0.71	0.86		0.740

Plot of average coefficient against zone

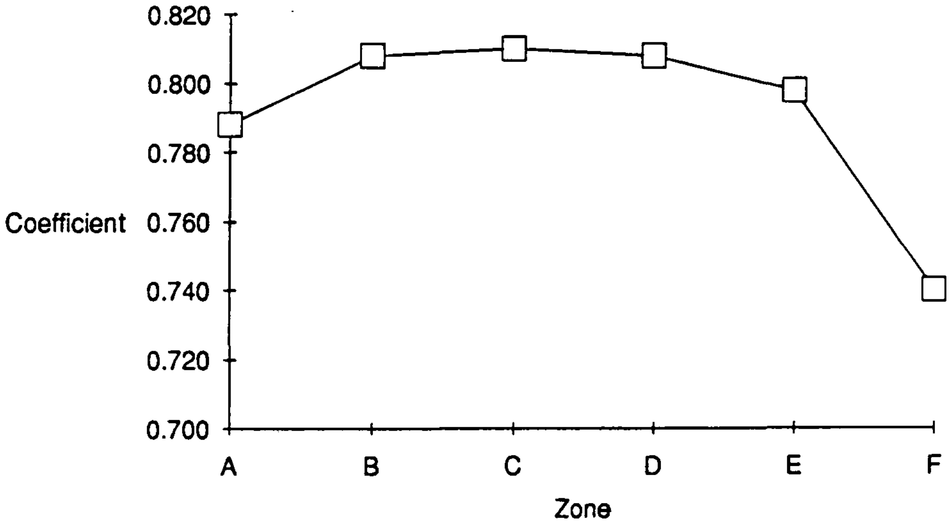


Fig. 13.5. Model 1

Mathematical matrix

F	E	D	C	B	A	Zone
5	«« 6	«« 7	«« 8	«« 9	«« 10	
1	«« 1	«« 1	«« 1	«« 1		
1	«« 1	«« 1	«« 1			
1	«« 1	«« 1				
1	«« 1					
1						
10	10	10	10	10	10	Total

Simpson Coefficient matrix

	A 10	B 10	C 10	D 10	E 10	F 10	Av
A	▨	9 0.90	8 0.80	7 0.70	6 0.60	5 0.50	0.700
B	0.90	▨	9 0.90	8 0.80	7 0.70	6 0.60	0.780
C	0.80	0.90	▨	9 0.90	8 0.80	7 0.70	0.820
D	0.70	0.80	0.90	▨	9 0.90	8 0.80	0.820
E	0.60	0.70	0.80	0.90	▨	9 0.90	0.780
F	0.50	0.60	0.70	0.80	0.90	▨	0.700

Plot of average coefficient against zone

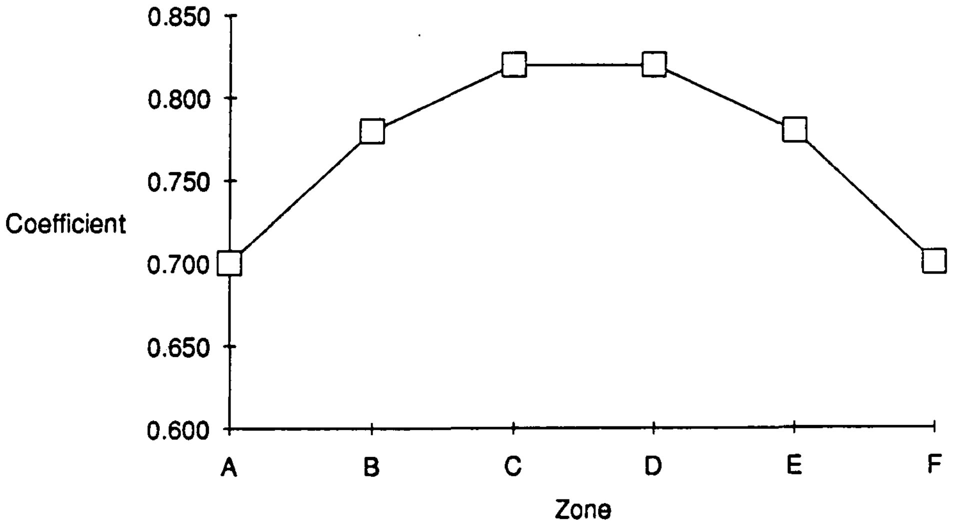


Fig. 13.6. Model 2

Mathematical matrix

F	E	D	C	B	A	Zone
10	«« 10	«« 10	«« 10	«« 10	«« 10	
1	«« 1	«« 1	«« 1	«« 1		
1	«« 1	«« 1	«« 1			
1	«« 1	«« 1				
1	«« 1					
1						
15	14	13	12	11	10	Total

Simpson Coefficient matrix

	A 10	B 11	C 12	D 13	E 14	F 15	Av
A	▨	10 1.00	10 1.00	10 1.00	10 1.00	10 1.00	1.000
B	1.00	▨	11 1.00	11 1.00	11 1.00	11 1.00	1.000
C	1.00	1.00	▨	12 1.00	12 1.00	12 1.00	1.000
D	1.00	1.00	1.00	▨	13 1.00	13 1.00	1.000
E	1.00	1.00	1.00	1.00	▨	14 1.00	1.000
F	1.00	1.00	1.00	1.00	1.00	▨	1.000

Plot of average coefficient against zone

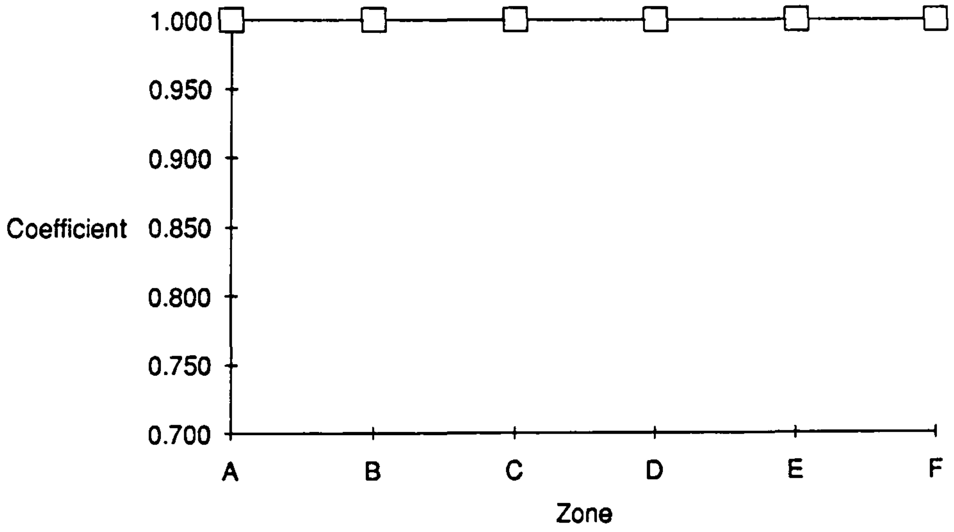


Fig. 13.7. Model 3

Mathematical matrix

F	E	D	C	B	A	Zone
5	«« 6	«« 7	«« 8	«« 9	«« 10	
				1		
			1			
		1				
	1					
1						
6	7	8	9	10	10	Total

Simpson Coefficient matrix

	A 10	B 10	C 9	D 8	E 7	F 6	Av
A		9 0.90	8 0.89	7 0.88	6 0.86	5 0.83	0.872
B	0.90		8 0.89	7 0.88	6 0.86	5 0.83	0.872
C	0.89	0.89		7 0.88	6 0.86	5 0.83	0.870
D	0.88	0.88	0.88		6 0.86	5 0.83	0.866
E	0.86	0.86	0.86	0.86		5 0.83	0.854
F	0.83	0.83	0.83	0.83	0.83		0.830

Plot of average coefficient against zone

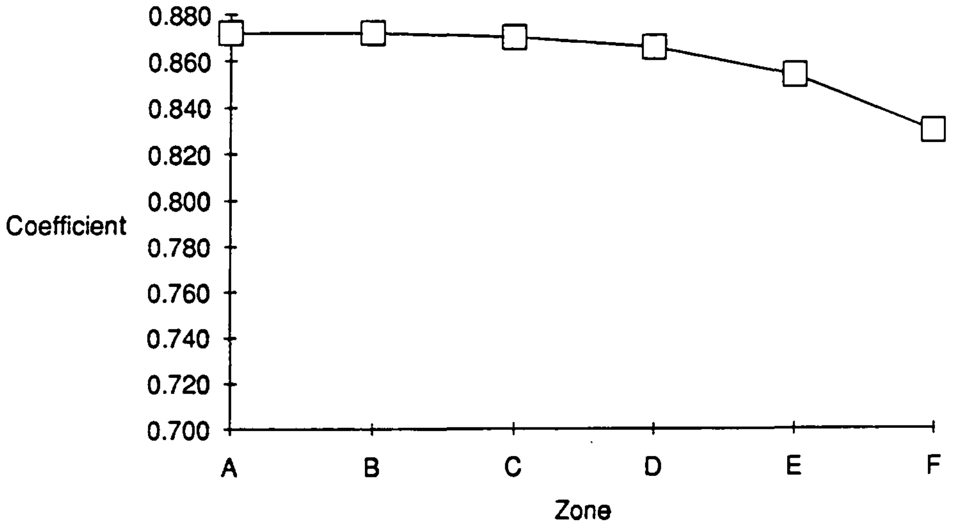


Fig. 13.8. Model 4

Thus, models 1 and 4, which have only limited distributions of species between the zones, produce the best fit with the patterns produced in figs. 13.1 and 13.2. However, it should be realised that not only is the Carboniferous data set far from complete, but the area under study is relatively small, and the relative geographical positioning of the zones on the bottom axes is only very crude, whereas the models have assumed a linear arrangement of the zones.

The notion that the trends are artefacts of an incomplete data set needs to be addressed. A plot of the number of taxa recorded in each area, against an alignment of the zones as in the above study (fig. 13.3) showed a similar trend to the coefficient/zone plots, with fewer species and fewer genera being recorded on the westerly regions than in the east. There is, however, much variation in this data, especially in the plots of number of species recorded. It may be argued that the trends seen in coefficient averages against geographical position may simply be due to a decrease in the number of taxa recorded in the west. However, a plot of the number of taxa recorded in an area against the corresponding coefficients of similarity (fig. 13.4) produced randomly scattered points, with no consistent trend amongst the data. This suggests that there is not, in fact, a relationship between the number of taxa in an area, and the Simpson and Jaccard Coefficients. Thus, the decreasing westward trend in the similarity coefficients is most likely due to biogeographical reasons, rather than to any mathematical relationship of coefficient value and number of taxa.

Figure 13.9 shows an inferred current circulation pattern for the region under study, which seems to be consistent with the generally accepted main easterly-derived currents, and the equatorial placing of the British Isles in the Lower Carboniferous (Scotese & McKerrow, 1990). The predominant currents are indicated with heavy lines, and subsidiary currents are shown by lighter lines. An inferred occasional connection between the Midland Valley and North Ireland is illustrated by a thin, broken line. The currents were probably pushed slightly to the southwest, in response to both the Coreolis effect acting on currents in the southern hemisphere, and to the northeast-southwest trend of the Laurasian shoreline. This circulation pattern can account for several features of the Simpson and Jaccard Coefficient results :

a. The low correlation between the bryozoan faunas of the Midland Valley and Northern Ireland. Despite the proximity of the two areas, and the palaeogeographical reconstructions (Johnson, 1982) showing an adjoining seaway, bryozoan faunal correlations between the two areas are consistently low. Wilson (1989) discussed the palaeogeographical setting of the Midland Valley, and observed the marine incursions to onlap from the east; the marine beds pinched out towards Kintyre, and only one limestone is present in the highly condensed sequence in Ballycastle, Northern Ireland. Thus, the Midland Valley of Scotland and the area of

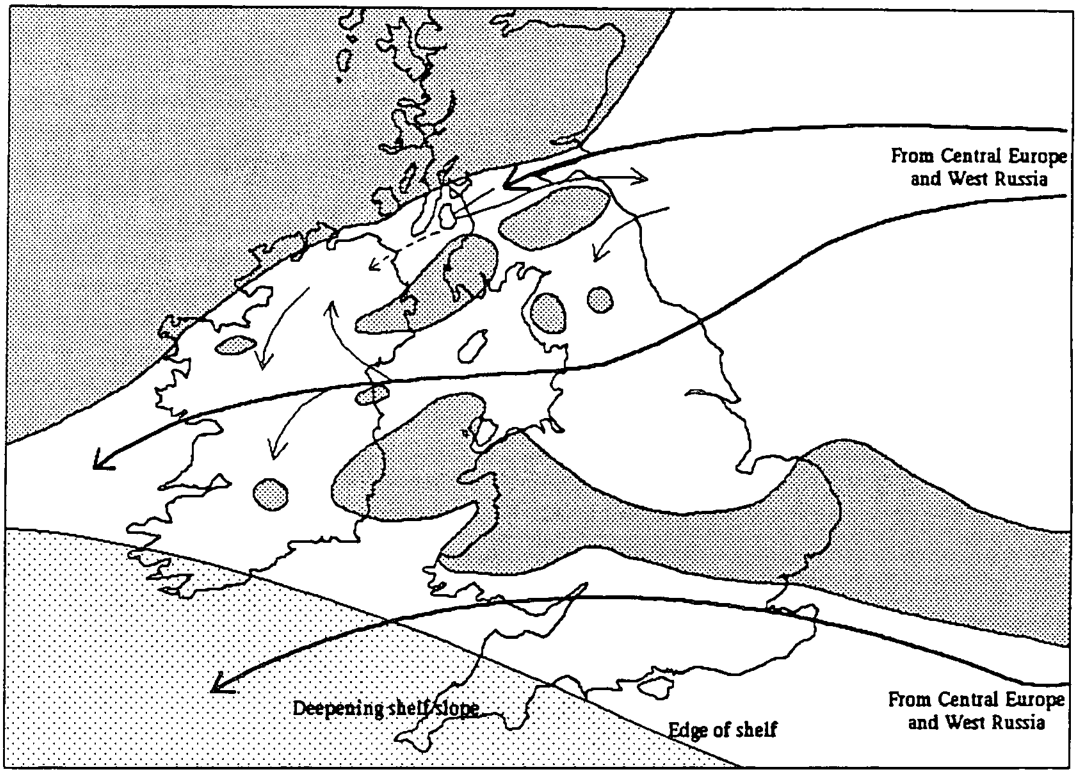


Fig. 13.9. Palaeocurrents across Britain in the Lower Carboniferous

North Ireland were only occasionally connected by a direct seaway. The Midland Valley was, in effect, a "blind alley", so species which originated there would have a low chance of being dispersed to North Ireland, though an accompanying return current could have swept some bryozoans out into the open sea. An additional consequence of a predominantly easterly current is that species from the east would have tended to be dispersed along the Longford Down Massif, by-passing North Ireland, and have a greater chance of settling in Central Ireland (fig. 13.9).

b. The high correlations between The Pennines, North Wales, and Central Ireland. The central position of these three areas, coupled with their northeast-facing aspect would have made them open to the easterly-derived ocean currents, which most probably swept between the Longford Down Massif and St. George's Land (fig. 13.9). As was discussed earlier, this ensured good bryozoan dispersals between the three areas.

c. The high correlations between South Wales and the Midland Valley. These two areas occur at opposite ends of the British Isles, yet the coefficients of similarity are rather high. There may be an overprint of collection data on the overall coefficients, since the two areas have been the subject of fieldwork for this project, and the majority of data on the two areas has been inputted from specimens noted during the fieldwork. Coefficients calculated from fieldwork species occurrences do show an expected pattern, with decreasing similarity gradients between South Wales, North Wales, Northumberland, and the Midland Valley. However, St. Georges Land, coupled with an easterly current, should have provided a barrier to the migration of Scottish bryozoans to South Wales, and therefore high similarities could be considered anomalous. This anomaly may be explained by a Central European/Baltic origin for the bryozoan faunas of Britain; similar bryozoans may have been swept westwards, with one branch of the current carrying bryozoans to the Midland Valley, and another sweeping around the southern shore of the Wales-Brabant massif to South Wales (fig. 13.9).

d. The low correlation between South Wales and South Ireland. Despite a similarity in the facies during the Courceyan (see section on South Wales distributions), the coefficients of similarity are abnormally low between the two areas, with a Simpson Coefficient at specific level of 0.364. Two species (*Fenestella multispinosa* and *Polypora verrucosa*) have possible occurrences in Hook Head, and this data was not been included in the coefficient calculations; however, even adding these to the equations, the Simpson Coefficient is still very low at only 0.417 (at specific level), though correlations are better with the Jaccard Coefficient. Low correlations may be due to the fact that most of the South Ireland data comes from the Courceyan of Hook Head, whilst the South Wales data is spread through several localities and spans the entire Dinantian. However, South Ireland does not have uniformly-low correlations, and in fact has a very high correlation with Central Ireland. The current circulation pattern detailed in fig. 13.9 could provide an answer to this problem; Southern Ireland species would be unable to migrate into South Wales, against the easterly current, and a southwest component to the general currents would tend to sweep the South Wales species away from South Ireland.

One remaining anomaly, which cannot be explained by current circulation patterns, is **the low correlations of Derbyshire.** Despite a relatively central position, Derbyshire has consistently low Simpson and Jaccard Coefficients with the other zones under study. Though the data may be affected by the area being under-studied, the coefficients give patterns consistent with the geographical positions of the regions, albeit of lower magnitude than expected; namely, that the lowest scores are with South Wales (from which Derbyshire was separated by St. George's Land), and higher scores with the neighbouring regions of the Pennines and North Wales. The facies of Derbyshire comprised the best developed Carboniferous reefs in Britain, and it is likely that the bryozoans which inhabited this region were predominantly reef-specialised forms, incapable of thriving in the non-reef facies of the rest of Britain. Much of the data for Derbyshire is provided by Owen (1966) and Bancroft (1984), who looked at the faunas around Castleton, and some additional information has been recorded from museum collections. Several species have been recorded only from Derbyshire, including *Rhombopora radialis*, *Streblotrypa pectinata*, *Penniretepora triserialis*, *Stenopora castletonensis*, *Amplexopora? discoidea*, and *Chainodictyon* sp. The other taxa which occur tend to be widespread forms, including *Fenestella multispinosa*, *F. plebeia*, *F. polyporata*, *Fistulipora incrustans* and the quiet-water forms *Hemitrypa hibernica* and *Ptylopora pluma*. However, it must be conceded that Derbyshire is grossly under-studied, and further research into the area will undoubtedly yield a more complete bryozoan faunal list.

Dissimilarities in Carboniferous Bryozoan Faunas

Current patterns have been used in the previous section to explain certain similarities and dissimilarities between the bryozoan faunas from different areas of the British Isles in the Carboniferous, but circulation patterns alone cannot account for the general low levels of similarity. As was mentioned earlier, Bambach (1990) cites Simpson Coefficients up to 0.97 and Jaccard Coefficients up to 0.70 (at generic level) between the faunas of adjacent provinces; the generic level averages in this study are only 0.750 and 0.433 for the Simpson and Jaccard Coefficients respectively. Since the zones under study are much smaller than classic "provinces", and the coefficients cover a unit of time some 35-40 million years, it might be expected that the levels of bryozoan similarity should be much higher. The possibility of lack of data has been discussed previously, and this may have some bearing on the low levels of similarity. However, there are certainly some species which are restricted to only a few of the nine regions, and some explanations need to be sought to explain this observation. These are discussed in the following sections.

Facies restriction and bryozoan faunas

Many marine animals are restricted in their distributions by facies type. Some taxa are not adapted to live on particular sediment types or in certain water depths. Do bryozoans show such facies restriction?

The sections in this thesis which discuss the bryozoans collected during fieldwork have tried to place the various bryozoan assemblages in their palaeoenvironmental settings. Many different facies have been recorded, ranging from deeper-water muddy deposits, to nearshore, energetic limestones. Fig. 13.10 shows a plot of 40 bryozoan species against nine facies groupings. The nine groupings are :

Nearshore Limestones : These are usually thin limestones, which are intercalated between deltaic sediments (eg. the Lickar Limestone), or succeed horizons which show abnormal salinities (eg. the Randerston Limestone).

Shaly Limestones : These are grey limestones which contain a large amount of terrigenous clastics, often including visible mica flakes; thus they are presumed to have either been formed near-shore, or to have been dominated by fluviatile run-off into the depositional basin. The clastic component is coarser than that found in micrites.

Limestone/Shale Beds : This term is used to describe sequences where there are small-scale alternations of limestones and shales. The alternations may be relatively regular (as in the Tumbler Beds over the Great Limestone), or may occur at irregular intervals (shown by the Hurlet Shales on Arran). The cyclicity may have some tectonic control, or may represent switching of terrigenous input into an area.

Low-clastics Limestones : These limestones are moderately pure bioclastic limestones, showing only a small degree of terrigenous input. They often preserve highly diverse faunas, and are usually buff-coloured to grey. They are coarser-grained than micrites.

High-energy Limestones : This group includes those limestones which can be demonstrated to have been deposited in a high-energy environment, indicated by fragmentation of the fauna, or showing evidence of current scouring or cross-bedding.

Clastic-free Limestones : These are pure white to light grey limestones, often massively-bedded and quite thick, with negligible amounts of terrigenous clastic material. Productid brachiopods and rugose corals are usually the dominant elements of the fauna. The matrix is usually composed of bioclastic débris, and this fact, combined with the observation that many corals are overturned (Ramsbottom, 1978), suggests a rather turbulent environment.

Micrites : This group encompasses dark-grey limestones composed of fine lime mud. They are inferred to have formed in quiet water conditions, with little terrigenous influence, but are not necessarily deep-water deposits.

Shales : This group includes fine-grained shales with only a limited amount of carbonate in the matrix; much of the clastic constituent is probably derived from a terrigenous source, rather than being autochthonously-generated. A quiet-water setting is indicated by these deposits, which are probably also formed in moderately-deep water, since a degree of terrigenous influence is evident.

Crinoid Bank Limestones : This facies encompasses the Waulsortian reef-flank deposits of Salthill Quarry, Clitheroe; the community is preserved *in situ*, and is dominated by a variety of crinoid taxa.

It is important to remember that very few of the beds surveyed during this fieldwork actually represent *in situ* deposits, and some degree of transportation has often taken place. However, in many cases the preservation of large fragments of delicate fenestellid fronds suggests that the transportation distance cannot have been very far; thus the facies in which the bryozoans have been recorded should give a fair indication of the environments in which they lived.

The plots of facies against species and against genera show that bryozoans are very widespread; however, no bryozoans were found in the very high-energy oolitic limestones of South Wales, nor are they common in crinoidal limestones, though *Minilya oculata* was recorded in the crinoid reef-flank facies in Clitheroe. Apart from these exceptions, bryozoans have been listed from all the common Carboniferous marine shelf facies.

Fig. 13.11, which shows the distributions of the genera in the various facies, indicates that the higher-energy deposits (High Energy Limestones, and Clastic-free Limestones) support the smallest number of genera, excepting the rare bryozoan from the Crinoid Bank Limestones. Additionally, the Nearshore Limestones would have had only eight genera recorded, if the unusually-diverse fauna of the Ironscars Limestone of Northumberland had been excluded. Thus, it is apparent that the relatively fragile colony architecture of many bryozoans limits their occurrence to the quieter-water deposits.

			Nearshore Lsts.						Shaly Lsts.				Lst/Shale Beds					Low clastics Lsts.					High Energy Lsts.			Clastic-free Lsts.				Micrites					Shales			Crinoid Bank Lst
	Avon Gorge	Randerston Lst	Index Lst	Dun Lst	Ironscars Lst	Lickar Lst	Stackpole Bryozoa Bed	Tears Point Lst	Acre Lst	Sandbanks Lst	Coplow Quarry	Hurlet Shales	Tumbler Beds	Redesdale	Witch Lake	Eelwell Lst	Oxford Lst	Sugar Sands Lst	Hendre: T,3,4	Cefn Mawr	Bryn Mawr: T,L,M	Three Cliffs Bay	Red Chamber & Mewslade	Charlestown Main Lst	St. Monans White	Loggerheads	Llandudno: 4	Mid Kinniny	Black Lias Quarry	Bryn Mawr: D,S,B	Llandudno: 1,2	Halkyn Quarry	Top Dun Lst.	Llandudno: 3	Ashes Quarry	Top St. Monans	Hendre: S	Salthill Quarry
Rhombopora similis							×	×														×	?					×										
Rhombopora incrassata					×			×											×											×				×				
Rhombopora bancrofti				×						×			×																×	×								
Rhabdomeson gracilis					×	×			×	×		×				×			×		×			×	×					×		×			×			
Rhabdomeson rhombifera	×			×					×	×		×		×			×														×		×					
Hyphasmopora buskii					×											×																	×					
Fenestella bicellulata								×					×	×		×			×		×	×						×							×		×	
Fenestella cf. *ivanovi*														×																								
Fenestella frutex				×	×			×	×			×	×	×		×		×	×										×	×	×						×	
Fenestella multispinosa				×	×	×	×	×	×	×			×	×		×	×		×		×	×	×			×				×		×	×					
Fenestella tuberculo-carinata			×		×							×			×	×									×			×								×		
Fenestella plebeia	×			×	×	×		×	×	×	×	×	×	×		×	×	×	×	×	×	×	×				×		×	×	×	×	×	×	×		×	
Fenestella polyporata									×					×						×										×	×	×						
Ignotifenestella sp.								×																														
Polyfenestella fenestelliformis										×																												
Hemitrypa hibernica																										×												
Polypora dendroides																			×		×	×			×			×			×							
Polypora verrucosa								×	×							×			×		×								×									
Polypora hexagonaria					×																																	
Minilya oculata																																						×
Diploporaria marginalis									×					×			×														×		×					
Baculopora sp.																				×										×								
Penniretepora spinosa					?				×							×				?								×		×							×	
Penniretepora flexicarinata								×	×				×	×		×	×		×		×								×	×	×	×	×				×	
Penniretepora pulcherrima				×													×															×						
Penniretepora laxa																															×							
Penniretepora grandis																														×	×							
Ptylopora pluma																							×						×									
Septopora carbonaria			×		×	×								×		×		×		×																		
Synocladia sp.																×																						
Tabulipora urii	?	?		?	?	?	?		?	?		×	?			?	?	?	×	?	×				×			×		?								
Tabulipora howsii														×														×										
Tabulipora minima?																																			×			
Stenodiscus tumida					×									×						×			×			×			×									
Dyscritella miliaria					×	×			×																													
Fistulipora incrustans			×	×	×			×					×	×		×			×	×	×		×							×					×			
Eridopora beilensis					×														×	×																		
Eridopora sp. nov.?																												×										
Sulcoretepora parallela				×					×	×				×		×																			×			
Goniocladia cellulifera													×																									

Fig. 13.10. Table of Carboniferous bryozoan species and their facies setting

Crinoid Bank Limestones	Shales	Micrites	Clastic-free Limestones	High Energy Limestones	Low clastics Limestones	Limestone/Shale Beds	Shaly Limestones	Nearshore Limestones	
	x	x		x	x	x	x	x	*Rhombopora*
	x	x	x	x	x	x	x	x	*Rhabdomeson*
	x				x			x	*Hyphasmopora*
	x	x	x	x	x	x	x	x	*Fenestella*
							x		*Ignotifenestella*
							x		*Polyfenestella*
			x						*Hemitrypa*
		x	x	x	x		x	x	*Polypora*
x									*Minilya*
	x	x			x	x	x		*Diploporaria*
		x			x				*Baculopora*
	x	x			x	x	x	x	*Penniretepora*
		x		x					*Ptylopora*
					x	x		x	*Septopora*
					x				*Synocladia*
	x	x	x		x	x	x	x	*Tabulipora*
		x	x	x	x	x		x	*Stenodiscus*
							x	x	*Dyscritella*
	x	x		x	x	x	x	x	*Fistulipora*
		x			x			x	*Eridopora*
	x				x	x	x	x	*Sulcoretepora*
						x			*Goniocladia*
1	9	12	6	7	15	11	12	13	Number of genera

Fig. 13.11. Table of Carboniferous bryozoan genera and their facies setting

The broad facies relations of the commoner genera are discussed below :

Rhombopora : This genus is not particularly abundant, but appears to have a wide facies distribution at generic level, though fig. 13.10 shows individual species to have a somewhat sporadic occurrence. Colonies have yet to be reported from the Clastic-free Limestones.

Rhabdomeson : The genus *Rhabdomeson* has a very wide facies distribution, with recorded occurrences in all the major facies types. *Rhabdomeson gracilis*, the stouter of the two British representatives of the genus, has the widest occurrence, while its slender counterpart, *R. rhombifera*, has not been observed in the higher-energy deposits. Some comparison may been drawn with the study on the Hurlet Shales of Arran (see Chapter 5), where it was shown that *R. gracilis* appeared in the pioneering succession before *R. rhombifera*; thus, *R. gracilis* seems to be the more generalised of the two species.

Fenestella : Fenestellids are the most dominant bryozoan taxa in most Carboniferous facies, and the order Fenestrata has representatives in all the recorded facies. Of these, the genus *Fenestella* has the widest distribution, which is to be expected, since there are several colony architectures within the genus. *Fenestella plebeia* and *F. multispinosa* have very broad facies distributions, and *F. tuberculo-carinata*, where it has been recorded in the north of Britain, has a similarly wide occurrence. These species can have variable colony shapes, as has been the major theme in the sections discussing the taxonomy of various representatives from around Britain (see Part II), and colony flexibility has undoubtedly contributed to the success of these species. The species *F. tuberculo-carinata* is a good example of the variation which can occur in a single taxon; a study of representatives from Arran (Chapter 5) has revealed that forms which occur in the Hurlet Shales tend to have thinner branches and dissepiments, smaller, more widely-spaced apertures, and closer nodes than their counterparts in the Index Limestone, which have thicker branches and dissepiments, closer-spaced apertures, and more widely-spaced nodes. The stouter meshwork parameters in the Index Limestone material may be adaptations for life in a more turbulent environment, or may represent colony morphology in environments with an excess of carbonate for skeletal growth; however, it is doubtful that lack of dissolved carbonate was a limiting factor on the architecture of specimens from the shales.

Fenestella frutex, a thinner-meshed bryozoan than *F. multispinosa*, does have a moderately-widespread facies distribution, but the thin meshwork did not enable the species to dwell in the higher-energy settings. Similarly, the finely-meshed species *F. bicellulata* and the wide-fenestruled, lax-meshed *F. polyporata* are excluded from the more energetic environments, where stronger current activity would have inflicted too much stress on the fine colony structures. It is likely that the moderate meshwork dimensions of *F. multispinosa*, *F. tuberculo-carinata*, and *F. plebeia* were of an optimum size for strength versus economy of growth, and thus were able to dominate the faunas in many Carboniferous environments.

Polypora : The genus *Polypora* has a wide facies distribution, the stout meshwork dimensions providing enough rigidity for species to survive even in the higher-energy environments; in these more turbulent settings, it is the shorter-fenestruled species *P. dendroides* that is present, rather than the lax-meshed *P. verrucosa*,and in the nearshore settings, the very stout-meshed *P. hexagonaria* has been recorded. No representatives of the genus have yet been recovered from the Limestone/Shale Beds, but since only three examples of this facies have been studied, this may be a collection bias, rather than a feature due to facies-exclusion. However, *Polypora* does not seem to occur in the Shale facies, and may prefer moderately energetic environments; Bancroft (1984) records that *P. verrucosa* is found in shallow water limestones and reef settings.

The arrangement of the autozooids into three or more rows on each branch may be a primitive character; the early phylloporinids, with multiserial rows of apertures, and a vestigial bilaminate skeletal arrangement (Tavener-Smith, 1975) are the likely ancestors of the Fenestellidae. Tavener-Smith (*ibid.*) also states that

> biserial forms such as *Fenestella* and its allies evolved from multiserial fenestelloids [eg. *Polypora*] by the suppression of one or more rows of zooecia.

The arrangement of the autozooids into two rows is an adaptation for a more efficient feeding strategy (Cowen & Rider, 1972). A biserial arrangement on a unilaminar colony would have allowed the ciliary action of everted tentacles into the fenestrules to draw a water current through the meshwork in a single direction. This adaptation would have been of greatest use in quiet-water settings; in more turbulent environments, the higher-velocity ambient currents would have interfered with the zooid-generated ones. Further, feeding may have been achieved passively in the higher currents, though this strategy has not been observed in modern bryozoans (Southwood, 1985). Stratton & Horowitz (1974) modelled the flow of water through plexiglass *Polypora* fronds, and concluded that the branch structure of the genus provided eddying, reduced velocity water from unidirectional current flows of 2 to 5 cm sec^{-1}. The more primitive *Polypora*, with three or more rows of zooids on each branch, would have produced less effective zooid-generated feeding currents, since the multiserial rows would have created interfering cross-currents.

This disadvantage, compared to *Fenestella*, would have been most obvious in the slack-water shale facies, since the difference in current efficiency between the two genera would be less obvious in the more turbulent environments; this may be an explanation of the scarcity of the genus *Polypora* in quiet-water settings, where it was most likely out-competed by the biserial fenestellids. Taylor (1979) also points out that extrazooecial currents may be additionally advantageous in quiet-water settings through a scouring action, which would have cleared the colony surfaces of fine-grained sediment, though this phenomenon would be of greater importance to sheet-like encrusting colonies, rather than erect forms such a *Polypora.* McKinney & Jackson (1989) have cited the regular arrangement of the apertures in *Fenestella* as a plausible reason for the overwhelming success of the group.

Diploporaria and ***Baculopora*** : These thin-branched acanthocladiids are restricted in their occurrences to the quieter-water facies, and have not been recorded in the more turbulent High Energy, Clastic-free, or Nearshore Limestones.

Penniretepora : The genus *Penniretepora* has a moderately wide facies occurrence, but has not been recorded in the more energetic environments. McKinney & Jackson (1989) discussed similar observations from the Chesterian deposits of eastern North America (see also McKinney & Gault, 1980), and concluded that the non-linked branches of *Penniretepora* created a colony that was weaker than the other linked-branched unilaminate colonies; thus the genus was restricted to the mud-dominated deposits that represented quieter-water areas.

Within the genus *Penniretepora,* there are some differences in facies-settlement patterns between species. The larger penniretepórids *P. laxa* and *P. grandis,* have been recorded only in the micritic facies, and have not been found in the more energetic limestones. Thus, as is the case with *Fenestella,* there is probably an optimum colony size which balances rigidity, stability, zooid current-generating potential, and economy of growth; the species *P. flexicarinata* and *P. pulcherrima* , both with lateral branch spacings in the order of 0.80mm (comparable with the magnitude of fenestrule lengths in the optimum *Fenestella* dimensions) have by far the widest facies distributions of the genus.

Septopora : This linked-branched acanthocladiid has a moderately-wide facies distribution, but, like *Penniretepora,* has not been found in the higher-energy deposits, though one specimen was noted in a thin, white bioclastic limestone in North Wales. The distribution differs from *Penniretepora* in that the genus does not commonly occur in shales. These observations are again similar to those made by McKinney & Jackson (1989), who recorded similar facies distributions between *Septopora* and the stout fenestellid *Polypora,* with the two genera being found predominantly in moderately-energetic environments.

Trepostomes : The trepostomes under study have wide facies distributions, and have been found in all environments, ranging from restricted-fauna, abnormal salinity limestones to high-energy, bioclastic, fully marine limestones. The same species can show several growth forms, with an initial encrusting habit being succeeded by an erect, dendritic habit; this flexibility in growth form has undoubtedly helped the taxon achieve a high degree of success regarding both numerical abundance and geographical distribution. The trepostomes, though occasionally occurring in shales, are not common in this facies, and may have been limited by the scarcity of suitably-large hard surfaces on which to settle and encrust.

Cystoporates : The cystoporates show a very similar facies distribution to the trepostomes; like this group, they are also predominantly encrusters. The species *Fistulipora incrustans* has a very wide distribution, but does not occur in the Clastic-free Limestone facies. Though encrusters are less likely to be physically-abraded in higher-energy environments than erect growth forms, they are more susceptible to burial by rapidly-shifting sediment, which is also associated with these facies. When specimens of encrusting cystoporates have been found growing on their original settlement surface, they have colonised areas which were presumably elevated above the sediment surface, and include chaetetids and rugose corals (see North Wales chapter 8, and Plate 9, figs. h. and i.), crinoid stems (as seen in the Ironscars Limestone, Northumberland) and fenestellid fans (see South Wales chapter 6, and Plate 10, fig. l.). The erect members of the order, *Sulcoretepora* and *Goniocladia*, have a comparatively limited facies distribution, and their slender, rather fragile colony forms seems to have generally limited their occurrences to the more muddy, quiet-water environments.

In summary, many bryozoan taxa have very wide facies distributions, and are excluded only from the most turbulent settings. Facies distributions can be shown to be related to colony architecture and feeding strategy, but there is no clear-cut relationship between individual species and facies. Fig. 13.10 demonstrates that it is not possible to take any single facies, and state the species which should occur in that environment; however, the colony habits, if not the exact species or genera, which should occur in that setting can be predicted with a fair degree of certainty.

It is improbable that facies-restrictions can solely account for the large scale bryozoan distributions throughout the Carboniferous strata of Britain and Ireland. The environments which are amenable to the locally-abundant species *Fenestella tuberculo-carinata* and *Tabulipora urii* are developed within all nine zones of study, yet these species are restricted to occurrences in the north of Britain. Thus, facies type cannot be a controlling influence on the geographical distribution of these species.

There may be an element of randomness in geographical facies-related distributions; Keough & Chernoff (1987) studying the modern bryozoan *Bugula neritina* found that the populations of the species were extremely patchy between apparently similar beds of seagrass, separated by only a few kilometres or less. Colonies which were transplanted into areas where *Bugula* did not normally occur actually grew and reproduced better than in the *Bugula*-inhabited areas; this suggests that the patchy distribution of the species is due not to subtle environmental differences, but is most probably related to very low dispersal between beds. Similarity, Winston & Jackson (unpublished data, cited in McKinney & Jackson, 1989) accounted for the disjunct local distributions of reef-associated bryozoans to limited dispersal, rather than to facies variations.

The possibility of limited bryozoan dispersal

As has been discussed in the previous section, certain bryozoan populations may show restricted distributions which cannot be related to facies variation, but are due to limited initial dispersal. The possibility of bryozoan brooding their larvae has been discussed earlier in this chapter, and there seem to be little difference in the distributions of those species which are known to brood larvae, and those which do not.

There is some evidence for limited larval distribution amongst Carboniferous bryozoans; McKinney (1981 ; see also McKinney & Jackson, 1989, p.115) reported several incidents of fusion of young colonies of fenestellids. This not only suggests polyembryony, as only colonies with identical genetic patterns could fuse, but also indicates that the larvae cannot have been dispersed very far from the parent, since the juvenile colonies have grown in close proximity. Further, allele studies on modern bryozoans from Cape Cod (Schopf, 1974) showed that there are statistically significant differences in the genetic constituents of the bryozoan *Schizoporella errata* over distances as little as 11 to 13 kilometres; this implies that there is a restricted gene flow between the populations, related to limited larval dispersal.

As was discussed earlier, the main mode of bryozoan dispersal is by rafting. Larvae may settle on floating objects, or encrusted plants may be uprooted and drift in the open seas, carrying healthy bryozoan colonies. Low bryozoan distributions could be related to a scarcity of suitable rafting objects in the Carboniferous.

The Carboniferous continents supported large forests of lycopods, ferns and calamitids. Drifted logs of these trees reaching the open sea may have acted as settlement surfaces for Carboniferous bryozoans. However, fossilised logs with encrusting species have not been reported in the Carboniferous, in contrast to the crinoid-encrusted driftwood of Germanic Jurassic deposits. It is possible that the pithy nature of the stems made Carboniferous pteridophtes more susceptible to waterlogging than the Jurassic gymnosperms with woody stems. Studies on modern pine trees floating in lakes after the Mount St. Helens eruption have shown that the logs can stay afloat for up to several years (Mike Simms, personal communication), but the length of time for which Carboniferous material could have floated has not been documented.

Attachment to floating logs may not have been a particularly important method of bryozoan dispersal. Studies on Baltic bryozoans of the Ordovician (Bassler, 1911) showed that there is a moderately high faunal similarity between the Baltic species and American faunas, with 35% of the species being common between the two areas. Since land plants had not evolved at this time, drifting logs can be discounted as the dispersal mechanism between the provinces. Further, the percentage of species similarity in the Ordovician is of a similar magnitude to the percentage of Carboniferous genera in common between China and Europe (44%) determined from Linhuang (1989), implying that similar dispersal mechanisms operated in the two periods.

Thus, attachment to floating pumice or algal fronds remain the two most likely methods for bryozoan dispersal. It is not possible to test the floating pumice hypothesis, though acidic vulcanism certainly took place in the Midland Valley during the Carboniferous. Dispersal from ripped-up algal fronds is a probable method of transportation, since Carboniferous bryozoans were known to have encrusted such fronds (see the Tears Point section in Chapter 6). It is not possible to reconstruct the soft-tissued flora, though, and therefore it is difficult to estimate how far such fronds could have been transported.

Carboniferous clines

The effect of temperature on bryozoan distributions may be fairly significant. Ryland (1970) cited a study of bryozoans from Norwegian fjords, concluding that the distributions were controlled by a thermal boundary layer; twenty six species were recovered exclusively above this layer, forty eight exclusively deeper, and only nine species in both regimes. The inference is that those species which lived below the boundary layer were unable to survive in the extremely low temperatures occurring during winter. However, Ryland also states that those bryozoans which are eurybathic also appear to be eurythermal.

Temperature is known to affect the size of Cenozoic cheilostome zooids (Okamura & Bishop, 1988); in lower-temperature regions, zooids have longer chambers than in those colonies which inhabit warmer areas. However, the study of bryozoan morphologies from outcrops of the British Carboniferous has failed to show any significant variation in chamber length (indicated by autozooecial aperture spacing) between the same species from different regions.

During periods of abnormal salinities and low temperatures, polypides may degenerate and form "brown bodies"; McKinney (1969a) reported finding organic remains in a trepostome of late Namurian age which may represent such degenerated polypides, and similar structures were reported in trepostomes by Cumings & Galloway (1915). Thus, it is possible that there may have been temperature fluctuations great enough to trigger polypide degeneration in the Middle Carboniferous.

Palaeoclimatic charts published in Scotese & McKerrow (1990) show that the global climate in the Dinantian and early Namurian was fairly equable; it was not until the late Namurian that the pole-to-equator temperature gradient began to strengthen, after an episode of high-latitude warming in the middle and late Viséan (Kelley *et al.*, 1990). Thus, there is no evidence of temperature clines in existence along the southern margin of Laurasia during the Lower Carboniferous, and temperature differences can probably be discounted as a factor affecting British Carboniferous bryozoan distributions.

Bryozoan Variations Through the Carboniferous

Geographical variation has been shown to be a major architect of bryozoan distributions throughout the British Carboniferous. However, the differences in bryozoan faunas through time also needs to be discussed. Can regional faunal variations, for instance, be explained by the timing of episodes of marine influence, and within long-lived species, are there any indications of morphological change ?

Species diversity through time

Fig. 13.12 summarises several plots of the variation in bryozoan diversities through time. Strictly, since the data is mathematically discrete, rather than continuous, the bars should not be joined; however, the linking of the top points of the bars does give a clearer impression of the overall trends in diversity. The majority of the charts show a very similar story, regarding relative variations through time :

a. An episode of slightly-high diversity during the Courceyan
b. Reduced species diversity through the Chadian to Holkerian
c. A rapid rise in diversity to a mid-Asbian peak
d. A slight faunal turnover across the Asbian/Brigantian boundary
e. A rise in diversity to a mid-Brigantian peak
f. A decline in species diversity through the Namurian, though some areas have late-Pendleian or early-Arnsbergian peaks.

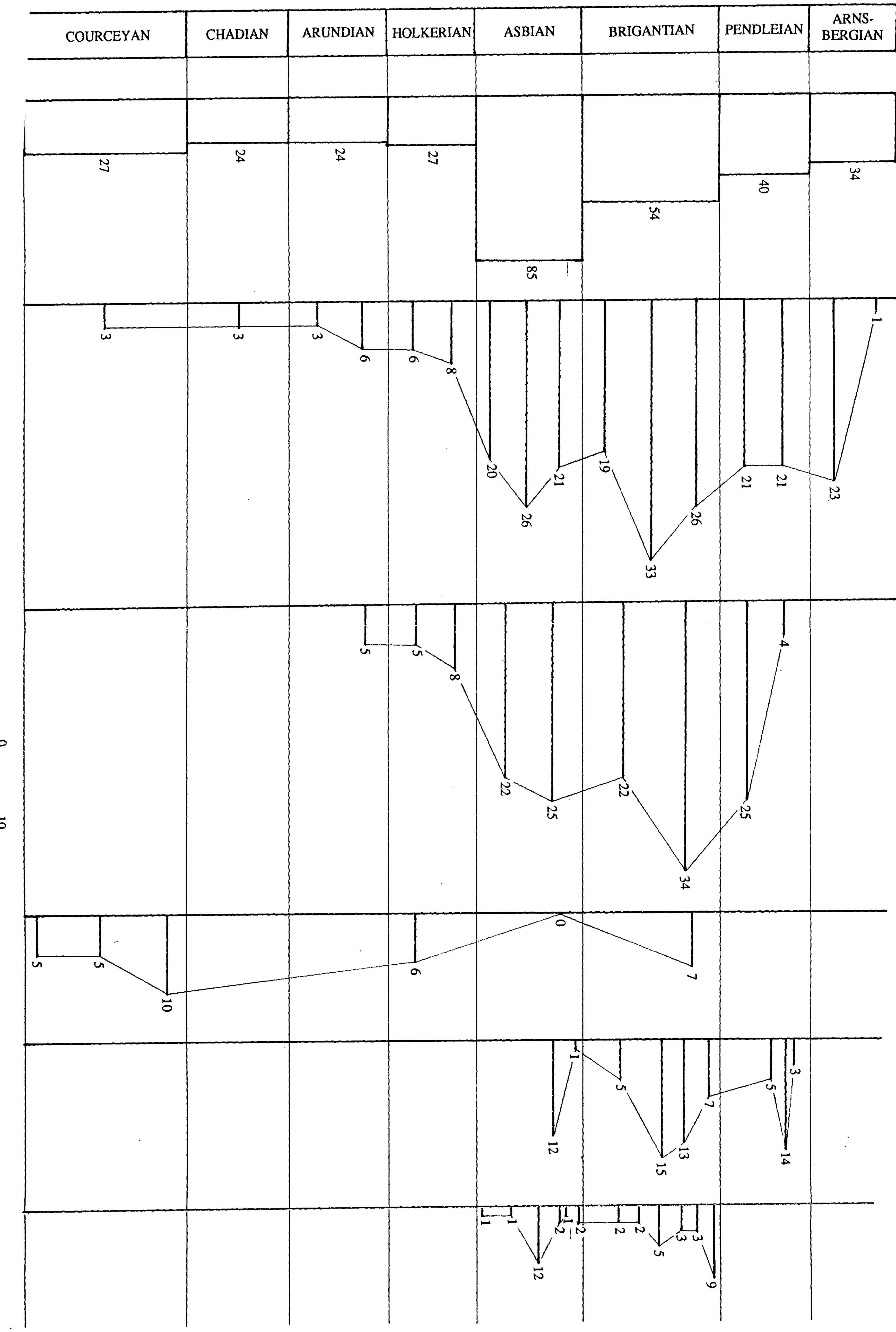


Fig. 13.12. Plots of Carboniferous bryozoan species diversity

Sea level changes during the Carboniferous

The fact that these patterns are repeated in several different studies, and are seen in several different field areas within Britain, suggests that the underlying causes for diversity variations through the Dinantian and Lower Silesian are due to large-scale effects, rather than local fluctuations. Palaeoclimatic causes are unlikely, since much data points to there being an equable climate over much of the globe during this time (Scotese & McKerrow, 1990). Eustatic sea level changes remain the most probable explanation for the temporal variations, but little has been published on global Carboniferous sea level fluctuations. Ross & Ross (1987) believe sea level fluctuations to be of low magnitude and with relatively long frequencies during the Dinantian, and that global sea level was high. Ramsbottom (1973) analysed the Dinantian in terms of six major cycles, which he believed to be related to eustatic sea level changes. The regressive phases coincide approximately with the stages erected by George *et al.* (1976), each succeeding transgression being accompanied by the influx of the migratory fauna used as the basis for Dinantian correlation. However, the Asbian and Brigantian were certainly the times of greatest marine influence over Carboniferous Britain, as exemplified by the development of widespread shallow-water carbonate platforms (see fig. 1.6, redrawn from Walkden, 1987, illustrating facies distributions in the Asbian).

The diachronous onset of marine conditions across Britain in the Carboniferous, with a northward transgression through the Dinantian (George *et al.*, 1976; Anderton *et al.*, 1979) is echoed in the reported bryozoan occurrences, illustrated by the Simpson Coefficient matrices at stage level (figs. 12.17 to 12.23). Courceyan data is restricted to the southern areas, with all areas not being represented until the Asbian. No bryozoan data has been found for the Brigantian of South and Central Ireland, and Namurian bryozoans have been recorded in only the north of Britain; further, Ramsbottom *et al.* (1978) illustrate shelf conditions in Ireland to be restricted to the north. The bryozoan species distribution maps (figs. 12.27 to 12.42) show that the first appearance of many species is in the southern regions, and they have progressively later appearances in the northern regions. This pattern of northward appearances is probably not a true migration trend, since such a phenomenon would involve distributions against the prevalent easterly ocean current. Rather, the first appearances of many bryozoan species in different areas is related to the progressively-northward onset of fully marine conditions across Britain.

A greater extent of shelf areas, during times of Carboniferous eustatic highs, would have provided a larger area which marine benthonic organisms could inhabit. A larger number of suitable habitats will result in less competition for space between the benthonic organisms; thus, shelves can support a more diverse fauna, since fewer taxa are excluded by direct competition. The Asbian is noted as a time of great species diversity in many taxa (G.A.L. Johnson, personal communication); thus, the high number of bryozoan species recorded in Asbian and Brigantian strata in Britain is therefore consistent with the episodes of maximum marine influence over the shallow shelf of southern Laurasia.

The patterns of Asbian and Brigantian peaks are similarly reflected in Northumberland and East Fife, but their magnitudes are different (fig. 13.12); the total species diversity is much greater in Northumberland. East Fife marine horizons are inferred to have been rather proximal to the Laurasian landmass, and as such were greatly influenced by the fluviatile runoff, with a major river system slightly to the east (Leeder, 1987; Wilson, 1989). Thus, a moderately-restricted bryozoan fauna is developed in Fife, while the greater marine influence in Northumberland allowed a more diverse fauna to flourish.

South Wales has a somewhat different temporal pattern than the other areas; though there is a diversity peak in the Courceyan (which is also seen in the plots for the whole of Britain), there is a sharp drop in bryozoan diversities in the Asbian. Firstly, it should be realised that the fieldwork patterns are plotted slightly differently to the larger-scale charts; the fieldwork graphs record the number of species known to occur at a particular horizon, whereas the British plots encompass the total stratigraphical range for a given species, whether it has actually been found in that stage or not. For example, if species X has occurrences in the Chadian and the Holkerian, but has not been found in the Arundian, then with the total-range charts, species X would have a positive occurrence in the Arundian, since it is known to have been in existence somewhere during that time. However, a local chart would record a negative occurrence for the same species in the Arundian, since it has not actually been found in strata of that age. Therefore, it may be argued that a straight line could be drawn from the Holkerian to the Upper Brigantian horizons on the South Wales chart, omitting the Asbian record. However, though there are well-developed marine limestones in the Asbian of Gower, with a good coral, crinoid, and brachiopod fauna, it is important to point out that no bryozoans have been recorded from these levels; not only would the high-energy crinoidal and oolitic limestone environments have been too turbulent for a high-diversity bryozoan fauna to thrive, but any bryozoans which did occur may have been severely fragmented by post-mortem agitation. Thus, the drop in bryozoan diversity during the Asbian can be attributed to the development of unsuitable facies within South Wales.

It is interesting to note that the overall patterns of species diversity through the Carboniferous closely mirror the global changes recorded at generic level by Ross (1981; see also Ross & Ross, 1990). Ross recorded relatively high generic diversities amongst the cosmopolitan faunas of the Tournasian, succeeded by greater generic diversity and broader distributions in the Viséan. However, in the Late Viséan, the joining of Gondwana and Euramerica at their southern suture reduced the available shelf area, closed the marine connection between Europe and western Euramerica, and diverted circumequatorial currents into higher-latitude waters; thus, Ross believes that greater precipitation occurred, resulting in general climatic cooling and the production of marked thermal clines and associated bryozoan provincialism. As a consequence, global generic diversity was reduced though the Namurian.

Species longevity and geographical coverage

The time ranges of the species utilised in this study are shown in figs. 12.2 and 12.3. From this original data, plots have been made showing the number of species compared with the number of geographical zones in which they occur (fig. 13.13) and of the number of species compared with the number of stages in which they occur (fig. 13.14). The plots show similar patterns, with the majority of species being confined to one stage and/or one geographical zone. Further, the decline is roughly exponential, seen best in fig. 13.13. This "hollow curve" (reviewed in Newton, 1990) is the characteristic shape for species geographical distribution plots, and was described by Flessa and Thomas (1985) for the occurrences of modern marine bivalve genera; most taxa occur in only a few areas, whereas a few are more widespread. The asymptopic nature of the exponential curve is also worthy of comment, and was modelled by Flessa and Thomas (*ibid.*); as more areas are plotted, the number of taxa present never actually reaches a zero value (though in real studies a zero value must be reached because of the discrete nature of the data). This is because the more widespread forms are more likely to be able to spread even further than the geographically-restricted forms, or as Flessa and Thomas quoted,

> Like the rich getting richer, the cosmopolitans become more cosmopolitan

Similarly, plots of species numbers against longevity have a similar, though less-pronounced asymptopic shape. There is a subsidiary peak for those species occurring in eight stages. This interval should more correctly be labelled "eight or more stages", since the interval is compressed; *Fistulipora incrustans* , for example, is known to occur into the Permian (Bancroft, 1984), and thus encompasses far more than just eight stages.

A study by Hansen (1980) on Tertiary neogastropod distributions and longevity revealed that the exponential "hollow" curve was best developed by those forms with non-planktotrophic life habits; planktotrophic species, while not possessing greater longevities, did have wider geographical coverage. The non-planktotrophic curves match closely with those shown in figs. 13.13 and 13.14, highlighting the limited

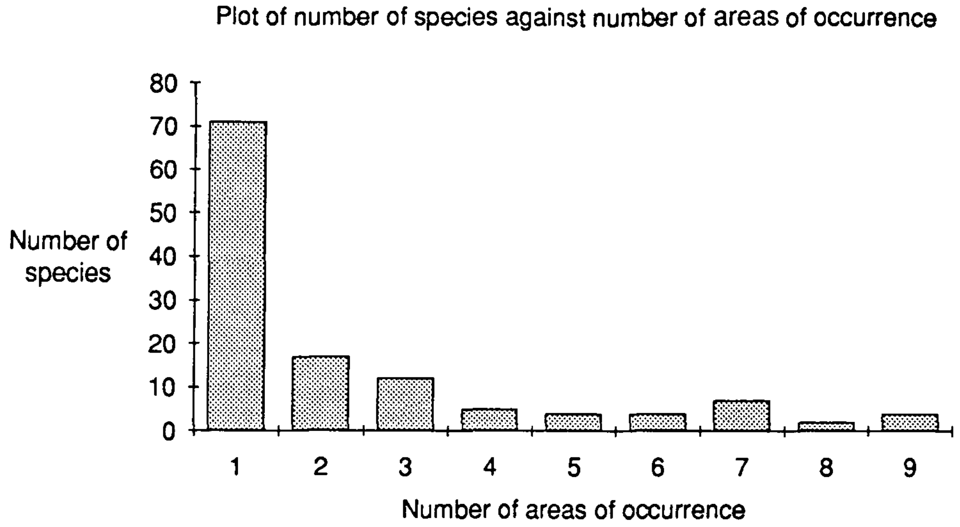


Fig. 13.13.

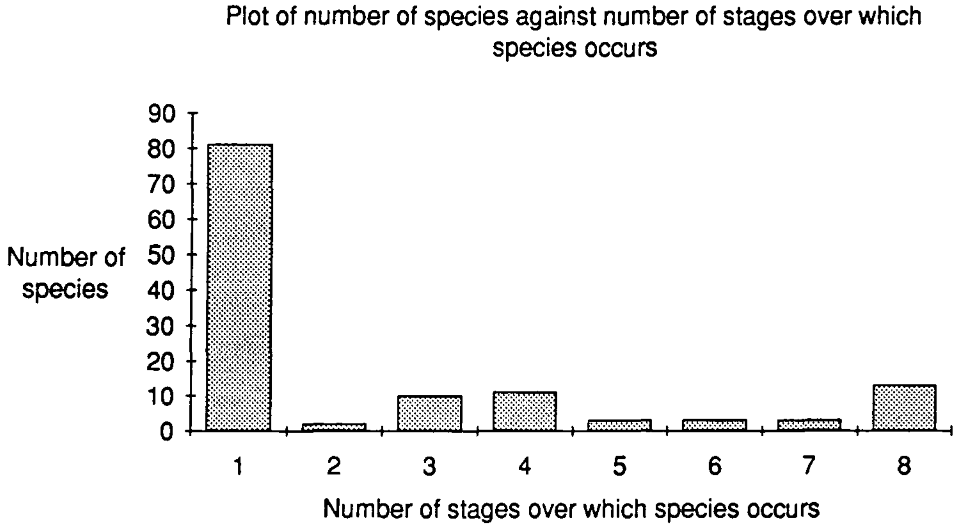
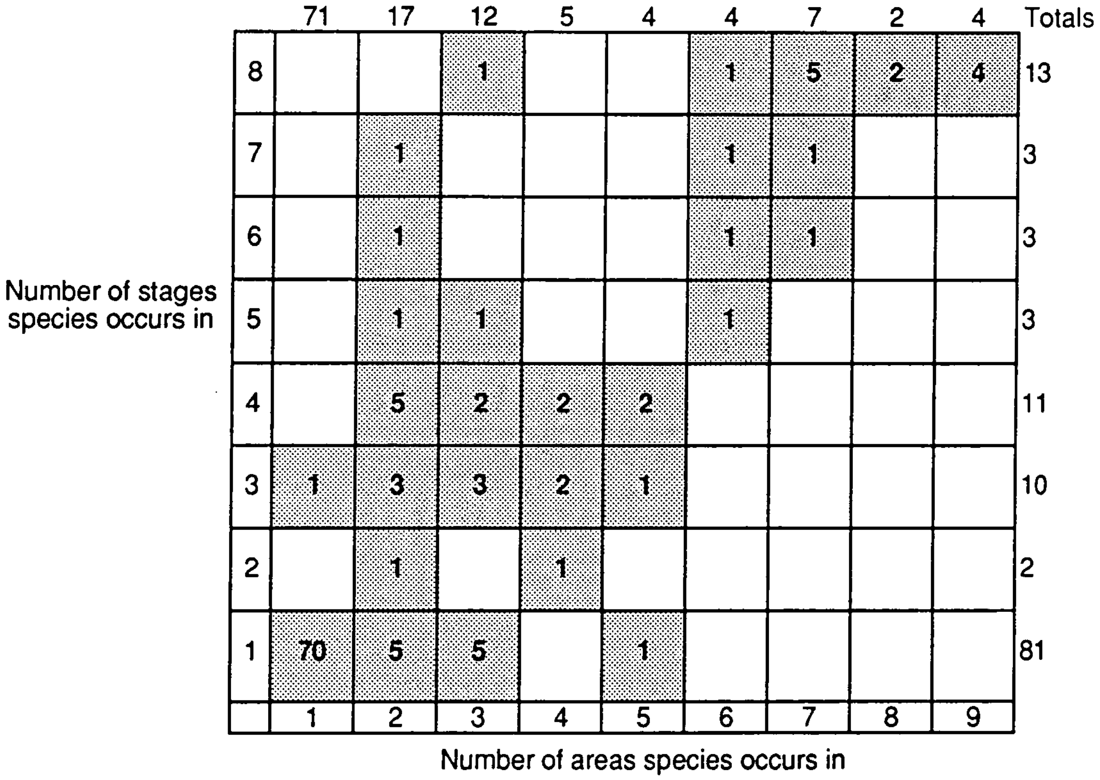


Fig. 13.14

dispersals of Carboniferous bryozoan species. Further, it is of some interest to note that while the geographical regions erected by Flessa and Thomas for their generic-level analysis were quite broad, those utilised by Hansen, for a study at specific level, are of a similar to smaller magnitude (each is 75km wide) than those used in this study, perhaps pointing to the fractal nature of distribution curves. Newton (1990), for instance, mentions the similar shape of geographical curves for species, genera, and families, thus indicating a common process affecting extinctions and distributions at all taxonomic levels.

The table below is a combined matrix of numbers of species against temporal stages and geographical areas in which those species occur:



Number of stages species occurs in

	71	17	12	5	4	4	7	2	4	Totals
8			1			1	5	2	4	13
7		1				1	1			3
6		1				1	1			3
5		1	1			1				3
4		5	2	2	2					11
3	1	3	3	2	1					10
2		1		1						2
1	70	5	5		1					81
	1	2	3	4	5	6	7	8	9	

Number of areas species occurs in

Fig. 13.15. Matrix of number of species versus number of stages of occurrence

There is a high correlation between number of stages in which a species occurs, and the number of areas it inhabits; the greater the geographical extent of a species, the greater the species longevity. Larger geographical coverage means that a species has a greater chance of surviving small-scale catastrophes, which could eliminate locally-concentrated populations. This phenomenon has been discussed by Jablonski (1986), who noted that during background extinctions, species with wide geographical ranges also had greater species longevities, but this effect was cancelled out when widescale mass extinctions took place, since such events seem to affect all geographical areas equally.

Anstey (1978) studied survivorship in Palaeozoic bryozoans, and noted that species which were morphologically complex had greater generic longevities than simple taxa during background extinction episodes. However, such specialisation was not advantageous across episodes of mass extinction, and it was the morphologically-simpler taxa which had the greater survivorship. Not enough taxa are shared between those cited by Anstey and those utilised in this study for a confident testing of Anstey's predictions during the Carboniferous. Further, Anstey omitted all members of the Fenestellidae, which were deemed an inappropriate group for study since they comprise simple autozooids in a complex extrazooidal skeleton. From amongst the taxa which are included in both studies, the British genera have revealed conflicting results; while the genus *Tabulipora*, identified by Anstey as a complex form, does have a great longevity, the genus *Fistulipora*, which Anstey regarded as being of simple morphology, actually has a greater longevity than *Tabulipora* across the British Carboniferous. Thus, it is unclear whether colony specialisation was a major factor affecting British Carboniferous temporal distribution patterns.

The observation that widespread bryozoan species tend to have greater species longevities has some bearing on the question of the use of bryozoans for biostratigraphical studies. Bancroft (1984; 1987b) proposed the possible use of Carboniferous bryozoans in stratigraphical studies, since he observed that many species had longevities of only one stage or less. He did, however, point out that the common occurrence of endemism within the group may hinder their application in larger-scale biostratigraphical studies. Results from this thesis suggest that bryozoans may be of only very limited use in biostratigraphy, since those forms which are geographically-widespread, and are thus potentially the most useful, also have long species durations. Further, the commonest bryozoan species, as exemplified by *Fenestella plebeia*, *F. multispinosa*, and *Fistulipora incrustans*, are also the most long-lived and widespread, their success undoubtedly linked with their wide geographical occurrences. However, several trepostome species tend to meet the compromise between species longevity and geographical extent; *Tabulipora howsii*, for example, occurs in five of the nine areas utilised in this study, but is restricted to Asbian strata.

It is interesting to note that bryozoans have been of some use in biostratigraphical studies; in the Lower Chickamauga Group (Middle Ordovician) of Alabama, for example, trepostome bryozoans are very common, and McKinney (1971b) used them to bracket the stratigraphical age of the Group. Similarly, Boardman (1960) studied the stratigraphical potential of trepostomes from the Hamilton Group (Middle

Devonian) of New York State; certain species had widespread occurrences, were relatively abundant, and were restricted to Member of the Group. However, those species which were most abundant in any one Member, also tended to be the longest-lived, often occurring throughout the whole Group. The relationship between species abundance and longevity was further highlighted by Anstey and Perry (1972) in a study of the trepostomes from the Eden Shale (late Middle Ordovician) of Ohio. The two dominant species, *Heterotrypa ulrichi* and *Hallopora nodulosa* (which constituted 52% of the material studied) and the next two most abundant species, all ranged throughout the vertical extent of the Eden Shale. However, the remaining eight species did have a more restricted stratigraphical range.

The complex internal morphology of the trepostomatous bryozoans may account for their greater speciation and extinction rates at species level, compared with the morphologically-simpler fenestrate taxa. Despite the difficulties with identifying trepostomes to specific level, which usually requires careful thin sectioning of well-preserved specimens, this order may prove to be the most useful bryozoan group for biostratigraphical analysis.

Morphological changes within species through the Carboniferous

Over the wide range of time encompassing the Dinantian and Lower Silesian, it may be expected that species should show some degree of gradualistic morphological change. Evidence amongst the Carboniferous Bryozoa for gradualism is scarce; Miller (1961) tentatively stated that there was a gradual decrease in the spacing of carinal nodes from Lower Tournasian to Upper Viséan specimens of *Fenestella plebeia*. However, he recorded very consistent measurements for the other meshwork parameters. Bancroft (1984) studied many specimens of *F. plebeia*, and noted that even specimens from the same geological horizon showed much variation in the carinal node spacing, and thus he believed Miller's gradualistic hypothesis to be unlikely.

The examination of specimens from different stratigraphical horizons and different geographical areas has failed to show any significant variation within bryozoan species. This is illustrated in the table overleaf, which documents a parametrical comparison of *Fenestella multispinosa* from the Eelwell Limestone (Brigantian) at Snook Point, Northumberland, with specimens attributed to the same genus from the Tears Point Limestone (Courceyan) of Tears Point, South Wales, and with standards from the Calp Shale (Asbian) of Carrick Lough, Northern Ireland (Tavener-Smith, 1973a).

	Fenestella multispinosa					
	Eelwell Lst. (Brigantian)				t-TEST PROBABILITY SCORES	
	N	n	σ	x	Tears Point (Courc)	Carrick Lough (Asb)
BW	15	60	0.0264	0.279	0.7097	0.0013
AD	5	16	0.0110	0.105	0.0009	0.3518
ID	7	42	0.0336	0.192	0.0008	0.0000
FL	15	138	0.0701	0.641	0.0092	0.6980
FW	15	94	0.0468	0.485	0.4474	0.3172
DW	15	94	0.0291	0.144	0.0140	0.0023
				TOTAL	0.1970	0.2284

The high probabilities returned between these species from different localities and horizons illustrates the lack of any consistent evidence for gradualism within the Carboniferous Bryozoa. This result is perhaps quite surprising, since it is not in keeping with the generally limited Carboniferous bryozoan distributions; clustered populations should have low gene flow between the isolated occurrences, and thus should have a high rate of speciation, as has been discussed earlier in this chapter. However, it should be realised that the longer-ranging taxa, on which this study has concentrated, are also the most widely-distributed, and thus would have had a more uniform and resistant gene pool across Britain; these forms are therefore more unlikely to undergo either allopatric speciation, or to show gradualistic evolution.

Summary

British Carboniferous bryozoans show a pattern of distributions which are best explained by a limited degree of dispersal, controlled by the prevalent South Equatorial easterly current system. The majority of species are limited to one geographical area, and to one stage. However, the broader the distribution of a species, the greater its longevity. There is little evidence for morphological variation within species from different areas or stages, though colonies may show some morphological adaptations related to their individual habitats.

PART IV : CONCLUSIONS

CHAPTER 14 : CONCLUSIONS AND FURTHER RESEARCH

British Carboniferous bryozoans are a common element in many marine faunas, and occur across a wide range of facies. Habitat energy level is the major control on morphology; the longer-lived taxa show no measurable change in colony parameters through the 30 million years which this study encompasses, nor are there any significant morphological differences between individual taxa from different geographical areas.

The use of the t-test has been evaluated for the comparison of species morphology. Bryozoans are well-suited for such a statistical method, since their colony parameters have been shown to be normally-distributed. Measurements can be made from relatively small fragments, and these parameters can be tested against published "standards". The t-test can discriminate between species, though the wide range of values for some parameters may sometimes return anomalous results. Basic colony morphology must remain of fundamental importance in the identification of bryozoan species, though it is proposed that the older "meshwork formula" be abandoned, and a standardised series of tables introduced in the taxonomic literature, showing means, standard deviations, and numbers of measurements taken from each species.

A new statistical method, the division t-test, has been devised, which compares the parameters of two "normalised" bryozoans; this routine is beneficial in identifying similarities between the relative ratios of bryozoan meshworks, which are often positively correlated. Thus, forms which are unusually large- or small-parametered representatives of a species may be correctly identified, while the original Student's t-test would not produce the correct species assignment. The division t-test may be useful for identifying "stunted" colonies, as may be expected in nutrient- or carbonate-depleted environments, but such stunting has not been positively observed in Carboniferous Bryozoa.

Studies on the faunas from nine regions within the British Isles have shown that bryozoan species are not uniformally-distributed throughout all nine areas. Gradients within the Simpson and Jaccard Coefficients of similarity between the areas indicate that the most-separated areas have the lowest number of common elements within their faunas, and that the average similarity coefficients for each of the nine areas decreases in a general westward direction. This gradient can be explained by bryozoan distributions being affected by an easterly current, but with limited species migration between the areas. The hypothesis of an easterly current system operating over the southern Laurasian shelf is now firmly established.

The Longford Down Massif, the western end of the Midland Valley, and St. Georges Land all provided slight barriers to species migration, as can be detected by the analysis of the similarity coefficients. The coefficients also suggest that there was a slight southwest gyre to the currents, a phenomenon which would be predicted for Britain's South Equatorial latitude in the Lower Carboniferous.

Plots of the commoner British Carboniferous Bryozoa indicate that many species make their first appearances in the southern districts, and the same species appear later in the more northerly areas. This south to north "migration" reflects the progressive marine transgression across Britain through the Lower Carboniferous, and does not represent true faunal migration, since many of the original species still remain in the southern districts throughout the transgression.

Species diversity within the British Carboniferous reached a peak during the Asbian and Brigantian stages. This peak correlates with a greater shelf area available for colonisation during an episode of higher relative sea levels over the area. There is a decline in the number of species within the British Silesian, as sea levels fell, and deltaic deposition reduced the available shelf area; many species may therefore have become extinct due to greater inter-specific competition for the remaining habitats. The reduction in species through the Silesian is parallelled by a global decrease in bryozoan genera, explained by continental collision which reduced shelf areas, diverted warm ocean currents, and is inferred to have produced global cooling.

Plots of the number of species against the range of areas in which they occur, and the relative length of time a species survives have produced exponential "hollow" curves; such a pattern is characteristic of taxa which have limited dispersal capabilities, and matches the inferred biologies of the Carboniferous bryozoan taxa. There seem to be no difference in the geographical coverage of species known to brood larvae, and those which are believed to have had free-swimming larvae. As at the present day, larval dispersal is not the major mechanism inferred for the distribution of species across seas; rather, rafting via colony attachment to floating material was the most likely method of increasing the geographical extent of a species. However, Carboniferous bryozoan species are not as widely distributed as their modern day counterparts, and there may have been fewer objects available which were suited for rafting. Comparisons with species distributions for Ordovician bryozoans show that the magnitudes of the dispersals are similar. Thus, it is suggested that floating logs, which are a major rafting material for present day bryozoans, were not suitable rafts in the Carboniferous; the pithy core of the Carboniferous lycopods may have become waterlogged very quickly. Bryozoan colonies were probably transported via detached plant fronds; colony origins have been found which indicate that some bryozoan larvae settled on soft-tissued plant stems or algal fronds.

A correlation between the number of areas in which a species occurs and the number of zones across which it is found match patterns predicted for episodes of normal background extinctions. The more widespread a species, the less chance it has of being wiped out during local small-scale catastrophic switches in the environment, and the greater its prospective longevity. The wide geographical coverage of such species, with frequent interchange of DNA between the populations, may have created a resistant gene pool; little morphological change through time should be expected with these taxa. This prediction seems to have been confirmed by the morphological study undertaken in this thesis.

A study of this nature cannot possibly hope to answer all the questions about Carboniferous bryozoan biogeography. Much work still remains to be undertaken, and this thesis represents a preliminary report on bryozoan distributions through the Carboniferous of Britain. As more data becomes available, and as various taxa are found to be synonymous, the similarity coefficients may change, and new interpretations sought to explain the patterns. Within this field, several areas need further research:

a. This thesis lists 126 bryozoan species which have been recorded in Britain. Many of these species have not been examined directly for this study, and a revision of these taxa would be very beneficial.

b. The bryozoan fauna of Derbyshire, though receiving some attention in the literature, remains understudied. Fieldwork collection around the reefs of this area would establish whether Derbyshire does have a distinct reef fauna of bryozoans. Similarly, the bryozoans of South and Central Ireland have received scant attention, and a thorough analysis of the Dinantian fauna would be of great benefit to biogeographical studies.

c. A study of the Carboniferous bryozoan faunas of eastern Europe would provide some answers about the suggested mid-European larval pool; the distribution models presented in this thesis indicate the existence of such a source for the British bryozoans, but without the available data, this model must remain hypothetical. A comparison of the British and Soviet faunas would be extremely useful.

Three further areas of study within this thesis could benefit from further research:

d. The work on the division t-test has established this technique as a valid statistical method, but an analysis of the mathematical distribution of this function has yet to be produced.

e. If the t-test is to be adopted as a standard method of comparing bryozoan morphometrical parameters, it will be essential to establish an international database incorporating information about the parameters of all bryozoan species holotypes.

f. This method, having been explored for Carboniferous Bryozoa, could possibly be applied to other groups of fossils.

BIBLIOGRAPHY

BIBLIOGRAPHY

ALLMAN, G.J. 1856. *A Monograph of the Freshwater Polyzoa, including all the known species, both British and foreign.* The Ray Society, London, 119pp.

ANDERTON, R., BRIDGES, P.H., LEEDER, M.R., and SELLWOOD, B.W. 1979. *A Dynamic Stratigraphy of the British Isles: A Study in Crustal Evolution.* George Allen & Unwin (Publishers) Ltd., London, 301pp.

ANNOSCIA, E. 1968. Problems of methodology in studying and describing Bryozoa. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale. Milano,* **108,** 237-240.

ANSTEY, R.L. 1978. Taxonomic survivorship and morphologic complexity in Paleozoic bryozoan genera. *Paleobiology,* **4,** 407-418.

——— and PERRY, T.G. 1970. Biometric procedures in taxonomic studies of Paleozoic bryozoans. *Journal of Paleontology,* **44,** 383-398.

——— ——— 1972. Eden Shale bryozoans: a numerical study (Ordovician, Ohio Valley). *Publications of the Museum - Michigan State University Paleontological Series,* **1** (1), 1-80.

ASTROVA, G.G. 1964. A new order of Palaeozoic Bryozoa. *Paleontologicheskii Zhurnal,* Moskva, **2,** 22-31.

BAMBACH, R.K. 1990. Late Palaeozoic provinciality in the Marine Realm. *In* McKERROW, W.S. and SCOTESE, C.R. (eds.) *Palaeozoic Palaeogeography and Biogeography.* Geological Society Memoir No. **12,** 307-323.

BANCROFT, A.J. 1984. *Studies in Carboniferous Bryozoa.* Unpublished Ph.D. thesis, University of Durham, U.K., 521pp.

——— 1985a. New Scottish Carboniferous fenestrate Bryozoa. *Scottish Journal of Geology,* **21,** 177-186.

——— 1985b. The Carboniferous fenestrate bryozoan *Ptylopora pluma* McCoy. *Irish Journal of Earth Sciences,* **7,** 35-45.

——— 1986a. A new Carboniferous fenestrate bryozoan genus. *Scottish Journal of Geology,* **22,** 99-106.

——— 1986b. *Hederella carbonaria* Condra and Elias, a rare ?bryozoan from the Carboniferous of Great Britain. *Proceedings of the Geological Association,* **97,** 243-248.

——— 1986c. Ovicells in the Palaeozoic bryozoan Order Fenestrata. *Palaeontology,* **29,** 155-164.

—— 1986d. Secondary nanozooecia in some Upper Palaeozoic fenestrate Bryozoa. *Palaeontology,* **29,** 207-212.

—— 1986e. The Carboniferous fenestrate bryozoan *Hemitrypa hibernica* McCoy. *Irish Journal of Earth Sciences,* **7,** 111-124.

—— 1986f. The Carboniferous cystoporate bryozoan *Eridopora macrostomata* Ulrich from the north of England. *Proceedings of the Yorkshire Geological Society,* **46,** 23-28.

—— 1987a. The fenestrate bryozoan *Septopora carbonaria* (Etheridge Jun.1873a) from the Carboniferous of Great Britain. *Geological Journal,* **22,** 1-10.

—— 1987b. Biostratigraphical potential of Carboniferous Bryozoa. *Courier. Forschungsinstitut Senckenberg,* **98,** 193-197.

—— 1988a. Ovicells in *Rectifenestella* from the Lower Carboniferous of Ireland. *Irish Journal of Earth Sciences,* **7,** 19-22.

—— 1988b. Palaeocorynid-type appendages in Upper Palaeozoic fenestellid Bryozoa. *Palaeontology,* **31,** 665-675.

—— 1988c. A reply to D.K. Graham regarding the validity of the Carboniferous fenestrate bryozoan genus *Lanarkopora* Graham (1975). *Geological Journal,* 67-68.

——, SOMERVILLE, I.D. and STRANK, A.R.E. 1988. A bryozoan buildup from the Lower Carboniferous of North Wales. *Lethaia,* **21,** 51-65.

BASSLER, R.S. 1911. The Early Palaeozoic Bryozoa of the Baltic Provinces. *Bulletin of the United States National Museum,* **77,** 1-382.

—— 1939. The Hederelloidea, a suborder of Palaeozoic cyclostomatous Bryozoa. *Proceedings of the United States National Museum,* **87,** 25-91.

—— 1952. Taxonomic notes on genera of fossil and recent Bryozoa. *Journal of the Washington Academy of Sciences,* **42,** 381-385.

—— 1953. Bryozoa. *In* MOORE, R.C. (ed.) *Treatise on Invertebrate Paleontology.* Part G. Bryozoa. Geological Society of America and University of Kansas Press, Boulder and Lawrence, xiii+253pp.

BILLING, I.M. 1991. Bryozoan growth on brachiopod spines in the Carboniferous of England. *In* BIGEY, F.P. (ed.) with D'HONDT, J-L. *Bryozoaires Actuels et Fossiles : Bryozoa Living and Fossil,.* Société des Sciences Naturelles de l'Ouest de la France, Nantes, 579pp.

BLAKE, D.B. 1980. Homeomorphy in Palaeozoic bryozoans : a search for explanations. *Paleobiology,* **6,** 451-465.

BOARDMAN, R.S. 1971. Mode of growth and functional morphology of autozooids in some Recent and Paleozoic tubular Bryozoa. *Smithsonian Contributions to Paleobiology,* **8,** 1-51.

——— 1960. Trepostomatous Bryozoa of the Hamilton Group of New York State. *Geological Survey Professional Paper,* **340,** 1-87. United States Government Printing Office, Washington.

——— and UTGAARD, J. 1964. Modifications of study methods for Paleozoic Bryozoa. *Journal of Paleontology,* **38,** 768-770.

——— CHEETHAM, A.H., BLAKE, D.B.,UTGAARD, J., KARKLINS, O.L., COOK, P.L., SANDBERG, P.A., LUTARD, G., and WOOD, T.S. 1983. Bryozoa. *In* ROBINSON, R.A. *Treatise on invertebrate paleontology.* Part G. Bryozoa (revised) I. Geological Society of America and University of Kansas Press, Boulder and Lawrence, xxvii+625pp.

——— and McKINNEY, F.K. 1985. Soft part characters in stenolaemate taxonomy. *In* NIELSEN, C. and LARWOOD, G.P. (eds.) *Bryozoa : Ordovician to Recent,* 35-44. Olsen and Olsen, Fredensborg, 364pp.

BORG, F. 1923. On the structure of cyclostomatous Bryozoa. *Arkiv för Zoologi,* **15** (11), 1-17.

——— 1926. Studies on recent cyclostomatous Bryozoa. *Zoologiska Bidrag från Uppsala,* **10,** 181-507.

——— 1933. A revision of the Recent Heteroporidae (Bryozoa) : II On the structure of the Heteroporidae. *Zoologiska Bidrag från Uppsala,* **14,** 353-385.

BOYDE, A. 1985. The Tandem Scanning Reflected Light Microscope. Part 2 - Pre-Micro '84 applications at UCL. *Proceedings of the Royal Microscope Society,* **20,** 131-139.

———, PETRAN, M., HADRAVSKY, M., BENES, and J., KUCERA, R. 1985. The Tandem Scanning Reflected Light Microscope. Part 1 - the principle, and its design. *Proceedings of the Royal Microscope Society,* **20,** 125-129.

BROWN, J.H. and GIBSON, A.C. 1983. *Biogeography.* The C.V. Mosby Company, St. Louis, 643 pp.

BRUNTON, C.H.C. 1966. Silicified productoids from the Viséan of County Fermanagh. *Bulletin of the British Museum (Natural History)* (Geology), **12,** 175-243.

BURCHETTE, T.P. and RIDING, R. 1977. Attached vermiform gastropods in Carboniferous marginal marine stromatolites and biostromes. *Lethaia,* **10,** 17-28.

BUSK, G. 1852. An account of the Polyzoa and Sertularian Zoophytes, collected in the voyage of the *Rattlesnake. In* MacGILLIVRAY, J. *Narrative of the voyage of H.M.S.* Rattlesnake...*during the years 1846-1850,* Volume **1,** Appendix No. 4. London.

BUSS, L.W. 1980. Competitive intransitivity and size-frequency distibutions of interacting populations. *Proceedings of the USA National Academy of Science,* **77,** 5355-5359.

CARRUTHERS, R.G., DINHAM, C.H., BURNETT, G.A., and MADEN, J. 1927. *The Geology of Belford, Holy Island and the Farne Islands.*. Geological Survey of England and Wales. Memoir for Sheet **4.** Her Majesty's Stationery Office, 195pp.

CHEETHAM, A.H. 1960. Time, migration and continental drift. *Bulletin of the American Association of Petroleum Geologists,* **44** (1), 244-251.

——— 1974. Taxonomic significance of autozooecial size and shape in some early multiserial cheilostomes from the Gulf coast of the USA. *Documents des Laboratoires de Géologie de la Faculité des Sciences de Lyons, Hors Série* **3,** 547-564.

———, HAYEK, L.C. and THOMSEN, E. 1981. Growth models in fossil arborescent cheilostome bryozoans. *Paleobiology,* **7,** 68-86.

——— and THOMSEN, E. 1981. Functional morphology of arborescent animals : strength and design of cheilostome bryozoan skeletons. *Paleobiology,* **7,** 355-383.

CLARKSON, E.N.K. 1986. *Invertebrate Palaeontology and Evolution.* George Allen and Unwin Ltd., London, 382pp.

COLE, G.A.J. 1893. On *Hemitrypa hibernica* McCoy. *Scientific Proceedings of the Royal Dublin Society,* **8** (10), 132-144.

COLL, J. and ALLEN, D. 1982. *The BBC Microcomputer User Guide.* British Broadcasting Corporation, London. 510pp.

CONDRA, G.E. 1902. New Bryozoa from the Coal Measures of Nebraska. *American Geologist,* **30,** 337-359.

——— and ELIAS, M.K. 1944. *Hederella* and *Corynotrypa* from the Pennsylvanian. *Journal of Paleontology,* **18,** 535-539

CORNELIUSSEN, E.F. and PERRY, T.G. 1970. The ectoproct *Batostoma? cornula* (Cumings and Galloway) and its enigmatic intrazooecial spines [Fort Atkinson Limestone (Cincinnatian), Wilmington, Illinois]. *Journal of Paleontology,* **44,** 997-1007.

COWEN, R. and RIDER, J. 1972. Functional analysis of fenestellid bryozoan colonies. *Lethaia,* **5,** 145-164.

CUFFEY, R.J. 1967. Bryozoan *Tabulipora carbonaria* in Wreford megacyclothem (Lower Permian) of Kansas. *University of Kansas Paleontological Contributions, Bryozoa, Article* **1,** 1-96.

CUMINGS, E.R. 1904. Development of some Paleozoic Bryozoa. *American Journal of Science,* **17,** 49-78.

——— 1905. Development of *Fenestella. American Journal of Science,* **20,** 169-177.

——— and GALLOWAY, J.J. 1915. Studies of the morphology and histology of the Trepostomata or Monticuliporoids. *Bulletin of the Geological Society of America,* **26,** 349-374.

DONOVAN, S.K. 1989. *A Field Guide to the Fossil Echinoderms of Coplow, Bellman, and Salthill Quarries, Clitheroe, Lancashire.* Unpublished excursion guide for the Palaeontological Association Annual Conference, Liverpool, December 1989. 12pp.

DRESSER, A.M. 1960. *The Polyzoa of the Lower Carboniferous Rocks of Hook Head, County Wexford, and Malahide, County Dublin.* Unpublished M.Sc. thesis, Trinity College, Dublin, Ireland, 75pp.

DUNAEVA, N.N. 1973. Carboniferous Bryozoa of the Donetz Basin. *In* LARWOOD, G.P. (ed.) *Living and fossil Bryozoa,* 73-77. Academic Press, London, 634pp.

DUNCAN, H. 1957. Bryozoans. *In* LADD, H.S. (ed.) *Treatise on Marine Ecology and Palaeoecology,* 783-800. Memoir **67,** Volume 2. Geological Society of America, Washington.

DUNCAN, P.M. 1871. Third report on the British fossil corals. *Report of the Fourty-First Meeting of the British Association for the Advancement of Science, Edinburgh, September 1871,* 116-137.

EHRENBERG, C.G. 1831. Symolae Physicae, seu Icones et descriptiones Corporum Naturalium novorum aut minus cognitorum, quae ex itineribus per Libyam, Aegyptum, Nubiam, Dongalam, Syriam, Arabiam et Habessiniam...studio annis 1820-25 redierunt. *Pars Zoologica,* **4,** Animalia Evertebrata excludis Insectis, 1-370, 10 Plates.

ELIAS, M.K. 1937. Stratigraphical significance of some Late Paleozoic fenestrate bryozoans. *Journal of Paleontology,* **11,** 306-334.

——— 1971. Concept of common bud and related phenomena in Bryozoa. *University of Kansas Paleontological Contributions, Paper* **52,** 1-21.

——— and CONDRA, G.E. 1957. *Fenestella* from the Permian of West Texas. *The Geological Society of America, Memoir* **70,** 158pp.

ETHERIDGE, R. 1873a. On a new species of *Synocladia* from the Carboniferous Limestone Series of Midlothian. *Annals and Magazine of Natural History,* **12,** 189-193.

——— 1873b. *Lanarkshire, Central Districts, Appendix III,* p101. Memoirs of the Geological Survey of Scotland, explanation to Sheet **23.**

——— 1873c. Description of *Carinella,* a new genus of Carboniferous Polyzoa. *The Geological Magazine,* **10,** 433-434.

——— 1875. Note on a new provisional genus of Carboniferous Polyzoa. *Annals and Magazine of Natural History,* **15,** 43-45.

FENGSHENG, X. 1987. Nipponostenoporidae, a new family of Trepostomida (Bryozoa) from Late Early Carboniferous of Zhanyi, Eastern Yunnan. *Acta Micropalaoontologica Sinica,* **4,** 375-385.

——— and XIAOLIANG, L. 1986. Late Carboniferous bryozoans from the vicinity of Urumqi, Xinjiang. *Memoirs of Nanjing Institute of Geology and Palaeontology, Academia Sinica, Number* **22,** 145-173.

FISHER, R.A. 1934. *Statistical Methods for Research Workers,* section 24.1, 120-125. Oliver and Boyd, London, 319pp.

FLEMING, J. 1828. *A History of British Animals.* Bell and Bradfute, Edinburgh, 565pp.

FLESSA, K.W. and THOMAS, R.H. 1985. Modelling the biogeographic regulation of evolutionary rates. *In* VALENTINE, J.W. (ed.) *Phanerozoic Diversity Patterns: Profiles in Macro-evolution,* 355-376. Princetown University Press, Princetown, New Jersey.

FORSYTH, I.H. and CHISHOLM, J.I. 1977. *The Geology of East Fife.* Geological Survey of Great Britain. Scotland. Memoir for Sheets **41** and **49.** Her Majesty's Stationery Office, Edinburgh, 284pp.

FOWLER, A. 1926. *The Geology of Berwick-on-Tweed, Norham and Scremerston.* Geological Survey of Great Britain. England. Memoir for Sheets **1** & **2.** Her Majesty's Stationery Office, 58pp.

——— 1966. The stratigraphy of the North Tyne Basin around Kielder and Falstone, Northumberland. *Bulletin of the Geological Survey of Great Britain,* **24,** 57-104.

FROST, D.V. and HOLLIDAY, D.W. 1980. *Geology of the country around Bellingham.*Geological Survey of Great Britain. Memoir for Sheet **13.** Her Majesty's Stationery Office, 112pp.

GARDINER, A.R. and TAYLOR, P.D. 1982. Computer modelling of branching growth in the bryozoan *Stomatopora. Neues Jahrbuch für Geologie und Paläontologie. Stuttgart,* **163,** 389-416.

GAUTIER, T.G. 1970. Interpretive morphology and taxonomy of bryozoan genus *Tabulipora. University of Kansas Paleontological Contributions, Paper* **48,** 1-21.

GEORGE, T.N. 1970. *British Regional Geology : South Wales.* Third edition. Institute of Geological Sciences, Her Majesty's Stationery Office, London, 152pp.

GEORGE, T.N., JOHNSON, G.A.L., MITCHELL, M., PRENTICE, J.E., RAMSBOTTOM, W.H.C., SEVASTOPULO, G.D., WILSON, R.B., 1976. A correlation of Dinantian rocks in the British Isles. *Geological Society of London, Special Report* **7,** 87pp.

GILBERT, N. 1973. *Biometric Interpretation.* Clarendon Press, Oxford, 125pp.

GORYUNOVA, P.B. 1985. Morphology, systematics and phylogeny of some Rhabdomesids. *Trudy Paleozoologicheskogo Instituta. Akademiya Nauk SSSR,* **208,** 1-152. [In Russian].

GRAHAM, D.K. 1975. A review of Scottish Carboniferous Acanthocladiid Bryozoa. *Bulletin of the Geological Survey of Great Britain,* **49,** 1-21.

——— 1987. Note on the Carboniferous bryozoan taxon *Lanarkopora carbonaria* (Etheridge Jun.). *Geological Journal,* **22,** 69.

GRANT, R.E. 1966. Spine arrangemnet and life habits of the productiod brachiopod *Waagenochona. Journal of Paleontology,* **40,** 1063-1069.

GRAY, D.I. 1980. Spicule pseudomorphs in a new Palaeozoic chaetetid, and its sclerosponge affinities. *Palaeontology,* **23,** 803-820.

GRAYSON, R.F. 1981. *Salthill Quarry Geology Trail.* Geology and Physiography Section, Nature Conservancy Council, 26pp.

——— and OLDHAM, L. 1987. A new structural framework for the Northern Birish Dinantian as a basis for oil, gas, and mineral exploration. *In* MILLER, J., ADAMS, A.E., and WRIGHT, V.P. (eds.) *European Dinantian Environments,* Geological Journal Special Issue No. **12,** 33-59. John Wiley & Sons Ltd., 402pp.

GUNN, W. 1903. *The geology of North Arran, South Bute, and the Cumbraes.* Geological Survey of Scotland, Memoir for sheet **21,** His Majesty's Stationery Office, Glasgow, 200pp.

HAGEMAN, S.J. 1988. Image processing and analysis with microcomputers. *Journal of Paleontology,* **62,** 474-477.

HALL, J. 1881. Bryozoans of the Upper Helderberg and Hamilton groups. *Abstracts and Transactions of the Albany Institute,* **10,** 1-26.

——— 1886. Bryozoa of the Upper Helderberg group; plates and explanations. *State Geologist of New York,* 5th Annual Report for 1885, Plates 25-53.

HALLAM, A. (ed.), 1973. *Atlas of Palaeobiogeography.* Elselvier Scientific Publishing Company, Amsterdam, 531pp.

HANSEN, T.A. 1980. Influence of larval dispersal and geographic distribution on species longevity in neogastropods. *Paleobiology,* **6,** 193-207.

HARTLEY, H.O. and PEARSON, E.S. 1950. Table of the probability integral of the t-distribution. *Biometrika,* **37,** 168-172.

HO, C. and COLEMAN, J.M. 1969. Consolidation and cementation of Recent sediments in the Atchafalaya Basin. *Bulletin of the Geological Society of America,* **80,** 183-192.

HOROWITZ, A.S. 1968. The ectoproct (bryozoan) genus *Actinotrypa* Ulrich. *Journal of Paleontology,* **42,** 356-373.

—— 1970. Nomenclaturial diversity within *Fistulipora* McCoy and allied genera. *Journal of Paleontology,* **44,** 776-778.

JABLONSKI, D. 1986. Background and mass extinctions: the alternation of macroevolutionary regimes. *Science,* **231,** 129-133.

——, FLESSA, K.W., and VALENTINE, J.W. 1985. Biogeography and paleobiology. *Paleobiology,* **11,** 75-90.

JACKSON, J.B.C. 1986. Modes of dispersal of clonal benthic invertebrates : consequences for species' distributions and genetic structure of local populations. *Bulletin of Marine Science,* **39,** 588-606.

JINGZHI, Y., ZHAOXUN, H. and FENGSHANG, X. 1988. Bryozoans from Late Devonian and Early Carboniferous of Central Hunan. *Palaeontologica Sinica,* **174,** *New Series B,* **23,** 1-197.

JOHNSON, G.A.L. 1958. Biostromes in the Namurian Great Limestone of northern England. *Palaeontology,* **1** (2), 147-157.

—— 1980a. Carboniferous Dinantian and Namurian rocks. *In* ROBSON, D.A. (ed.) *The Geology of North East England,* 11-23. Special publication of the Natural History Society of Northumbria, The Hancock Museum, Newcastle, 113pp.

—— 1980b. Carboniferous geography and terrestrial migration routes. *In* PANCHEN, A.L. (ed.) *The Terrestrial Environment and the Origin of Land Vertebrates.* Systematics Association Special Volume No. **15,** 39-54.

—— 1982. Geographical change in Britain during the Carboniferous Period. *Proceedings of the Yorkshire Geological Society,* **44,** 181-203.

—— and TARLING, D.H. 1985. Continental convergence and closing seas during the Carboniferous. *Compte Rendu. 10^{e} Congrès International de Stratigraphie et de Géologie Carbonifère. (Madrid, Spain 1983),* **4,** 163-168.

KELLEY, P.H., RAYMOND, A., and LUTKEN, C.B. 1990. Carboniferous brachiopod migration and latitudinal diversity: a new palaeoclimatic method. *In* McKERROW, W.S. and SCOTESE, C.R. (eds.) *Palaeozoic Palaeogeography and Biogeography.* Geological Society Memoir No. **12,** 325-332.

KELLY, S.M. and HOROWITZ, A.S. 1987. Growth forms and paleoecology of Mississippian bryozoans : critical application of Stach's 1936 model, Eastern United States. *In* ROSS, J.R.P. (ed.) *Bryozoa : Present and Past,* 137-144. Western Washington University, Bellingham, 333pp.

KEOUGH, M.J. 1984. Effects of patch size on the abundance of sessile marine invertebrates. *Ecology,* **65** (2), 423-437.

——— 1986. The distribution of a bryozoan on seagrass blades : settlement, growth, and mortality. *Ecology,* **67,** 846-857.

——— and BUTLER, A.J. 1983. Temporal changes in species number in an assemblage of sessile marine invertebrates. *Journal of Biogeography,* **10,** 317-330.

——— and CHERNOFF, H. 1987. Dispersal and population variation in the bryozoan *Bugula neritina. Ecology,* **68,** 199-210.

KIRKBY, J.W. 1880. On the zones of marine fossils in the Calciferous Sandstone Series of Fife. *Quarterly Journal of the Geological Society of London,* **36,** 559-590.

——— 1901. On Lower Carboniferous strata and fossils at Randerstone, near Crail, Fife. *Transactions of the Edinburgh Geological Society,* **8,** 61-75.

KOENIG, J.W. 1958. Fenestrate Bryozoa in the Chouteau Group of Central Missouri. *Journal of Paleontology,* **32,** 126-143.

de KONINCK, L.G. 1842. *Descriptions des Animaux Fossiles qui se trouvent dans le Terrain Carbonifère de la Belgique.* Liége. iv+650pp, 55pl.

LAGAAIJ, R. and COOK, P.L. 1973. Some Tertiary to Recent Bryozoa. *In* HALLAM, A. (ed.) *Atlas of Palaeobiogeography,* 489-498. Elselvier Scientific Publishing Company, Amsterdam, 531pp.

LEE, G.W. 1912. The British Carboniferous Trepostomata. *Memoirs of the Geological Survey of Great Britain, Palaeontology* **1,** 135-195.

LEEDER, M.R. 1987. Tectonic and palaeogeographic models for Lower Carboniferous Europe. *In* MILLER, J., ADAMS, A.E., and WRIGHT, V.P. (eds.) *European Dinantian Environments,* Geological Journal Special Issue No. **12,** 1-20. John Wiley & Sons Ltd., 402pp.

LEES, A., HALLET, V., and HIBO, D. 1985. Facies variation in Waulsortian buildups, Part 1 ; a model from Belgium. *Geological Journal,* **20,** 133-158.

——— and MILLER, J. Facies variation in Waulsortian buildups, Part 2 ; Mid-Dinantian buildups from Europe and North America. *Geological Journal,* **20,** 159-180

LINHUANG, L. 1989. Bryozoans from Chouniugou Formation of Late Early Carboniferous on the northern slope of Mt. Qilian. *Palaeontologica Cathayana,* **4,** 327-433.

MADSEN, L. 1987. Growth and polypide morphology in some ramose trepostome bryozoans from the Permo-Carboniferous of the Arctic. *In* ROSS, J.R.P. (ed.) *Bryozoa : Present and Past,* 169-176. Western Washington University, Bellingham, 333pp.

MARSAL, D. 1987. *Statistics for Geoscientists.* Permagon Press, Oxford, 176pp.

MEEK, F.B. 1872. Report on the paleontology of eastern Nebraska. *In* HAYDEN, F.V. (ed.) *Final Report of the United States Geological Survey of Nebraska and Portions of the Adjacent Terrotories,* 81-239. U.S. Government Printing Office (Washington).

MILLER, J. and GRAYSON, R.F. 1972. Origin and structure of the Lower Viséan "reef" limestones near Clitheroe, Lancashire. *Proceedings of the Yorkshire Geological Society,* **38** (4), 607-638

MILLER, T.G. 1961a. Type specimens of the genus *Fenestella* from the Lower Carboniferous of Great Britain. *Palaeontology,* **4,** 221-242.

——— 1961b. New Irish Tournasian fenestellids. *Geological Magazine,* **98,** 493-500.

——— 1962a. North American species of *Fenestella* from the Carboniferous of Great Britain. *Journal of Paleontology,* **36,** 120-125.

——— 1962b. On *Hemitrypa hibernica* McCoy. *Geological Magazine,* **99,** 313-321.

——— 1963. The bryozoan genus *Polypora. Palaeontology,* **6,** 166-171.

MITCHELL, M. 1971. Stratigraphical palaeontology of the Carboniferous Limestone Series in the Warlingham Borehole. Appendix C. *Bulletin of the Geological Survey of Great Britain,* **36,** 139-146.

MOORE, R.C. 1929. A bryozoan faunale from the Upper Graham Formation, Pennsylvanian of North Central Texas. *Journal of Paleontology,* **3,** 1-27, 121-154.

MOROZOVA, I.P. 1974. Revision of the bryozoan genus *Fenestella. Paleontologicheskii Zhurnal,* Moskva, **2,** 54-67.

McCOY, F. 1844. *Synopsis of the characters of the Carboniferous Limestone fossils of Ireland.* University Press, Dublin, 207pp.

MacGREGOR, M. and MacGREGOR, A.G. 1948. *British Regional Geology : The Midland Valley of Scotland.* Her Majesty's Stationery Office, Edinburgh, 93pp.

McKINNEY, F.K. 1969a. Late Mississipian Ectoprocta (Bryozoa) from Alabama. *Geological Society of America special Paper* **121** : Abstracts for 1968, p57.

——— 1969b. Organic structures in a Late Mississipian trepostomatous ectoproct (bryozoan). *Journal of Paleontology,* **43,** 285-288.

——— 1969c. Bibliography and list (1900 - 1965) of the families Constellariidae and Dianulitidae (Ectoprocta, Order Cystoporata). *Southeastern Geology,* **10,** 175-184.

——— 1971a. *Stenoporella,* a Late Mississipian trepostomatous ectoproct (bryozoan). *Journal of Paleontology,* **45,** 713-723.

——— 1971b. Bryozoan stratigraphy of the Lower Chickamaugh Group, Wills

Valley, Alabama. *In* DRAHOVZAL, J.A. and NEATHERY, T.L. (eds.) *The Middle and Upper Ordovician of the Alabama Appalachians*. Guidebook for the Ninth Annual Field Trip of the Alabama Geological Society., 101-114.

——— 1977. Functional interpretation of lyre-shaped Bryozoa. *Paleobiology,* **3,** 90-97.

——— 1981a. Intercolony fusion suggests polyembryony in Paleozoic fenestrate bryozoans. *Paleobiology,* **7,** 247-251.

——— 1981b. Planar branch systems in colonial suspension feeders. *Paleobiology,* **7,** 344-354.

——— 1983. Asexual colony multiplication by fragmentation : an important mode of generic longevity in the Carboniferous bryozoan *Archimedes. Paleobiology,* **9,** 35-43.

——— 1986a. Evolution of erect marine bryozoan faunas : repeated success of unilaminate species. *The American Naturalist,* **128,** 795-809.

——— 1986b. Historical record of erect bryozoan growth forms. *Proceedings of the Royal Society of London,* **228,** 133-149.

——— and BOARDMAN, R.S. 1985. Zooidal biometry of stenolaemata. *In* NIELSEN, C. and LARWOOD, G.P. (eds.) *Bryozoa : Ordovician to Recent,* 35-44. Olsen and Olsen, Fredensborg, 364pp.

——— and GAULT, H.W. 1980. Paleoenvironment of Late Mississipian fenestrate bryozoans, Eastern United States. *Lethaia,* **13,** 127-146.

——— and JACKSON, J.B.C. 1989. *Bryozoan Evolution.* Unwin Hyman, Boston, 238pp.

———, LISTOKIN, M.R.A., and PHIFER, C.D. 1986. Flow and poypide distribution in the cheilostome bryozoan *Bugula* and their inference in *Archimedes. Lethaia,* **19,** 81-93.

———, McKINNEY, M.J., and LISTOKIN, M.R.A. 1987. Erect bryozoans are more than baffling : enhanced sedimentation rate by a living unilaminate branched bryozoan and possble implications for fenestrate bryozoan mudmounds. *Palais,* **2,** 41-47.

NEKHOROSHEV, V.N. 1932. Die Bryozoen des deutschen Unterkarbons. *Abhandlungen der Preussischen Geologischen Landesanstalt. Berlin.* **141,** 1-

NEVES, R., GUEINN, K.J., CLAYTON, G., IOANNIDES, N.S., NEVILLE, and R.S.W., KRUSZEWSKA, K. 1973. Palynological correlation within the Lower Carboniferous of Scotland and Northern England. *Transactions of the Royal Society of Edinburgh,* **69,** 23-70.

NEWTON, C.R. 1990. Palaeobiogeography. *In* BRIGGS, D.E.G., and CROWTHER, P.R. (eds.) *Palaeobiology: A Synthesis,* 452-460. Blackwell Scientific Publications, Oxford, 583pp.

NEWTON, G.B. 1971. Rhabdomesonid bryozoans of the Wreford Megacyclothem (Wolfcampian, Permian) of Nebraska, Kansas and Oklahoma. *University of Kansas Paleontological Contributions, Article* **56** (Bryozoa 2), 1-71.

NICHOLS, D. (ed.) 1962. *Taxonomy and Geography.* The Systematics Association, Publication No. **4**, London, 160pp.

NICHOLS, R.A.H. 1965. Petrology of a Lower Carboniferous bryozoan limestone and adjacent limestones in North Wales, Great Britain. *Journal of Sedimentary Petrology,* **35,** 887-899.

NICHOLSON, H.A. 1881. *On the structure and affinities of the genus Monticulipora and its sub-genera, with critical descriptions of illustrative species.* William Blackwood and Sons, Edinburgh, 240pp.

——— and ETHERIDGE, R. Jun. 1877. On *Ascodictyon,* a new provisional and anomalous genus of Palaeozoic fossils. *Annals and Magazine of Natural History,* Series 4, **19,** 464-465.

NIKIFOROVA, A.I. 1938. Types of Carboniferous Bryozoa in the European part of the U.S.S.R. *Paleontologiya SSSR,* **4,** 1-290 [in Russian, with English summary]

NITECKI, M.H. and McKINNEY, F.K. 1975. *Cucumulites* Gurley 1884 : A bryozoan, not a sponge. *Journal of Paleontology,* **49,** 561-563.

NUDDS, J.R. and JOHNSON, G.A.L. 1985. Carboniferous coral provinces and the geography of the period. *Compte Rendu. 10^e Congrès International de Stratigraphie et de Géologie Carbonifère. (Madrid, Spain 1983),* **4,** 83-88.

NYE, O.B. 1976. Generic revision and skeletal morphology of some cerioporid cyclostomes (Bryozoa). *Bulletins of American Paleontology,* **69** (No. 291), 1-224.

OKAMURA, B. and BISHOP, J.D.D. 1988. Zooid size in cheilostome bryozoans as an indicator of relative palaeotemperature. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **66,** 145-152.

OLALOYE, F. 1974. Some *Penniretepora* (Bryozoa) from the Viséan of County Fermanagh, with a revision of the generic name. *Proceedings of the Royal Irish Academy,* **74-B,** 471-506.

OSBURN, R.C. 1957. Marine Bryozoa. *In* HEDGPETH, J.W. (ed.) *Treatise on Marine Ecology and Palaeoecology,* 1109-1112. Memoir **67,** Volume 1. Geological Society of America, Washington.

OWEN, D.E. 1966. New Carboniferous Polyzoa from Derbyshire. *Geological Journal,* **5,** 135-148.

——— 1969. Lower Carboniferous Bryozoa from Scotland. *Geological Journal,* **6,** 257-266.

—— 1973. Lower Carboniferous Bryozoa from County Tyrone. *Geological Journal,* **8,** 297-306.

OWEN, T.R. and RHODES, F.H.T. 1960. *Geologists' Association Guides No. 17 : Geology around the University Towns : Swansea, South Wales.* Benham and Company Limited, Colchester, 20pp.

PACHNT, J.F. and HOROWITZ, A.S. 1987. Multivariate discrimination and classification of some North American Mississipian species of *Fistulipora* McCoy. *In* ROSS, J.R.P. (ed.) *Bryozoa : Present and Past,* 205-212. Western Washington University, Bellingham, 333pp.

PATZKOWSKY, M.E. 1987. Inferred water flow patterns in the fossil *Fistulipora* McCoy (Cystoporata, Bryozoa). *In* ROSS, J.R.P. (ed.) *Bryozoa : Present and Past,* 213-219. Western Washington University, Bellingham, 333pp.

PERKINS, R.D., PERRY, T.G. and HATTIN, D.E. 1962. Some bryozoans from the Beal Limestone Member of the Lecompton Limestone (Virgillian) of Kansas. *State Geological Survey of Kansas, Bulletin* **157** (5), 1-25.

PERRY, T.G. and HOROWITZ, A.S. 1963. Bryozoans from the Glen Dean Limestone (Middle Chester) of Southern Indiana and Kentucky. *Indiana Department of Conservation, Geological Survey Bulletin* **26,** 1-51.

—— —— and ANSTEG, R.L. 1973. Restudy of some Nicholson's types of Palaeozoic bryozoans. *In* LARWOOD, G.P. (ed.) *Living and Fossil Bryozoa,* 429-436. Academic Press, London, 634pp.

PHILLIPS, J. 1836. *Illustrations of the geology of Yorkshire. Part I, the Yorkshire Coast.* John, Murray, London, 254pp.

—— 1841. *Figures and description of the Palaeozoic fossils of Cornwall, Devon, and West Somerset.* Ordnance Geological Survey Publication. Longman, Brown, Green and Longmans, London. 231pp.

POWER, G. and SOMERVILLE, I.D. 1975. A preliminary report on the occurrence of minor sedimentary cycles in the "Middle White Limestone" (D1, Lower Carboniferous) of North Wales. *Proceedings of the Yorkshire Geological Society,* **40,** 491-497.

PROUT, H.A. 1859. Four series of descriptions of Bryozoa from the Paleozoic rocks of the western states and territories. *Transactions of the St. Louis Academy of Science,* **1,** 235-237, 266-273, 443-452, 571-581.

RAMSBOTTOM, W.H.C. 1969. The Namurian of Britain. *Compte Rendu. 6^e^ Congrès International de Stratigraphie et de Géologie Carbonifère. (Sheffield, England 1967),* **1,** 71-77.

—— 1973. Transgressions and regressions in the Dinantian: a new synthesis of British Dinantian stratigraphy. *Proceedings of the Yorkshire Geological Society,* **39,** 567-607.

—— 1978. Carboniferous. *In* McKERROW, W.S. (ed.) *The Ecology of Fossils,* 146-183. Duckworth, London, 384pp.

——, CALVER, M.A., EAGER, R.M.C., HODSON, F., HOLLIDAY, D.W., STUBBLEFIELD, C.J. and WILSON, R.B. 1978. A correlation of Silesian rocks in the British Isles. *Geological Society of London, Special Report* **10,** 82pp.

RAMSAY, A.T.S. 1987. Depositional environments of Dinantian Limestones in Gower, South Wales. *In* MILLER, J., ADAMS, A.E., and WRIGHT, V.P. (eds.) *European Dinantian Environments,* Geological Journal Special Issue No. **12,** 33-59. John Wiley & Sons Ltd., 402pp.

ROSS, C.A. and ROSS,J.R.P. 1981. Biogeographical influences on Late Palaeozoic faunal distributions. *In* LARWOOD, G.P. and NIELSEN, C. (eds.) *Recent and Fossil Bryozoa,* 199-212. Olsen and Olsen, Fredensborg, 334pp.

—— —— 1985. Carboniferous and Early Permian biogeography. *Geology,* **13,** 27-30.

—— —— 1987. Late Paleozoic sea levels and depositional sequences. *Cushman Foundation for Foraminiferal Research,* Special Publication **24,** 151-168.

ROSS, J.R.P. 1981. Biogeography of Carboniferous Ectoproct Bryozoa. *Palaeontology,* **24,** 313-341.

—— and ROSS, C.A. 1990. Late Palaeozoic bryozoan biogeography. *In* McKERROW, W.S. and SCOTESE, C.R. (eds.) *Palaeozoic Palaeogeography and Biogeography.* Geological Society Memoir No. **12,** 353-362.

RUDWICK, M.J.S. 1961. The anchorage of articulate brachiopods on soft substrata. *Palaeontology,* **4,** 475-476.

—— 1970. *Living and fossil brachiopods.* Hutchinson University Library, London, 199pp.

RYLAND, J.S. 1970. *Bryozoans.* Hutchinson University Library, London, 175pp.

—— 1973. The analysis of spatial distribution patterns. *In* LARWOOD, G.P. (ed.) *Living and Fossil Bryozoa,* 165-172. Academic Press, London, 634pp.

SCHOPF, T.J.M. 1974. Survey of genetic differentiation in a coastal zone invertebrate: the ectoproct *Schizoporella errata. Biological Bulletin,* **146,** 78-87.

—— 1979. Fossil Communities. *Science,* **203,** 999-1000.

—— and BASSETT, E.L. 1973. F.A. Smitt, marine Bryozoa, and the introduction of Darwin into Sweden. *Transactions of the American Philosophical Society,* **63** (7), 3-30.

——— COLLIER, K.O. and BACH, B.O. 1980. Relation of the morphology of stick-like bryozoans at Friday Harbor, Washington, to bottom currents, suspended matter and depth. *Paleobiology,* **6** (4), 466-476.

SCOLARO, R.J. 1968. Palaeoecological interpretation of some Florida Miocene Bryozoa. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale. Milano,* **108,** 174-177.

SCOTESE, C.R. and McKERROW, W.S. 1990. Revised World maps and introduction. *In* McKERROW, W.S. and SCOTESE, C.R. (eds.) *Palaeozoic Palaeogeography and Biogeography.* Geological Society Memoir No. **12,** 1-21.

SHRUBSOLE, G.W. 1879. A review of the British Carboniferous Fenestellidae. *Quarterly Journal of the Geological Society of London,* **35,** 275-284.

SHULGA-NESTERENKO, M.I. 1936. *Fenestella* and *Archimedes* from the Middle Pechora region of the North Urals. *Acad. Nauk. SSSR. Polyararya. Komissiia. Trudy,* **28,** 233-285.

——— 1941. Lower Permian Bryozoa of the Urals. *Paleontologiya SSSR,* **5,** 1-266.

——— 1951. Carboniferous fenestellids of the Russian Platform. *Trudy Paleozoologicheskogo Instituta. Akademiya Nauk SSSR,* **32,** 1-61. [In Russian].

——— 1955. Carboniferous Bryozoa of the Russian Platform. *Paleontologiya SSSR,* **57,** 1-207.

SINCLAIR, D.A. and SMITH, I.R. 1979. Scanning acoustic Microscopy. *Proceedings of the Royal Microscope Society,* **14** (1), 34-39.

SMITH, S. 1910. The faunal succession of the Upper Bernician. *Transactions of the Natural History Society of Northumberland, Durham, and Newcastle-upon-Tyne,* **3,** 591-645.

SMYTH, L.B. 1925. A contribution to the geology of Great Orme's Head. *Scientific Proceedings of the Royal Dublin Society,* **18** (12), 141-164.

SOMERVILLE, I.D. 1979a. A cyclicity in the Early Brigantian (D2) limestones east of the Clwydian Range, North Wales, and its use in correlation. *Geological Journal,* **14,** 69-86.

——— 1979b. Minor sedimentary cyclicity in Late Asbian (Upper D1) limestones in the Llangollen district of North Wales. *Proceedings of the Yorkshire Geological Society,* **42,** 317-341.

——— 1979c. A sedimentary cyclicity in Early Asbian (Lower D1) limestones in the Llangollen District of North Wales. *Proceedings of the Yorkshire Geological Society,* **42,** 397-404.

——— and STRANK, A.R.E. 1984. Discovery of Arundian and Holkerian faunas from a Dinantian platform succession in North Wales. *Geological Journal,* **19,** 85-104.

——— ——— 1984. The recognition of the Asbian/Brigantian boundary fauna and marker horizons in the Dinantian of North Wales. *Geological Journal,* **19,** 227-237.

SOUTHWOOD, D. 1985. *The taxonomy and palaeoecology of Bryozoa from the Upper Permian Zechstein reef of N.E. England.* Unpublished Ph.D. thesis, University of Durham, U.K., 407pp.

STEELE, R.P. 1978. *The geology of North-East Arran.* Unpublished B.Sc. dissertation, University of Durham, 86pp.

STRATTON, J.F. and HOROWITZ, A.S. 1974. Studies of the flow of water through models of *Polypora. Documents des Laboratoires de Géologie de la Facultié des Sciences de Lyons, Hors Série* **3,** 425-438.

——— ——— 1977. Astogenetic variability in a frond of *Polypora laevinodata* (Hall) (Bryozoa). *Proceedings of the Indiana Academy of Science,* **86,** 290-292.

SYLVESTER-BRADLEY, P.C. (ed.) 1956. *The Species Concept in Palaeontology.* The Systematics Association, Publication No. 4, London, 145pp.

TAIT, D. and WRIGHT,J. 1923. Notes on the structure, character and relationship of the Lower Carboniferous Limestones of St. Monans, Fife. *Transactions of the Edinburgh Geological Society,* **11,** 165-184.

TAVENER-SMITH, R. 1965. A new fenestrate bryozoan from the Lower Carboniferous of County Fermanagh. *Palaeontology,* **8,** 478-491.

——— 1965. A revision of *Retepora nodulosa* Phillips, 1836. *Geological Magazine,* **102,** 135-142.

——— 1966a. The micrometric formula and the classification of fenestrate cryptostomes. *Palaeontology,* **9,** 413-425.

——— 1966b. Ovicells in fenestrate cryptostomes of Viséan age. *Journal of Paleontology,* **40** (1), 190-198.

——— 1969a. Skeletal structure and growth in the Fenestellidae (Bryozoa). *Palaeontology,* **12,** 281-309.

——— 1969b. Wall structure and acanthopores in the bryozoan *Leioclema asperum. Lethaia,* **2,** 89-97.

——— 1971. *Polypora stenostoma* : a Carboniferous bryozoan with cheilostomatous features. *Palaeontology,* **14,** 178-187.

——— 1973a. Fenestrate Bryozoa from the Viséan of County Fermanagh, Ireland. *Bulletin of the British Museum (Natural History)* (Geology), **23,** 389-493.

——— 1973b. Some aspects of skeletal organization in Bryozoa. *In* LARWOOD, G.P. (ed.) *Living and fossil Bryozoa,* 349-359. Academic Press, London, 634pp.

——— 1974. Early growth stages in rhabdomesoid bryozoans from the Lower Carboniferous of Hook Head, Ireland. *Palaeontology,* **17,** 149-164.

——— 1975. The phylogenetic affinities of fenestelloid bryozoans. *Palaeontology,* **18,** 1-17.

——— and WILLIAMS, A. 1970. Structure of the compensation sac in two ascophoran bryozoans. *Proceedings of the Royal Society of London,* **175,** 235-254.

——— ——— 1973. The secretion and structure of the skeleton of living and fossil Bryozoa. *Philosophical Transactions of the Royal Society of London. Series B,* **264,** 97-159.

TAYLOR, P.D. 1977. The palaeobiology and systematics of some Jurrasic Bryozoa. Unpublished Ph.D. thesis, University of Durham, U.K., 518pp.

——— 1979. The inference of extrazooidal feeding currents in fossil bryozoan colonies. *Lethaia,* **12,** 47-56.

——— 1985a. Carboniferous and Permian species of the cyclostome bryozoan *Corynotrypa* Bassler, 1911, and their clonal propagation. *Bulletin of the British Museum (Natural History)* (Geology), **38,** 359-372.

——— 1985b. Bryozoa. *In* MURRAY, J.W. (ed.) *Atlas of Invertebrate Macrofossils,* 47-52. The Palaeontological Association, Longman Group Ltd., Essex, 241pp.

——— 1988. Major radiation of cheilostome bryozoans : triggered by the evolution of a new larval type ? *Historical Biology,* **1,** 45-64.

———, LARWOOD, G.P. and BALSON, P.S. 1981. Some British field localities with fossil Bryozoa. *In* LARWOOD, G.P. and NIELSEN, C. (eds.) *Recent and Fossil Bryozoa,* 249-262. Olsen and Olsen, Fredensborg, 334pp.

THORSON, G. 1961. Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents. *In* SEARS, M. (ed.) *Oceanography,* 455-474. American Association for the Advancement of Science, Publication **67.**

TROTTER, F.M. and HOLLINGWORTH, S.E. 1932. *The geology of the Brampton district.* Geological Survey of Great Britain. Memoir for Sheet **18.** Her Majesty's Stationery Office, 223pp.

ULRICH, E.O. 1882. American Paleozoic Bryozoa. *Journal of the Cincinnati Society of Natural History,* **5,** 121-175, 232-257.

——— 1890. Paleozoic Bryozoa. *Bulletin of the Geological Survey of Illinois,* **8,** 283-688.

——— and BASSLER, R.S. 1904. A revision of the Paleozoic Bryozoa : Part 1. On genera and species of Ctenostoma. *Smithsonian Miscellaneous Collections,* **45,** 256-294.

——— ——— 1905. A revision of the Paleozoic Bryozoa : Part 2. On genera and species of Trepostomata. *Smithsonian Miscellaneous Collections,* **47,** 15-55.

UTGAARD, J. and PERRY, T.G. 1960. Fenestrate bryozoans from the Glen Dean Limestone (Middle Chester) of Southern Indiana. *Indiana Department of Conservation, Geological Survey Bulletin* **19,** 1-46.

VAUGHAN, A. 1905. The palaeontological sequence in the Carboniferous Limestone of the Bristol Area. *Quartery Journal of the Geological Society,* **61,** 181-307.

VINE, G.R. 1881. Notes on the Carboniferous Polyzoa of North Yorkshire. *Proceedings of the Yorkshire Geological Society,* **7,** 329-341.

——— 1883. Fourth report of the committee consisting of Dr. H.C. Sorby and Mr. G.R. Vine, appointed for the purpose of reporting of fossil Polyzoa. *Report of the Fifty-Third Meeting of the British Association for the Advancement of Science , Southport, September 1883,* 161-209.

——— 1885. Notes on the Yoredale Polyzoa of North Lancashire. *Proceedings of the Yorkshire Geological Society,* **9,** 70-98.

——— 1887. Notes on the classification of cyclostomatous Polyzoa; old and new. *Proceedings of the Yorkshire Geological Society,* **9,** 346-362.

——— 1888a. Notes on the classification of the Palaeozoic Polyzoa. *Proceedings of the Yorkshire Geological Society,* **11,** 20-44.

——— 1888b. A monograph of Yorkshire Carboniferous and Permian Polyzoa. Part I. *Proceedings of the Yorkshire Geological Society,* **11,** 68-85.

——— 1889. A monograph of Yorkshire Carboniferous and Permian Polyzoa. Part II. *Proceedings of the Yorkshire Geological Society,* **11,** 184-200.

——— 1891. British Palaeozoic ctenostomatous Polyzoa. *Proceedings of the Yorkshire Geological Society,* **12,** 74-93.

VOIGT, E. 1981. Upper Cretaceous bryozoan-seagrass association in the Maastrichtian of the Netherlands. *In* LARWOOD, G.P. and NIELSEN, C. (eds.) *Recent and Fossil Bryozoa,* 281-298. Olsen and Olsen, Fredensborg, 334pp.

WALKDEN, G.M. 1987. Sedimentary and diagenetic styles in Late Dinantian carbonates of Britain. *In* MILLER, J., ADAMS, A.E., and WRIGHT, V.P. (eds.) *European Dinantian Environments,* Geological Journal Special Issue No. **12,** 131-155. John Wiley & Sons Ltd., 402pp.

WHITE, A.G. 1990. *The palaeoecology of the Great Limestone and overlying shales in the Stanhope area, with particular reference to the crinoids of the Ashes Quarry Shales.* Unpublished B.Sc. dissertation, University of Durham, U.K., 80pp.

WILSON, H.H. 1952. The Cove Marine Bands in East Lothian and their relation to the Ironstone Shale and Limestone of Redesdale, Northumberland. *Geological Magazine,* **89,** 305-319.

WILSON, R.B. 1961. Palaeontology of the Archerbeck borehole, Canonbie, Dumfrieshire. *Bulletin of the Geological Survey of Great Britain,* **18,** 90-106.

——— 1966. A study of the Neilson Shell Bed, a Scottish Lower Carboniferous Marine Shale. *Bulletin of the Geological Survey of Great Britain,* **24,** 105-131.

——— 1974. A study of the Dinantian marine faunas of South-East Scotland. *Bulletin of the Geological Survey of Great Britain,* **46,** 35-65.

——— 1989. A study of the Dinantian marine macrofossils of Central Scotland. *Transactions of the Royal Society Of Edinburgh : Earth Sciences,* **80,** 91-126.

WILLIAMS, A. 1962. The Barr and Lower Ardmillan Series (Caradoc) of the Girvan District, South-West Ayrshire, with descriptions of the Brachiopoda. *Geological Society of London, Memoir* **3,** 1-267.

WOOD, A. 1942. The algal nature of the genus *Koninkopora* Lee; its occurrence in Canada and Western Europe. *Quartery Journal of the Geological Society of London,* **98,** 205-222.

WYSE-JACKSON, P.N. 1988. New fenestrate Bryozoa from the Carboniferous of County Fermanagh. *Irish Journal of Earth Sciences,* **9,** 197-208.

———, BANCROFT, A.J. and SOMERVILLE, I.D. 1991. Bryozoan zonation in a trepostome-dominated buildup from the Lower Carboniferous of North Wales. *In* BIGEY, F.P. (ed.) with D'HONDT, J-L. *Bryozoaires Actuels et Fossiles : Bryozoa Living and Fossil,* . Société des Sciences Naturelles de l'Ouest de la France, Nantes, 579pp.

YOUNG, J. 1877. Notes on a new method of fixing fronds of Carboniferous Polyzoa on a layer of asphalt, to show the celluliferous face. *Proceedings of the Natural History Society of Glasgow,* **3,** 207-210.

——— 1881. Remarks on the genus *Synocladia* and other allied forms, with description of a new species. *Proceedings of the Natural History Society of Glasgow,* **5,** 30-35.

——— 1882. Remarks on some of the external characters which distinguish *Fenestella plebeia* of McCoy from those of *F. tuberculo-carinata* of Etheridge, Jun.. *Transactions of the Geological Society of Glasgow,* **8,** 182-188.

——— and ROBERTSON, D. 1874. Notes on the Polyzoa of the Hairmyres Limestone Shale, East Kilbride. *Transactions of the Geological Society of Glasgow,* **5,** 173-175.

——— and YOUNG, J. 1874a. On *Palaeocoryne* and other polyzoal appendages. *Quarterly Journal of the Geological Society of London,* **30,** 684-688.

——— ——— 1874b. New Carboniferous Polyzoa. *Quarterly Journal of the Geological Society of London,***30,** 681-683.

——— ——— 1875a. New species of *Glauconome* from Carboniferous Limestone strata of the West of Scotland. *Proceedings of the Natural History Society of Glasgow,* **2,** 325-335.

——— ——— 1875b. On new Carboniferous Polyzoa. *Annals and Magazine of Natural History,* **14,** 333-336.

——— ——— 1878. On two new species of Carboniferous Polyzoa. *Proceedings of the Natural History Society of Glasgow,* **3,** 353-356.

PLATES

PLATE 1

Bryozoans from the Isle of Arran

Fig. a. *Rhabdomeson gracilis* (left) and *Rhabdomeson rhombifera* (right). AS^45. Hurlet shales (Lower Brigantian), Laggan Cottage. x6.3

Fig. b. *Rhabdomeson gracilis*. AS11. Hurlet shales (Lower Brigantian), Laggan Cottage. x6.3

Fig. c. *Fenestella tuberculo-carinata*. Hexagonal-meshed reverse surface. AS^214. Hurlet shales (Lower Brigantian), Laggan Cottage. x5.6

Fig. d. *Fenestella plebeia*. Striated reverse surface. AS^412. Hurlet shales (Lower Brigantian), Laggan Cottage. x5.6

Fig. e. *Septopora carbonaria*. Meshwork aspect, obverse surface. AL3, 24, & 25. Index Limestone (Pendleian), 1.7 kilometres northwest of Laggan Cottage. x2.2

Fig. f. *Tabulipora urii*. Dendritic colony. AS^432. Hurlet shales (Lower Brigantian), Laggan Cottage. x4.2

Bryozoans from East Fife

Fig. g. *Tabulipora urii*. Cylindrical colony. PCB3. St. Monance White Limestone (Brigantian), Parton Craig. x8.4

Fig. h. *Tabulipora urii*. Cylindrical colony. MMK13. Mid Kinniny Limestone (Upper Brigantian), St. Monans. x6.3

Fig. i. *Tabulipora urii*. Cylindrical colony. MMK41. Mid Kinniny Limestone (Upper Brigantian), St. Monans. x8.4

Fig. j. *Tabulipora howsii*. Sheet-like colony. MMK39. Mid Kinniny Limestone (Upper Brigantian), St. Monans. x8.4

Fig. k. *Eridopora* sp. nov.? MMK30. Mid Kinniny Limestone (Upper Brigantian), St. Monans. x13.3

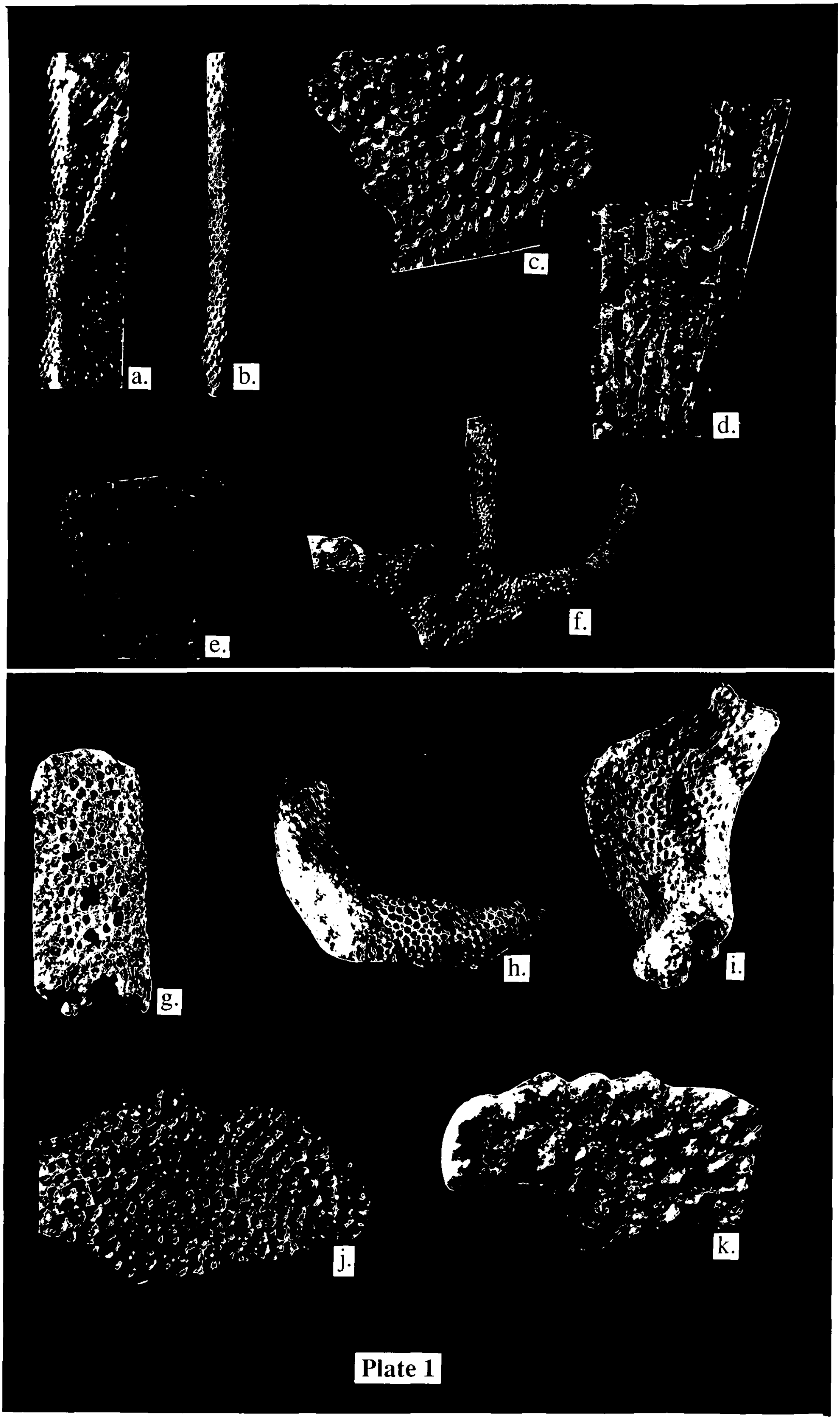


Plate 1

PLATE 2

Bryozoans from East Fife

Fig. a. *Rhabdomeson gracilis.* Recrystallised colony. PMW^{T}3. St. Monance White Limestone (Brigantian), Pathhead. x11.9

Fig. b. *Rhabdomeson gracilis.* MMK38. Mid Kinniny Limestone (Upper Brigantian), St. Monans. x12.6

Fig. c. *Rhombopora incrassata?.* Small stylets are present around the autozooecial apertures. PCM1. Charlestown Main Limestone (Brigantian), Pathhead. x12.6

Fig. d. *Fenestella bicellulata.* Reverse surface. MMK44. Mid Kinniny Limestone (Upper Brigantian), St. Monans. x4.2

Fig. e. *Fenestella tuberculo-carinata.* Reverse surface of non-secondarily calcified colony. MRW3. Witch Lake Marine Band (Asbian), Maiden Rock. x4.2

Fig. f. *Fenestella tuberculo-carinata.* Reverse surface of secondarily-calcified colony. PMW^{T}5. St. Monance White Limestone (Brigantian), Pathhead. x6.3

Fig. g. *Fenestella tuberculo-carinata.* Obverse surface detail. MRW1. Witch Lake Marine Band (Asbian), Maiden Rock. x14.0

Fig. h. *Fenestella tuberculo-carinata.* Obverse surface, with very closely-spaced carinal nodes. PMW^{S}1. St. Monance White Limestone (Brigantian), Pathhead. x6.3

Fig. i. *Polypora dendroides.* Thick-branched reverse surface. PCB8. St. Monance White Limestone (Brigantian), Parton Craig, St. Monans. x10.5

Fig. j. *Penniretepora spinosa.* Striated reverse surface. MMK30. Mid Kinniny Limestone (Upper Brigantian), St. Monans. x19.6

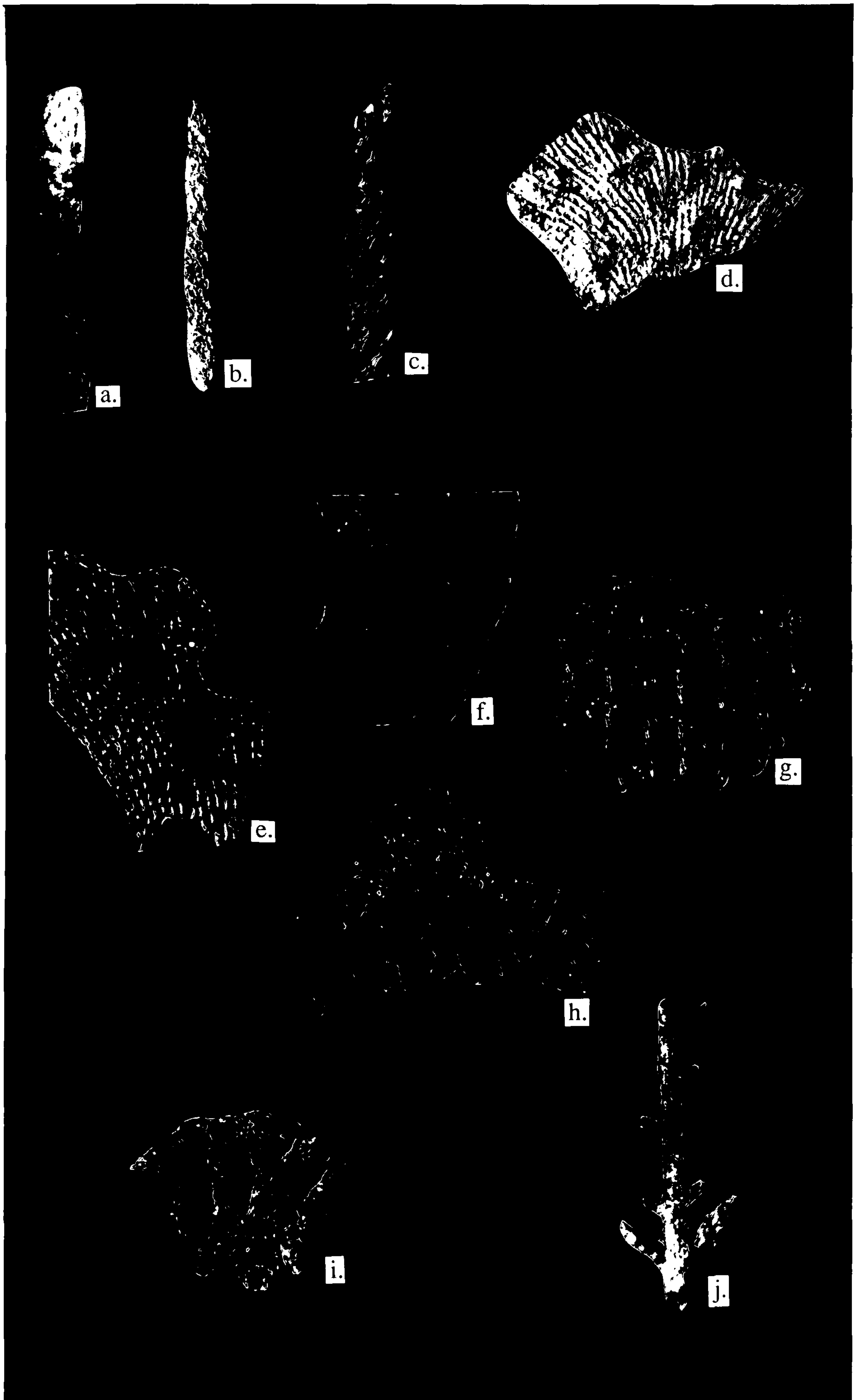


Plate 2

PLATE 3

Bryozoans from the Northumberland Coast

Fig. a. *Rhombopora bancrofti.* Partially-weathered colony. HB7. Dun Limestone (Upper Asbian), Hilton Bay, Burnmouth. x17.5

Fig. b. *Rhombopora incrassata.* Zooarial surface detail. LH5. Sandbanks Limestone (Upper Brigantian), Lady's Hole, Beadnell. x35

Fig. c. *Rhombopora incrassata.* LH5. Sandbanks Limestone (Upper Brigantian), Lady's Hole, Beadnell. x17.5

Fig. d. *Rhabdomeson gracilis.* Colony with single stylet at distal end of apertures. LH6. Sandbanks Limestone (Upper Brigantian), Lady's Hole, Beadnell. x25.2

Fig. e. *Hyphasmopora buskii.* Note the abundance of exilazooecia between the autozooecial apertures. BH7. Shales above the Dun Limestone (Upper Asbian), Bears Head, Spittal. x17.5

Fig. f. *Hyphasmopora buskii.* Surface detail. BH5. Shales above the Dun Limestone (Upper Asbian), Bears Head, Spittal. x17.5

Fig. g. *Fenestella bicellulata.* Reverse surface. SP^{M}7. Eelwell Limestone (Brigantian), Snook Point, Seahouses. x17.5

Fig. h. *Fenestella frutex.* Reverse surface. SP^{T}11. Eelwell Limestone (Brigantian), Snook Point, Seahouses. x8.4

Fig. i. *Fenestella multispinosa.* "Palaeocorynid" spine developing from reverse surface. SP^{1}23. Eelwell Limestone (Brigantian), Snook Point, Seahouses. x16.8

Fig. j. *Fenestella multispinosa.* Obverse surface, with thin carina. SSB30. Ironscars Limestone (Pendleian), Sugar Sands Bay, Howick. x17.5

Fig. k. *Fenestella tuberculo-carinata.* Secondarily-calcified reverse surface. SSB42. Ironscars Limestone (Pendleian), Sugar Sands Bay, Howick. x11.9

Fig. l. *Fenestella tuberculo-carinata.* Obverse surface, with broad carina. SSB40. Ironscars Limestone (Pendleian), Sugar Sands Bay, Howick. x11.9

Fig. m. *Fenestella polyporata.* Reverse surface. CPA4. Acre Limestone (Brigantian), Cullernose Point, Howick. x4.2

Fig. n. *Fenestella plebeia.* Reverse surface. BH3. Shales above the Dun Limestone (Upper Asbian), Bears Head, Spittal. x8.4

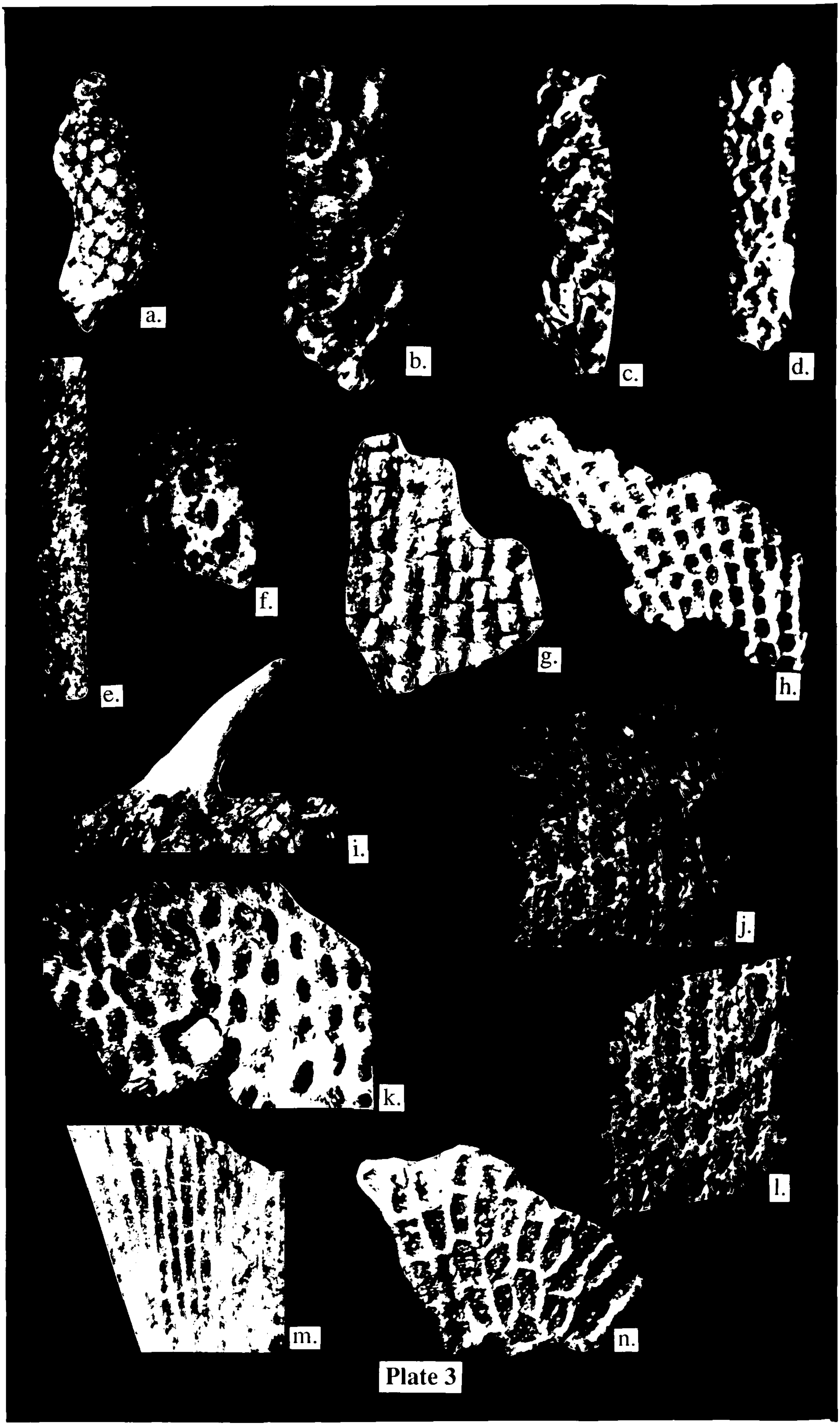


Plate 3

PLATE 4

Bryozoans from the Northumberland Coast

Fig. a. *Polypora hexagonaria.* Reverse surface, showing the development of a hexagonal meshwork. SSB13. Ironscars Limestone (Pendleian), Sugar Sands Bay, Howick. x4.2

Fig. b. *Polypora hexagonaria.* Partially weathered obverse surface. SSB12. Ironscars Limestone (Pendleian), Sugar Sands Bay, Howick. x4.2

Fig. c. *Polypora hexagonaria.* Detail of branch obverse surface. SSB10. Ironscars Limestone (Pendleian), Sugar Sands Bay, Howick. x18.3

Fig. d. *Polypora hexagonaria.* Tangential thin section, showing initially rhombic autozooecial chamber bases (bottom) developing into hexagonal chambers (top). SSB13. Ironscars Limestone (Pendleian), Sugar Sands Bay, Howick. x4.2

Fig. e. *Polypora verrucosa.* Reverse surface. SP^15. Eelwell Limestone (Brigantian), Snook Point, Seahouses. x8.4

Fig. f. *Polyfenestella fenestelliformis.* Reverse surface, with the development of randomly placed cyclozooecia (circled for clarity). LH4. Sandbanks Limestone (Upper Brigantian), Lady's Hole, Beadnell. x17.5

Fig. g. *Penniretepora spinosa.* Reverse surface. SP^T12. Eelwell Limestone (Brigantian), Snook Point, Seahouses. x21.0

Fig. h. *Penniretepora flexicarinata.* Obverse surface. BH5. Shales above the Dun Limestone (Upper Asbian), Bears Head, Spittal. x19.6

Fig. i. *Penniretepora flexicarinata.* Reverse surface. BH5. Shales above the Dun Limestone (Upper Asbian), Bears Head, Spittal. x10.5

Fig. j. *Penniretepora pulcherrima.* Pustulose reverse surface. SH2. Marl below the Oxford Limestone (Brigantian), Sharpers Head, Berwick. x10.5

Fig. k. *Diploporaria marginalis.* Obverse surface, showing protruding peristomes. LSP5a. Acre Limestone (Brigantian), Snipe Point, Lindisfarne. x12.6

Fig. l. *Diploporaria marginalis.* Striated reverse surface. GR5. Oxford Limestone (Brigantian), Greenhill Rocks, Seahouses. x33.6

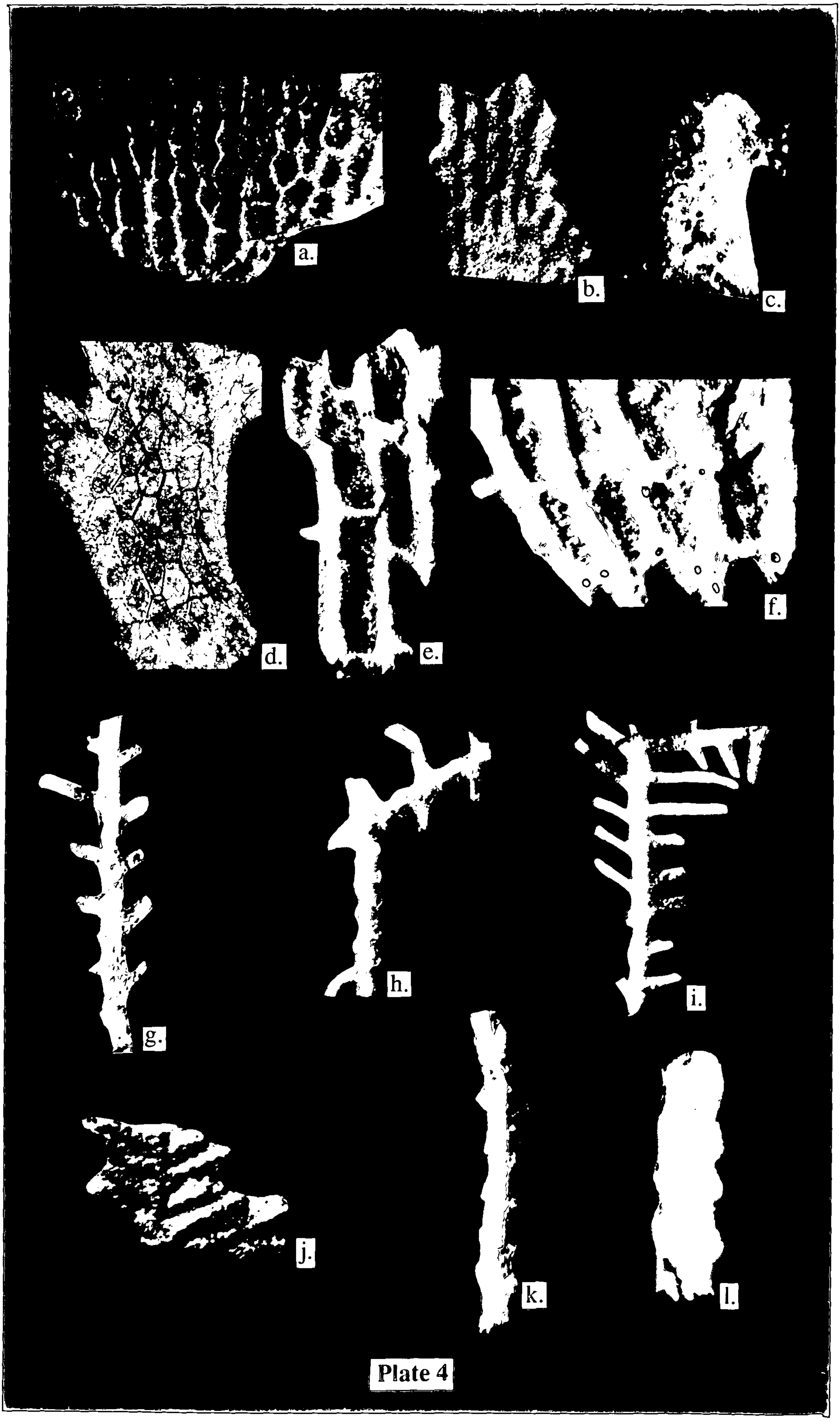


Plate 4

PLATE 5

Bryozoans from the Northumberland Coast

Fig. a. *Synocladia* sp. Fragment of branch showing three rows of apertures on the obverse surface. DP11. Eelwell Limestone (Brigantian), Dell Point, Beadnell. x8.4

Fig. b. *Septopora carbonaria.* Obverse surface of partially-eroded colony. HLL1. Lickar Limestone (Pendleian), Howick. x7.0

Fig. c. *Septopora carbonaria.* Obverse surface detail, showing autozooecia on dissepiment-like lateral branches. SSB30. Ironscars Limestone (Pendleian), Sugar Sands Bay, Howick. x8.4

Fig. d. *Septopora carbonaria.* Obverse surface. SSB32. Ironscars Limestone (Pendleian), Sugar Sands Bay, Howick. x6.3

Fig. e. *Septopora carbonaria.* High-angle conical colony. SSB34. Ironscars Limestone (Pendleian), Sugar Sands Bay, Howick. x1.7

Fig. f. *Tabulipora urii.* Transverse colony acetate peel, showing a wide exozone. SP6. Eelwell Limestone (Brigantian), Snook Point, Seahouses. x7.0

Fig. g. *Tabulipora urii.* Exozone detail, showing the development of ring septa within the zooecial chambers. SP6. Eelwell Limestone (Brigantian), Snook Point, Seahouses. x7.0

Fig. h. *Tabulipora* sp. Colony surface detail. DP17. Eelwell Limestone (Brigantian), Dell Point, Beadnell. x26.6

Fig. i. *Stenodiscus tumida.* Dendritic colony fragment. SSB49. Ironscars Limestone (Pendleian), Sugar Sands Bay, Howick. x4.2

Fig. j. *Stenodiscus tumida.* Surface detail. SSB49. Ironscars Limestone (Pendleian), Sugar Sands Bay, Howick. x4.2

Fig. k. *Dyscritella miliaria.* Cylindrical colony fragment. LSP1. Acre Limestone (Brigantian), Snipe Point, Lindisfarne. x4.2

Fig. l. *Dyscritella miliaria.* Surface detail. LSP1. Acre Limestone (Brigantian), Snipe Point, Lindisfarne. x4.2

Fig. m. *Eridopora beilensis.* Surface detail. SSB44. Ironscars Limestone (Pendleian), Sugar Sands Bay, Howick. x9.8

Fig. n. *Fistulipora incrustans.* Partially weathered fragment. SP^{1}18. Eelwell Limestone (Brigantian), Snook Point, Seahouses. x8.4

Fig. o. *Sulcoretepora parallela.* Colony fragment showing alternate rows of zooecia separated by prominent ridges. DP3. Eelwell Limestone (Brigantian), Dell Point, Beadnell. x23.1

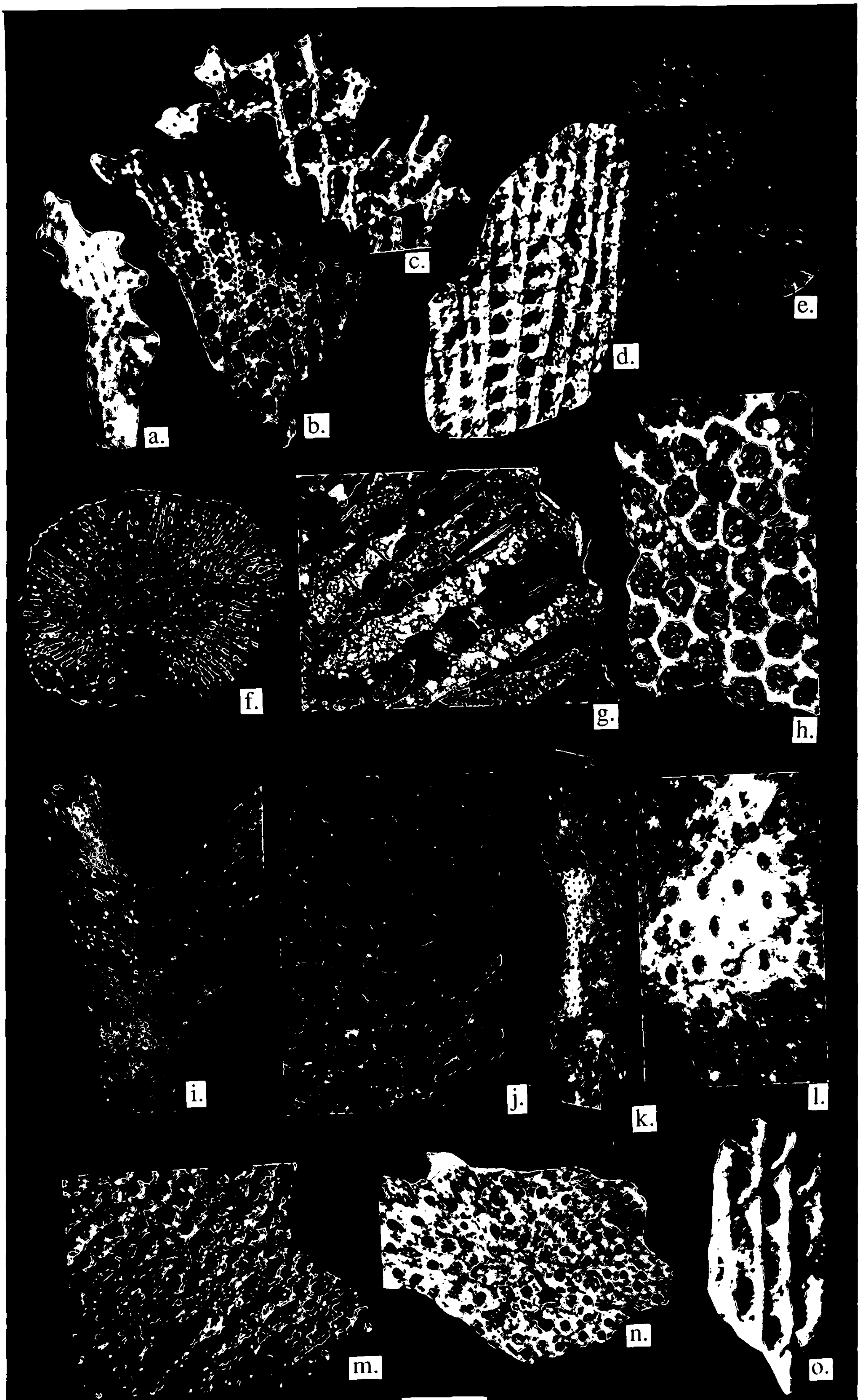


Plate 5

PLATE 6

Bryozoans from North Wales

Fig. a. *Rhombopora incrassata.* Transverse colony acetate peel, illustrating budding from a central point. HQ^{T}2.1. Cefn Mawr Limestone (Brigantian), Hendre Quarry, Clwyd. x35.0

Fig. b. *Rhombopora incrassata.* Laterally-branching colony. HQ^{T}2. Cefn Mawr Limestone (Brigantian), Hendre Quarry, Clwyd. x10.5

Fig. c. and **Fig. d.** *Rhabdomeson rhombifera.* Two photographs of opposite faces of a cylindrical colony, illustrating the variation in aperture size. LLD^{1}1. Bishop's Quarry Beds (Lower Brigantian), Bishop's Quarry, Llandudno. x24.5

Fig. e. *Rhabdomeson gracilis.* Bifurcating cylindrical colony. HQ^{T}8. Cefn Mawr Limestone (Brigantian), Hendre Quarry, Clwyd. x5.6

Fig. f. *Rhabdomeson gracilis.* Bedding surface crowded with branching colonies. HMQ4. Cefn Mawr Limestone (Brigantian), Halkyn Mountain Quarry, Clwyd. x1.7

Fig. g. *Penniretepora laxa.* Poorly-preserved reverse surface. LLD^{1}5. Bishop's Quarry Beds (Lower Brigantian), Bishop's Quarry, Llandudno. x12.6

Fig. h. *Penniretepora* cf. *grandis.* Poorly-preserved reverse surface. LLD^{1}4. Bishop's Quarry Beds (Lower Brigantian), Bishop's Quarry, Llandudno. x12.6

Fig. i. *Penniretepora pulcherrima.* Branching colony. HMQ5. Cefn Mawr Limestone (Brigantian), Halkyn Mountain Quarry, Clwyd. x4.2

Fig. j. *Penniretepora pulcherrima.* Pustulose reverse surface, with a central row of nodes. HMQ5. Cefn Mawr Limestone (Brigantian), Halkyn Mountain Quarry, Clwyd. x27.3

Fig. k. *Penniretepora flexicarinata.* Branching colony reverse surface. BMQ^{D}2. Cefn Mawr Limestone (Brigantian), Bryn Mawr Quarry, Halkyn Mountain, Clwyd. x4.2

Fig. l. *Diploporaria marginalis.* Obverse surface. LLD^{2}1. Bishop's Quarry Beds (Lower Brigantian), Bishop's Quarry, Llandudno. x16.8

Fig. m. *Baculopora* sp. Obverse surface, with faint striations developed. CMQ4. Cefn Mawr Limestone (Brigantian), Cefn Mawr Quarry, Clwyd. x17.5

Fig. n. *Baculopora* sp. Obverse surface, with rounded apertures. BMQ^{B}2. Cefn Mawr Limestone (Brigantian), Bryn Mawr Quarry, Halkyn Mountain, Clwyd. x8.4

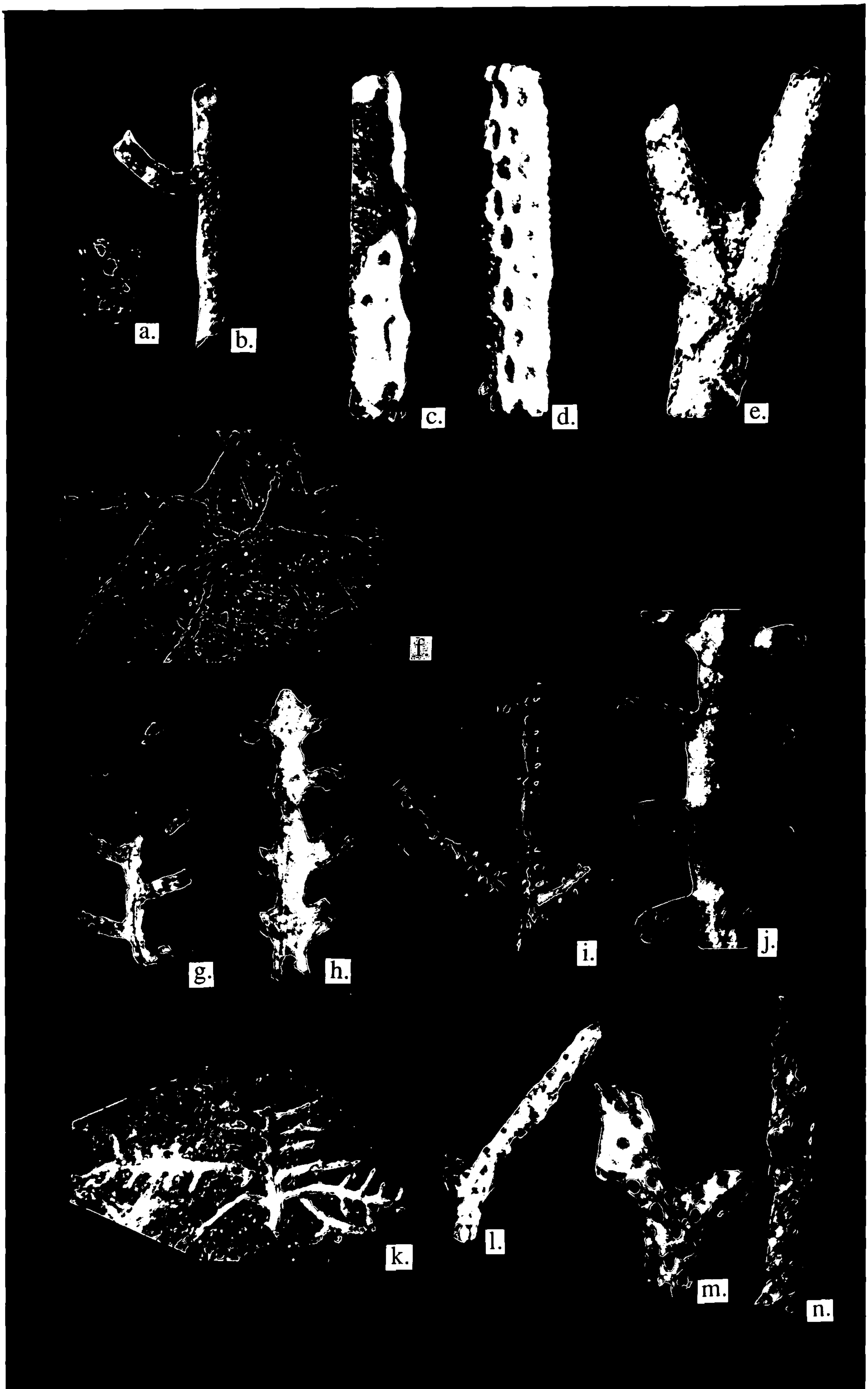


Plate 6

PLATE 7

Bryozoans from North Wales

Fig. a. *Fenestella bicellulata.* Well-preserved obverse surface. HQ^T13. Cefn Mawr Limestone (Brigantian), Hendre Quarry, Clwyd. x18.2

Fig. b. *Fenestella bicellulata.* Reverse surface. HQ^T19. Cefn Mawr Limestone (Brigantian), Hendre Quarry, Clwyd. x7.0

Fig. c. *Fenestella multispinosa.* Hexagonal-meshed, secondarily calcified reverse surface. HQ1. Cefn Mawr Limestone (Brigantian), Hendre Quarry, Clwyd. x2.2

Fig. d. *Fenestella multispinosa.* Detail of partially eroded meshwork, showing hemi-hexagonal zooecial chamber bases. HQ1. Cefn Mawr Limestone (Brigantian), Hendre Quarry, Clwyd. x14.0

Fig. e. *Fenestella multispinosa.* Initial stages of non-secondarily calcified fan-shaped colony; reverse surface. HMQ3 .Cefn Mawr Limestone (Brigantian), Halkyn Mountain Quarry, Clwyd. x10.5

Fig. f. *Fenestella polyporata.* Wide-fenestruled reverse suface. HMQ1. Cefn Mawr Limestone (Brigantian), Halkyn Mountain Quarry, Clwyd. x4.2

Fig. g. *Fenestella polyporata.* Obverse surface. BMQ^B1a. Cefn Mawr Limestone (Brigantian), Bryn Mawr Quarry, Halkyn Mountain, Clwyd. x4.2

Fig. h. *Fenestella polyporata.* Obverse surface. CMQ3. Cefn Mawr Limestone (Brigantian), Cefn Mawr Quarry, Clwyd. x4.9

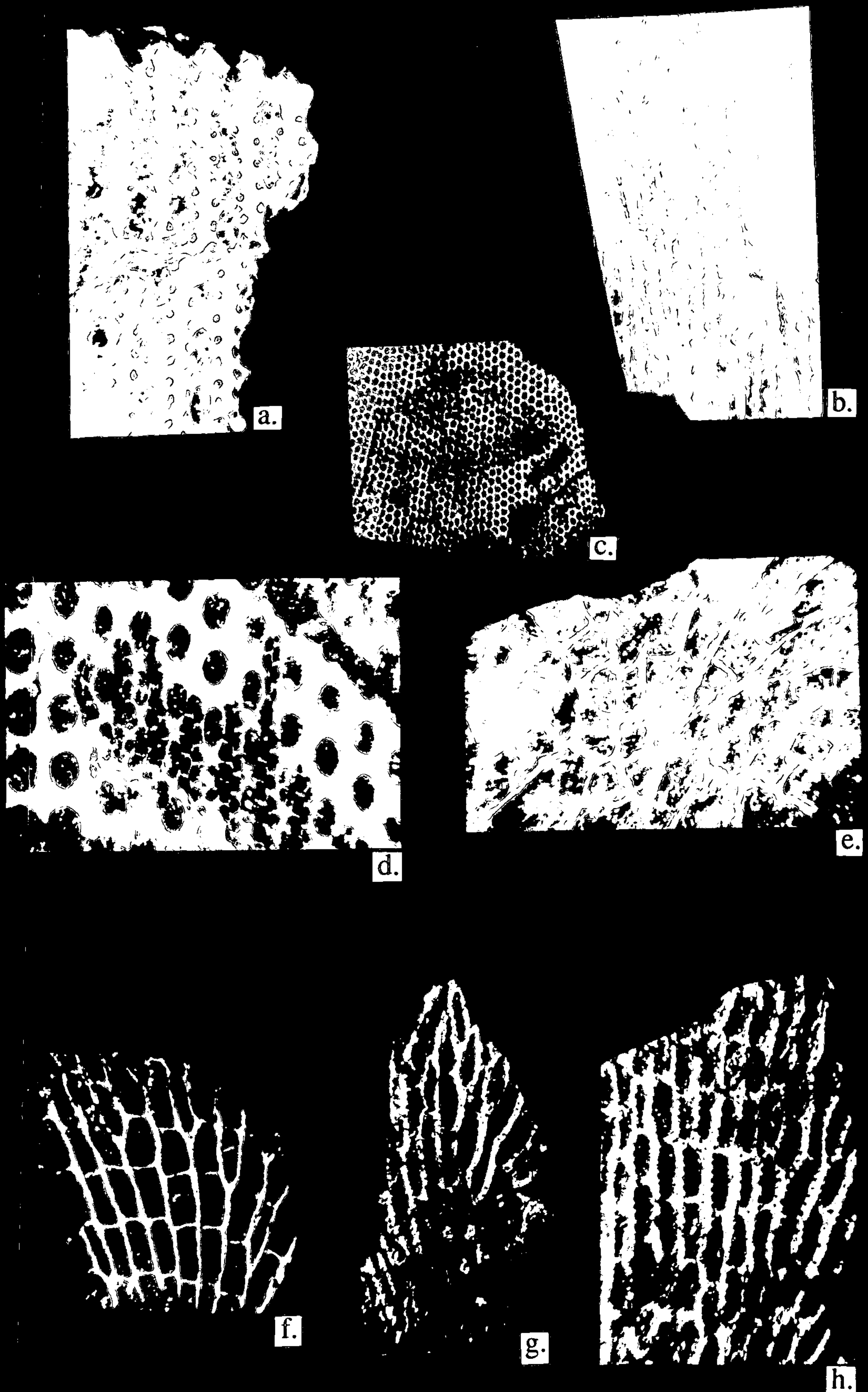


Plate 7

PLATE 8

Bryozoans from North Wales

Fig. a. *Fenestella plebeia.* Bedding surface covered with flattened colony fronds. BMQ^{S}1. Cefn Mawr Limestone (Brigantian), Bryn Mawr Quarry, Halkyn Mountain, Clwyd. x1.7

Fig. b. *Fenestella plebeia.* Colony origin, initiating from a cylindrical basal sheath (indicated by arrow); obverse surface. BMQ^{L}3. Cefn Mawr Limestone (Brigantian), Bryn Mawr Quarry, Halkyn Mountain, Clwyd. x7.0

Fig. c. *Fenestella plebeia.* Fused proximal portion of colony (origin indicated by arrow); obverse surface. BMQ^{L}4. Cefn Mawr Limestone (Brigantian), Bryn Mawr Quarry, Halkyn Mountain, Clwyd. x2.8

Fig. d. *Fenestella* sp. Colony origin, initiating from a large, curved basal sheath (indicated by arrow); reverse surface. HQ^{T}5. Cefn Mawr Limestone (Brigantian), Hendre Quarry, Clwyd. x10.5

Fig. e. *Fenestella frutex.* Colony origin, initiating from a cylindrical basal sheath (indicated by arrow); reverse surface. BMQ^{D}1. Cefn Mawr Limestone (Brigantian), Bryn Mawr Quarry, Halkyn Mountain, Clwyd. x10.5

Fig. f. *Polypora dendroides.* Obverse surface, showing three to four rows of apertures on each branch. HQ^{T}17. Cefn Mawr Limestone (Brigantian), Hendre Quarry, Clwyd. x8.4

Fig. g. *Polypora verrucosa.* Reverse surface. BMQ^{M}16. Cefn Mawr Limestone (Brigantian), Bryn Mawr Quarry, Halkyn Mountain, Clwyd. x4.2

Fig. h. *Hemitrypa hibernica.* Detail of hexagonal superstructure meshwork. LLG2. Loggerheads Limestone (Asbian), Loggerheads Country Park, Clwyd. x10.5

Fig. i. *Septopora carbonaria.* Partially broken fragment of the reverse surface; "dissepiments" are actually zooid-bearing lateral branches. CMQ2. Cefn Mawr Limestone (Brigantian), Cefn Mawr Quarry, Clwyd. x4.9

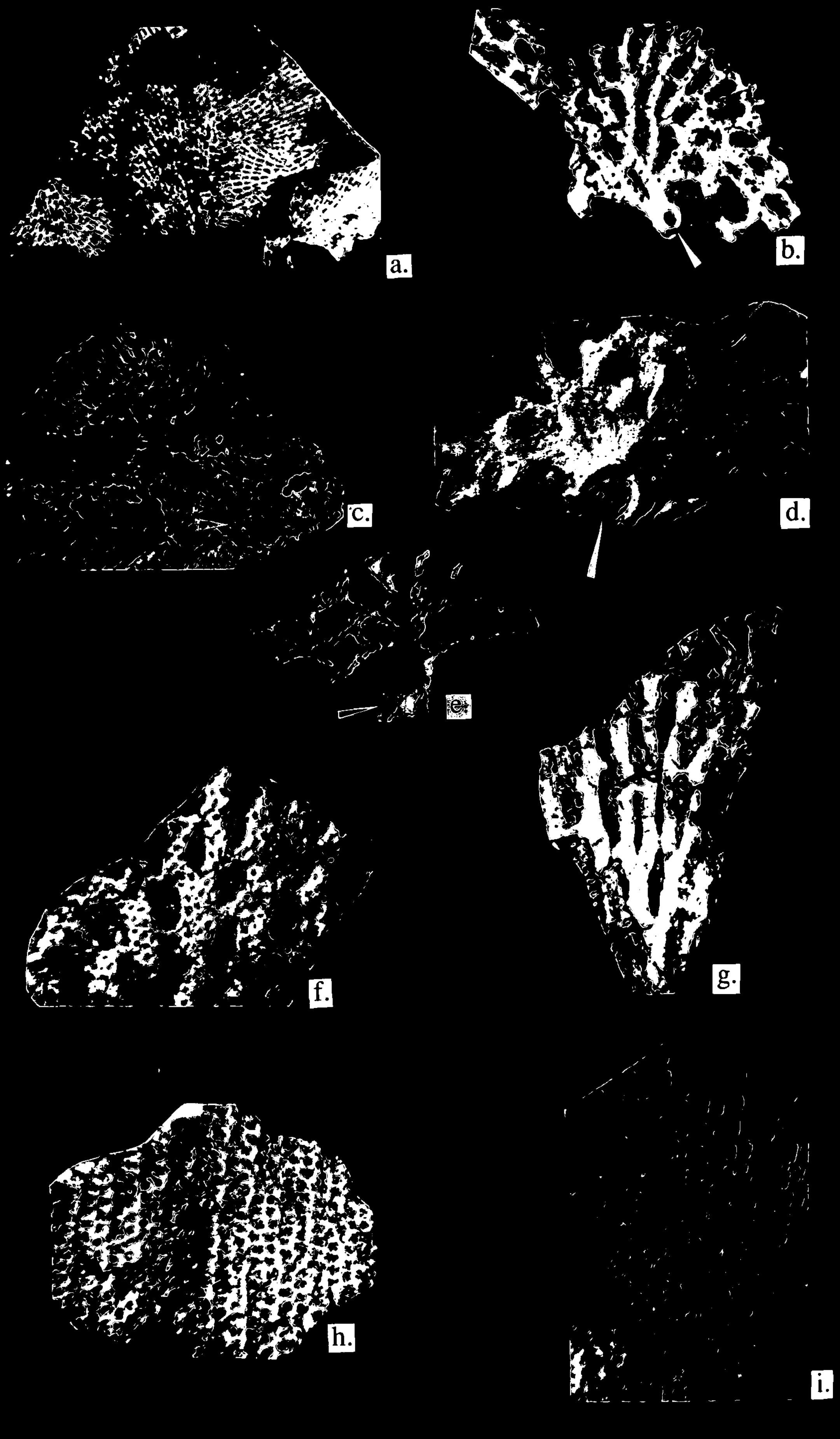


Plate 8

PLATE 9

Bryozoans from North Wales

Fig. a. *Tabulipora* sp. Colony encrusting brachiopod (*Brachythyris*) shell. HQ^{T}1. Cefn Mawr Limestone (Brigantian), Hendre Quarry, Clwyd. x10.5

Fig. b. *Tabulipora urii.* Acetate peel of transverse colony section. BMQ^{L}2.1. Cefn Mawr Limestone (Brigantian), Bryn Mawr Quarry, Halkyn Mountain, Clwyd. x10.5

Fig. c. *Tabulipora urii.* Detail of section, illustrating the development of ring septa in the exozone. BMQ^{L}2.1. Cefn Mawr Limestone (Brigantian), Bryn Mawr Quarry, Halkyn Mountain, Clwyd. x19.6

Fig. d. *Tabulipora urii.* Cylindrical colony. BMQ^{L}1. Cefn Mawr Limestone (Brigantian), Bryn Mawr Quarry, Halkyn Mountain, Clwyd. x2.2

Fig. e. *Tabulipora* sp. Acetate peel, cut transversely, showing a colony encrusting over a gastropod shell. HQ^{3}1.1. Cefn Mawr Limestone (Brigantian), Hendre Quarry, Clwyd. x5.6

Fig. f. *Stenodiscus* sp. Cylindrical colony. LLG1. Loggerheads Limestone (Asbian), Loggerheads Country Park, Clwyd. x16.8

Fig. g. *Stenodiscus* sp. Acetate peel through transverse section of colony, showing a thick, well-defined endozone. LLG1. Loggerheads Limestone (Asbian), Loggerheads Country Park, Clwyd. x35.0

Fig. h. *Fistulipora incrustans.* Sheet-like colony, found encrusting a rugose coral. CMQ1. Cefn Mawr Limestone (Brigantian), Cefn Mawr Quarry, Clwyd. x4.2

Fig. i. *Fistulipora incrustans.* Colony encrusting over a chaetetid sclerosponge; details of the growing edge can be seen. HQ^{3}3. Cefn Mawr Limestone (Brigantian), Hendre Quarry, Clwyd. x4.2

Fig. j. *Eridopora beilensis.* Sheet-like colony, with zooecial apertures partially covered by hood-like lunarii. HQ^{3}2. Cefn Mawr Limestone (Brigantian), Hendre Quarry, Clwyd. x7.7

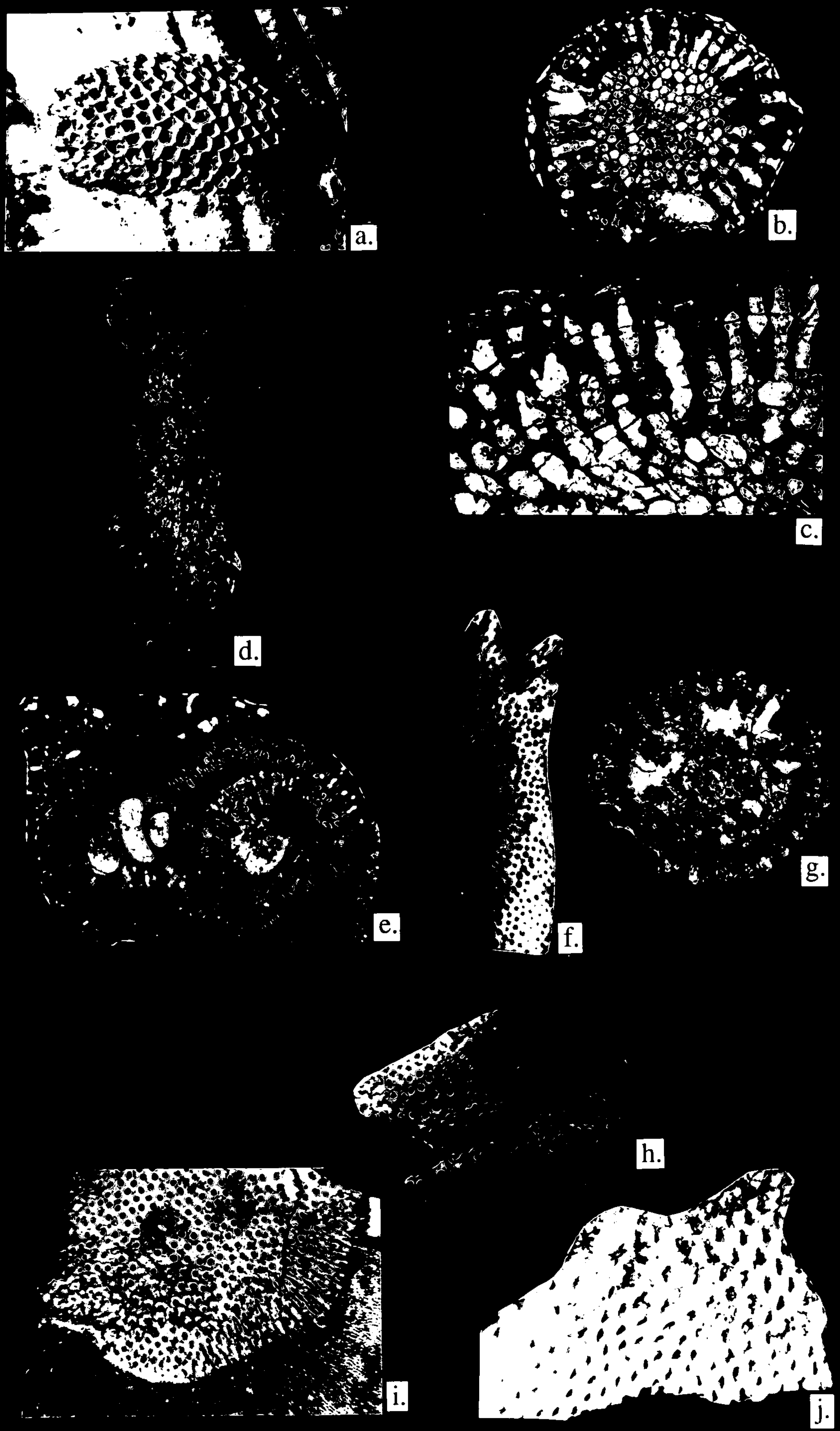


Plate 9

PLATE 10

Bryozoans from South Wales & Avon

Fig. a. *Rhombopora bancrofti.* BLQ15. Oystermouth Beds (Upper Brigantian), Black Lias Quarry. x17.5

Fig. b. *Rhombopora incrassata.* TP23. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x4.2

Fig. c. *Rhombopora incrassata.* Surface detail, highlighting the small stylets around the apertures. TP23. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x21.0

Fig. d. *Rhombopora similis.* TP28. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x13.3

Fig. e. *Rhombopora similis.* TP1. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x8.4

Fig. f. *Fenestella bicellulata.* Very weathered obverse surface. TCB^{1}3. Shipway Limestone (Z1, Courceyan), Three Cliffs Bay. x6.3

Fig. g. *Fenestella frutex.* Very weathered reverse surface. TP6. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x8.4

Fig. h. *Fenestella multispinosa.* Obverse surface detail. TP23. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x14.0

Fig. i. *Fenestella plebeia.* Obverse surface detail. TP21. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x10.5

Fig. j. *Fenestella* cf. *plebeia.* Obverse surface. AG4. Lower Limestone Shales (K, Lower Courceyan), Avon Gorge. x13.3

Fig. k. *Fenestella plebeia.* Partially secondarily-calcified obverse surface. TP24. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x7.7

Fig. l. *Fenestella plebeia.* Reverse surface, with an encrusting *Fistulipora* colony. TP12. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x6.3

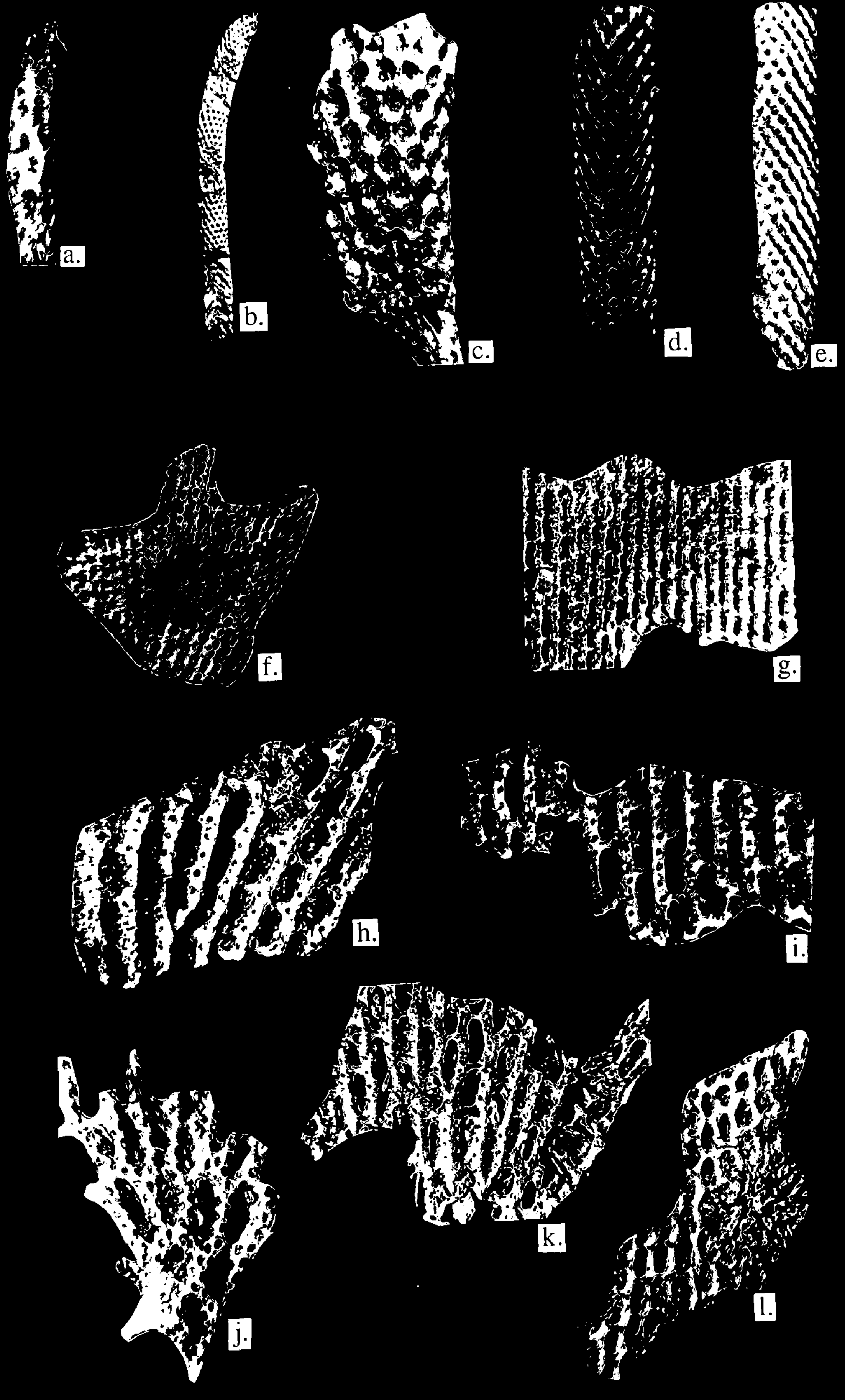


Plate 10

PLATE 11

Bryozoans from South Wales & Avon

Fig. a. *Fenestella plebeia.* Secondarily calcified reverse surface. TP 13. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x12.6

Fig. b. *Fenestella plebeia.* Weathered reverse surface. TP 13. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x8.4

Fig. c. "Palaeocorynid" fenestellid spine. TP 28. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x8.4

Fig. d. *Ignotifenestella?.* Reverse surface with spine development. TP28. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x9.1

Fig. e. Fenestellid colony origin, showing the development of supporting spines. TP28. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x3.4

Fig. f. Fenestellid colony, with the development of a calcareous sheath within the meshwork. TP28. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x10.5

Fig. g. *Polypora verrucosa.* Reverse surface. TP19. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x5.3

Fig. h. *Polypora verrucosa.* Partially ground down meshwork, showing the development of three to four rows of apertures on each branch. TP10. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x7.4

Fig. i. *Ignotifenestella* sp. Reverse surface, with the development of cyclozooecia at the dissepiment/branch junctions. TP13. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x28.0

Fig. j. to **Fig. m.** *Ignotifenestella* sp. A series of serial sections through a colony, illustrating the development of the cyclozooecia from initial lateral budding off the autozooecia (**Fig. j.**), migrating outwards towards the centre of the dissepiments (**Fig. m.**). TP13.2,3,6,&7. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x35.0

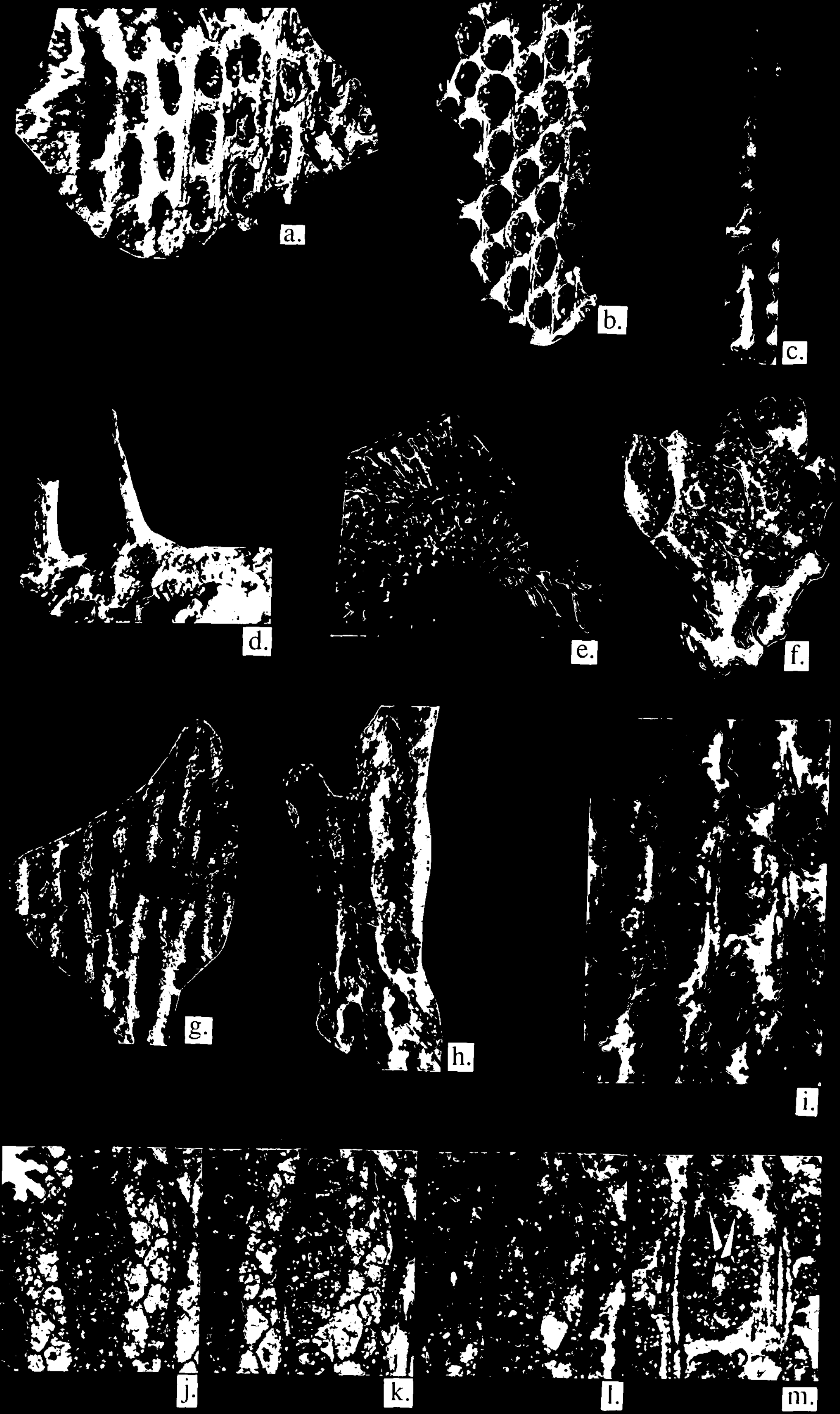


Plate 11

PLATE 12

Bryozoans from South Wales & Avon

Fig. a. *Penniretepora flexicarinata.* Reverse surfaces. BLQ8. Oystermouth Beds (Upper Brigantian), Black Lias Quarry. x8.4

Fig. b. *Penniretepora flexicarinata.* Branch obverse surface, illustrating the development of a strong central carina, and two weaker lateral carinae. TP11. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x20.3

Fig. c. *Ptylopora? pluma.* Reverse surface. BLQ17. Oystermouth Beds (Upper Brigantian), Black Lias Quarry. x18.9

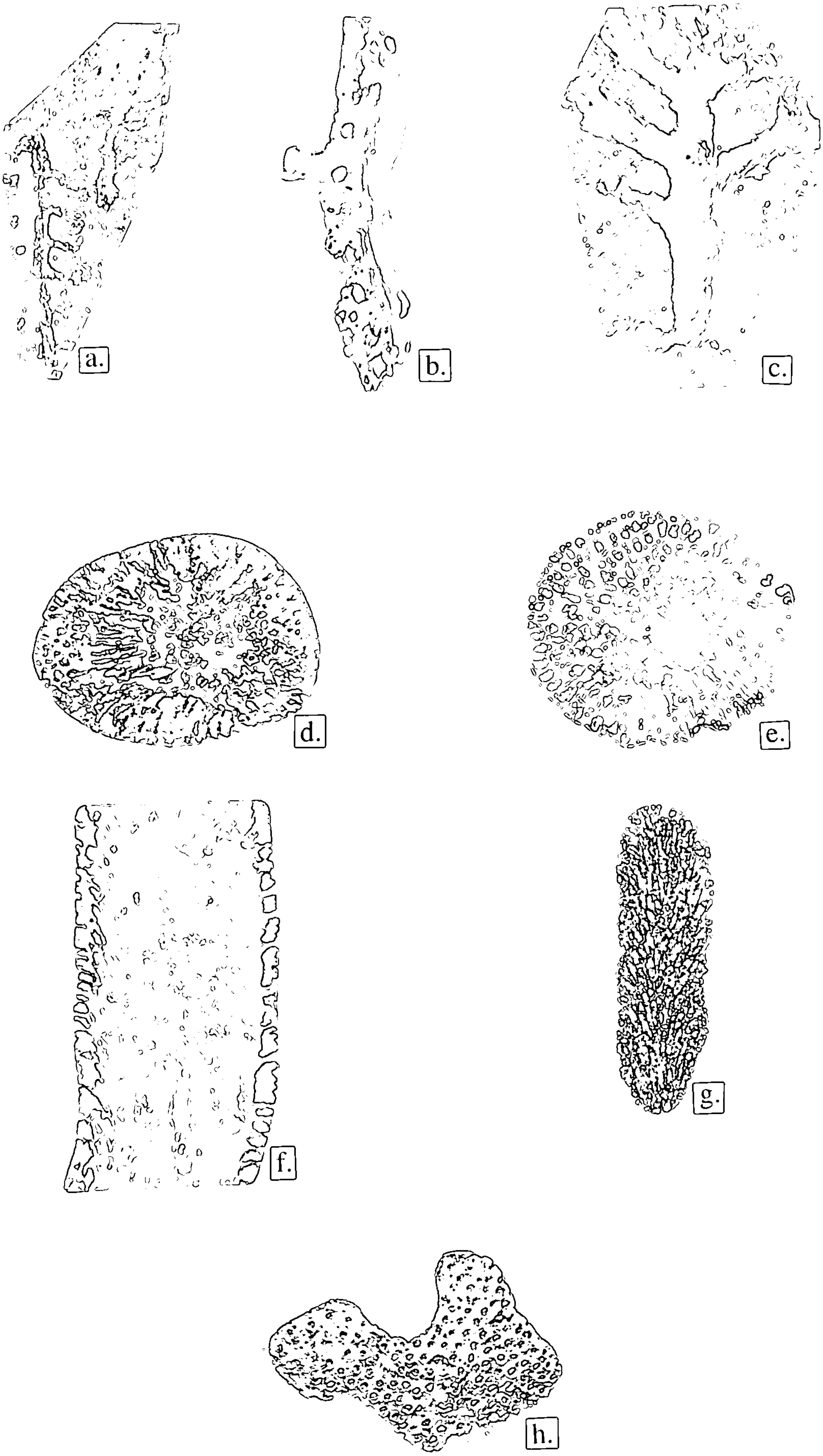
Fig. d. *Stenodiscus tumida.* Naturally-weathered transverse section though a cylindrical colony. BLQ22. Oystermouth Beds (Upper Brigantian), Black Lias Quarry. x8.4

Fig. e. *Stenodiscus tumida.* Acetate peel of a transverse section through a colony. BLQ21. Oystermouth Beds (Upper Brigantian), Black Lias Quarry. x8.4

Fig. f. *Stenodiscus tumida.* Naturally-weathered longitudinal section though a colony, showing abrupt oral flexure of the zooecial chambers into the thin exozone from an initially recumbent axial position. BLQ20. Oystermouth Beds (Upper Brigantian), Black Lias Quarry. x2.2

Fig. g. *Stenodiscus tumida.* Acetate peel of a longitudinal section through the axial endozone of a colony. BLQ20. Oystermouth Beds (Upper Brigantian), Black Lias Quarry. x7.7

Fig. h. *Fistulipora incrustans.* Sheet-like colony, with thin, circula lunarii around the apertures. TP^{U}3. Tears Point Limestone (C1, Upper Courceyan), Tears Point. x4.2



a. b. c. d. e. f. g. h.

Plate 12

APPENDICES

APPENDIX A : LIST OF BRYOZOAN TAXA CITED IN THIS STUDY

CLASS STENOLAEMATA

Order Cryptostomata

Suborder Rhabdomesina

Family Rhabdomesidae

- *Rhabdomeson gracilis* (Phillips, 1841)
- *Rhabdomeson rhombifera* (Phillips, 1836)

Family Rhomboporidae

- *Rhombopora similis* (Phillips, 1841)
- *Rhombopora incrassata* Ulrich, 1890
- *Rhombopora radialis* Owen, 1966
- *Rhombopora bancrofti* sp. nov.

Family Hyphasmoporidae

- *Hyphasmopora buskii* Etheridge Jun., 1875
- *Streblotrypa nicklisii* Vine, 1885
- *Streblotrypa ?* var. *minuta* Vine, 1885
- *Streblotrypa pectinata* Owen, 1966

Order Fenestrata

Family Fenestellidae

- *Fenestella bicellulata* Etheridge Jun., 1873a
- *Fenestella ivanovi* Shulga-Nesterenko, 1951
- *Fenestella frutex* McCoy, 1844
- *Fenestella multispinosa* Ulrich, 1890
- *Fenestella tuberculo-carinata* Etheridge Jun., 1873a
- *Fenestella plebeia* McCoy, 1844
- *Fenestella papillata* (McCoy, 1844)
- *Fenestella morrisii* McCoy, 1844
- *Fenestella polyporata* (Phillips, 1836)
- *Fenestella quadridecimalis* McCoy, 1844
- *Fenestella modesta* Ulrich, 1890
- *Fenestella hemispherica* McCoy, 1844
- *Fenestella parallela* Hall, 1881
- *Fenestella rudis* Ulrich *multinodosa* Tavener-Smith, 1973a
- *Fenestella* cf. *arthritica* Phillips, 1841
- *Fenestella praemagna* Shulga-Nesterenko, 1951

Fenestella fanata Whudborne *carrickensis* Tavener-Smith, 1973
Fenestella cf. *spinacristata* Moore, 1929
Fenestella cf. *funicula* Ulrich, 1890
Fenestella cf. *filistriata* Ulrich, 1890
Fenestella subspeciosa Shulga-Nesterenko, 1955
Fenestella pseudovirgosa Nikiforova, 1938
Fenestella cf. *albida* Hall, 1886
Fenestella oblongata Koenig, 1958
Fenestella cf. *delicatula* Ulrich, 1890
Fenestella irregularis Nekhoroshev, 1932
Fenestella polynodosa Miller, 1961
Fenestella rossica Shulga-Nesterenko, 1936
Levifenestella undecimalis (Shulga-Nesterenko, 1941)
Levifenestella maeve Miller, 1961
Polyfenestella fenestelliformis (Young, 1881)
Ptilofenestella carrickensis Tavener-Smith, 1965
Ignotifenestella sp.
Rectifenestella sp.
Minilya plummerae (Moore, 1929)
Minilya nodulosa (Phillips, 1836)
Minilya binodata (Condra, 1902)
Minilya oculata (McCoy, 1844)
Ptiloporella varicosa (McCoy, 1844)
Hemitrypa hibernica McCoy, 1844
Polypora dendroides McCoy, 1844
Polypora verrucosa McCoy, 1844
Polypora marginata McCoy, 1844
Polypora tuberculata Prout, 1859
Polypora stenostoma Tavener-Smith, 1971
Polypora binodus Bancroft, 1985a
Polypora hexagonaria sp. nov.
Thamniscus rankini Young & Young, 1875b
Thamniscus gracilis Vine, 1885
Thamniscus colei Wyse-Jackson, 1988

Family Acanthocladiidae
Diploporaria marginalis (Young & Young, 1875a)
Diploporaria tenella Wyse-Jackson, 1988

Penniretepora stellipora (Young & Young, 1874a)
Penniretepora spinosa (Young & Young, 1874a)
Penniretepora wilsoneri Bancroft, 1985
Penniretepora flexicarinata (Young & Young, 1875a)
Penniretepora pulcherrima (McCoy, 1844)
Penniretepora robusta (Young & Young, 1878)
Penniretepora elegans (Young & Young, 1875a)
Penniretepora laxa (Young & Young, 1875a)
Penniretepora grandis (McCoy, 1844)
Penniretepora triserialis Owen, 1966
Penniretepora pluma Phillips, 1836
Penniretepora gracilis (McCoy, 1844)
Penniretepora frondiformis Olaloye, 1974
Penniretepora normalis Olaloye, 1974
Penniretepora cucullea Olaloye, 1974
Penniretepora sinuosa Hall, 1887
Penniretepora rotunda Olaloye, 1974
Penniretepora tortuosa Olaloye, 1974
Ptylopora pluma McCoy, 1844
Ptylopora pluma McCoy *parva* Tavener-Smith, 1973a
Septopora hibernica Tavener-Smith, 1973a
Septopora carbonaria (Etheridge Jun., 1873a)
Icthyorachis newenhami McCoy, 1844
Baculopora megastoma (McCoy, 1844)

Order Trepostomata

Tabulipora urii (Fleming, 1828)
Tabulipora howsii (Nicholson, 1881)
Tabulipora minima Lee, 1912
Tabulipora youngi Lee, 1912
Tabulipora tenuimuralis Lee, 1912
Tabulipora maeandria Lee, 1912
Tabulipora sparsitabulata Lee, 1912
Tabulipora crassimuralis Lee, 1912
Tabulipora multitabulata Lee, 1912
Tabulipora wexfordensis Lee, 1912
Tabulipora debilis Lee, 1912
Tabulipora hessilheadensis Owen, 1969

Stenodiscus tumida (Phillips, 1836)
Dyscritella miliaria (Nicholson, 1881)
Dyscritella multifida Lee, 1912
Dyscritella ambigua Lee, 1912
Dyscritella tyronei Owen, 1973
Koninckopora inflata (de Koninck, 1842)
Leeporina nana (Lee, 1912)
Stenopora haddingtonensis Lee, 1912
Stenopora dubia (McCoy, 1844)
Stenopora castletonensis Lee, 1912
Stenopora obliqua Lee, 1912
Stenopora tenuipora Lee, 1912
Batostomella bundorensis Lee, 1912
Leioclema avonense Lee, 1912
Amplexopora? discoidea Owen, 1966
Stenophragmidium incrustans Owen, 1973
Stenophragmidium ramosum Owen, 1969

Order Cystoporata

Fistulipora incrustans (Phillips, 1836)
Eridopora beilensis Perkins & Perry, 1962
Eridopora macrostomata Ulrich, 1882
Eridopora sp. nov.
Goniocladia cellulifera (Etheridge Jun., 1873a)
Sulcoretepora parallela (Phillips, 1836)
Sulcoretepora? ramosa Owen, 1973

Order Cyclostomata

Hederella carbonaria Condra & Elias, 1944

CLASS GYMNOLAEMATA

Order Ctenostomata

Ascodictyon youngii Vine, 1891
Ascodictyon stellatum Nicholson & Etheridge Jun., 1877

APPENDIX B : THE TFENDIV COMPUTER PROGRAM

A copy of the TFENDIV computer program, for analysing t-test scores between bryozoan species, is deposited in the offices of the Department of Geological Sciences, Durham University.

To run the program it is best to install all the information from the 3.5" disc onto the computer's hard disc :

Put the disc into the A drive of the computer and then type

```
xcopy a:*.* c:\ /s/e
```

This will copy all the files, directories, and sub-directories onto the C drive.

Then to change the working drive to C

```
c:\
```

and to change the working directory to the one with the source files

```
cd bbasic
```

To run BBASIC, type

```
bbasic
```

and finally to execute the analysis program, type

CH."TFENDIV" or **CH."TF"** (remembering to put the Caps Lock on)

Alternatively, once in the BBASIC directory, type **tf** and TFENDIV.BBS will automatically load and run. On subsequent runs of the program, it is not necessary to copy everyting from a: to c: ,just enter the C drive and follow the instructions above from there.

Once TFENDIV has been exited, to escape from BBASIC mode, type *sys and the computer will return to DOS mode.

A program listing is given in the following pages.

```
 100 REM T.FEN.DIV
 101 @%=&A90
 102 MODE 19
 103 CLEAR :DIM P(3,9):DIM X(9):DIM N1(9):DIM SIGMA(9):DIM XS(9):DIM SIGMAS(9):DIM
        N2(9):DIM T(9):DIM FENSP$(9):DIM P00(13):DIM P11(13):DIM BLANK(9,9):DIM
        XA(9):DIM SIGMAA(9):DIM N1A(9):DIM XAS(9):DIM SIGMAAS(9):DIM N2A(9):LET
        TAG =0
 104 DIM BL(9):DIM PROB(9):LET TYPE =0:LET SPEC1$=" ":LET SPEC2$=" ":LET EXTRA1$="
        ":LET EXTRA2$=" "
 106 GCOL 0,132:COLOUR 7
 107 CLOSE#0
 110 REM THIS PROGRAM CALCULATES VALUES OF T FOR TWO FENESTELLID
BRYOZOANS
 115 CLS
 117 ON ERROR GOTO 9500
 120 PRINT TAB(33,8);"T.FEN.DIV"
 122 PRINT TAB(16,11);"A program designed for calculating probability"
 123 PRINT TAB(18,12);"coefficients for Carboniferous fenestellid"
 124 PRINT TAB(21,13);"bryozoans, based on Student's t-test"
 130 PRINT TAB(25,16)"PRESS SPACE BAR TO CONTINUE "
 150 REPEAT UNTIL GET=32
 160 CLS
 190 LET dir =0:LET SWITCH =0
 191
 192
 200 REM BIT FOR INPUTTING SPECIMEN DATA
 201 *CD\BBASIC\SAMPLES
 202 IF SWITCH =1 THEN PROCspec1data :GOTO 330
 203 LET BOB =0
 204 PRINT TAB(0,0);"DATA FOR SPECIMEN 1"
 205 PRINT TAB(2,5);"LOAD DATA FROM DISK ? (y/n)"
 207 inp$=INKEY$(1):PRINT TAB(2,7);:IF inp$="Y" OR inp$="y" THEN GOTO 300
 208 IF inp$="N" OR inp$="n" THEN GOTO 210
 209 GOTO 207
 210 CLS:PRINT TAB(0,0);"DATA FOR SPECIMEN 1"
 215 PRINT TAB(2,5);"ENTER NAME OR NUMBER OF SPECIMEN"
 220 INPUT LINE(8)TAB(2,7)SPEC1$:LET SP$=SPEC1$
 225 CLS
 230 GOSUB 6000
 232 PRINT TAB(0,0);"DATA FOR SPECIMEN ";SPEC1$
 240 FOR KOUNT =1 TO 9
 242  PRINT TAB(6,2+KOUNT );"_____":INPUT TAB(6,2+KOUNT )X(KOUNT )
 244  PRINT TAB(16,2+KOUNT );"______":INPUT TAB(16,2+KOUNT )SIGMA(KOUNT )
 246  PRINT TAB(26,2+KOUNT );"___":INPUT TAB(26,2+KOUNT )N1(KOUNT )
 248 NEXT KOUNT
 249 PRINT TAB(0,12);"EXTRA DATA : ":PRINT TAB(0,13)STRING$(29,"_"):INPUT
        LINE(39)TAB(0,13)EXTRA1$
 250 PRINT TAB(0,12);SPC(13):PRINT TAB(21,22);"SAVE DATA ON DISK ? (y/n)"
 252 inp$=INKEY$(1):IF inp$="N" OR inp$="n" THEN PRINT TAB(21,22);SPC(26):GOTO 322
 254 IF inp$="Y" OR inp$="y" THEN PRINT TAB(21,22);SPC(26):GOTO 258
 256 GOTO 252
 258 PROCsavedir
 260
 261 f1%=OPENOUT SPEC1$:PTR#f1%=0:PRINT#f1%,SPEC1$
```

```
262 FOR KOUNT =1 TO 9
264  PRINT#f1%,X(KOUNT )
266  PRINT#f1%,SIGMA(KOUNT )
268  PRINT#f1%,N1(KOUNT )
270 NEXT KOUNT
271 PRINT#f1%,EXTRA1$
272 CLOSE#0
274 GOTO 322
275
299 REM INPUTTING FILE DATA FOR SPEC1
300 ON ERROR PROCcorrection :RESUME :GOTO 301
301 PRINT TAB(0,0);"DATA FOR SPECIMEN 1";SPC(13)
302 GOSUB 8000:PRINT TAB(2,7);SPC(10)
303 PRINT TAB(0,5);"ENTER NAME OF SPECIMEN OR DIRECTORY":INPUT
      TAB(2,7)SPEC1$:LET SP$=SPEC1$
304 FOR LOOP =12 TO 23:PRINT TAB(0,LOOP );SPC(79):NEXT LOOP :PRINT
      TAB(0,5);SPC(36):PRINT TAB(2,7);SPC(30)
307 f1%=OPENIN SPEC1$
308 PTR#f1%=0:INPUT#f1%,SPEC1A$
309 PRINT TAB(0,0);"DATA FOR SPECIMEN ";SPEC1$;SPC(5)
311 CLS:FOR KOUNT =1 TO 9
313  INPUT#f1%,X(KOUNT ):IF X(KOUNT )<=0 THEN INPUT#f1%,SIGMA(KOUNT ),N1(KOUNT
      ):NEXT KOUNT :GOTO 319
314 @%=&20309:PRINT TAB(6,2+KOUNT );X(KOUNT )
315 INPUT#f1%,SIGMA(KOUNT ):@%=&20409:PRINT TAB(16,2+KOUNT );SIGMA(KOUNT )
317 INPUT#f1%,N1(KOUNT ):@%=&A90:PRINT TAB(26,2+KOUNT );N1(KOUNT )
318NEXT KOUNT
319 INPUT#f1%,EXTRA1$:PRINT TAB(0,13)EXTRA1$
320 CLOSE#0:ON ERROR GOTO 9500
321 PRINT TAB(0,0);"DATA FOR SPECIMEN ";SPEC1$:GOSUB 6000
322 *CD\BBASIC\SAMPLES
323 PRINT TAB(20,21)"PRESS n FOR NEW DATA FOR SPEC 1"
324 PRINT TAB(20,22)"PRESS ANY OTHER KEY TO CONTINUE "
325 A =GET
326 IF A =78 OR A =110 THEN CLS:GOTO 200
327 PRINT TAB(20,21);SPC(33):PRINT TAB(20,22);SPC(33)
328
329
330 REM BIT FOR DATA FOR SPEC2
331 LET BOB =40
332 IF SWITCH =2 THEN PROCspec2data :GOTO 425
335 PRINT TAB(40,0);"DATA FOR SPECIMEN 2":PRINT TAB(42,5);"LOAD DATA FROM DISK ?
      (y/n)"
336 inp$=INKEY$(1):PRINT TAB(42,7);:IF inp$="Y" OR inp$="y" THEN GOTO 390
338 IF inp$="N" OR inp$="n" THEN GOTO 342
340 GOTO 336
342 PRINT TAB(40,0);"DATA FOR SPECIMEN 2"
344 PRINT TAB(40,5);"ENTER NAME OR NUMBER OF SPECIMEN"
346 INPUT LINE(8)TAB(42,7)SPEC2$:LET SP$=SPEC2$
348 PRINT TAB(40,5);SPC(33):PRINT TAB(40,7);SPC(10)
350 GOSUB 6000
352 PRINT TAB(40,0);"DATA FOR SPECIMEN ";SPEC2$;SPC(5)
354 FOR KOUNT =1 TO 9
356  PRINT TAB(46,2+KOUNT );"_____":INPUT TAB(46,2+KOUNT )XS(KOUNT )
```

```
358  PRINT TAB(56,2+KOUNT );"______":INPUT TAB(56,2+KOUNT )SIGMAS(KOUNT )
360  PRINT TAB(66,2+KOUNT );"___":INPUT TAB(66,2+KOUNT )N2(KOUNT )
362 NEXT KOUNT
363 PRINT TAB(40,12);"EXTRA DATA : ":PRINT TAB(40,13)STRING$(29,"_"):INPUT
        LINE(39)TAB(40,13)EXTRA2$
364 PRINT TAB(40,12);SPC(13):PRINT TAB(21,22);"SAVE DATA ON DISK ? (y/n)"
366 inp$=INKEY$(1):IF inp$="N" OR inp$="n" THEN PRINT TAB(21,22);SPC(26):GOTO 418
368 IF inp$="Y" OR inp$="y" THEN PRINT TAB(21,22);SPC(26):GOTO 372
370 GOTO 366
372 PROCsavedir
373 f2%=OPENOUT SPEC2$:PTR#f2%=0:PRINT#f2%,SPEC2$
374 FOR KOUNT =1 TO 9
376  PRINT#f2%,XS(KOUNT )
378  PRINT#f2%,SIGMAS(KOUNT )
380  PRINT#f2%,N2(KOUNT )
382 NEXT KOUNT
383 PRINT#f2%,EXTRA2$
384 CLOSE#0
386 GOTO 418
388
390 REM INPUTTING FILE DATA FOR SPEC2
391 FOR LOOP =15 TO 17:PRINT TAB(0,LOOP );SPC(79):NEXT LOOP
392 PRINT TAB(40,0);"DATA FOR SPECIMEN 2"
393 GOSUB 8000
394 PRINT TAB(40,5);"ENTER NAME OF SPECIMEN OR DIRECTORY":INPUT
        TAB(42,7)SPEC2$:LET SP$=SPEC2$
395 PRINT TAB(40,5);SPC(36):PRINT TAB(40,7);SPC(35)
396 FOR LOOP =12 TO 23:PRINT TAB(0,LOOP );SPC(79):NEXT LOOP
400 ON ERROR PROCcorrection :RESUME :GOTO 392
401 f2%=OPENUP SPEC2$
402 PTR#f2%=0:INPUT#f2%,SPEC2A$
403 PRINT TAB(40,0);"DATA FOR SPECIMEN ";SPEC2$;SPC(5)
405 FOR KOUNT =1 TO 9
406  INPUT#f2%,XS(KOUNT ):IF XS(KOUNT )<=0 THEN INPUT#f2%,SIGMAS(KOUNT
        ),N2(KOUNT ):NEXT KOUNT :GOTO 412
407 @%=&20309:PRINT TAB(46,2+KOUNT );XS(KOUNT )
408 INPUT#f2%,SIGMAS(KOUNT ):@%=&20409:PRINT TAB(56,2+KOUNT );SIGMAS(KOUNT )
410 INPUT#f2%,N2(KOUNT ):@%=&A90:PRINT TAB(66,2+KOUNT );N2(KOUNT )
411NEXT KOUNT
412 INPUT#f2%,EXTRA2$:PRINT TAB(40,13)EXTRA2$:PRINT TAB(0,13)EXTRA1$
413 CLOSE#0:ON ERROR GOTO 9500
414 GOSUB 6000
416
418 PRINT TAB(21,21)"PRESS n FOR NEW DATA FOR SPEC 2"
419 PRINT TAB(21,22)"PRESS ANY OTHER KEY TO CONTINUE"
420 A =GET
421 IF A =78 OR A =110 THEN CLS:PROCspec1data :EXEC "*CD\BBASIC\SAMPLES":GOTO 330
424 EXEC "*CD\BBASIC":GOTO 431
425
426 PRINT TAB(20,22)"PRESS SPACE BAR TO CONTINUE"
427 REPEAT UNTIL GET=32:GOTO 431
429
431 REM DIVISION OPTION BIT
432 ON ERROR GOTO 9500
```

```
 433 CLS
 434 FOR KOUNT =1 TO 9
 435  LET XA(KOUNT )=X(KOUNT ):LET SIGMAA(KOUNT )=SIGMA(KOUNT ):LET
N1A(KOUNT     )=N1(KOUNT ):LET XAS(KOUNT )=XS(KOUNT ):LET SIGMAAS(KOUNT
          )=SIGMAS(KOUNT ):LET N2A(KOUNT )=N2(KOUNT ):LET BLANK(1,KOUNT )=0
 436 NEXT KOUNT
 437 PRINT TAB(0,2);"ENTER OPTION :-"
 438 PRINT TAB(10,8);"1.GO STRAIGHT TO T-TEST"
 439 PRINT TAB(10,10);"2.RESULTS OF DIVISION BY ONE FEATURE"
 441 PRINT TAB(10,12);"3.TOTAL PROBABILITIES FROM DIVISION"
 442 PRINT TAB(10,14);"4.QUIT PROGRAM"
 443 PRINT TAB(10,16);"5.EDIT DATA"
 444 INP$=INKEY$(1):PRINT TAB(0,16);:IF INP$="1" THEN LET TYPE =1:GOTO 502
 445 IF INP$="2" THEN LET TYPE =2:GOTO 450
 446 IF INP$="3" THEN PRINT TAB(1,22);"CALCULATING VALUES...PLEASE WAIT":PRINT
          TAB(15,24);:LET TYPE =3:GOTO 7000
 447 IF INP$="4" THEN GOTO 9500
 448 IF INP$="5" THEN PROCupdate :GOTO 103
 449 GOTO 444
 450 REM BIT FOR CHOOSING DIV FEATURE
 451 CLS:PRINT TAB(0,2);"ENTER FEATURE TO DIVIDE DATA WITH :-"
 453 IF LEFT$(SPEC1$,2)="S-" OR LEFT$(SPEC1$,2)="s-" THEN RESTORE 915:ELSE RESTORE
910
 454 FOR D =1 TO 9:LET BLANK(1,D )=0
 456  READ FEATURE$:PRINT TAB(10,7+D );D ;".";FEATURE$
 458 NEXT D
 469 INP$=INKEY$(1):PRINT TAB(0,15);:IF INP$="1" THEN LET CHOICE =1:LET
         CHOICE$="BW":GOTO 7000
 470 IF INP$="2" THEN LET CHOICE =2:LET CHOICE$="AD":GOTO 7000
 471 IF INP$="3" THEN LET CHOICE =3:LET CHOICE$="ID":GOTO 7000
 472 IF INP$="4" THEN LET CHOICE =4:LET CHOICE$="FL":GOTO 7000
 473 IF INP$="5" THEN LET CHOICE =5:LET CHOICE$="FW":GOTO 7000
 474 IF INP$="6" THEN LET CHOICE =6:IF LEFT$(SPEC1$,2)="S-" OR LEFT$(SPEC1$,2)="s-"
         THEN LET CHOICE$="LBW":GOTO 7000:ELSE LET CHOICE$="DW":GOTO 7000
 475 IF INP$="7" THEN LET CHOICE =7:LET CHOICE$="IND":GOTO 7000
 476 IF INP$="8" THEN LET CHOICE =8:IF LEFT$(SPEC1$,2)="S-" OR LEFT$(SPEC1$,2)="s-"
         THEN LET CHOICE$="CD":GOTO 7000:ELSE LET CHOICE$="ZB1":GOTO 7000
 477 IF INP$="9" THEN LET CHOICE =9:LET CHOICE$="ZB2":GOTO 7000
 500 GOTO 469
 501
 502
 510 LET KOUNT =1
 515 FOR MARK =1 TO 9
 520  IF XS(MARK )=0 OR SIGMAS(MARK )=0 OR N2(MARK )=0 THEN LET T(MARK
         )=10000:LET BLANK(KOUNT ,MARK )=1:GOTO 600
 525  IF X(MARK )=0 OR SIGMA(MARK )=0 OR N1(MARK )=0 THEN LET T(MARK )=10000:LET
         BLANK(KOUNT ,MARK )=1:GOTO 600
 527  IF N1(MARK )=1 OR N2(MARK )=1 THEN LET T(MARK )=10000:LET BLANK(KOUNT
         ,MARK )=1:GOTO 600
 530  REM TFORM CALCULATES VALUE OF T
 535  IF X(MARK )=XS(MARK ) THEN LET T(MARK )=0:GOTO 600
 537  IF N1(MARK )<30 THEN LET SIGMA(MARK )=SIGMA(MARK )*SQR(N1(MARK
         )/(N1(MARK )-1))
 538  IF N2(MARK )<30 THEN LET SIGMAS(MARK )=SIGMAS(MARK )*SQR(N2(MARK
```

```
        )/(N2(MARK )-1))
 540  LET E =((SIGMA(MARK ))^2)*(N1(MARK ))
 550  LET ES =((SIGMAS(MARK ))^2)*(N2(MARK ))
 560  LET S2 =(E +ES )/(N1(MARK )+N2(MARK )-2)
 570  LET S =SQR(S2 )
 580  LET NUM =SQR((N2(MARK )*N1(MARK ))/(N1(MARK )+N2(MARK )))
 590  LET T(MARK )=ABS(((X(MARK )-XS(MARK ))*NUM )/S )
 600 NEXT MARK
 610 GOSUB 3000:IF TYPE =3 THEN RETURN:ELSE GOTO 710
 622
 710 REM BIT FOR SHOWING TWO SAMPLE RES.
 720 CLS
 730 PRINT TAB(47,0);"T-TEST PROBABILITY VALUES"
 740 IF LEFT$(SPEC1$,2)="S-" OR LEFT$(SPEC1$,2)="s-" THEN RESTORE 915:ELSE RESTORE
910
 745 LET KOUNT =1
 747 IF TYPE <>3 THEN LET BL =0:LET TPROB =0
 750 FOR MARK =1 TO 9
 760  READ FEATURES$
 761  LET P(KOUNT ,MARK )=2*(1-(P(KOUNT ,MARK ))):@%=&20409
 770  PRINT TAB(42,2+MARK *2);FEATURES$;STRING$(38-LEN(FEATURES$),".")
 771  IF TYPE =3 THEN LET CHOICE$="ALL":GOTO 773
 772  IF BLANK(KOUNT ,MARK )=1 THEN LET BL =BL +1:GOTO 777
 773  IF XA(MARK )=0 OR XAS(MARK )=0 THEN GOTO 777
 774  IF TYPE =3 AND BL(MARK )=9 THEN GOTO 777
 775  PRINT TAB(74,2+MARK *2);P(KOUNT ,MARK )
 776  IF TYPE <>3 THEN LET TPROB =TPROB +P(KOUNT ,MARK )
 777 NEXT MARK
 778 IF TYPE <>3 AND BL <9 THEN LET TPROB =TPROB /(9-BL ):ELSE IF TYPE <>3 THEN LET
        TPROB =0
 781 PRINT TAB(52,2);"TOTAL PROB=";TPROB
 783 LET CHOICE =1
 800 REM GRAPH-DRAWING PROCEDURE
 802 PRINT TAB(43,22);SPC(33)
 804 REM PLOT AXES
 805 PRINT TAB(0,4);"PROB.":PRINT TAB(8,0);"T-TEST PROBABILITY GRAPH"
 806 FOR KOUNT =0 TO 10
 807  @%=&20109
 808  PRINT TAB(0,(15-KOUNT ));(KOUNT /10):MOVE 64,(399+(KOUNT *42)):DRAW
        48,(399+(KOUNT *42))
 809  @%=&A90:NEXT KOUNT
 810 MOVE 64,399:DRAW 64,818:MOVE 64,399:DRAW 640,399
 812 REM PLOT BAR CHART
 813 LET Q =399:LET D =64
 814 IF LEFT$(SPEC1$,2)="S-" OR LEFT$(SPEC1$,2)="s-" THEN RESTORE 905:ELSE RESTORE
900
 816 FOR KOUNT =1 TO 9
 818  READ FEATURES$
 820  LET Y1 =P(CHOICE ,KOUNT ):IF P(CHOICE ,KOUNT )>1E-4 AND P(CHOICE ,KOUNT
)<8E-3  THEN LET Y1 =8E-3
 830  MOVE(16+D *KOUNT ),Q :DRAW(16+D *KOUNT ),(Q +Y1 *420):DRAW(48+D *KOUNT
),(Q      +Y1 *420):DRAW(48+D *KOUNT ),Q
 833  IF TYPE =3 AND BL(KOUNT )=9 THEN GOTO 840
 834  IF TYPE =3 THEN GOTO 837
```

```
 835  IF BLANK(1,KOUNT )=1 THEN GOTO 840
 837  PRINT TAB(1+(KOUNT *4),16);FEATURES$
 840 NEXT KOUNT
 847 IF TYPE =3 OR TYPE =2 THEN PRINT TAB(13,2);"DIVIDED BY ";CHOICES$
 850 PRINT TAB(10,18);SPEC1$;" vs ";SPEC2$
 852 PRINT TAB(0,22);"SPEC 1 : ";EXTRA1$:PRINT TAB(0,23);"SPEC 2 : ";EXTRA2$
 860 PRINT TAB(50,22);"1=MAIN MENU : 2=NEW DATA":PRINT TAB(50,23);"     3=REVIEW
         DATA":PRINT TAB(79,23);
 862 INP$=INKEY$(1):IF INP$="2" THEN GOSUB 1000:PROCnewdata
 864 IF INP$="1" THEN CLS:GOSUB 1000:GOTO 437
 865 IF INP$="3" THEN CLS:GOSUB 1000:PROCspec1data :PROCspec2data :GOTO 425
 866 IF INP$="P" OR INP$="p" THEN PROCdump
 867 GOTO 862
 899 PRINT TAB(0,28):END
 900 DATA BW,AD,ID,FL,FW,DW,IND,ZB1,ZB2
 905 DATA BW,AD,ID,FL,FW,LBW,IND,CD," "
 910 DATA BRANCH WIDTH,AUTOZOOECIAL APERTURE DIAMETER,INTERAPERTURAL
        DISTANCE,FENESTRULE LENGTH,FENESTRULE WIDTH,DISSEPIMENT
        WIDTH,INTERNODAL DISTANCE,ZOOECIAL CHAMBER LENGTH,ZOOECIAL
        CHAMBER WIDTH
 915 DATA BRANCH WIDTH,APERTURE DIAMETER,INTER-APERTURAL
        DISTANCE,FENESTRULE LENGTH,FENESTRULE WIDTH,LATERAL BRANCH
        WIDTH,INTERNODAL DISTANCE,CYCLOZOOECIAL DIAMETER,,
1000 REM RESETTING VALUES OF PARAMETERS
1020 FOR KOUNT =1 TO 9
1030  LET X(KOUNT )=XA(KOUNT ):LET SIGMA(KOUNT )=SIGMAA(KOUNT ):LET N1(KOUNT
        )=N1A(KOUNT )
1040  LET XS(KOUNT )=XAS(KOUNT ):LET SIGMAS(KOUNT )=SIGMAAS(KOUNT ):LET
        N2(KOUNT )=N2A(KOUNT )
1050  LET BLANK(1,KOUNT )=0:LET BL(KOUNT )=0
1055  LET PROB(KOUNT )=0
1060 NEXT KOUNT
1070RETURN
2000 DEF PROCsavedir
2010  PRINT TAB(20,21);"PRESS d TO CHANGE DIRECTORY":PRINT TAB(18,22);"PRESS ANY
        OTHER KEY TO CONTINUE"
2020  A =GET
2030  PRINT TAB(20,21);SPC(34):PRINT TAB(18,22);SPC(34):FOR LOOP =13 TO 22:PRINT
        TAB(0,LOOP );SPC(80):NEXT LOOP
2040  IF A =68 OR A =100 THEN GOTO 2050:ELSE ENDPROC
2050 VDU 31,0,12
2060 EXEC "*DIR *. /W"
2070 PRINT TAB(45,13);"ENTER NAME OF DIRECTORY":INPUT TAB(45,14);SP$
2080 LET DIR$="*CD "+SP$:LET MDIR$="*MD "+SP$
2083 VDU 31,45,13
2085 EXEC MDIR$
2090 EXEC DIR$
2105 PRINT TAB(45,13);SPC(34):PRINT TAB(45,14);SPC(34):FOR LOOP =13 TO 22:PRINT
        TAB(0,LOOP );SPC(79):NEXT LOOP
2110ENDPROC
2998 END
2999
3000 REM subroutine to use tables
3001 FOR MARK =1 TO 9
```

```
3003 IF T(MARK )=0 THEN LET P(KOUNT ,MARK )=0.5:NEXT MARK :RETURN
3005 IF T(MARK )=10000 THEN LET P(KOUNT ,MARK )=1:NEXT MARK :RETURN
3006 IF X(MARK )=0 OR SIGMA(MARK )=0 OR N1(MARK )=0 THEN LET T =10000:LET
P(KOUNT ,       MARK )=1:NEXT MARK :RETURN
3007 IF T(MARK )>8 THEN LET P(KOUNT ,MARK )=1:NEXT MARK :RETURN
3010 LET N =N1(MARK )+N2(MARK )
3015 IF N >500 THEN LET NUMB =500
3020 IF N <24 THEN GOTO 3300
3030 IF N >24 THEN GOTO 3500
3299
3300 REM subroutine for N<24
3301 RESTORE(5000+(N *10))
3310 FOR LOOP =0 TO 12
3320  READ P00(LOOP )
3330 NEXT LOOP
3340 IF T(MARK )<4 THEN LET GAP =0.5
3350 IF T(MARK )>4 THEN LET GAP =1
3360 LET T1 =(INT((T(MARK )+GAP )*2))/2
3370 IF T(MARK )>4 THEN LET T1 =INT(T1 )
3380 LET THETA =(T(MARK )-(T1 -GAP ))/(GAP )
3385 IF T(MARK )<4 THEN LET REL1 =T1 *2
3387 IF T(MARK )>4 THEN LET REL1 =T1 +4
3390 LET P(KOUNT ,MARK )=((P00(REL1 -1)*(1-THETA ))+(P00(REL1 )*THETA ))
3400NEXT MARK :RETURN
3499
3500 REM subroutine for N>24
3510 REM N can be in intervals 24-30,30-40,40-60,60-120,and 120-500
3515 IF T(MARK )>8 THEN LET P(KOUNT ,MARK )=1:NEXT MARK :RETURN
3520 IF N <=30 THEN LET NUMB =30:LET LAST =24
3530 IF N >30 AND N <=40 THEN LET NUMB =40:LET LAST =30
3540 IF N >40 AND N <=60 THEN LET NUMB =60:LET LAST =40
3550 IF N >60 AND N <=120 THEN LET NUMB =120:LET LAST =60
3560 IF N >120 AND N <=500 THEN LET NUMB =500:LET LAST =120
3570 RESTORE(5300+NUMB )
3590 FOR LOOP =0 TO 12
3600  READ P11(LOOP )
3610 NEXT LOOP
3615 IF N >500 THEN GOTO 3660
3620 RESTORE(5300+LAST )
3630 FOR LOOP =0 TO 12
3640  READ P00(LOOP )
3650 NEXT LOOP
3660 IF T(MARK )<4 THEN LET GAP =0.5
3670 IF T(MARK )>4 THEN LET GAP =1
3680 LET T1 =(INT(((T(MARK ))+GAP )*2))/2
3690 IF T(MARK )>4 THEN LET T1 =INT(T1 )
3700 LET THETA =(T(MARK )-(T1 -GAP ))/(GAP )
3710 IF T(MARK )<4 THEN LET REL1 =T1 *2
3720 IF T(MARK )>4 THEN LET REL1 =T1 +4
3725 IF N >500 THEN GOTO 3800
3730 LET PSI =120*(NUMB -N )/(NUMB *N )
3740 LET FIRST =(P00(REL1 -1))*(1-THETA -PSI +THETA *PSI )
3750 LET SECOND =(P00(REL1 ))*(THETA -THETA *PSI )
3760 LET THIRD =(P11(REL1 -1))*(PSI -THETA *PSI )
```

```
3770 LET FOURTH =(P11(REL1 ))*(THETA *PSI )
3780 LET P(KOUNT ,MARK )=FIRST +SECOND +THIRD +FOURTH
3785 IF P(KOUNT ,MARK )>1 THEN LET P(KOUNT ,MARK )=1
3790NEXT MARK :RETURN
3800 LET P(KOUNT ,MARK )=((P11(REL1 -1))*(1-THETA ))+(P11(REL1 )*THETA )
3810NEXT MARK
3820RETURN
5000 REM N=1
5010 DATA
        0.50000,0.64758,0.75000,0.81283,0.85242,0.87888,0.89758,0.91141,0.92202,0.93717,0.94743,
        0.95483,0.96042
5019 REM N=2
5020 DATA
        0.50000,0.66667,0.78868,0.86380,0.90825,0.93519,0.95227,0.96358,0.97141,0.98113,0.98666,
        0.99010,0.99237
5029 REM N=3
5030 DATA
        0.50000,0.67428,0.80450,0.88471,0.93034,0.95615,0.97116,0.98026,0.98600,0.99230,0.99536,
        0.99701,0.99796
5039 REM N=4
5040 DATA
        0.50000,0.67834,0.81305,0.89600,0.94194,0.96662,0.98003,0.98755,0.99193,0.99625,0.99806,
        0.99890,0.99934
5049 REM N=5
5050 DATA
        0.50000,0.68085,0.81839,0.90305,0.94903,0.97275,0.98495,0.99136,0.99484,0.99795,0.99908,
        0.99954,0.99975
5059 REM N=6
5060 DATA
        0.50000,0.68256,0.82204,0.90786,0.95379,0.97674,0.98800,0.99359,0.99644,0.99877,0.99952,
        0.99979,0.99990
5069 REM N=7
5070 DATA
        0.50000,0.68380,0.82469,0.91135,0.95719,0.97950,0.99003,0.99500,0.99741,0.99922,0.99973,
        0.99990,0.99996
5079 REM N=8
5080 DATA
        0.50000,0.68473,0.82670,0.91400,0.95974,0.98153,0.99146,0.99596,0.99803,0.99947,0.99984,
        0.99994,0.99998
5089 REM N=9
5090 DATA
        0.50000,0.68546,0.82828,0.91608,0.96172,0.98307,0.99252,0.99664,0.99845,0.99963,0.99990,
        0.99997,0.99999
5099 REM N=10
5100 DATA
        0.50000,0.68605,0.82955,0.91775,0.96331,0.98428,0.99333,0.99714,0.99874,0.99973,0.99993,
        0.99998,0.99999
5109 REM N=11
5110 DATA
        0.50000,0.68654,0.83060,0.91912,0.96460,0.98525,0.99396,0.99751,0.99896,0.99980,0.99995,
        0.99999,1.00000
5119 REM N=12
5120 DATA
        0.50000,0.68694,0.83148,0.92027,0.96567,0.98604,0.99447,0.99781,0.99912,0.99985,0.99997,
```

```
        0.99999,1.00000
5129 REM N=13
5130 DATA
        0.50000,0.68728,0.83222,0.92125,0.96658,0.98671,0.99488,0.99804,0.99924,0.99988,0.99998,
        1.00000,1.00000
5139 REM N=14
5140 DATA
        0.50000,0.68758,0.83286,0.92209,0.96736,0.98727,0.99522,0.99823,0.99934,0.99990,0.99998,
        1.00000,1.00000
5149 REM N=15
5150 DATA
        0.50000,0.68783,0.83341,0.92282,0.96803,0.98775,0.99551,0.99839,0.99942,0.99992,0.99999,
        1.00000,1.00000
5159 REM N=16
5160 DATA
        0.50000,0.68806,0.83390,0.92346,0.96861,0.98816,0.99576,0.99852,0.99948,0.99993,0.99999,
        1.00000,1.00000
5169 REM N=17
5170 DATA
        0.50000,0.68826,0.83433,0.92402,0.96913,0.98853,0.99597,0.99863,0.99954,0.99995,0.99999,
        1.00000,1.00000
5179 REM N=18
5180 DATA
        0.50000,0.68843,0.83472,0.92452,0.96959,0.98885,0.99616,0.99872,0.99958,0.99995,0.99999,
        1.00000,1.00000
5189 REM N=19
5190 DATA
        0.50000,0.68859,0.83506,0.92498,0.97000,0.98913,0.99632,0.99880,0.99962,0.99996,1.00000,
        1.00000,1.00000
5199 REM N=20
5200 DATA
        0.50000,0.68873,0.83537,0.92538,0.97037,0.98938,0.99646,0.99887,0.99965,0.99997,1.00000,
        1.00000,1.00000
5209 REM N=21
5210 DATA
        0.50000,0.68886,0.83565,0.92575,0.97070,0.98961,0.99659,0.99893,0.99967,0.99997,1.00000,
        1.00000,1.00000
5219 REM N=22
5220 DATA
        0.50000,0.68898,0.83591,0.92608,0.97100,0.98982,0.99670,0.99899,0.99970,0.99998,1.00000,
        1.00000,1.00000
5229 REM N=23
5230 DATA
        0.50000,0.68909,0.83614,0.92639,0.97128,0.99000,0.99681,0.99904,0.99972,0.99998,1.00000,
        1.00000,1.00000
5239 REM N=24
5240 DATA
        0.50000,0.68919,0.83636,0.92667,0.97153,0.99017,0.99690,0.99908,0.99974,0.99998,1.00000,
        1.00000,1.00000
5323 REM N=24
5324 DATA
        0.50000,0.68919,0.83636,0.92667,0.97153,0.99017,0.99690,0.99908,0.99974,0.99998,1.00000,
        1.00000,1.00000
5329 REM N=30
```

```
 5330 DATA
        0.50000,0.68964,0.83735,0.92797,0.97269,0.99094,0.99730,0.99926,0.99981,0.99999,1.00000,
        1.00000,1.00000
 5339 REM N=40
 5340 DATA
        0.50000,0.69009,0.83834,0.92927,0.97384,0.99169,0.99768,0.99942,0.99987,0.99999,1.00000,
        1.00000,1.00000
 5359 REM N=60
 5360 DATA
        0.50000,0.69055,0.83934,0.93057,0.97498,0.99241,0.99804,0.99956,0.99991,1.00000,1.00000,
        1.00000,1.00000
 5419 REM N=120
 5420 DATA
        0.50000,0.69100,0.84034,0.93188,0.97612,0.99312,0.99836,0.99967,0.99995,1.00000,1.00000,
        1.00000,1.00000
 5799 REM N=500
 5800 DATA
        0.50000,0.69146,0.84134,0.93319,0.97725,0.99379,0.99865,0.99977,0.99997,1.00000,1.00000,
        1.00000,1.00000
 6000 REM BIT FOR DRAWING UP DATA ARRAY
 6003 IF LEFT$(SP$,2)="S-" OR LEFT$(SP$,2)="s-" THEN RESTORE 6075:ELSE RESTORE 6070
 6010 FOR KOUNT =1 TO 9
 6020  READ FEATURES$
 6030  PRINT TAB(BOB +1,2+KOUNT );FEATURES$
 6040 NEXT KOUNT
 6050 PRINT TAB(BOB +6,2);"MEAN":PRINT TAB(BOB +16,2);"S.D.":PRINT TAB(BOB
        +26,2);"NO."
 6052 IF LEFT$(SP$,2)="S-" OR LEFT$(SP$,2)="s-" THEN RESTORE 6065:ELSE RESTORE 6060
 6054 FOR LOOP =15 TO 17:READ FEATURES$:PRINT TAB(0,LOOP );FEATURES$:NEXT LOOP
 6060 DATA "BW=branch width  AZ=autozooecial aperture diameter  ID=interaperture distance"
 6061 DATA "FL=fenestrule length  FW=fenestrule width  DW=dissepiment width  IND=internodal"
 6062 DATA "distance  ZB1=zooecial chamber base length  ZB2=zooecial chamber base width"
 6065 DATA "BW=branch width  AZ=autozooecial aperture diameter  ID=interaperture distance"
 6067 DATA "FL=fenestrule length  FW=fenestrule width  LLB=lateral branch width"
 6068 DATA "IND=internodal distance  CD=cyclozooecial aperture diameter"
 6070 DATA BW,AD,ID,FL,FW,DW,IND,ZB1,ZB2
 6075 DATA BW,AD,ID,FL,FW,LBW,IND,CD," "
 6080RETURN
 7000
 7001 REM BIT FOR CALULATING DIVISION
 7003 LET TPROB =0
 7005 IF TYPE =3 THEN FOR CHOICE =1 TO 9
 7007  LET SUM =9
 7010  FOR TICK =1 TO 9
 7040   IF XA(CHOICE )>0 THEN LET X(TICK )=XA(TICK )/XA(CHOICE )
 7045   IF XAS(CHOICE )>0 THEN LET XS(TICK )=XAS(TICK )/XAS(CHOICE )
 7050   IF XAS(CHOICE )>0 THEN LET SIGMAS(TICK )=SIGMAAS(TICK )/XAS(CHOICE )
 7055   IF XA(CHOICE )>0 THEN LET SIGMA(TICK )=SIGMAA(TICK )/XA(CHOICE )
 7060   LET X(CHOICE )=0:LET XS(CHOICE )=0
 7070   IF X(TICK )=0 OR SIGMA(TICK )=0 OR SIGMAS(TICK )=0 THEN LET BL(TICK
)=BL(TICK        )+1
 7080  NEXT TICK :IF TYPE =2 THEN GOTO 7100
 7082  GOSUB 510
 7085  FOR T =1 TO 9
```

```
7087  LET PROB(T )=(PROB(T )+2*(1-(P(1,T ))))
7089  NEXT T
7090  IF TYPE =3 THEN NEXT CHOICE
7092 LET TBL =9:FOR T =1 TO 9
7094  IF BL(T )=9 THEN LET PROB(T )=0:ELSE LET PROB(T )=PROB(T )/(9-BL(T ))
7095  LET TPROB =TPROB +PROB(T ):IF BL(T )=9 THEN LET TBL =TBL -1
7096  LET P(1,T )=1-(PROB(T )/2)
7097 NEXT T :LET TPROB =TPROB /TBL
7098 GOTO 710
7100 CLS
7110 LET BOB =0:GOSUB 6000
7120 PRINT TAB(2,0);SPEC1$;" DIVIDED BY ";CHOICE$
7125
7130 FOR LOOP =1 TO 9
7135  IF X(LOOP )=0 THEN GOTO 7170
7140  @%=&20409:PRINT TAB(6,2+LOOP );X(LOOP )
7150  @%=&20409:PRINT TAB(16,2+LOOP );SIGMA(LOOP )
7160  @%=&A90:PRINT TAB(26,2+LOOP );N1(LOOP )
7170 NEXT LOOP
7200
7210 LET BOB =40:GOSUB 6000
7220 PRINT TAB(42,0);SPEC2$;" DIVIDED BY ";CHOICE$
7230 FOR LOOP =1 TO 9
7235  IF XS(LOOP )=0 THEN GOTO 7270
7240  @%=&20409:PRINT TAB(46,2+LOOP );XS(LOOP )
7250  @%=&20409:PRINT TAB(56,2+LOOP );SIGMAS(LOOP )
7260  @%=&A90:PRINT TAB(66,2+LOOP );N2(LOOP )
7270 NEXT LOOP
7280 PRINT TAB(18,22)"PRESS SPACE BAR TO CONTINUE"
7290 REPEAT UNTIL GET=32
7300 GOSUB 510
8000 REM list of disc contents
8010 IF EXTRA1$=" " THEN GOTO 8020:ELSE PRINT TAB(0,13);SPC(79)
8020 VDU 31,0,12:EXEC "*DIR *. /W"
8030RETURN
9000 DEF PROCcorrection
9001  REM error correction procedure
9005  IF ERR=17 THEN GOTO 9500
9010  CLOSE#0
9015  FOR LOOP =12 TO 23:PRINT TAB(0,LOOP );SPC(79):NEXT LOOP
9017  FOR LOOP =1 TO 12:PRINT TAB(BOB ,LOOP );SPC(39):NEXT LOOP
9018  RESUME
9022  LET DIR$="*CD "+SP$
9024  EXEC DIR$
9025 ENDPROC
9500 REM winding up procedure
9510 *CD\BBASIC
9520 MODE 3
9540 END
10000 DEF PROCdir_change
10010  IF SPEC1$="TAVENER" OR SPEC2$="TAVENER" THEN EXEC "*CD
TAVENER":ENDPROC
10020  IF SPEC1$="BANCROFT" OR SPEC2$="BANCROFT" THEN EXEC "*CD
        BANCROFT":ENDPROC
```

```
10040 ENDPROC
11000 DEF PROCrestore
11010  *CD..
11015  LET dir =0
11020 ENDPROC
12000 DEF PROCdir_drop
12010  *CD..
12020 ENDPROC
13000 DEF PROCspec1data
13010  LET SP$=SPEC1$
13020  LET BOB =0:GOSUB 6000
13060  FOR KOUNT =1 TO 9
13063   IF X(KOUNT )=0 THEN GOTO 13140
13065   @%=&20309
13070   PRINT TAB(6,2+KOUNT );X(KOUNT )
13085   @%=&20409
13090   PRINT TAB(16,2+KOUNT );SIGMA(KOUNT )
13105   @%=&A90
13110   PRINT TAB(26,2+KOUNT );N1(KOUNT )
13140  NEXT KOUNT
13145  PRINT TAB(0,13)EXTRA1$
13150  PRINT TAB(0,0);"DATA FOR SPECIMEN ";SPEC1$
13170 ENDPROC
14000 DEF PROCspec2data
14010  LET SP$=SPEC2$
14020  LET BOB =40:GOSUB 6000
14060  FOR KOUNT =1 TO 9
14063   IF XS(KOUNT )=0 THEN GOTO 14140
14065   @%=&20309
14070   PRINT TAB(46,2+KOUNT );XS(KOUNT )
14085   @%=&20409
14090   PRINT TAB(56,2+KOUNT );SIGMAS(KOUNT )
14105   @%=&A90
14110   PRINT TAB(66,2+KOUNT );N2(KOUNT )
14140  NEXT KOUNT
14145  PRINT TAB(40,13)EXTRA2$
14150  PRINT TAB(40,0);"DATA FOR SPECIMEN ";SPEC2$
14170 ENDPROC
15000 DEF PROCnewdata
15020  PRINT TAB(50,22);"0=NEW DATA : 1=KEEP SPEC 1":PRINT TAB(50,23);"      2=KEEP
SPEC   2"
15030  INP$=INKEY$(1)
15040  IF INP$="0" THEN LET SWITCH =0:GOTO 103
15050  IF INP$="1" THEN LET SWITCH =1:LET SPEC2$=" ":CLS:GOTO 200
15060  IF INP$="2" THEN LET SWITCH =2:LET SPEC1$=" ":CLS:GOTO 200
15070  GOTO 15030
20000  DEF PROCupdate
20010   ON ERROR GOTO 20500
20020   CLS
20030   *CD\BBASIC\SAMPLES
20050   PRINT TAB(0,12);:EXEC "*DIR *. /W"
20060   INPUT TAB(0,0){"ENTER FILE TO UPDATE : "}FILE$
20105   PRINT TAB(0,0);SPC(79):FOR KOUNT =12 TO 23:PRINT TAB(0,KOUNT );SPC(79):NEXT
         KOUNT
```

```
20110  f%=OPENUP FILE$:PTR#f%=0
20120  INPUT#f%,SPEC$
20125  ON ERROR PRINT TAB(13,22)"CANNOT READ FILE : PRESS SPACE BAR TO
        CONTINUE":RESUME :REPEAT UNTIL GET=32:GOTO 20020
20130  FOR KOUNT =1 TO 9
20140   INPUT#f%,X(KOUNT ):@%=&20309:PRINT TAB(6,2+KOUNT );X(KOUNT )
20150   INPUT#f%,SIGMA(KOUNT ):@%=&20409:PRINT TAB(16,2+KOUNT );SIGMA(KOUNT )
20160   INPUT#f%,N1(KOUNT ):@%=&A90:PRINT TAB(26,2+KOUNT );N1(KOUNT )
20170  NEXT KOUNT
20180  LET EXTRA$="     "
20185  WHILE NOT EOF#f%
20190   INPUT#f%,EXTRA$
20210   PRINT TAB(1,13);EXTRA$
20213  WEND
20215  ON ERROR OFF
20220  PRINT TAB(0,0);"DATA FOR SPECIMEN ";SPEC$:LET BOB =0:GOSUB 6000
20225  PRINT TAB(42,6);"Press ENTER to confirm data":PRINT TAB(42,7);"Press SPACE BAR to
edit    data"
20230  FOR KOUNT =1 TO 9
20240   PRINT TAB(5,2+KOUNT );"*"
20242   A =GET:IF A =13 OR A =32 THEN GOTO 20244:ELSE GOTO 20242
20244   IF A =13 THEN GOTO 20250:IF A =32 THEN PRINT TAB(6,2+KOUNT );SPC(6):INPUT
        TAB(6,2+KOUNT );X(KOUNT )
20246   IF A =32 THEN PRINT TAB(6,2+KOUNT );SPC(6):INPUT TAB(6,2+KOUNT );X(KOUNT )
20250   PRINT TAB(5,2+KOUNT );" ":PRINT TAB(15,2+KOUNT );"*"
20252   A =GET:IF A =13 OR A =32 THEN GOTO 20254:ELSE GOTO 20252
20254   IF A =13 THEN GOTO 20260
20256   IF A =32 THEN PRINT TAB(16,2+KOUNT );SPC(7):INPUT TAB(16,2+KOUNT
        );SIGMA(KOUNT )
20260   PRINT TAB(15,2+KOUNT );" ":PRINT TAB(25,2+KOUNT );"*"
20262   A =GET:IF A =13 OR A =32 THEN GOTO 20264:ELSE GOTO 20262
20264   IF A =13 THEN GOTO 20270
20266   IF A =32 THEN PRINT TAB(26,2+KOUNT );SPC(3):INPUT TAB(26,2+KOUNT
);N1(KOUNT     )
20270   PRINT TAB(25,2+KOUNT );" "
20280  NEXT KOUNT
20290  PRINT TAB(0,13);"*"
20292  A =GET:IF A =13 OR A =32 THEN GOTO 20294:ELSE GOTO 20292
20294  IF A =13 THEN GOTO 20300
20296  IF A =32 THEN PRINT TAB(1,13);SPC(40):INPUT LINE(39)TAB(1,13);EXTRA$
20300  PRINT TAB(0,13);" ":PRINT TAB(42,6);SPC(30):PRINT TAB(42,7);SPC(30)
20310  PRINT TAB(21,22);"SAVE DATA ON DISC ? (y/n)"
20320  A$=INKEY$(1):IF A$="N" OR A$="n" THEN GOTO 20410
20330  IF A$="Y" OR A$="y" THEN GOTO 20340:ELSE GOTO 20320
20340  PRINT TAB(21,21);"PRESS n FOR NEW FILE NAME":PRINT TAB(21,22);"ANY OTHER
        KEY TO CONTINUE "
20341  A =GET:IF A =78 OR A =110 THEN GOTO 20342:ELSE GOTO 20348
20342  PRINT TAB(21,21);SPC(26):PRINT TAB(21,22);SPC(26):INPUT
        LINE(8)TAB(21,22){"ENTER NEW FILE NAME : "}SPEC$
20348  CLOSE#0:f%=OPENOUT SPEC$:PTR#f%=0
20350  PRINT#f%,SPEC$
20360  FOR KOUNT =1 TO 9
20370   PRINT#f%,X(KOUNT ),SIGMA(KOUNT ),N1(KOUNT )
20380  NEXT KOUNT
```

```
20390  PRINT#f%,EXTRA$
20400  CLOSE#0
20410  PRINT TAB(21,21);SPC(26):PRINT TAB(21,22)"NEW FILE TO APPEND (y/n) ?        "
20420  A$=INKEY$(1):IF A$="Y" OR A$="y" THEN CLS:GOTO 20010
20430  IF A$="N" OR A$="n" THEN EXEC "*CD\BBASIC":ENDPROC
20440  GOTO 20420
20500  REM directory change
20503  IF ERR=17 THEN GOTO 9500
20505  RESUME
20510  LET DIR$="*CD "+FILE$
20515  PRINT TAB(0,0);SPC(79):FOR KOUNT =12 TO 23:PRINT TAB(0,KOUNT );SPC(79):NEXT
        KOUNT
20520  EXEC DIR$
20530  PRINT TAB(0,0)SPC(50):PRINT TAB(0,1)SPC(50):PRINT TAB(0,2)SPC(50)
20540  GOTO 20050
59000  DEF PROCdump
59010   LOCAL I%,J%,A%
59020   PROCLIST (CHR$(27)+"A"+CHR$(8))
59030   FOR I%=0 TO 79
59040    PROCLIST (CHR$(27)+"K"+CHR$(400 MOD 256)+CHR$(400 DIV 256))
59050    FOR J%=199 TO 0STEP -1
59060     A%=?(&B8000000+&2000*(J% MOD 2)+80*(J% DIV 2)+I%)
59070     VDU 1,A%,1,A%
59080    NEXT
59090    VDU 1,13,1,10
59100   NEXT
59110   VDU 1,12
59120  ENDPROC
59199
59200  DEF PROCLIST (A$)
59210   LOCAL I%
59220   FOR I%=1 TO LEN(A$)
59230    VDU 1,ASC(MID$(A$,I%,1))
59240   NEXT
59250  ENDPROC
59299
```

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BRYOZOAN GROWTH ON BRACHIOPOD SPINES IN THE CARBONIFEROUS OF ENGLAND

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ABSTRACT. – Bryozoans encrusting brachiopod spines are described from the Redesdale Ironstone Shale, a highly fossiliferous horizon within Carboniferous rocks of Asbian (D1) age, exposed in quarries at Redesdale, Northumberland, England. The most abundant constituents of this diverse Redesdale fauna are broken brachiopod spines and bryozoan debris. There are many different genera of Bryozoa represented, encompassing several families and orders, but they all share one thing in common; the earliest growth stages encrust brachiopod spines. It is proposed that the bryozoans grew on these spines while the spines were still attached to the brachiopods, having been exposed as potential substrates because of sediment winnowing.

KEY-WORDS. – Bryozoa, encrusting, brachiopod spines, Carboniferous, England.

RÉSUMÉ. – Les Bryozoaires encroûtant des épines de Brachiopodes, décrits ici, proviennent du Redesdale Iron Shale, un horizon très fossilifère dans les couches carbonifères d'âge asbien (D1). Cet horizon affleure en carrière à Redesdale, Northumberland (Angleterre). Les éléments les plus abondants de cette faune variée sont des épines cassées de Brachiopodes et des fragments de Bryozoaires. Il y a beaucoup de genres différents de Bryozoaires représentés, recouvrant plusieurs familles et ordres. Tous partagent une même caractéristique : ils encroûtent des épines de Brachiopodes à leurs premiers stades de croissance. Il est avancé que les Bryozoaires se sont développés sur les épines quand elles étaient encore fixées aux Brachiopodes, se présentant alors comme substrat potentiel en raison de l'instabilité du sédiment meuble.

MOTS-CLÉS. – Bryozoa, encroûtement, épines de Brachiopodes, Carbonifère, Angleterre.

THE AVAILABILITY OF SUBSTRATA

Throughout geological time, bryozoan larvae have faced the problem of finding a suitable substrate on which to settle and grow. Modern bryozoans can be observed attached to a wide variety of objects and substrata, but during the processes of transport, burial, and fossilization, colonies are often detached from their original holdfasts, which may themselves be biodegradable with little chance of preservation.

It is uncommon to find the colony origins of Carboniferous bryozoans. CUMINGS (1904, 1905) described early growth stages of Bryozoa from the Middle Devonian Hamilton Formation of Ontario, but did not fully discuss the attachment of juvenile forms. He observed that some fenestellids grew on other Bryozoa (*Orthopora* HALL, 1886, which is probably *Rhombopora* MEEK, 1872 and "*Callopora*" HALL, 1851) but more commonly found only isolated basal discs.

Encrusting Bryozoa such as *Fistulipora* and *Tabulipora* can occasionally be observed to have grown on brachiopod shells (chonetids and productids) and sometimes on coral epithecae. More rarely, they have encrusted crinoid stems. However, the chosen substrata of erect bryozoans is not so obvious, especially in soft-sediment facies where they can occur in great abundance. McKINNEY (1983) attributed the scarcity of colony origins in *Archimedes* to asexual colony multiplication by fragmentation, but it is not certain whether this phenomenon occurred in other fenestellids. CUFFEY (1967), in describing a Lower Permian bryozoan fauna from Kansas, noted a possible variety of bryozoan substrates, and recorded that the more delicate-branching forms sometimes encrusted productid spines.

The fauna described here is from the Redesdale Ironstone Shales of Northumberland, and a substantial number of colony origins are present. Commonly, the bryozoans show attachment to brachiopod spines, and this mode of life is not solely restricted to one family. An analogous situation is described by VOIGT (1981) for the Maastrichtian bryozoan fauna of the Netherlands, where many different genera and growth forms encrust sea grass stems and roots; brachiopod spines and sea grass roots are both thin cylindrical structures, which are easy for bryozoan colonies to wrap around, also providing firm anchorages in areas of sediment instability.

STRATIGRAPHY

"The Steel" quarry in Redesdale, Northumberland (grid reference NY 8936 8290) exploited the Redesdale Ironstone, an iron-rich biomicrite, in the last century. Today it is disused, and much of the overburden lies in large spoil heaps.

The Ironstone is overlain by the Redesdale Ironstone Shale, a group of dark grey, sporadically shelly shales, with iron-rich nodules and lens-shaped accumulations of fragmented fossils. One such shelly horizon is particularly noticeable, being an iron-poor biomicritic limestone up to 25 cm in thickness. This stratigraphy is shown in FROST & HOLLIDAY (1980), and the deposits are regarded as Asbian in age. This Shell Band is thought to correlate with the widespread Bryozoa Bed which extends over much of the Northumberland Trough (TROTTER & HOLLINGWORTH, 1932).

Because of its low iron content, the Shell Band was discarded onto the waste piles, where the fauna has been weathered out. It is from this horizon that the bryozoan fauna described in this paper has been recovered.

PALAEOECOLOGY

The Redesdale Ironstone Shale group is thought to represent slow sediment accumulation in stagnant waters, probably as a deposit in a lagoon with limited current circulation of the type described in HO & COLEMAN (1969). However, it is rather unlikely that the fauna is preserved *in situ* since not only are crinoid stems usually completely disarticulated, and bryozoan colonies fragmented, but the brachiopods do not "nest" together, as is their mode of life in soft substrata (RAMSBOTTOM, 1978; RUDWICK: 1961, 1970). Some guesses must therefore be made as to the original habitat represented by these fossils. Though the fossils are fragmentary, they are probably not swept into the ironstone accumulation area by strong storm currents, since large pieces of delicate fenestellid fans remain intact, and there is no current sorting. Instead, slow build-up of material removed from its habitat by more gentle bottom currents is envisaged.

SMITH (1910), in his paper on the fauna of Northumberland, viewed the Redesdale Ironstone Shale fauna as being representative of a shallow water bivalve-dominated

	ABUNDANCE	MODE OF LIFE
CRYPTOSTOMATA		
Rhabdomeson rhombifera (Phillips, 1836)	***	sp
FENESTRATA: FENESTELLIDAE		
Fenestella bicellulata Etheridge jun., 1873	**	sp
Fenestella cf. ivanovi Shulga-Nesterenko, 1951	*	sp
Fenestella frutex McCoy, 1884	*****	sp
Fenestella multispinosa Ulrich, 1890	****	sp
Fenestella plebeia McCoy, 1844	***	sp
Fenestella polyporata (Phillips, 1836)	***	?
FENESTRATA: ACANTHOCLADIIDAE		
Penniretepora flexicarinata (Young & Young, 1875)	**	?
Diploporaria marginalis (Young & Young, 1875)	*****	sp
Septopora carbonaria (Etheridge jun., 1873)	**	sp
TREPOSTOMATA		
Tabulipora cf. howseii (Nicholson, 1881)	*****	sp & cr
Stenodiscus tumida (Phillips, 1836)	***	? & fl
CYSTOPORATA		
Fistulipora incrustans (Phillips, 1836)	**	? & sh & fl
Sulcoretepora parallela (Phillips, 1836)	*	?

KEY

*=rare
**=moderatley rare
***=rare
****=moderately common
*****=common

sp=attached to spine
cr=attached to crinoid
sh=attached to shell
fl=free-lying
?=not seen attached to spine

Table 1. List of bryozoans from the Redesdale Shale Shell Band ; Northumberland (England).

Tableau 1. Liste des Bryozoaires provenant de l'horizon coquillier du Redesdale Ironstone Shale ; Northumberland (Angleterre).

community. However, it is proposed here that the assemblage of the Shell Band is more probably typical of a deeper water muddy bottom community, comprising spinose productid brachiopods and shallow-burrowing edmondiid bivalves, together with less abundant crinoids, fish, and orthoconic nautiloids in addition to the rich bryozoan fauna. Corals are very rare.

The "Lower Reef Slope Brachiopod Community" of RAMSBOTTOM (1978) provides the closest analogy to the palaeoenvironment, with a diverse brachiopod community, but though *Fenestella* fans are shown by RAMSBOTTOM, no indication is given of their substrata.

THE BRYOZOANS

Bryozoans are very abundant, and occur mainly as fragments rather than entire colonies. Early stages of colony growth almost invariably show attachment to brachiopod spines. SMITH (1910) lists only three bryozoans from this locality; *Fistulipora incrustans* (PHILLIPS, 1836) NICHOLSON & FOORD, 1885, *Heterotrypa tumida* (PHILLIPS), which is probably *Stenodiscus tumida* (PHILLIPS, 1836), and *Fenestella* LONSDALE, 1839. BANCROFT (1984) gives a fairly comprehensive bryozoan faunal list, which has been largely verified in this study. Table 1 lists the recognised forms, together with an estimate of their relative abundances and modes of attachment.

In the palaeoenvironment discussed here, the only commonly exposed surfaces suitable for settling must have been protruding brachiopod spines. A few forms settled on the less common crinoid stems (Pl. 1, Fig. 2c) and some more rarely on brachiopod shells themselves. Did the bryozoans encrust spines still attached to brachiopod shells, or to loose spines lying free on the sea-floor? Spines are usually found fragmented, often only being one cm or so long, but spine bases are very commonly seen on the productid brachiopods. Though no brachiopod-attached

⁂

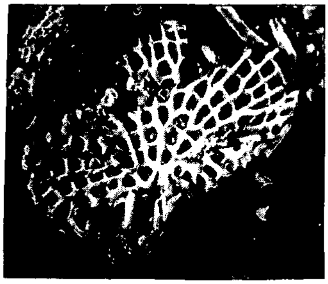
PLATE 1

Fig. 1a-d. Fenestellids, Redesdale Ironstone Shale (Carboniferous) ; Northumberland (England). **a**, Fenestellid fan (RIS 14), x 5.5. **b**, Fenestellid fan encircling spine (RIS 12), x 5.5. **c**, Fenestellid fan growing perpendicular to spine (RIS 10), x 5.5. **d**, Fenestellid fan growing parallel to spine (RIS 16), x 5.5. **Fig. 2a-c.** *Tabulipora*, Redesdale Ironstone Shale (Carboniferous) ; Northumberland (England). **a**, *Tabulipora* encrusting single spine (RIS 3), x 5.5. **b**, *Tabulipora* encrusting two parallel spines (RIS 1), x 5.5. **c**, *Tabulipora* growing crinoid stem (RIS 4), x 5.5. **Fig. 3.** Spinose productid brachiopod *Productus productus redesdalensis* (RIS 20), Redesdale Ironstone Shale (Carboniferous) ; Northumberland (England), x 1.6.

PLANCHE 1

Fig. 1a-d. Fénestellides, Redesdale Ironstone Shale (Carbonifère) ; Northumberland (Angleterre). **a**, Fénestellide en éventail (RIS 14), x 5.5. **b**, Fénestellide en éventail encerclant une épine (RIS 12), x 5.5. **c**, Fénestellide en éventail se développant perpendiculairement à une épine (RIS 10), x 5.5. **d**, Fénestellide en éventail se développant parallèlement à une épine (RIS 16), x 5.5. **Fig. 2a-c.** *Tabulipora*, Redesdale Ironstone Shale (Carbonifère) ; Northumberland (Angleterre). **a**, *Tabulipora* encroûtant une seule épine (RIS 3), x 5.5. **b**, *Tabulipora* encroûtant deux épines parallèles (RIS 1), x 5.5. **c**, *Tabulipora* se développant sur une tige de Crinoïde (RIS 4), x 5.5. **Fig. 3.** Brachiopode productide avec épines : *Productus productus redesdalensis* (RIS 20), Redesdale Ironstone Shale (Carbonifère) ; Northumberland (Angleterre), x 1.6.

1a



1b

1c

1d

2a

2b

3

2c

spines have been observed to be encrusted by bryozoans, other evidence points to this mode of life being the preferred one:

a) trepostomes such as *Tabulipora* encrust around all surfaces of the spine (Text-Figs. 1b, 1d) suggesting that the spine must have been clear of the substrate.

b) the basal discs of fenestellids also wrap completely around the spines (Text-Figs. 1a, 1e; Pl. 1, Figs. 1a-d). If the spines had been free-lying on the sediment, with one side partially buried, then the basal disc could not envelop all of the spine.

c) a loose spine could not support a fan-shaped colony or a towering *Diploporaria* (Text-Figs. 1c, 1f) without being susceptible to toppling over in even very gentle currents. The fenestellids appear not to have developed supporting spines in this environment, suggesting that their anchorage was fairly stable.

d) encrusting trepostomes generally cover only one spine, and the colony grows along this spine (e.g. *Tabulipora*, Pl. 1, Fig. 2a). If the spine had been lying loose on the sediment, then once the colony had established itself, it would have spread out from the spine onto the seafloor, also overgrowing any other loose spines; this is not observed. One specimen (another *Tabulipora*, Pl. 1, Fig. 2b) is interesting in that it does overgrow two spines, but these spines are parallel and probably represent their original orientation when still attached to the brachiopod.

e) bryozoans have not been observed growing close to the spine bases, suggesting that either only the distal ends of the spines were exposed, or that larvae preferred to settle some distance from the brachiopod shell along the spine.

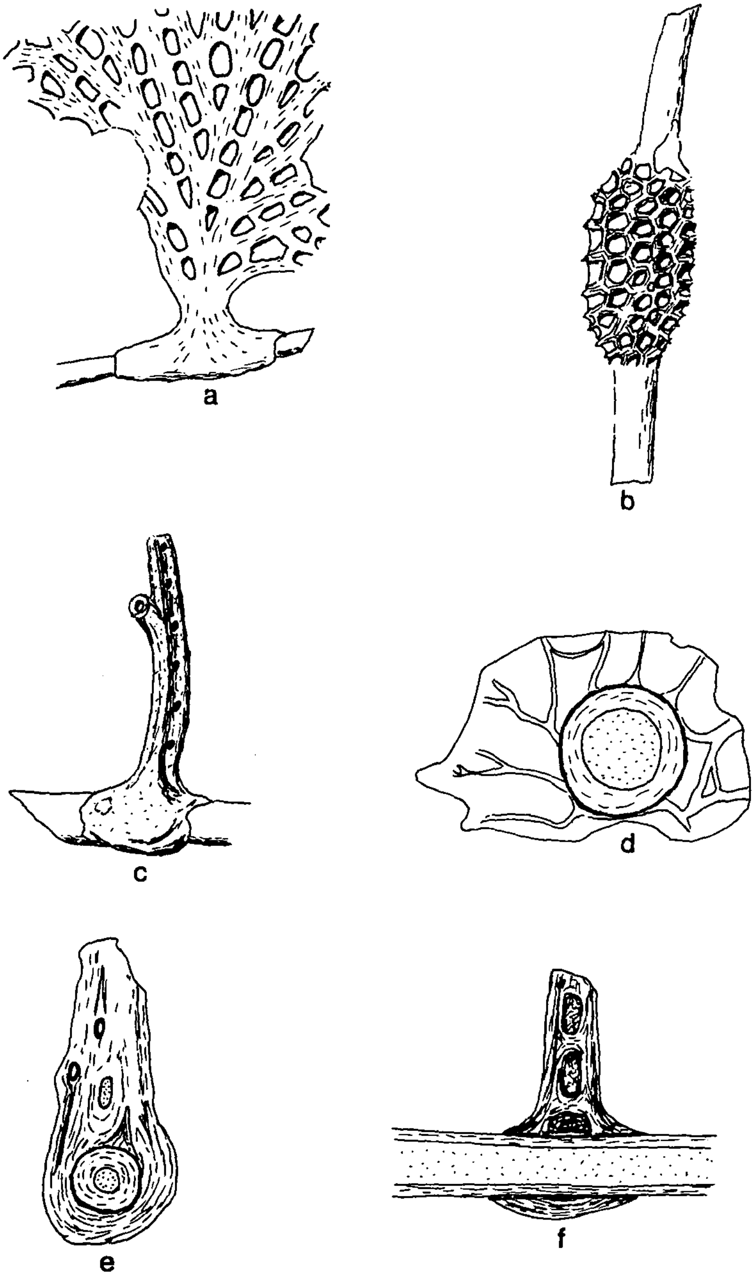
Though larger fragments are found, the portions which are attached to the spines are rather small, the largest fenestellid fan having a radius of only 1 cm. It is possible that once the colony reached a critical size, the spine would no longer be able to support the weight, snap off, and leave the colony lying free on the muddy bottom. Growth must have continued in some way, to account for the larger fragments, which are up to several cm in length. Multilaminar forms would have had a better chance of recovery from this position than unilaminar forms, which needed to land in a favourable orientation to survive. Unless colonies had grown in a suitable form, as in *Lyroporella* (described in McKINNEY, 1977) then on falling from a snapped spine, unilaminar colonies would die if the zooid-bearing face came to lie on the substratum: by contrast, multilaminar colonies such as *Tabulipora* would have had the majority of zooids still facing away from the substratum. Yet despite the apparent lack of adaptive colony growth, with some fenestellid fans developing parallel to spine length, and others perpendicular (Pl. 1, Figs. 1b-c), unilaminar fenestellids still seem to predominate over the potentially better-adapted multilaminar bryozoans.

No colonies have yet been found which show signs of rejuvenation, even in free-lying trepostomes or fistuliporids. This, however, may simply be because a bend in a colony at a point of rejuvenation is not only more likely to be a point of weakness during transportation to the burial site, but would also be snapped during compaction of the shale.

⁂

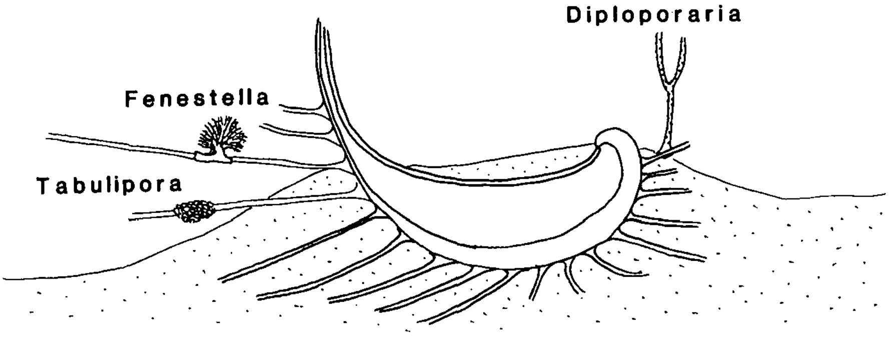
Text-Fig. 1a-c. Representative bryozoans encrusting brachiopod spines. **a**, Fenestellid fan (RIS 16), x 13. **b**, *Tabulipora* (RIS 3), x 12. **c**, *Diploporaria* (RIS 2), x 19. **1d-f**. Thin sections showing complete encirclement of spines by bryozoans. **d**, *Tabulipora* (RIS 19), x 36. **e**, *Fenestella* (RIS 17), x 33. **f**, *Diploporaria* (RIS 18), x 27.

Texte-Fig. 1a-c. Bryozoaires représentatifs de l'encroûtement des épines de Brachiopodes. **a**, Fenestellide en éventail (RIS 16), x 13. **b**, *Tabulipora* (RIS 3), x 12. **c**, *Diploporaria* (RIS 2), x 19. **1d-f**. Lames minces montrant l'encerclement complet des épines par les Bryozoaires. **d**, *Tabulipora* (RIS 19), x 36. **e**, *Fenestella* (RIS 17), x 33. **f**, *Diploporaria* (RIS 18), x 27.


a
b
c
d
e
f

IMPLICATIONS

Productid brachiopods, such as the one shown in Pl. 1, Fig. 3, are thought to have lived quasi-infaunally, spines being developed to anchor the animals in soft sediment, with only the edges of the valves projecting above the surface (GRANT, 1966). Either partial winnowing of the sediment exposed the spines of these brachiopods, or their spines naturally grew above the sediment surface; in either case, exposed spines provided attachment areas in a muddy environment. Text-Fig. 2 shows a possible reconstruction of this mode of life. It may have been the case that the brachiopods lived epifaunally, and that spines acted as buttress-like supports. However, the brachial valves, which are not spinose, have not been observed to be encrusted, suggesting that the animal was indeed quasi-infaunal, or that the shells had been eroded out by currents and flipped over, leaving only the spinose pedicle valves available for encrustation.



Text-Fig. 2. Reconstruction showing exposed productid spines encrusted by bryozoans.

Texte-Fig. 2. Reconstitution montrant les épines de Productide extérieures au substrat, encroûtées par les Bryozoaires.

Some questions, though, remain unanswered. Spiriferids, chonetids, and early terebratulids certainly also lived in this community, and they are epifaunal (RAMSBOTTOM, 1978), with exposed shell surfaces. Yet the bryozoans appear not to have encrusted these brachiopods, but rather chosen the productid spines for attachment. Spines would certainly allow better anchorage, since the basal disc could have quickly wrapped around the spine. Attachment to spines also gave greater clearance from the sea-bed than exposed brachiopod shells, at an age when colonies would have been most susceptible to burial by sediment, and would have also elevated colonies into areas of faster current flow above the boundary layer.

AFTERWORD. – BRUNTON (1966) reported juvenile brachiopods from the Carboniferous of County Fermanagh attaching themselves to fenestellid fans and to towering bryozoans by clasping spines; it is fitting that a fauna has now been discovered in which juvenile bryozoans attach themselves to brachiopod spines !

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REFERENCES

BANCROFT, A.J. (1984). – Studies in Carboniferous Bryozoa. Unpubl. Ph. D thesis, Univ. Durham.

BRUNTON, C.H.C. (1986). – Silicified Productoids from the Visean of County Fermanagh. *Bull. Br. Mus. (Nat. Hist.), Geol.*, 12, 5: 173-243.

CUFFEY, R.J. (1967). – Bryozoan *Tabulipora carbonaria* in Wreford megacyclothem (Lower Permian) of Kansas. *Univ. Kansas. Pal. Contrib.* Article 1: 1-96.

CUMINGS, E.R. (1904). – Development of some Paleozoic Bryozoa. *Am. J. Sci.*, (4), 17: 48-78.

CUMINGS, E.R. (1905). – Development of *Fenestella. Am. J. Sci.* (4), 20: 169-177.

FROST, D.V. & HOLLIDAY, D.W. (1980). – Geology of the country around Bellingham. *Geol. Surv. G.B. Memoir for Sheet 13*, H.M.S.O.: 1-112.

GRANT, R.E. (1966). – Spine arrangement and life habits of the productoid brachiopod *Waagenoconcha. J. Paleont.*, 40: 1063-1069.

HO, C. & COLEMAN, J.M. (1969). – Consolidation and cementation of Recent sediments in the Atchafalaya Basin. *Bull. Geol. Soc. Am.*, 80: 183-192.

MCKINNEY, F.K. (1977). – Functional interpretation of lyre-shaped Bryozoa. *Paleobiology*, 3: 90-97.

MCKINNEY, F.K. (1983). – Asexual colony multiplication by fragmentation: an important mode of genetic longevity in the Carboniferous Bryozoan *Archimedes. Paleobiology*, 9: 35-43.

RAMSBOTTOM, W.H.C. (1978). – Carboniferous: Lower Reef slope Brachiopod Community. *In* W.S. MCKERROW (Ed.), *The Ecology of Fossils*, Duckworth, London: 47-48.

RUDWICK, M.J.S. (1961). – The anchorage of articulate brachiopods on soft substrata. *Palaeontology*, 4: 475-476.

RUDWICK, M.J.S. (1970). – *Living and Fossil Brachiopods*, Hutchinson University Library, London: 1-119.

SMITH, S. (1910). – The faunal succession of the Upper Bernician. *Trans. Nat. Hist. Soc. Northumberland*, (N.S.), 3: 591-645.

TROTTER, F.M. & HOLLINGWORTH, S.E. (1932). – The Geology of the Brampton District. *Geol. Surv. G.B. Memoir for Sheet 18*, H.M.S.O.: 1-223.

VOIGT, E. (1981). – Upper Cretaceous bryozoan-seagrass association in the Maastrichtian of the Netherlands. *In* G.P. LARWOOD & C. NIELSEN (Eds.): *Recent and fossil Bryozoa*, Olsen & Olsen, Fredensborg: 281-298.