

Durham E-Theses

The taxonomy and palaeoecology of Bryozoa from the upper Permian zechstein reef of N.E. England

Southwood, David Ashley

How to cite:

Southwood, David Ashley (1985) *The taxonomy and palaeoecology of Bryozoa from the upper Permian zechstein reef of N.E. England*, Durham theses, Durham University. Available at Durham E-Theses Online: <http://etheses.dur.ac.uk/6816/>

Use policy

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a [link](#) is made to the metadata record in Durham E-Theses
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the [full Durham E-Theses policy](#) for further details.

**THE TAXONOMY AND PALAEOECOLOGY OF BRYOZOA FROM THE UPPER PERMIAN
ZECHSTEIN REEF OF N.E. ENGLAND**

by

David Ashley Southwood, B.A.

**A thesis presented for the degree of Doctor of Philosophy in the
University of Durham**

Volume 1 - Text

The copyright of this thesis rests with the author.
No quotation from it should be published without
his prior written consent and information derived
from it should be acknowledged.

**Department of Geological Sciences
University of Durham**

September 1985



17 11 1986

ABSTRACT

Eighteen species of Bryozoa are described from the Upper Permian Zechstein reef - they are assigned to ten genera in the Orders Fenestrata, Trepostomata and Cyclostomata. Emended diagnoses are given at various levels and superspecific taxonomic categories within the Fenestrata are discussed. The examination of type specimens and of a large suite of new material has allowed the limits of intraspecific morphological variability to be defined and has resulted in the synonymising of several species. Three new taxa are described, for which holotypes have been designated:- Ryhopora delicata gen. nov., sp. nov. Acanthocladia magna sp. nov. and Penniretepora waltheri nodata subsp. nov. The genera Penniretepora and Kalvariella are recorded for the first time from the Zechstein reef in N.E. England.

Aspects of bryozoan palaeobiology and functional morphology have been inferred at zooid and colony level. A type of ovicell, new in the Fenestrata, is described and is compared with those of the Cheilostomata; the taxonomic significance of this character is assessed. Patterns of zooid-generated feeding currents are inferred and some correlation of intraspecifically varying zoarial morphology with environment is suggested.

The characteristic distribution of Bryozoa in relation to Zechstein reef sub-environments is described. An analysis of species abundance and diversity demonstrates a marked faunal impoverishment in reef-flat communities; new evidence for contemporaneous reef lithification is assessed.

ACKNOWLEDGEMENTS

I am very grateful to Dr. G.P. Larwood for his supervision throughout this project.

I wish to thank especially Dr. A.J. Bancroft for advice and discussions during three years at Durham. Dr. P.D. Taylor (British Museum, Natural History) provided much valuable help and Miss P.L. Cook (B.M.N.H.) gave advice on several occasions. Discussions on the Zechstein reef with Dr. D.B. Smith and Mr. N.T.J. Hollingworth proved very useful.

The thesis was typed skilfully, and against all the odds, by Carole Blair.

I am grateful to the technical staff of the Department of Geological Sciences, and in particular to Gerry Dresser (photography), George Randall and Ron Lambert (thin sections).

Material from several museums was examined; I extend my thanks to:- University College, Galway, Sue Nelson of the Hancock Museum (Newcastle), Tim Pettigrew (Sunderland Museum), Dr. P.D. Taylor and Andrea Burgess-Faulkner (B.M.N.H.), Miss P. Pyrah (York Museum), Mr. H.P. Powell (Oxford University Museum), Dr. Pietrzeniuk (Museum für Naturkunde, Humboldt-Universität, Berlin), Dr. Hartmut Hauboldt and Dr. Krumbiegel kindly arranged a visit to the Geiseltalmuseum, Martin-Luther-Universität, Halle.

I am indebted to Mr. N.T.J. Hollingworth for the donation of several particularly good specimens and to Irina Sokolov for translation of several Russian papers.

I thank Prof. J. F. Dewey and Prof. M.H.P. Bott for the use of facilities in the Department of Geological Sciences, and the Natural Environment Research Council for three years' financial support.

Last, and least I would like to thank Chris, Adrian, Roger, Kevin, Sally, Neville and Ian (Room 223) for their tolerance during the most anguished moments of thesis writing, and the decurator for not throwing my specimens away, yet.

CONTENTS

VOLUME 1

	Page No.
ABSTRACT	i
ACKNOWLEDGEMENTS	ii
CONTENTS	iv
DECLARATION AND COPYRIGHT	viii
<u>CHAPTER 1</u> INTRODUCTION	1
<u>CHAPTER 2</u> MATERIAL AND METHODS	14
<u>CHAPTER 3</u> EXPLANATION OF SOME TERMS	21
<u>CHAPTER 4</u> ORDER FENESTRATA	24
Order Fenestrata versus Order Cryptostomata	25
Basic elements of the morphology of the	
Fenestrata	30
Families in the Fenestrata	61
FAMILY FENESTELLIDAE	69
GENUS <u>Fenestella</u>	76
Generic level subdivision of <u>Fenestella</u>	77
<u>Fenestella retiformis</u>	84
Aspects of the morphology of <u>Fenestella</u>	
<u>retiformis</u>	107
<u>Fenestella geinitzi</u>	118
FAMILY POLYPORIDAE	126
SUBFAMILY RETEPORIDRINAE	127
GENUS <u>Kingopora</u>	128
<u>Kingopora ehrenbergi</u>	133

Aspects of the morphology of <u>Kingopora</u>	
<u>ehrenbergi</u>	144
SUBFAMILY ACANTHOCLADIINAE	149
GENUS <u>Synocladia</u>	150
<u>Synocladia virgulacea</u>	152
Aspects of the morphology of <u>Synocladia</u>	
<u>virgulacea</u>	166
GENUS <u>Thamniscus</u>	170
<u>Thamniscus dubius</u>	173
<u>Thamniscus geometricus</u>	182
<u>Thamniscus siccus</u>	187
GENUS <u>Acanthocladia</u>	191
<u>Acanthocladia anceps</u>	195
<u>Acanthocladia minor</u>	208
<u>Acanthocladia magna</u>	215
<u>Acanthocladia laxa</u>	221
<u>Acanthocladia diffusus</u>	230
Discussion of the possibility that species	
of <u>Acanthocladia</u> and <u>Thamniscus</u> are synonymous	239
Comparison of the genera <u>Thamniscus</u> King	
and <u>Acanthocladia</u> King	244
GENUS <u>Kalvariella</u>	251
<u>Kalvariella typica</u>	253
GENUS <u>Penniretepora</u>	257
<u>Penniretepora waltheri</u>	258
<u>Penniretepora waltheri nodata</u>	263

GENUS <u>Ryhopora</u>	268
<u>Ryhopora delicata</u>	269
<u>CHAPTER 5</u> ORDER TREPOSTOMATA	273
Basic elements of the morphology of the	
Trepostomata	274
Taxonomic procedure in the Trepostomata	287
FAMILY DYSCRITELLIDAE	290
GENUS <u>Dyscritella</u>	291
<u>Dyscritella columnaris</u>	292
Secondary overgrowths in <u>Dyscritella</u>	
<u>columnaris</u>	305
<u>CHAPTER 6</u> ORDER CYCLOSTOMATA	308
SUBORDER PALEOTUBULOPORINA	309
FAMILY CORYNOTRYPIDAE	310
GENUS <u>Corynotrypa</u>	311
<u>Corynotrypa voigtiana</u>	313
<u>CHAPTER 7</u> PALAEOECOLOGY	318
Introduction	318
Locality descriptions and faunal lists	323
Interpretation of diversity patterns	335
Distribution of bryozoan species through	
the reef	339
The nature of substrata and evidence for	
contemporaneous lithification	344
Substrata for bryozoan attachment and	
bryozoa as substrata	348
Feeding behaviour of some fenestrates	351

Predators of the Bryozoa	372
<u>CHAPTER 8</u> SUMMARY AND CONCLUSIONS	375
REFERENCES	379

VOLUME 2

FIGURES	1-103
PLATES	1-147

DECLARATION

The content of this thesis is the original work of the author (other people's work is acknowledged by reference). It has not been submitted previously for a degree at this or any other University.

D.A. SOUTHWOOD

Durham, September 1985

COPYRIGHT

The copyright of this thesis rests with the author. No quotation from it should be published without his prior written consent and information from it should be acknowledged.

CHAPTER 1

INTRODUCTION

The purpose of the present study is to revise the taxonomy of bryozoa from the Upper Permian Zechstein reef (Tunstall Member of the Ford Formation, Harwood et al. (1982)) and where possible to elucidate aspects of their palaeoecology.

The Tunstall Member consists of a basin facies of coquinoid dolomite packstone which thins sharply eastwards to a dolomitic mudstone (this has not been examined in the present study), a back-reef facies of oolitic packstone/grainstone with a limited shelly fauna but locally small patch reefs and a reef facies with an abundant invertebrate fauna. The reef is considered by Smith (1981) to have been a major linear feature along the western margin of the Zechstein basin in England during the middle and later parts of Zechstein cycle 1. Deposition in the Zechstein basin is generally considered to be coeval with the Guadalupian of N. America, the Kazanian of the Russian platform, the Neoschwagerina zone in Japan and the Middle Productus limestone of the Salt Range, Pakistan (e.g. Ross (1979), Taylor (1984)). Deposition commenced when a barrier was breached in the North, probably close to Spitzbergen and Greenland (in their pre-drift positions). A rise in sea level and/or rifting between Spitzbergen and Greenland allowed the desert basins of the Rotliegend to be flooded by waters from the Boreal Ocean (see fig. 1A), Taylor (1984).

The suggested spatial and stratigraphical relationships of the reef with other units of the Zechstein are shown in fig. 1B. Reefs,



which are presumably equivalent to that of N.E. England, are also known from Denmark, Germany and Poland; their occurrence along the North Sea high is suggested by seismic data, Taylor (1984). The outcrop of the reef in N.E. England is approximately 25 km long (see Fig. 2) with a further 5-10 km known from onshore boreholes at its southern end, Smith (1981). Its width reaches a maximum of about 800 metres and its thickness 100 metres. The reef dips gently eastwards and southwards and is displaced by several E-W trending faults.

Previous Research

Schlotheim (1813) was the first author to publish descriptions of the reef fauna which he had collected in Germany. Goldfuss (1826-1833) supplemented Schlotheim's work while Sedgwick (1829) described the fauna from exposures in N.E. England. Geinitz (1846, 1848, 1861) established several new taxa from the reef as did Howse (1848), King (1849, 1850) and Kirkby (1859, 1860). Little was added to the knowledge of the reef until Trechmann (1913, 1925, 1942, 1944) described some new taxa and discussed changes in faunal diversities - he was the first author to suggest that the invertebrates had inhabited and built an organic reef. Korn (1930) established several new bryozoan species, some of which are rejected in Chapter 4; although he examined the bryozoa in more detail than previous authors his lack of use of thin sections and his poor understanding of bryozoan biology and the nature of reef diagenesis led him to several erroneous conclusions. Dreyer (1961) added further bryozoan taxa but had little understanding of the basic principles of classification within the phylum. Logan (1962) revised the systematics of reef

bivalves and brachiopods. Kerkmann (1967, 1969) suggested a 3-dimensional model of the reef and the characteristic occurrences of faunal elements in relation to this model. However, his bryozoan identifications are only at genus level or above and are probably incorrect in several cases. Pattison (1977) revised the systematics of several elements of the reef fauna. Smith (1958, 1981) elucidated many of the aspects of the reef structure, evolution and diagenesis but did no detailed palaeontological work. Aplin (1981) discussed the diagenesis of the reef and Tucker and Hollingworth (1986, in press) have described the occurrence of undolomitized limestones near the reef base. Permian bryozoan faunas have been described from Australia by Crockford (1941a, 1941b, 1943, 1944a, 1944b, 1944c, 1945a, 1945b, 1951), from the far east by Sakagami (1961, 1968a, 1968b, 1968c, 1970a, , 1973a, 1973b, 1975, 1976a, 1976b), and from the Soviet Union by Gorjunova (1975), Shulga-Nesterenko (1941, 1952), Morozova (1970), Shishova (1960). The distribution and roles of bryozoans in modern reefs have been described by Cuffey (1971, 1972, 1974a, 1974b, 1977), who also attempted comparisons with fossil reefs.

It is clear that little palaeontological research has been carried out on the fauna of the Permian reef in N.E. England; the bryozoa have been particularly neglected. Bryozoan faunas have not been examined from a systematic point of view since King (1850), during which time techniques have changed drastically as has the understanding of bryozoan biology.

The Present Study

The present study is concerned primarily with the Systematics of the bryozoan fauna though aspects of their palaeobiology and palaeoecology are also considered. Where possible, comparisons are made with Permian taxa from other parts of the world e.g. Australia, Russia, Thailand, Japan and the U.S.A. After an introduction to the phylum (Chapter 1), basic principles of classification are discussed. Chapter 2 is a description of material and methods, Chapter 3 explains some of the terms used in the study. Chapter 4 is concerned with the Order Fenestrata, Chapter 5 with the Trepostomata and Chapter 6 with the Cyclostomata. Some aspects of the bryozoan palaeoecology are discussed in Chapter 7. Chapter 8 presents the conclusions of the study.

The Phylum Bryozoa

Three classes are distinguished in the phylum Bryozoa:- the Phylactolaemata, Gymnolaemata and Stenolaemata. The Phylactolaemata are exclusively freshwater forms and have no calcified skeleton. They range from the ? Mesozoic to the Recent. Fossil examples are only very rare.

The Gymnolaemata are sub-divided into two orders - the Ctenostomata and the Cheilostomata. Ctenostomes are uncalcified and quite abundant today. They have a sparse geological record, known only from mould preservation, extending from the Ordovician. Not all fossil forms placed in the order have many morphological features clearly supporting such assignment. Cheilostomes are the most abundant bryozoans of Recent marine environments. They are known from

the late Jurassic (e.g. Pohowsky (1973)) and are abundant from the Cretaceous onwards. They have a calcified skeleton and box-like zooecia. Polymorphs are a feature of the order - Kenozooids, avicularia and vibraculae occur (avicularia and vibraculae occur in no other bryozoan Order). Interzoooidal communication occurs via funicular material which passes through mural pores. Fig. 3C shows zooid structure in an anascan cheilostome.

All known calcified Palaeozoic bryozoans belong to the Class Stenolaemata. Five Orders are generally recognized:- Cyclostomata (= Tubuliporata of the Treatise), Trepostomata, Cryptostomata, Fenestrata and Cystoporata. Cyclostomes range from the Ordovician to the Recent - they are very rare in the Palaeozoic, common in the Jurassic and quite common thereafter. They are important in being the only extant members of their Class and are thus used as an analogy for the soft-part interpretations of the other extinct Orders of the Stenolaemata (see p. 8). The Trepostomata are one of the most abundant groups of Palaeozoic bryozoans, ranging from the Ordovician to the Triassic (see Chapter 5). The composition of the Cryptostomata has been the subject of considerable debate (some of which is reviewed on p. 25) - the Treatise recognizes two suborders:- the Ptilodictyina, which have an erect bifoliate habit and range from the Ordovician to ? Permian and the Rhabdomesina which have zoaria composed of erect, slender, cylindrical bifurcating branches, this suborder ranges from Ordovician to Permian (Shishova (1968) considers the Rhabdomesonata to be a distinct Order). In spite of their quite common occurrence in Permian rocks of the Soviet Union and Spitsbergen, rhabdomesids are not known from the Zechstein of Britain or Germany. Controversy over the

ordinal status of the Fenestrata is reviewed on p. 25. Bryozoa of this Order are common throughout the Palaeozoic, ranging from Ordovician to Triassic; they are particularly common in the Upper Palaeozoic and comprise the great majority of the taxa described in the present study (see Chapter 4). Utgaard (in the Treatise) recognises two suborders within the Order Cystoporata - the Ceramoporina and the Fistuliporina. The Order ranges from Ordovician to Permian with only the Fistuliporina occurring in the Upper Palaeozoic. Fistuliporids and hexagonellids are quite abundant in Permian rocks of the Soviet Union and Spitsbergen but are not known from the Zechstein of Britain or Germany.

Bryozoa are colonial aquatic filter-feeding invertebrates which are nearly always sedentary. A colony usually develops from a sexually produced larva (though some colonies may develop asexually by fragmentation, McKinney (1983)) which attaches itself to a substratum and then metamorphoses to produce the ancestrula, the first zooid of the colony. A number of zooids are then asexually budded, each colony consisting of autozooids with or without a variety of different polymorphs reflecting various degrees of colonial integration. Autozooids exhibit a gradient of increasing size distally throughout a zone known as the zone of astogenetic change, this usually lasts only for a few zooidal generations after which size stabilizes in the zone of astogenetic repetition (the zooids of this zone usually comprise the bulk of a colony). Basic bryozoan autozooid body plan is demonstrated by the ctenostome genus Bowerbankia, Ryland (1970) (see fig. 3). The distal end of the zooid consists of a number of slender ciliated tentacles which arise from an annular lophophore surrounding

the mouth. The alimentary canal makes a loop inside the coelomic cavity, it consists of ciliated pharynx, oesophagus, tripartite stomach, intestine and rectum. The gizzard which occurs is not a characteristic feature of the phylum. A nerve ganglion occurs between the mouth and the anus. The tentacle sheath surrounds the pharynx and the terminal part of the rectum - it can be considered an introvert because it completely encloses the tentacles when they are retracted. The collar (see Fig. 3) is a feature which is not characteristic of other groups within the Phylum. The retractor muscle extends from the proximal end of the cystid to the base of the lophophore, it is largely responsible for the retraction of the tentacles. The body wall consists of an inner peritoneum and an outer epidermis which is surrounded externally by cuticle. The funiculus is a cord of mesenchymatous tissue which extends from the stomach and serves to link zooids throughout the colony. The fertilized egg passes through the supraneural pore on its way from the coelom to the atrium where it matures.

Modern cyclostomes show some differences from the basic plan of an autozoid of Bowerbankia. The body wall incorporates a calcified layer and a terminal membrane closes the distal end of the zooid when the polypide is withdrawn (see fig. 4). The simple situation in Fig. 4 is complicated further in free-walled cyclostomes (= double - walled cyclostomes) (see Fig. 5). The polypide is enclosed in a membranous sac which is fastened to the zooid wall by short ligaments; at its proximal end it hangs freely in the coelom. The membranous sac divides the metacoel into an exosaccal cavity and an entosaccal cavity.

As well as normal feeding autozooids several different types of polymorph are developed in the phylum. Gonozooids in cyclostomes have no polypide and are the large swollen chambers in which embryos develop. Nanozooids are single-tentacled polymorphs, in some cases keeping the colony surface free of sediment and larval settlement, in other cases performing an unknown function (see p.50). Avicularia are mandibular polymorphs which occur only in cheilostomes. Vibraculae are also restricted to cheilostomes, they consist of a long seta which originates from a basal chamber and appears to serve the function of discouraging larval settlement on the colony surface. A kenozooid is any polymorph lacking a lophophore, gut, orifice and usually muscles.

Cyclostomes as analogues of Palaeozoic stenolaemates

In his work on the structure of modern cyclostomes, Borg (1926) described two types of wall arrangement - single-walled and double-walled (= fixed-wall and free-walled). In a single-walled cyclostome the wall structure is as follows:- outermost cuticle, calcareous layer, epidermis (consisting of ectodermal epithelium and mesoderm). In a double-walled cyclostome (e.g. hornerids and lichenoporids) the wall structure is as follows:- outermost cuticle, epidermis (eustegal epithelium), a narrow slit-like cavity called the hypostegal coelom which is continuous with the zooidal exosaccal coelom, epidermis (hypostegal epithelium), calcareous layer, epidermis (zooidal epithelium) then the body cavity of the zooid (see Fig. 5). It is this double-walled model which is considered an analogue for the condition of ^{most} Palaeozoic stenolaemates. Elias and Condra (1957) and Tavener-Smith (1969a) both applied the model to bryozoans of the Order

Fenestrata - the occurrence of large amounts of extrazoidial skeleton suggests the existence of a depositing epithelium external to outer walls. Colony-wide transfer of nutrients could only take place via a hypostegal coelomic space because no inter-zoidial pores have been observed in bryozoans of the Order; a double-walled model for fenestrate bryozoans best explains the growth of their skeleton (see p.38). Boardman (1971) applied the double-walled model to trepostomes for reasons similar to those used for the Fenestrata (see p.278).

A cyclostome analogy is generally accepted for the interpretation of soft parts throughout the Stenolaemata - the correlations of polypide-skeleton relationships by McKinney and Boardman (1985, in press) support this idea. However, not all morphological features of the Fenestrata are best explained by analogy with cyclostomes - ovicells of Synocladia virgulacea and other species are here compared with those of the Cheilostomata (see p.53) and Tavener-Smith (1971) suggested that Polypora stenostoma Tavener-Smith had cheilostomatous features.

Taxonomic Procedure

Simpson (1961) provides a definition of taxonomy as " ... the theoretical study of classification ..."; Sokal and Sneath (1963) define classification as "... the ordering of organisms into groups (or sets) on the basis of their relationships, that is, of their associations by contiguity, similarity, or both". According to these definitions most of the present study is concerned with classification. However, authors frequently use "taxonomy" in the sense of classification as defined above.

Earliest classifications of organisms simply grouped together those which were most similar. A hierarchical arrangement of these organisms was achieved on the same basis. A dramatic change in the philosophical basis of classification was made possible when Darwin identified the phenomenon of evolution. However, the application of the theory of evolution had very little material effect on already existing classifications; this was because proximity of evolutionary relationship was usually inferred from similarity in morphological characters, i.e. the same practical methodology was employed as existed prior to the acceptance of the theory of evolution.

At the present day there are two main approaches to classification:- Numerical taxonomy and cladistic taxonomy.

Sokal and Sneath (1963) discuss the theory of numerical taxonomy at great length. Its main aim is the elimination of subjectivity from classifications which is supposedly achieved by considering all morphological characters to be of equal importance. A group of organisms is arranged into higher taxonomic categories by assessment of the number of characters in common. The grouping of species into higher taxonomic categories is an obvious source of subjectivity in numerical taxonomic procedure since the choice of level of subdivision is made by the taxonomist. Thus, classification achieved by numerical taxonomic methods is purely phenetic and has no regard for the supposed evolutionary relationships of the organisms. Although this is an approach which is fundamentally different from the evolutionary approach to taxonomy where higher classificatory categories are defined by inferences of phylogenetic relationships, classifications achieved by the two methods need not be dissimilar because of their

common basic principle that closeness of morphology equals closeness of relationship (except for the recognition of convergent evolution in evolutionary classifications).

Cladistic taxonomists do not consider all morphological characters to be of equal importance in the formation of groups within a classification. Hennig (1966) was one of the pioneers of this approach which aims to construct monophyletic groups which are descendants of a common "stem species". The relative positions of these groups within the hierarchical arrangement of the phylogenetic system are controlled by the positions of the stem species and are deduced by a consideration of certain character states which are common to some taxa and not others. Character states are considered to be by symplesiomorphs (i.e. taken over unchanged by all descendants) or synapomorphs (changed in a descendant). The concept is a relative one, e.g. a character could be a symplesiomorph at genus level but a synapomorph at family level. The more "derived" (synapomorphic) characters that are shared by two groups the more closely they are related. In its purest form cladistics takes no account of actual stratigraphic relationships between taxa, though cladograms (reconstructions of phylogeny) can be checked against stratigraphical data. The problems of this approach to taxonomy lie in the difficulty of recognizing synapomorphies and symplesiomorphies with confidence and, according to Mayr (1968), in its recognition of branching but not the variable degrees of subsequent divergence of branches (though it seems likely that Mayr (op. cit.) misinterpreted aspects of cladistics).

It is possible to consider a third school of thought, that of

evolutionary classification. This appears to combine features of both the above types of classification with the aim of elucidating evolutionary relationships. It is a relatively flexible approach in which emphasis on a particular methodology is not a precondition.

The present study has been concerned largely with classification at the level of the species. Specimens have been grouped together on the basis of morphological similarity with as many characters as possible being used. The characters are weighted, greater significance being attributed to those which are likely to reflect most closely the genotype of the taxon and less significance being attributed to those which probably include a large component of ecophenotypic variation. A knowledge of bryozoan biology and the possible effects of ecology on morphology have been components taken into account throughout the study. The goal of species-level taxonomy in palaeontology must be to achieve groupings which are as similar as possible to those of the original biological species. The difficulties in achieving this are obvious - a large number of morphological characters are not preserved in fossils and the relationship between morphology and genetics is not always a simple one (e.g. pleiotropy allows the same genotype to have different phenotypes; sibling species are genetically and morphologically indistinguishable but reproductively isolated). Problems with ecophenotypic variation can be particularly acute with colonial organisms such as bryozoans where a number of characters which can be considered zoarial rather than zooecial may be particularly susceptible to environmental effects. Type specimens have been selected for new species though the concept of a single specimen being

most typical of a species is rejected as inadequate and often misleading. Higher taxonomic categories have been defined on the basis of morphology with reference to their original definitions - internal consistency has been the main aim as the incorporation of an evolutionary dimension is beyond the scope of the study. Considerable problems have been encountered with the genus concept e.g. in Thamniscus versus Acanthocladia (see p.244) and with Dyscritella (see p.297) - these problems have highlighted the relative artificiality of the concept and the difficulties of the typological approach (e.g. type specimens of "Keratophytes dubius" which have been examined are all truly referable to Synocladia virgulacea). Taxonomy above genus level has been achieved using other authors' work since detailed investigations of this kind are beyond the scope of the present study.

When morphological characters have been selected for a taxonomic group they are described qualitatively and quantitatively. Quantitative description consists of counts of features and/or measurement of the features' dimensions which are then plotted on histograms in order to identify discontinuities (see p.72 for general procedure in fenestellids). Large sample sizes have been used to allow the fullest possible appraisal of intraspecific morphological variability, and coefficients of variation are calculated to give some indication of the relative constancy of morphological characters. Considerable problems with specific level subdivision arise from the poor preservation of characters in a large number of specimens; this makes comparisons with other Permian faunas difficult and the specific assignments only tentative in many cases. Diagnoses at various taxonomic levels are given throughout the study.

CHAPTER 2

MATERIAL AND METHODS

Material

The material examined in the present study was from museum collections and from field collecting in N.E. England.

Type and figured specimens from several museums were examined:- some of Schlotheim's material was borrowed from the Museum für Naturkunde der Humboldt-Universität, Berlin, the King Collection of bryozoa was borrowed from University College, Galway and Korn's (1930) figured specimens were examined in the Geiseltalmuseum, Martin-Luther-Universität, Halle, East Germany - Korn's specimens have unfortunately been labelled with the figure numbers from Korn (op. cit.), this may lead to some confusion where individual specimens are referred to. Dreyer's (1961) type material could not be located. Geinitz's type material was destroyed during World War II.

Other museum material included the Kirkby-Howse collection, Hancock Museum, the Phillips Collection, York Museum, material from the British Museum (Natural History) and the Oxford University Museum.

Material was collected from about twenty localities in N.E. England. Descriptions of the in situ fauna were made for palaeoecological purposes then counts of individuals were made on exposed faces as well as counts from whole blocks. A conscious effort was made to reduce the natural bias towards larger specimens and towards bryozoans in the collecting procedure for palaeoecological analysis. After species diversities had been assessed, specific

bryozoan collecting was undertaken.

The state of preservation of bryozoans from the Tunstall Member presents considerable problems. A complex and varied diagenetic history, including dolomitisation, dedolomitisation and redolomitisation leaves many specimens with few observable morphological features. Specimens are often preserved only as moulds; cast preservation occurs frequently, though this has the advantage of allowing 3-D observation of features which can usually only be interpreted from 2-D thin sections, e.g. zooecial chamber shapes and ovicells. The precipitation of dolomite on zoaria obscures many characters which might be of use taxonomically e.g. pustules and small nodes. Only the reverse surface is observable in most specimens, the obverse surface tends to remain in the rock (in such cases it can rarely be revealed by the making of asphalt peels (see below)). The general lack of well-developed bedding planes (cf. e.g. Carboniferous shales) means that blocks often fracture across specimens, rendering their complete observation impossible.

Methods

Cleaning and Preparation

Specimens were cleaned by scrubbing with a toothbrush in warm water with detergent. Care was taken not to scrub the surface of specimens with delicate morphological features - an ultrasonic bath was used in most cases. A tungsten needle was used to pick out matrix.

Only the reverse surface is visible in most of the material - the technique of taking asphalt peels was used to expose the obverse

surface, but with only very limited success. This technique was described by Bancroft (1984) and first used by Young (1877). The specimen is heated to ensure it is perfectly dry. Pure asphalt is heated in a container until it is completely molten - this is then poured onto the specimen using a previously heated spoon (this ensures the asphalt does not solidify on the spoon). A layer about 5 mm thick is formed which cools and solidifies in a few minutes. The asphalt is then peeled off the rock, hopefully with the bryozoan remaining attached to the asphalt. This may then be cleaned in an ultrasonic bath and obverse surface details observed.

Silicone rubber casts

Silicone rubber casts were made of specimens in mould preservation. In several cases this technique revealed a surprising amount of morphological detail e.g. the imprints of skeletal rods. The material used was the silicone rubber compound 'lastic'.

Examination of external morphology

Specimens were examined with a Zeiss citoval binocular microscope. Possible magnifications range from 10X to 100X.

Measurements were made using an eyepiece graticule at a magnification of 80X. The smallest graticule subdivision at this magnification is 0.02 mm, thus measurements were accurate to 0.01 mm. A small source of error in measurements results from the 3-D shape of many specimens - attempts were made to manipulate specimens so that the dimension being measured was as nearly perpendicular to the plane of observation as possible. A graticule with a grid pattern was used

in counts of zooecial apertures of trepostome bryozoans.

Drawing external morphology

Drawings are necessary as an interpretive tool to show morphological features which are not adequately demonstrated by photographs. These were made at a magnification of 32X using the eyepiece grid and a sheet of paper overlaying paper with a similar grid pattern. Camera ludicra drawings were unsuccessful because of insufficient lighting of the subject.

Photography of external morphology

FP4 ASA 125 black and white film was used. For low magnification photography a 35 mm S.L.R. camera was used with a varioprox lens attached. Aperture setting was f 16 to allow maximum depth of focus - exposure time was 1-2 seconds. Magnifications up to 3X were achieved with this arrangement.

For high magnification photography an S.L.R. camera was used with 1-3 extension tubes and a Leitz 24 mm 'Sumnar' lens. Magnifications of 14X to 20X were achieved with this arrangement. Exposure times varied from 9-30 seconds.

Lighting was by two lamps, one either side of the specimen and with different intensities to achieve some relief in the photographs.

A number of difficulties were experienced in the photography - nearly all bryozoa are the same colour as the rock matrix around them such that most photographs have a very poor contrast, dusting of specimens with ammonium chloride proved unsuccessful. The complicated 3-D shape of many specimens meant that focussing was often possible on

only a part of the specimen.

Scanning electron microscopy

External morphology was examined with a scanning electron microscope. Magnifications up to 400X were achieved using a Cambridge 600 S.E.M.

Examination of internal morphology

Internal morphology was examined by means of thin sections and acetate peels. Where the observation of a feature in a particular orientation was necessary resin encapsulation was often used:- the specimen was separated from the rock matrix by the use of a tungsten needle and/or a Burgess powerline vibrotool then set in a small block of pre-activated polyester resin (Trylon EM 306). This could then be manipulated easily, being ground to the required level by a horizontal grinding wheel and using abrasive (grit size 400 and 1200). Acetate peels could then be taken from this prepared surface, though in many cases with only limited success because of the state of preservation of the material. Thin sections were also prepared from such surfaces, these were not always successful because of the behaviour of the resin when heated.

Thin section preparation

Thin sections were prepared at various thicknesses (30 μ to approx. 5 μ), depending on the lithology and on the scale of observations required (some morphological features of poorly preserved material were better observed in relatively thick sections). Numerous

random sections were made at standard thickness of 30μ then ground further with fine abrasive (grit size 1200) if they contained features of interest. Orientated sections were prepared by grinding a specimen on an abrasive wheel and then using corundum powder until the desired level was reached.

Acetate Peels

Acetate peels were made by grinding the appropriate surface flat with a fine abrasive. This was then etched with 10% hydrochloric acid for 5-15 seconds. The specimen was then washed in water and left to dry. When dry the surface was flooded with acetone and the acetate sheet rolled onto the surface ensuring no air bubbles were trapped. When the peel was dry it was removed from the specimen and placed between two glass slides, sellotaped together to keep it flat.

The advantage of acetate peels is that serial sections can be made, allowing the interpretation of internal features in 3-D. They are also quicker to make than thin sections and can be made without the complete destruction of a specimen. However, only limited success was achieved with the material of the present study, partly because of the great porosity of many specimens and because of their preservation as dolomite (which does not etch in 10% HCl).

Measurement of internal morphological features

A Swift polarising microscope with an eyepiece graticule was used to measure features in thin sections and acetate peels. Magnifications of up to 400X were used, the maximum accuracy of measurement was to 1μ .

Photography of internal morphological features

Photographs of thin sections and acetate peels were taken with a Zeiss Ultraphot II microscope which has an automatic exposure camera. Magnifications up to 300X were used.

CHAPTER 3

EXPLANATION OF SOME TERMS

- Cystid: The name sometimes used for zooid walls - they can be either internal or external body walls.
- Fossula: A fossula is a notch which may occur proximal to and continuous with an autozooecial aperture in acanthocladiid fenestrates (see. p. 46).
- Skeletal Rods: Skeletal rods are equivalent to the 'styles' of the Treatise, i.e. rodlike skeletal structures orientated approximately perpendicular to the zoarial surface. The term 'style' has not been used in order to avoid confusion which might arise because of its different meaning as a word in common use in the English Language.
- Longitudinal striae: Longitudinal striae occur in the Fenestrata, they are narrow ridges in the primary granular layer, extending parallel to branch length. They are most prominent on the reverse surface but may occur on the sides of branches (e.g. in Fenestella retiformis, see p.84). They occur in all species of the Fenestrata examined in the present study but are usually only visible in hand specimen when the outer laminated layer is thinly developed or has been removed by diagenetic effects. They are always visible in correctly orientated thin sections.

- Nanate Zooecium: Nanate zooecium is a new term suggested for a zooecial chamber which is normal apart from being sealed by a thin, terminal, calcareous plate with a small central pore. It is interpreted to have housed a secondary nanozoid (see p.50). The new term is suggested in order to prevent usage of the soft-part interpretation for the skeletal structure, i.e. secondary nanozoid (e.g. Bancroft (1984)) and as a more accurate alternative to nanozooecium, the term used by Bancroft (1986, in press).
- Reef: The word is often used in a general sense to refer to any rocks of the reef complex, e.g. including patch reefs of the back-reef environment.
- 'Sub-colony': 'Sub-colony' has been used in a sense which is not that generally accepted by many authors, i.e. a grouping of zooids with a function related to the production of excurrent water outlets. It is used here for a part of a colony which expands rapidly from a point on a branch, consequently having an aspect similar to that of a colony origin. 'Sub-colonies' occur in Synocladia virgulacea (see p. 167).
- Vestibule: The vestibule is the tubular distal part of an autozooecial chamber. In the Fenestrata the base of the vestibule is usually defined by the presence of a hemiseptum - hemisepta have not been

observed in the present study but the term 'vestibule' is maintained for the distal part of a chamber.

Zoarial lamina: This term is used to describe the way in which a number of branches of a zoarium grow in a single plane (it is applied to Fenestella and Synocladia).

Multilaminar growth: This refers to the sub-parallel growth of zoarial laminae - one inside another in conical colonies or one above another in flat colony expansions. It may occur in Fenestella retiformis but is most common in Synocladia virgulacea. It is not to be confused with multilaminate growth which is the superimposed growth of two or more layers of zooids in cheilostomes.

Figure 6 gives pictorial examples of shapes used in the description of zooecial chambers, e.g. triangular, pentagonal, elongate hexagonal, hemi-hexagonal, rhombic, etc.

CHAPTER 4

ORDER FENESTRATA Elias and Condra, 1957

Diagnosis

Stenolaemata with zoaria composed of branches which are dichotomous, pinnate or in a reticulate expansion. Branches may be connected by dissepiments with or without apertures " or may fuse with neighbouring branches to form fenestrules. Autozooecia are fairly short, composed of an initially recumbent, box-like proximal part and a distal tubular part which meets the obverse surface at a high angle. Autozooecial apertures open only on the obverse surface. Obverse surfaces may be smooth, finely granular, pustulose or nodose. Reverse surfaces may be smooth, finely granular, pustulose, nodose or longitudinally striate. Internal microstructure of branches consists of a continuous thin primary granular layer surrounded by thin inner laminated skeleton in zooecial chambers and thicker outer laminated skeleton around the outside of branches. The outer laminated skeleton is traversed by numerous small rods of primary granular layer, extending roughly perpendicular to branch surfaces. Ovicells and nanate zooecia may be abundant. Heterozooecia may occur.

Range

Ordovician to Permian (?Triassic).

Order Fenestrata versus Order Cryptostomata

The bryozoan Suborder Cryptostomata was first proposed by Vine (1883). Ulrich (1890) maintained this Suborder, contrary to popular belief, and increased its number of families by assigning the fenestellids, amongst others, to it. The Cryptostomata achieved ordinal status at a later date, not in Ulrich's (op. cit.) work.

Three zoarial types within the Order were recognised by McNair (1937) - cylindrical e.g. rhabdomesids, bifoliate, e.g. ptilodictyids and unilaminar e.g. fenestellids. These different zoarial types were the basis upon which Astrova and Morozova (1956) erected three Suborders of the Cryptostomata, attributing phylogenetic significance to their sub-division. The Order Fenestrata was proposed by Elias and Condra (1957). The basis for its creation was the suggested homology of the colonial plexus of fenestrate forms with the common bud of Cyclostomata and the claim that this colonial plexus was absent in other members of the Cryptostomata. However, Blake (1975) mentioned the presence (though often reduced in extent) of a primary granular layer (colonial plexus) in hyphasmoporids, arthrostylids, rhabdomesids and ptilodictyids. Tavener-Smith (1975) commented on the difference between the localized distribution of a primary granular layer in most cryptostomatous groups and its zoarium-wide extent in the fenestellids but showed that certain genera, e.g. the ptilodictyid Taeniodictya have a tendency towards a more fenestellid-like arrangement of this layer. In view of these observations the ordinal status of the Fenestrata, on the basis of the occurrence of the primary granular layer, must be considered somewhat controversial. Other features which have been considered to support the ordinal status of the

Fenestrata are:-

- (a) The zoarial morphology - which is usually fenestrate, but there are several exceptions to this, e.g. Penniretepora, Acanthocladia and Thamniscus and there are ptilodictyids which have a grossly fenestrate form, e.g. Clathropora and Coscinella.
- (b) The short box-like shape of the zooecia - some species of Fenestella have relatively tubular zooecia and some species of phylloporinid do not have box-like zooecia, Tavener-Smith (1975).
- (c) The presence of apertures on one side only of the branches - according to Tavener-Smith (op. cit.) the longitudinal striations in the primary granular layer of fenestellids represent vestigial interzooecial walls which suggests that an ancestral stock of this group could have been bifoliate. As evidence in support of this theory, Tavener-Smith (op. cit.) cites the condition of the phylloporinid Pseudohornera which has, on the reverse sides of branches, stunted obsolete zooecial chambers separated by walls of a primary granular layer with the appearance of the characteristic fenestellid longitudinal striae.

Blake (1975) described several features of the early Arthrostylidae which also occur in comparable states of development or in a closely related form in other rhabdomesids, the ptilodictyids and the fenestellids and concluded that the three groups show a degree of unity which is greater than any that can be demonstrated between the Trepostomata and Cystoporata at the earliest stage in their history. In view of this he believes that the Fenestrata, Rhabdomesonata and Ptilodictyoidea ought to be reunited, as suborders, into the order Cryptostomata. Tavener-Smith and Williams (1972) also retained the

order Cyptostomata containing the three suborders of Astrova and Morozova (1956). Cuffey (1973), in a new classification of the higher taxa of Bryozoa, which he suggested was an interim measure until phylogenies could be better understood, retained the order Cryptostomata with two suborders - Fenestrina and Habrovirgatina - the ptilodictyids and rhabdomesids were united in the Habrovirgatina as infraorders. Cuffey's classification was essentially a numerical-taxonomic analysis of a large number of morphological features of each taxon but has generally been ignored by most authors.

If the interpretations of Blake (1975) and Tavener-Smith (1975) are both correct then the ordinal status of the Fenestrata must be considered a little doubtful, but there are some reasons for scepticism.

The details of the astogeny of the arthrostylids are not known and only a relatively small amount of material of this group is available, to some extent weakening Blake's arguments about their significance. The early astogeny of taxa is considered important by many authors in the definition of higher taxa, e.g. McKinney (1978) comments on the observation of Gautier (1972) that there is a difference between the protoecium of Trepostomata (not enveloped by hypostegal coelom) and that of Fenestrata (enveloped by hypostegal coelom) and suggests that this difference implies a large phyletic separation between the groups. The lack of sufficient knowledge about the astogeny of ptilodictyids and rhabdomesids still leaves uncertainty as to the higher taxonomic positions of these groups. The idea of reverse surface longitudinal striae in fenestellids as vestigial interzooecial walls can be criticised. Their occurrence can

be explained as simply an adaptation for structural strength of the typically long and slender fenestellid branch. Longitudinal striae are straight and parallel to branch length in the genus Fenestella but the interzooecial wall zig-zags along the branch length. The obsolete and reduced zooecial chambers on the reverse surface of Pseudohornera are not necessarily an intermediate stage between the bifoliate state and the unilaminar fenestellid state.

There are undoubtedly significant morphological differences between the fenestellids, the ptilodictyids and the rhabdomesids - the scale of these differences (admittedly a subjective assessment) is not much less than that between the Trepostomata and some ptilodictyids and rhabdomesids. Since the Trepostomata are worthy of ordinal status on the basis of these differences it is possible to consider similar status for the fenestellids, ptilodictyids and rhabdomesids. The occurrence of the distinct orders Trepostomata and Cystoporata early in the geological record along with the arthrostylids, which appear to have features in common with the fenestellids, ptilodictyids and rhabdomesids is not necessarily an argument against the ordinal status of the Fenestrata. There is no reason to believe that orders of bryozoans should arise at comparable periods in time and the arthrostylids may be an aberrant or a polyphyletic group, in which case the Fenestrata can reasonably be considered distinct from the Cryptostomata. Further uncertainty exists about the vital early record of these groups and their relative positions in time because of poor stratigraphic control and the low abundance of material. If, as Tavener-Smith (1975) claims, the Trepostomata are close to the rhabdomesoids in morphology and the fenestelloids are close to the

ptilodictyoids then the unification of those three suborders into the order Cryptostomata is probably less appropriate than the retention of the orders Fenestrata and Rhabdomesonata with the ptilodictyoids remaining in the Cryptostomata.

Until more is known of the early representatives of all these Bryozoa the higher taxonomy of these families must remain open to some speculation. A more detailed investigation is beyond the scope of the present study but the order Fenestrata is recognised here in accordance with the 'Treatise' and with the majority of current authors.

Basic elements of the morphology of the Fenestrata

The Microstructure and Growth of the Skeleton

The microstructural elements of the skeleton in the Fenestrata, and their possible mode of growth will be considered separately for the Fenestellidae and Acanthocladiinae. It is evident though that there are very few differences between the representatives of the two groups studied (cf. Gautier, 1972, 1973).

Fenestellidae

Two fundamentally different types of skeletal tissue have been recognised in the Fenestrata ever since they were first studied in thin section. Nicholson and Lydekker (1889), and Ulrich (1890) commented on this. Ulrich described the differentiation thus "In transverse sections of the branches the original basal or germinal plate is generally quite distinct from the subsequently added layers of calcareous tissue". He recognised a laminated structure in the outer layers of skeleton which was penetrated by 'tubuli'. This basic division into outer laminated layers and inner non-laminated material was described further by several authors including Likharev (1926), Shulga-Nesterenko (1941), Condra and Elias (1944), Elias and Condra (1957) and Tavener-Smith (1969a). Likharev (op. cit.) recognised some faint laminar structure within the non-laminated layer when sections were very thin - Elias and Condra (1957) comment on this at greater length. Tavener-Smith (op. cit.) studied the ultrastructure of the skeleton and maintained a three fold division of inner

laminated skeleton which lined the zooecial chamber, primary granular skeleton and outer laminated skeleton traversed by rods of granular material. He also attempted to reconstruct growth processes in the Fenestellidae. Tavener-Smith's terminology will be used below as each element of microstructure is considered in turn. Figs. 8 and 9 show the disposition of microstructural elements in a stylized fenestrate.

Primary Granular Skeleton

This corresponds to the colonial or germinal plexus described by Elias and Condra (1957). In plane polarised light it is clear and shows only weak structure. It completely surrounds zooecial chambers (apart from their apertures) and extends the whole length of a zoarium. The granular skeleton extends from the interzooecial walls to form the core of the carina and its nodes (the extent of its development in nodes is uncertain). On the reverse side of the branch, beneath the zooecial chamber bases, the primary granular skeleton is corrugated to form ridges which extend longitudinally and parallel to one another along a branch - these are referred to as longitudinal striae. The layer is continuous into dissepiments, spines and other processes of fenestellid zoaria where it forms the core of their structure. Electron microscopic study of this layer by Tavener-Smith (1969a) has shown it to be composed of roughly equidimensional calcite particles which present a granular or rubbly appearance; he comments "A distinctive feature is the total absence of laminar structure". However, when it is viewed in crossed polars, with very thin sections, there is a possible further subdivision of structure. Likharev (1926) first mentioned this and Elias and Condra

(1957) described the division as "inner platy core, a concentration of fine dark particles whose calcification results in a single crystalline unit and thin outer walls, generally optically different and usually somewhat laminated". Tavener-Smith (1969a) made no comment on this subdivision but it has been observed in Fenestella retiformis during the present study (see p. 88). This platy core occurs in the centres of the longitudinal striae and is continuous through to the core of carinal nodes. Its extent is easily traced, as Elias and Condra (1957) found, because it is observed to go into extinction uniformly in transverse sections. In tangential sections the same feature is apparent; when the branch is parallel to the plane of polarization there is a thin dark line of calcite in the interzooecial walls in extinction more or less uninterrupted for the length of the branch; this extends to the outer wall of the zooecial chambers where it forms a thin dark layer outside of which is the rest of the primary granular layer and then the outer laminated layer. The present study has found some evidence of the fine dark granules which occur in the inner platy core (see p. 88) - these are visible in plane polarized light.

Inner Laminated Skeleton

The inner laminated skeleton forms a thin lining around the zooecial chamber on the inside of the primary granular skeleton. Elias and Condra (1957) used the term "Inner Sclerenchyma" for this layer but only showed its distribution in a figure rather than describing it. Tavener-Smith (1969a) described it as a separate entity having essentially the same construction as the outer laminated layer, that is, it consists of calcite particles with a platy texture

as opposed to the granular texture of the primary granular layer. The banding is regular in this layer which is always very thin - as Tavener-Smith (1969a) points out, this must be because of a physiological check exercised on deposition as the maximum thickness possible to allow accommodation of the zooid was achieved.

Outer Laminated Skeleton

This is the outer sclerenchyma of Elias and Condra (1957). They attribute the laminated appearance to the higher refractive index of the laminae compared to the structureless substance in which they are embedded. The division between primary granular layer and outer laminated skeleton is visible in plane polarised light - in crossed polars the individual dark laminae remain unchanged in appearance. Tavener-Smith's (1969a) study of the ultrastructure of this layer revealed that "each lamina consists of a thin, sheet-like mosaic of calcite particles" - presumably the lamina of Tavener-Smith corresponds to the "structureless substance" of Elias and Condra. The outer laminated layer surrounds the primary granular layer producing a thick covering on the reverse surfaces of branches and usually a slightly thinner covering on the sides and obverse surfaces. It surrounds the carina, nodes, dissepiments and spinose processes. In the proximal parts of zoaria it may be very thick forming a substantial holdfast and overgrowing autozooeal apertures. It was partly this last observation which led Tavener-Smith (1969a) to propose that the outer laminated skeleton was deposited by external colony-wide tissues which were analogous in their structure and disposition to those of the modern cyclostome Hornera (see fig. 5).

Traversing the outer laminated layer are slender rods of granular calcite called skeletal rods.

Skeletal Rods

Elias and Condra used the terms spicules or filaments for these structures. They consist of granular calcite similar to that of the primary granular skeleton and radiate from this layer through the outer laminated layer; they may protrude at the branch surface. Tavener-Smith used the term 'pustules' for the protruberances of the skeletal rods however this term is used for "equidimensional skeletal structures consisting of crinkled segments of skeletal laminae" in the 'Treatise' (1984). Skeletal rods usually have diameters of approximately 10μ but may range from 1μ to 20μ according to Elias and Condra (1957). Where laminae are in contact with the rods they tend to be deflected distally forming a cone-in-cone structure - Tavener-Smith (1969a) interprets this as indicative of growth of the rod being slightly in advance of that of the surrounding laminae. He believes them to be an integral part of fenestellid wall structure and not algal in origin as Elias and Condra (op. cit.) suggested. Only very poorly developed skeletal rods have been observed in Fenestella in the present study.

Dark Granules

Elias and Condra (1957) referred to fine dark granules which occurred in the inner platy core of the primary granular layer. These may be just discernible in comparable positions in the present study of Fenestella. Tavener-Smith (1969a) referred several times to

'trails of dark granules' which are in a different position to those of Elias and Condra - they extend from the junction between the primary layer and the inner laminated layer into the cores of carinal nodes, dissepiments and spinose processes. These granules are inferred by Tavener-Smith to represent the former position of a thin cuticular spindle. In the present study, dark granules have not been observed in such positions in Fenestella.

Acanthocladiinae

The basic elements of microstructure are the same in the Acanthocladiinae as in the Fenestellidae.

Primary Granular Layer

This is clear in plane polarized light and usually shows faint laminar structure in longitudinal sections. The laminar calcite gives way to structureless calcite in the interzooecial walls and close to the zooecial chamber bases. In crossed polars the laminar structure is still weakly visible and thin rods of calcite can be seen to extend towards the boundary with the outer laminated layer where they can no longer be traced. The disposition of these rods is fairly irregular and their point of origin is not certain; they do not go into extinction as the rest of the layer does in crossed polars. As in the Fenestellidae, the primary granular layer extends around zooecia into dissepiments and into the cores of nodes; it is continuous for the length of the zoarium.

Inner Laminated Skeleton

This is as in the Fenestellidae.

Outer Laminated Skeleton

This is easily distinguished from the primary granular layer in plane polarized light; it consists of numerous dark laminae immersed in structureless calcite. In crossed polars the division is still clear - the laminae remain as dark lines. Rarely, skeletal rods are visible traversing this layer in longitudinal sections; they are more commonly visible in tangential sections of branches. The outer laminated layer surrounds the zooecial chambers as it does in the Fenestellidae and does not extend into interzooecial walls as Gautier describes (1972, 1973). Close to zoarial origins the outer laminated skeleton may seal off zooecial chamber apertures and form a thick holdfast. It occurs on the outside of spines, nodes and dissepiments.

Skeletal Rods

These are visible in tangential sections of branches close to the reverse surface. They have been seen only rarely in longitudinal or transverse sections. They appear as circles of calcite surrounded by dark haloes. The calcitic core is presumably granular and usually has a diameter of approximately 2μ . The dark halo probably represents laminated skeleton - the diameter of the whole structure is approximately 8μ . They are seen to protrude at the branch surface in some places. They have not been found in interzooecial walls cf. Gautier (1972).

Dark Granules

Gautier (1972, 1973) did not comment on dark granules in the Acanthocladidiids. They have been seen rarely in the present study and it is apparent that their distribution is variable.

Mode of Growth

The mode of growth to be inferred for both the Fenestellidae and the Acanthocladiinae is essentially the same, there being only superficial differences. Therefore, they will be considered together.

A fundamental and reasonable assumption is that the calcareous skeleton of bryozoa is secreted by a closely associated epithelium. The disposition and function of the epithelium must be such that it can produce the skeletal features of the Fenestrata described above. One of the most striking features of fenestrate Bryozoa is the often very great thickness of laminated skeleton on the reverse surface and around the proximal parts of zoaria. To explain this Shulga-Nesterenko (1949) suggested that there was an epithelium on the outside of branches which deposited successive skeletal increments. Elias and Condra (1957) also favoured an 'ectoderm', stretched over the whole zoarium, which was responsible for the deposition of the outer laminated layer. They drew attention to the striking parallels between the fenestrate skeleton and that of the atypical cyclostome families Horneridae and Lichenoporidae and suggested that Borg's work (1926) could be applied to fenestrate Bryozoa. Borg elucidated the wall structure and nature of the soft parts of many cyclostome genera. He found that the wall of the cystid in hornerids and lichenoporids was different from that of most other cyclostomes, consisting of a doubled layer of ectodermal epithelium on the outside of zooecial walls, separated by a small slit-like cavity, on the inside of the zooecial wall was another layer of ectodermal epithelium. Since the ectodermal epithelium is responsible for the deposition of the skeleton it is possible to see that calcareous material can be

deposited on the inside of the zooecial chambers and all around the exterior of the zoarium. The sequence of layers in the wall, from the inside of the zooecial chamber outwards is:- the body cavity of the zooid, mesoderm, ectodermal epithelium, calcareous layer, ectodermal epithelium, mesoderm, a narrow slit-like cavity called the hypostegal coelom (this is in communication with the zooidal coelom), mesoderm, ectodermal epithelium then the outermost thin cuticle. This kind of wall structure is that which typifies the "double wall" concept - it is this concept of wall structure and growth which was applied to fenestellids in detail by Tavener-Smith (1969a) see Fig. 10. The sealing of autozooecial apertures by secondary skeletal material is seen as evidence in favour of an external epithelium. Tavener-Smith's study of the ultrastructure of the fenestellid wall enabled him to suggest some of the possible fine details of the process of calcareous wall deposition. At the highest magnifications the junction between the primary granular layer and the outer laminated layer is seen to be gradational - Tavener-Smith suggests that the primary granular layer, consisting of roughly equidimensional calcite particles, represents fairly rapid continuous deposition and that a decrease in the rate of secretion leads to intermittent deposition producing the outer laminated layer. He suggests that the epithelium remained fixed in position relative to the calcareous wall and that its secretory regime changed with time. He describes lenses of granular skeleton within the outer laminated layer - similar lateral discontinuities of the laminated layer have been seen in the present study (see e.g. Pl. 65) and show that the change in secretory regime could often be variable and irregular. The skeletal rods in the outer laminated layer are

explained by Tavener-Smith as the products of continuous growth outward from the primary granular layer while intermittent deposition was occurring around them. He suggests that, analogously to the taleolae of strophomenid brachiopods, they served as attachment points for the soft tissues where they protruded at the zoarial surface. He comments on the occurrence of trails of dark granules in the axial regions of dissepiments which extend from the junction of the primary granular layer and the inner laminated layer of a neighbouring zooecial chamber. He considers the granules to represent the former position of cuticle which was present between the inner laminated layer and the primary granular layer and extended as a narrow spindle into dissepiments. As evidence in support of a cuticular partition here he cites the absence of skeletal rods in the inner laminated layer. This evidence could be circumstantial. The trails of dark granules have not been observed in any of the well-preserved specimens of Fenestella seen in the present study, nor have they been seen in any of the numerous well-preserved specimens of Carboniferous Fenestella examined in thin section by Bancroft (1984).

Calcium carbonate crystallites are seeded by the hypostegal epithelium (Ryland's terminology is preferred here to Tavener-Smith's "inner mantle epithelium"). In Tavener-Smith's growth model calcification at the growing tips of branches began only after the developing zooids had attained adult size and shapes (see fig. 10). The evidence in favour of this is weak, being that no partly formed zooecial chambers have been observed in the tips of zoaria and that zooecial chambers next to dissepiments appear to be slightly deformed towards the dissepiment. This distortion of zooecia is supposed to

have been caused by outward drag of the soft parts of the zooecial chamber due to formation of a bud from the epithelial tissue which produces the dissepiment. In order to accommodate his hypothesis Tavener-Smith's growth model for interzooecial walls is very complicated, involving the fusion of layers of epithelium and then the development of perforations in their structure. The figures 4 E-H (see fig. 10) drawn to explain this process are misleading in suggesting that a single row of zooecial chambers occurred in a branch. The modified model developed here (which is hypothetical, but explains the observed skeletal elements) is one in which calcification takes place continually at the growing margin; the developing zooids arise after the formation of the skeleton of the zooecial chamber by continued addition to existing skeleton by the hypostegal epithelium. The sequence of events is shown in Figs. 11 & 12 - the hypostegal and eustegal epithelium surround the whole branch tip, the primary granular layer at the base of the zooecial chambers is continually increased, extending in a distal direction; the same applies to the longitudinal interzooecial wall which continuously extends in a distal direction, zig-zagging between the zooecial chambers and growing laterally and distally to form their roof. The walls on the outside of the zooecial chambers grow in a similar way. The extension of the epithelium in this region is presumably by intussusception i.e. the interpolation of new material among the cuticular elements already present, as described in Bugula by Schneider (1959), Ryland (1976). As each calcified zooecial chamber is formed the new zooid develops from the hypostegal coelom and the eustegal and hypostegal epithelium. This is in contrast to Tavener-Smith's model where the new zooid

develops from a parent zooid. Gautier's (1972, 1973) model of growth in the Acanthocladidae has the new zooid developing from the colonial tissues rather than from a parental zooid and is thus similar to that described above. Once the chamber is formed, what was previously the hypostegal epithelium becomes the zooidal epithelium, and, when the primary granular layer is completed, a change in secretory regime takes place from continuous to intermittent deposition giving the inner laminated skeleton. Tavener-Smith (1973b) later modified his ideas on growth and suggested that the zooidal epithelium could have been partly responsible for the deposition of the primary granular layer. Though his explanation of this change of viewpoint was not very detailed, it seems to represent a growth model which is closer to that described here.

The mode of development of the epithelial tissues with their associated hypostegal coelom was suggested by Tavener-Smith (1969a). The zooidal epithelium was considered to be an extension of the ancestrular ectoderm; the hypostegal and eustegal epithelium originated as a peripheral evagination of ectodermal epithelium from the vestibular region of the ancestrula ('ancestrula' in the sense of Tavener-Smith 1969a is equivalent to 'protooecium' in the sense of Cumings, 1905). In Fig. 12 Tavener-Smith's text fig. 4A-D has been modified to accommodate the present growth model. Diagram 'A' is as in Tavener-Smith - evagination of the ancestrular epithelium begins, thus forming two layers of epithelium - the hypostegal and eustegal, which are continuous all around the ancestrula and with the zooidal epithelium. Between these two layers is the narrow hypostegal coelom - this is continuous with the coelom of the ancestrula. In diagram

'B' the hypostegal and eustegal epithelium continue to extend by intussusception over the surface of the ancestrula to the substrate. The epithelia may extend over the substrate for a short distance and calcification commences with the deposition of primary granular layer around the outside of the ancestrula. This primary granular layer forms the basal wall of the first zooecial chamber. In diagram 'C' deposition of the lateral walls of the first zooecial chamber commences in two upfolds of the hypostegal and eustegal epithelia. These walls extend into the plane of the paper. In diagram 'D' the walls of the first zooecial chamber are complete and the first asexually budded zooid is formed by expansion of the hypostegal coelom. The hypostegal epithelium remains in the zooecial chamber where it becomes the zooidal epithelium. The zooidal coelom is continuous with the hypostegal coelom. Successive zooecia are added in this way around the ancestrula, presumably in the manner described by Cumings (1904). (No zoarial origins have been observed in thin section during the present study so it is assumed that their development in Permian species of Fenestella was the same as that in the Palaeozoic fenestellids studied by Cumings (1904, 1905)), these earliest zooecia may have all been in contact with the substrate or some may have been up on the side of the protooecium as described in Lyroporella by McKinney (1978). When the initial circle of zooecia was completed budding took place to produce the branches of the zoarium, growing free of the substrate. According to Cumings (1904) the autozooecial apertures always open onto the outside of an infundibuliform zoarium in Fenestella. In the present study of Fenestella they have been observed only on the inside of

infundibuliform zoaria and have been found in this orientation very close to zoarial origins (see Pl. 29). If Cumings's description of the initial development of zooecia in Fenestella is correct for all species of the genus then the zooecia in F. retiformis must undergo some slight torsion as they grow free of the substrate, directing the autozooecial apertures towards the inside of the zoarium.

Gautier's (1972) description of the ancestrular development of Permian acanthocladids is very similar to the modification of Tavener-Smith's model given above. The difference is in the occurrence of laminated skeleton in the interzooecial walls of the ancestrular complex - in the hypothetical model presented above there is only non-laminated skeleton in interzooecial walls; this is consistent with observations on more mature parts of zoaria.

Gautier's (1972, 1973) general growth model for acanthocladids is similar to that described above for fenestrate Bryozoa. The occurrence of laminated skeleton in interzooecial walls which is continuous with similar deposits on laterally adjacent skeletal units and with similar, but thicker, deposits which envelop the nest of zooecia is a fundamental difference. The primary granular layer in the acanthocladids he studied is considerably reduced in thickness relative to that seen in the present study. Gautier also described skeletal rods in inter-zooecial walls - these have not been seen in fenestellids or acanthocladids in the present study.

Zoaria

Zoaria are always erect, distal to the ancestrular complex. They consist of branches which may be pinnate, dichotomously divided or part of a reticulate meshwork. The reticulate meshwork may be formed by the coalescence of adjacent branches or by the joining of adjacent branches by dissepiments. Dissepiments may have autozooecia or may be sterile. Two or more usually longitudinal rows of autozooecia occur on branches and some dissepiments. Spines are commonly developed from the reverse surfaces of branches, in particular close to zoarial origins. Large amounts of extrazoooidal skeleton may be developed around zoarial origins (e.g. in Kingopora).

Autozooecial Chambers

Autozooecial chambers are relatively short. They consist of a box-like or flask-shaped to roughly tubular proximal part which tends to be recumbent, sub-parallel to the reverse surface. The chamber bends sharply into the distal tubular part, referred to here as the vestibule. This meets the obverse surface at a high angle. The base of the vestibule is usually defined by the presence of a hemiseptum - hemisepta have not been seen in the present study but the term 'vestibule' is maintained for this distal tubular part of an autozooecial chamber. Autozooecial apertures all open onto the same side of the colony - the obverse surface. Zooecial chambers usually have the same shape intraspecifically, though there may be a quite marked variation in morphologically less regular species (e.g. Kingopora ehrenbergi) and between zooecial chambers on the edge of a branch and those in the centre of a branch (e.g. in Acanthocladia

and Synocladia).

Autozooecial Apertures

Autozooecial apertures in the Fenestrata are usually relatively small (e.g. compared to trepostomes or cystoporates); they are circular to oval. A peristome is often developed around an aperture - it is a narrow rim-like projection above the obverse surface which often completely surrounds the aperture. However, in acanthocladids, it is often incomplete at its proximal edge, where a small notch may be variably developed. This notch may truly be a fossula, as described by Gautier (1972), (see fig. 7) though it is not so well developed in any of the species of the present study (i.e. Acanthocladia anceps, A. magna) as it is in the Permian "Adlatipora" of Gautier (op. cit.). The fossula described by Gautier in Permian acanthocladids may be a well-developed, quite long trough (e.g. in "Adlatipora"), or a small notch at the proximal edge of an aperture. Occasionally, a small isolated pore occurs proximal to the aperture - Gautier considers this to represent possibly a stage in the ontogenetic development of a fossula. He proposes a number of alternatives for the function of the fossula:

- (i) It served to connect the coelom in the main zooidal cavity to the coelom on the outer side of the zooecial wall, posterior to the aperture.
- (ii) It connected the external environment with some structure within the zooidal cavity.

In several species of acanthocladids the proximal notch in the aperture is only very weakly developed. Gautier considered these

species to be closely related to "Adlatipora" and thus suggested that the function of the fossula was unlikely to have been one which could not have been performed by a relatively normal aperture and zooecial chamber alone.

Gautier (op. cit.) suggested that the fossula might have acted as a passageway for the anal end of the gut, but pointed out that this would require a proximal separation of the anus from the tentacle sheath - an arrangement unknown in living cyclostomes or cheilostomes. In support of such an interpretation he cited the condition of some species of Fenestella from the Permian of Texas. These have apertures with eight marginal holes (denticulated apertures of other authors), one central hole and a pore behind each aperture in a position equivalent to that of the fossula in "Adlatipora". If the eight marginal holes represent the positions of each tentacle and the central hole the position of the mouth then the pore proximal to each aperture may represent the position of the anus. A similar arrangement of pores may exist in the genus Septatopora Engel (1975). However, in several species with denticulated apertures there is no evidence of a pore proximal to the aperture or a notch in the peristome (e.g. (Fenestella ivanovi Shulga-Nesterenko, Fenestella bicellulata Etheridge and Penniretepora spinosa Young and Young, Bancroft (1984)). Thus, the argument in favour of an anal opening separated from and proximal to the tentacle sheath may be weakened.

Gautier (op. cit.) compared the fossula to the sinus of ascophoran cheilostomes which links the compensation sac to the external environment. He concluded that the shape of the zooecial chamber would cause a compensation sac to bend sharply if it were

present and so rejected this idea.

Tavener-Smith (1971) described the new species Polypora stenostoma from the Viséan of Ireland - this has an elongate opening proximal to the autozooeal aperture. Tavener-Smith (op. cit.) suggested that this opening had a membranous covering during life which functioned like the frontal membrane of anascan cheilostomes. It is unlikely that a similar situation would have existed in "Adlatipora" or any of the acanthocladids of the present study since the size of the fossula is probably too small to allow depression of a membrane sufficient to cause protrusion of the lophophore.

In spite of not being comparable to the known condition of modern cheilostomes and cyclostomes it is felt here that the proximal notch (?fossula) in apertures of several species of acanthocladids may have had a function related to the anal opening of the gut of an autozoid.

Nodes

Nodes are spinose structures projecting above the level of the obverse surface, occasionally they occur on the reverse surface (e.g. in Penniretepora waltheri nodata subsp. nov.). They are usually elongate parallel to branch length at their base but tend to be approximately circular in cross-section higher up. They may reach great lengths (up to 0.5 mm above the obverse surface in Fenestella retiformis) and may bifurcate, trifurcate or have lateral projections (see fig. 19). They are situated at the apex of a median carina in species of Fenestella and Penniretepora but may form two longitudinal rows in Acanthocladia or may be situated at the inner margins of apertures in Kalvariella and Ryhopora. Their distribution may be more

irregular in species of Thamniscus.

Carinal nodes were considered by some authors e.g. Miller (1961) to be homologous with the acanthostyles of the Trepostomata which were originally thought to be hollow and to have housed some type of heterozoid. This was shown not to be the case by Tavener-Smith (1969b) who demonstrated the acanthostyles of the trepostome Leioclema aspera Hall to be solid structures. Carinal nodes of the fenestellids were shown as early as 1926 (Likharev) to be solid structures and Tavener-Smith (op. cit.) suggested that they were unlikely to be homologous with trepostome acanthostyles because of the relative timing of deposition of their skeletal elements - carinal nodes have a primary granular core which is completely formed before any deposition of outer laminated skeleton around them (see fig. 8) whereas the laminated skeleton around acanthostyles is formed approximately contemporaneously with the granular core.

Several authors have suggested that nodes served to protect the obverse surface from predators e.g. Chronic (1949), Tavener-Smith (1969a). This interpretation is accepted here as very likely though they may also have served a function related to the generation of feeding currents - they may have created eddies from unidirectional ambient flow and thus improved feeding efficiency (see p.357 for detailed interpretation).

Polymorphs

Several different types of polymorphic zooecia may be developed in species of the Fenestrata:-

Heterozooecia

Fenestella retiformis and Fenestella geinitzi may both develop abnormally large zooecia with atypical morphologies. These usually occur in branches prior to bifurcation and appear to have acted as 'space-fillers' (see Pl. 10). They may also occur where a bifurcation fails to take place e.g. in F. geinitzi (see Pl. 34 fig. a). It is very unlikely that such a zooecium would have housed a normal feeding autozoid, in which case it could be considered a kenozooecium - it is not known whether these zooecia truly lack an aperture though, and it is impossible to be sure that their polymorphs lacked a lophophore, gut and muscles.

Abnormally small apertures may occur in Ryhopora delicata sp. nov. prior to bifurcation points. They are 0.04-0.06 mm in diameter compared to the 0.085 mm of autozooecial apertures (see fig. 69). These may be heterozooecia of some unknown type - they are not comparable in size or morphology to nanate zooecia, described below.

Nanate zooecia

Otherwise normal zooecial chambers are quite often sealed at their aperture by a calcareous terminal diaphragm - this diaphragm has a small (usually about 20 μ) sub-centrally placed, roughly circular hole (see Pls. 8 and 64). Such chambers are interpreted as having housed secondary nanozooids (e.g. in Silén and Harmelin, 1974). The new term "Nanate zooecium" is suggested here for the chamber of the polymorphic zooid instead of "secondary nanozooid", as used by Bancroft (1984), since this term is descriptive of the soft-part interpretation of the structure and not the structure itself. The

term "nanozooecium" used by Bancroft (1986 in press) is also rejected as an inaccurate description of the polymorphic chamber.

Silén and Harmelin (1974) and Bancroft (1984) described a low peristome around the opening of the nanate zooecium - such a peristome has not been seen in the present study. Nanate zooecia are described here in Fenestella retiformis, Fenestella geinitzi, Kingopora ehrenbergi, Synocladia virgulacea, Acanthocladia anceps, A. minor, A. diffusus, A. magna sp. nov. and ? Kalvariella typica. Bancroft (1984, 1986) described them in several species of Carboniferous fenestrates and McKinney (1977) described them in Lyroporella quincuncialis Hall (1857). It seems likely that they are a common feature of fenestrate bryozoans and remain to be described in many taxa.

Silén and Harmelin (1974) described different types of nanozoids in the diastoporid cyclostome genera Diplosolen and Plagioecia - they attempted functional interpretations of these nanozoids by observation in the laboratory. Nanozoids in Diplosolen obelium are primary in origin, they occur in zooecial chambers which are smaller than autozooecial chambers and are often regularly distributed in a colony in a 1:1 ratio with autozoids. They have a single, fairly long tentacle which sweeps regularly over the colony surface, apparently to keep it free from sediment or larval settlement.

Secondary nanozoids occur in Plagioecia sarniensis. These occupy normal autozooecial chambers (apart from the terminal diaphragm) and differ from nanozoids S.S. in being part of a degeneration-regeneration cycle. The autozoid polypide degenerates leaving the body wall of the proximal part of the zooid and the atrial sphincter unchanged, a polypide with retractor muscles and membranous

sac is regenerated with only a single unciliated tentacle and a rudimentary alimentary canal. Secondary nanozooids are shorter than nanozooids S.S. and appear not to perform a similar cleaning function. They have no male sex cells. Their function remained a mystery to Silén and Harmelin (1974).

Mckinney (1977) suggested secondary nanozooids in Lyroporella quincuncialis may have been male polymorphs, but there is no evidence to support this point of view.

It is suggested here that secondary nanozooids in Permian Fenestrata need not have been as short as those of Plagioecia sarniensis and may thus have performed a defensive and/or cleaning function. Bancroft (1984, 1986) considered secondary nanozooids to be more abundant in the proximal parts of colonies. Other patterns of their distribution have been noted in the present study. In Fenestella retiformis nanate zooecia appear to occur preferentially close to bifurcations - in this position a nanozooid could have discouraged larval settlement on the increased area of available substratum. If the model proposed for feeding current patterns in Fenestella is correct (see p.351) then it is possible that an autozooid at a branch bifurcation could not have fed normally - a secondary nanozooid in such a position would be advantageous. Large areas of a zoarium of Synocladia virgulacea may have nanate zooecia to the exclusion of normal autozooecia. These are not necessarily the most proximal parts of zoaria - they may represent the lower zoarial lamina of a colony which is composed of several such laminae (see p. for discussion); the occurrence of secondary nanozooids here may be related to the proposed model of feeding current generation in S.

virgulacea (see p.351) where it is suggested that refiltration of water is inefficient and usually avoided by a colony.

Mckinney (1977) claimed that secondary nanozooids in Lyroporella quincuncialis were merely an ephemeral stage in the ontogeny of a zooid, just prior to the complete sealing by outer laminated skeleton of the zooecial chamber. This interpretation is doubted here in view of their widespread occurrence and their occurrence away from the proximal parts of zoaria. It is believed that they were an integral part of a colony, performing a definite function or functions.

Ovicells

Structures interpreted as ovicells have been described from relatively few genera in the Fenestrata; they are considered to be the skeletal indications of brood chambers where embryonic products were incubated prior to their discharge to the external environment.

Tavener-Smith (1966a) was the first author to describe ovicells in the Fenestrata in detail. However, their occurrence in Fenestella basloensis var. shaktauensis had been suggested earlier by Elias and Condra (1957) - they described, as ovicells, hemispherical swellings projecting into fenestrules. McCoy (1844) was probably the first author to describe an ovicell in a fenestrate bryozoan when he wrote of Parafenestalla formosa - "at each setting off of a dissepiment, is one pore, nearly twice the size of the others". Tavener-Smith (op. cit.) described large cyst-like inflations of branches in Fenestella cf. fanata Whidborne, they have an average length of 0.675 mm and a width of 0.575 mm, three or four apertures open at the surface of this inflation but only one zooecial chamber, interpreted as the

gonozooecium, has an intimate connection with the ovicell (see fig. 13). He described similar structures in Fenestella cf. delicatula Ulrich though these are much smaller than those of F. cf. fanata and do not effect the disposition of adjacent zooecia. He also described ovicells of a similar type in Hemitrypa hibernica McCoy which appeared to be an inflation of the vestibular or sub-vestibular region and affected the disposition of adjacent zooecia. Tavener-Smith (op. cit.) rightly drew attention to the general morphological similarities between these ovicells and the inflated gonozooids of cyclostomes.

Stratton (1975) described ovicells in Fenestella sp. from the Devonian of Southern Indiana; they were similar to those described by Tavener-Smith (op. cit.) but adjacent zooecia were not disrupted by the swelling of the ovicell. Stratton (1981) found inflated chambers or bowl-like depressions on the dissepiments of Polypora shumardii Prout, these were joined by narrow canals to zooecia which he considered to be gonozooecia.

Bancroft (1984, 1985 pers. comm.) described ovicells similar to the above types in Penniretepora spinosa Young and Young and Penniretepora sp. nov. B. In all the above cases the ovicells are rare in a zoarium.

In the present study Synocladia virgulacea, Acanthocladia anceps, ?A. minor, A. diffusus, Thamnisucs geometricus, ?Penniretepora waltheri nodata, ?Penniretepora waltheri and ?Kalvariella typica all have structures which are interpreted as ovicells but which differ quite markedly from the type described above. These structures are small hemispherical cavities immediately proximal to and partly in continuity with the vestibules of zooecia. They usually have a depth

equivalent to 1/2-3/4 of the vestibule length. In most cases they appear to be enclosed within the branch but undoubtedly project above it in some specimens. Uncertainty about their true relationship to the branch obverse surface is caused by the cast preservation in which most of these structures have been observed (see fig. 14 and Pl. 68). Observations in slightly oblique tangential thin sections confirm deductions made about their morphology from specimens in cast preservation (see fig. 14 and Pl. 69). The base of the vestibule is circular in tangential section, as the obverse surface is approached the ovicell appears, circular in section, with a thin line of skeletal material separating it from the vestibule, closer to the obverse surface this disappears and the ovicell and vestibule are in continuity. Longitudinal sections appear to show the ovicell as a small depression proximal to the aperture rather than as a cavity within the branch. However, such sections are not numerous and it is possible that a thin skeletal covering of the ovicell has not been preserved. Well-preserved specimens of the obverse surface of species with ovicells have not shown such depressions proximal to apertures.

The length, width and depth of these ovicells were measured (see fig. 14) and a statistical analysis of their size undertaken. There was found to be no significant variation between species. Measurements from only nine zoaria were considered in the analysis because of the very small amount of variation found.

Maximum variation in length = 0.12 - 0.18 mm

Inter-colonial average = 0.154 mm

S.D. = 3.54×10^{-3} , C.V. = 2.3

Maximum variation in width = 0.14 - 0.20 mm

Inter-colonial average = 0.165 mm

S.D. = 7.0×10^{-3} , C.V. = 4.2

Accurate measurement of depth was not possible in many cases, but where it was, a constant value of 0.08 mm was found.

Although variation in the state of preservation is a factor which must be considered when attempting to assess the distribution of these ovicells, there is undoubtedly a real variation in their abundance and distribution between zoaria. They are often very abundant and have been found in almost every zooecium in a zoarial fragment of S. virgulacea 6.5 x 3 cm in size - they are only rarely absent from zooecia at branch margins. Their distribution may be more sparse and irregular and they may be clustered into small groups. No distinct zonation in a zoarium has been noted. They occur on both branches and dissepiments in Synocladia virgulacea. The nearest that ovicells have been found to the origin of a zoarium is at the eighteenth zooecial generation - this fact may be considered evidence in support of the interpretation of these structures as ovicells.

These ovicells are strikingly different from those described by Tavener-Smith (1966a) - they are much smaller and much more abundant within a zoarium. They are not morphologically comparable with the gonozooecia of cyclostomes but their size and distribution recall the aspect of ovicells in the Cheilostomata. However, cheilostome ovicells occur at the distal margin of a chamber and those described above occur at the proximal margin. Hemispherical depressions on the branch surface, proximal to the aperture were described by Engel (1975) in the Carboniferous Septatopora flemingi Engel and Septatopora acarinata Crockford (see fig. 14). These depressions are connected to

the lower vestibule by an auxiliary tube and are interpreted as ovicellular structures by Engel (op. cit.); they have a similar size and disposition to the ovicells described in the present study. The occurrence of septate apertures in these species was considered by Engel (op. cit) to be a limiting factor on the possible degree of protrusion of the polypide, because of this the anus of Septatopora would have been enclosed within the vestibule and the development of a separate anal opening would have been expedient. The auxiliary tube may also have served as a passageway for the release of fertilized ova to the ovicell. These interpretations of Engel (op. cit.) probably require the polypide to be in a degenerated state while embryos are developing in the ovicell, they also require the anus and supraneural pore to be situated proximally, rather than distally as is the case with modern bryozoans. A similar departure from known polypide construction need not be postulated here for Permian species with ovicells though it appears to be necessary for the supraneural pore to be proximally rather than distally situated. The frequent occurrence of an ovicell associated with almost every zooecial chamber in these Permian species suggests that zooids may have been feeding normally at the same time as an embryo was developing in an adjacent ovicell (as occurs in numerous cheilostomes). It is also possible that zooids of these species followed some sort of degenerative-regenerative cycle - the zooid was in a degenerated state when an embryo was developing and was regenerated when the ovicell was redundant. If this was true then there would probably have been a zonation of polypides in different states within a colony such as that described in cheilostomes by Dyrynda (1981).

The morphology of ovicells has been used by several authors for taxonomic discrimination at species level. However, Silén (1944) doubts their significance at this level and Larwood (1962), for example, found both endozooïdal and hyperstomial ovicells in species of the genus Pelmatopora. Viskova (1981) suggested that the general type of brood chamber may be of some value at higher taxonomic rank. The occurrence of identical ovicells in several species and genera of the present study shows, in this case, that their morphology cannot be used for taxonomic purposes at or below the level of the genus. They may be of significance at the sub-family level - all species with these ovicells are considered to be acanthocladids whereas Kingopora is not, and appears to have a different type of ovicell (see below); Fenestella belongs to the family Fenestellidae and may have large gonozooïd-like brood chambers. The fact that the ovicell described in Penniretepora waltheri and P. waltheri noda is different from that described by Bancroft (1984) in Penniretepora sp. nov. B may suggest some complexity of the relationship between these structures, taxonomy and phylogeny.

The type of ovicell described above in Permian fenestrates may be more widespread in its occurrence. Crockford (1944a) appears to describe them in Synocladia spinosa Crockford and Ulrich (1890) refers to similar structures on the branch surface of Thamniscus octonarius Ulrich. Gautier (1972) described ovicells in "Adlatipora". These are generally similar in morphology to those described above but are larger and less abundant in a zoarium. They may be on the branch surface or immersed within the branch to varying degrees. Gautier (op. cit) compared them to brood chambers of cyclostomes rather than

cheilostomes because he considered the polypide to have been in a degenerated state when the embryo was developing (this assumption was made because the ovicell occludes the fossula, thus preventing normal feeding of the polypide (see p.46)).

Inflated mound-like structures are developed in one zoarium of Kingopora ehrenbergi; they extend from branches to cover adjacent fenestrules. They may be roughly circular in shape or may form a narrow prominent band. Apertures occur on the surface of these structures, they have the same inter-apertural distance as apertures on a normal branch. A polished section of one of these structures revealed thin partitions forming at least three chambers and a thin section (see p.147 and Pls. 51 and 52) revealed a similar feature, though this could not be confirmed as representing such a structure. These are interpreted here as ovicells, of a different type from those described above in the acanthocladids, being, at least superficially, more similar to the inflated gonozooids of cyclostomes (see also p. 147).

Accessory Pores

Morozova (1973) described accessory pores in fenestellid genera and mentioned their occurrence in Acanthocladia. She considered them to be the apertures of regularly developed heterozooecia which could occur on the reverse or obverse surface of a species. Her work on internal microscopic structure confirms these 'pores' to be related to some kind of chamber and thus an integral part of Bryozoan morphology. In contrast, apparent accessory pores in Fenestella retiformis, Synocladia virgulacea and Thamniscus dubius have been shown to be

unrelated to bryozoan structure and probably result from the activity of a boring organism (see p.114). Thus, it is important, when identifying accessory pores, to make observations in thin section.

Families in the Fenestrata

The family Fenestellidae was erected by King in 1849 to unite Palaeozoic genera which were reticulated and had "the cellules planted on a basal plate composed of vertical capillary tubuli". The "vertical capillary tubuli" are the longitudinal striae. Fenestella was designated the type genus and other genera included in the family were Polypora, Ptylopora, Synocladia and Phyllopora (Kingopora). For genera similar to these but with free stems and branches King erected the family Thamniscidae - this contained Thamniscus and Acanthocladia. Zittel (1880) created the family Acanthocladiidae on the basis (according to Waagen and Pichl 1885) of his belief that Thamniscus was identical to Acanthocladia and therefore that the genus Thamniscus should be discarded. The characteristics of his Acanthocladiidae were the same as those of King's Thamniscidae. However, Thamniscus is in fact not the same as Acanthocladia so that Zittel's reason for the new family name is not valid. Because of this, Waagen and Pichl (1885) suggested the earlier name 'Thamniscidae' ought to take precedence. The family name Acanthocladiidae is thus a subjective synonym of the Thamniscidae. However, the Acanthocladiidae will be retained here as the subfamily Acanthocladiinae in accordance with the usage of Dunaeva and Morozova (1975) and in order to cause minimum taxonomic upset. Waagen and Pichl (1885) considered the main characteristic distinguishing the fenestellids from the thamniscids to be the presence of fenestrules in the former. They suggested three subfamilies; the Fenestellinae, Polyporinae and Goniocladinae. Fenestella was placed in the Fenestellinae and Synocladia and

Phyllopora (Kingopora) were placed in the Polyporinae. The chief characteristic separating the two sub-families is that, in the Polyporinae, "the branches are covered all over with pores on one side" whereas, in the Fenestellinae, the obverse surface has a keel with regular rows of zooecia on either side. This is not an adequate distinction since they describe also the presence of a keel in Synocladia virgulacea. It may be that they saw the difference between the sub-families as the number of rows of apertures (two in the Fenestellinae and more than two in the Polyporinae) but expressed this badly. However, Phyllopora (Kingopora) usually has two rows of apertures and is placed in the Polyporinae and Lyropora has more than two rows of apertures and is in the Fenestellinae. These sub-families must be considered inadequately defined on the basis of the inconsistencies between their definitions and the genera contained within them.

Ulrich (1890) placed Fenestella, Phyllopora (Kingopora) and Thamniscus in the Fenestellidae and Penniretepora, Acanthocladia and Synocladia in the Acanthocladiidae. The main characters used to distinguish these two families were the absence of non-poriferous dissepiments and the presence of lateral branches in the acanthocladiids. Ulrich denied the claims of most earlier authors that Thamniscus and Acanthocladia are closely related. He believed that Thamniscus was closer to Polypora because he observed rare dissepiments in Thamniscus dubius. In the present study they have been seen only very rarely and so their significance is doubted. Ulrich also believed the "cell structure" (zooecial chamber structure) to be identical in T. dubius and some species of Polypora - in the

present study the zooecial chambers of T. dubius and Acanthocladia have been found to be very similar and are less similar to those of several species of Polypora. In view of this the placing of Thamniscus in the Fenestellidae is considered erroneous here. Ulrich's familial assignments of genera appear to have been generally accepted for quite a long time e.g. Bassler (1953) in "The Treatise". Morozova (1962) recognized some inconsistencies in the generic assignments to the Fenestellidae and reinstated the family Polyporidae to contain those genera with more than two rows of zooecia. Morozova was mistaken in believing that the family was erected by Waagen and Pichl (1885), it was originally created by Vine (1883) for precisely the same reason as that used by her. Phyllopora (Kingopora) ehrenbergi was placed in this family by Vine; an untenable assignment because it usually has two rows of zooecia, not three. Morozova (op. cit.) maintained the family Acanthocladiidae but removed Synocladia from it to her new family Septoporidae which was characterised by zooecia-bearing dissepiments.

Termier and Termier (1971) wrongly believed that they had erected the new family Polyporidae - they considered it to consist of forms with or without fenestrules, with zooecia in more than two rows, the reverse surface being characterized by longitudinal striae, carinae and nodes are absent. They placed Thamniscus and Protoretepora (which they wrongly believed was synonymous with Phyllopora (Kingopora)) in this group. Fairly conspicuous nodes have been found in Kingopora during the course of the present study, they occur also in Polypora, Bancroft (pers. comm.); for this reason, and because there is no formal diagnosis, the description of the family Polyporidae by Termier

and Termier is untenable. They considered the characteristics of the Acanthocladiidae to comprise a zoarium composed of main branches from which arise oblique secondary branches which could be free, or fused with those from a neighbouring branch to form fenestrules. They placed Septopora, Acanthocladia, Penniretepora and Ptylopora in this group.

The structure of zooecia and budding pattern were considered the main criteria for recognition of higher taxa within the Fenestrata by Dunaeva and Morozova (1975). They placed the families Fenestellidae, Polyporidae, Septoporidae and Fenestraliidae in the suborder Fenestelloidea. They also distinguished three subfamilies in both the Fenestellidae and Polyporidae on the basis of 'colony structure'. The different types of structure were:- reticulate colonies with branches connected by regularly spaced dissepiments without zooecia, reticulate colonies with anastomosing branches bearing zooecia (or with branches connected by very short wide dissepiments), or branched colonies without dissepiments. The occurrence of similar 'colony structure' types in two separate families was explained as homeomorphy due to analogous functional and environmental adaptations. The main characteristic of the Fenestellidae is the presence of two rows of zooecia divided by a distinct median keel according to Dunaeva and Morozova (op. cit.). Penniretepora is placed in the subfamily Diploporinae on the basis of its pinnate zoarial morphology. The family Polyporidae is characterized, and differentiated from the Fenestellidae, by having three or more rows of zooecia. The zooecial base is described as rhombic or hexagonal in shape in the diagnosis. In the present study the zooecial base shape of Penniretepora has been

observed as hexagonal/oval and is much closer to that of Acanthocladia and Synocladia than it is to that of Fenestella retiformis. On this basis Penniretepora seems more closely related to the Polyporidae than the Fenestellidae. Kingopora is placed in the subfamily Reteporidrinae of the Polyporidae by Dunaeva and Morozova. This assignment contradicts their own diagnosis. Morozova herself (1970) described Kingopora with two to three rows of zooecia and the only species of it seen in the present study has usually two rows of zooecia with more rarely a third developed. The zooecial chamber base shape of Kingopora is irregular but tends to be rhombic/pentagonal in most cases. It is quite different from that of Fenestella retiformis and is also different from that found in Thamniscus, Acanthocladia and Synocladia. Thus Kingopora fits uneasily into the Polyporidae with the diagnosis of Dunaeva and Morozova as it stands. Acanthocladia and Thamniscus are both assigned to the polyporid subfamily Acanthocladinae by Dunaeva and Morozova, which is characterized by the lack of regular dissepiments. Synocladia is placed in the family Septoporidae whose main distinguishing characteristic appears to be the presence of dissepiments which have zooecia. This is a fairly weak characteristic for definition of the family since the presence of wide short dissepiments with zooecia is considered a sub-familial character in the polyporid subfamily Reteporidrinae. The other characters of this family given in the diagnosis are not very useful for differentiation at higher taxonomic levels e.g. "Heterozooecia (cyclozooecia) opening on the obverse as well as on the reverse colony sides are usually present". Morozova herself (1973) claims that "accessory pores" (heterozooecia) are invariably present in both

Septopora and Acanthocladia, but Acanthocladia is assigned to the Polyporidae, not the Septoporidae, by Dunaeva and Morozova. The number of rows of zooecia (two or more) is not unique to the Septoporidae and the occurrence of branches which are derived from the points of connection of the opposite halves of dissepiments is a variable character which is unlikely to be of any taxonomic significance even at the species level, let alone that of the family.

The consistent placing of genera into families which have a closely constrained and exclusive diagnosis is very difficult. The small number of species observed in the present study means that the total limits of intrageneric variability of morphological parameters can be estimated only using other authors' work. On the basis of zooecial chamber morphologies and ovicell type seen in the present study, several of the genera considered are distinct and others can be grouped together. Acanthocladia, Synocladia, Thamniscus and Penniretepora all have almost identical zooecial chamber morphologies and have identical ovicells (see p.53 for discussion of ovicells). The zooecial chamber of Kingopora is different from these and is also different from that of Fenestella - Kingopora has ovicells of a different type to those of Acanthocladia and none have been found in Permian species of Fenestella. The placing of Synocladia in the family Septoporidae by Dunaeva and Morozova (1975) is rejected here on the basis of the zooecial chamber shape in the genus and because of the poor definition of that family. It is suggested that it be united in a family with Acanthocladia, Thamniscus and Penniretepora and, very tentatively, with Kingopora (until more genera can be studied Dunaeva and Morozova's general conclusions have to be accepted). Fenestella

is quite distinct from these genera and should be retained in the family Fenestellidae. The family Polyporidae will be used here for the other genera but with an amendment of the diagnosis given for it by Dunaeva and Morozova (op. cit.) so that it may contain genera with two rows of zooecia. A subdivision of this family is warranted on the basis of the distinct form of the zooecial chamber and ovicell in Kingopora - it will be placed in the subfamily Reteporidrinae Dunaeva and Morozova. Acanthocladia, Thamniscus, Penniretepora and Synocladia have constant and obvious differences in zoarial morphology and number of rows of zooecia but these are considered features of generic taxonomic significance and so these genera are placed in the subfamily Acanthocladiinae.

Table I
Families in the Fenestrata

Author	Families	Characteristics	Some of Genera Assigned to Family
King, 1849	Fenestellidae Thamniiscidae	Reticulated Free stems and branches	<u>Fenestella</u> , <u>Polypora</u> , <u>Phyllopora</u> , <u>Synocladia</u> <u>Phyllopora</u> (<u>Kingpora</u>) <u>Thamniiscus</u> , <u>Acanthocladia</u>
Zittel, 1850	Acanthocladiidae	As for King's (1849) Thamniiscidae	<u>Acanthocladia</u>
Naupen and Pichl, 1885	Fenestellidae King's Subfamilies Fenestellinae Polyporinae	Differentiated from Thamniiscidae by fenestrules keel and 2 rows of apertures No keel, more than 2 rows of apertures	<u>Fenestella</u> , <u>Lycopora</u> <u>Synocladia</u> , <u>Phyllopora</u> (<u>Kingpora</u>) <u>Fenestella</u> , <u>Phyllopora</u> (<u>Kingpora</u>), <u>Thamniiscus</u> <u>Acanthocladia</u> , <u>Synocladia</u> , <u>Penniretepora</u>
Pichl, 1890	Fenestellidae King Acanthocladiidae Zittel	Non-poriferous dissimilants Lateral branches	<u>Polypora</u> , <u>Phyllopora</u> (<u>Kingpora</u>) <u>Synocladia</u> , <u>Septopora</u>
Neretova, 1962	Polyporidae Vine (1883) Septoporidae	More than 2 rows of zooecia Zooecia-bearing dissimilants	<u>Polypora</u> , <u>Phyllopora</u> (<u>Kingpora</u>) <u>Synocladia</u> , <u>Septopora</u>
Terrier and Terrier, 1971	Polyporidae Vine Acanthocladiidae Zittel	More than 2 rows of zooecia Carinae and nodes absent Main branches and oblique secondary branches with zooecia.	<u>Thamniiscus</u> , <u>Protoretepora</u> (<u>Phyllopora</u> , <u>Kingpora</u>), <u>Polypora</u> , <u>Septopora</u> , <u>Acanthocladia</u> , <u>Penniretepora</u> , <u>Phyllopora</u> .
Donovan and Norton, 1975	Fenestellidae King Polyporidae Vine Subfamilies Acanthocladiinae Reteporidiinae Septoporidae Norton	2 rows of zooecia and distinct median keel. 3 or more rows of zooecia zooecial bases rhombic or hexagonal. Lack regular dissimilants Reticulated, branches and fenestrules joined by wide short dissimilants. Zooecia-bearing dissimilants. <u>Penniretepora</u> branches may be derived from dissimilants.	<u>Fenestella</u> , <u>Penniretepora</u> <u>Acanthocladia</u> , <u>Thamniiscus</u> <u>Kingpora</u> <u>Synocladia</u>

Family Fenestellidae King, 1849

Type Genus

Fenestella Lonsdale, 1839

Diagnosis

Fenestrata with zoaria forming reticulate expansions of branches connected at regular intervals by sterile dissepiments. Autozooecial apertures in two rows on the obverse surface, separated by a median carina with nodes at its apex. Nodes may be extended to form a superstructure. The reverse surface may be granular, pustulose, nodose or longitudinally striate. Nanate zooecia and ovicells may occur.

Range

Ordovician to Permian (? Triassic).

Procedure followed historically in the Taxonomy of
fenestellids

The very earliest descriptions of fenestellids were entirely qualitative e.g. Schlotheim (1816/17), but authors soon became aware that the geometric regularity of the fenestellid zoarium could be expressed quantitatively and that it had taxonomic significance. McCoy (1844) was probably the first to appreciate this when he quoted the number of apertures per fenestrule in his species. In 1881 Shrubsole tabulated data giving the number of apertures per fenestrule, the number of fenestrules in a unit distance and the number of branches in a unit distance. The tabulation of his data facilitated comparisons between five species of Carboniferous Fenestella. This basic format has been revised in many ways ever since, but many authors still present data in tabulated form, e.g. Morozova (1970). A greater variety and accuracy of measurements were achieved by Ulrich (1890) for numerous species of Fenestella. Cumings (1904) sounded a cautionary note with regard to the proliferation of species made possible by increasing accuracy of measurement. He suggested that several Palaeozoic species of Fenestella were erected on the basis of small fragments of zoaria and no account was taken of the intra-colonial variation of dimensions. He wrote, "The only reliable criterion of a species is the entire zoarium". Nekhoroshev (1926) separated some of the measured parameters for special consideration (number of fenestrules in unit length, number of branches in unit width and number of apertures in unit length), these were used as a means of indexing a species and became known later as

the meshwork formula, Condra and Elias (1944) and then the micrometric formula, Miller (1961). The formula was stated thus:-

No. Branches in 10mm/No. Dissepiments in 10mm/

No. Apertures in 5mm/ No. Nodes in 5mm.

e.g. 14-17/16-20/23-25/20-24

However, the micrometric formula was not always a convenient or accurate means of comparing or defining species. Methods of measurement differed between authors - some using the "space-count" method where, for example, the number of spaces between apertures would be counted instead of the number of apertures themselves, e.g. Condra and Elias (1944) and others counting the actual number of features in a fixed distance. The range of values found in a species was often all that was given with no indication of a mean. Elias and Condra (1957) stressed the need for awareness of the variability that might occur in a meshwork intraspecifically. Utgaard and Perry (1960) used the micrometric formula but also drew histograms to show the mode of a series of measurements. Tavener-Smith (1966b) drew attention to the shortcomings of the micrometric formula when it was used in comparative work; he suggested that more direct measurement was required, e.g. measurement of Fenestrule Length, Fenestrule Width, Inter-Apertural-Distance, Inter-Nodal-Distance, Branch Width and Dissepiment Width and that minima, maxima and averages should be stated for individual colonies and the colony averages for measured parameters should be grouped together to give the average value for a species. The distribution of such values should be approximately a normal distribution unless there is more than one species present in the sample. A standard t-test can then be used to test the

significance of any apparent discontinuities in a measured parameter. Tavener-Smith stressed the need to state sample size when attempting comparisons of data - a procedure which was ignored by most other authors. Although Tavener-Smith's taxonomic procedure was sound with regard to the external form of a colony he made almost no mention of the characteristics of species which are observable in thin sections. Russian workers have been aware of the taxonomic significance of these features since the early part of the twentieth century, e.g. Likharev (1926), Nekhoroshev (1926, 1932). The shape of the zooecial chamber, in particular its base, was considered useful in taxonomy at species level by many authors, although some considered it to be of generic significance (see p. 77). Another feature observable in thin section which has been used for specific subdivision is the morphology and distribution of skeletal rods. At the present day most authors now combine a statistical analysis of external features with those observed in thin sections, although new species are still erected on the basis of dangerously small sample sizes; taxonomic procedure of this kind is partly responsible for recent great proliferation in the number of species of Fenestella. It is very likely that a number of synonyms exist in the publications of authors who work with such small sample sizes and who examine only imperfectly preserved oblique thin sections.

Taxonomic Procedure Followed in the Present Study

The procedure followed is essentially that described by Tavener-Smith (1966b) for fenestrate cryptostomes.

A qualitative assessment is made of the morphology of elements of the zoarium in the taxon. Elements whose morphology is described include: branches, dissepiments, fenestrules, apertures, peristomes, carinae, nodes, ornamentation, autozooecial chambers, the chambers of polymorphic zooecia and the microstructure of the skeleton. The morphology of the zoarium as a whole is considered also. Most of these elements are defined quantitatively and a statistical analysis of the data may be undertaken to assess the significance of any apparent morphological discontinuities. Minima, maxima and averages are calculated within a colony. Colony average values are then used to calculate the minimum, maximum and average values for a sample. Standard deviations (S.D.) and Coefficients of variation (C.V.) are quoted for these data - Standard deviation is a measure of the spread about the mean and is the square root of the variance. Variance may be regarded as the average squared deviation of all possible observations from the population mean, Davis (1973). A large value of Standard deviation indicates that values have a large spread about the mean and a weak tendency for clustering. Coefficient of Variation is another measure of the spread of the data about the mean and is

$$\frac{\text{S.D.}}{\text{Mean}} \times 100$$

Histograms of colony means are plotted to provide an indication of the distribution of the data and a t-test may be used to assess the probability of more than one species being represented in the data.

Fig. 15 shows parameters measured on the genus Fenestella.

Branch Width (B.W.) is measured perpendicular to branch length in the mature part of a zoarium, away from bifurcation points and

dissepiments. The juvenile part of a zoarium is avoided for such measurements because the branch here is susceptible to a thick accretion of outer laminated skeleton. The branch width increases significantly prior to bifurcation and to a lesser extent where a dissepiment joins the branch. Branch width is closely correlated with the size of zooecial chambers and is likely to be a useful parameter for specific determinations.

Dissepiment width (D.W.) is measured perpendicular to a dissepiment's length at its mid-point, where it is thinnest.

Fenestrule length (F.L.) is measured from the mid-points of adjacent dissepiments in the direction of branch growth. Proximal parts of zoaria are avoided in favour of mature regions where fenestrule length becomes stabilized. Fenestrules close to bifurcation points are also avoided.

Fenestrule width (F.W.) is measured from the centres of adjacent branches, perpendicular to the direction of branch growth. Proximal parts of zoaria are avoided in favour of more mature parts where fenestrule width becomes stabilized. Bifurcation points are avoided and so are areas of a zoarium where fenestrules are constricted.

Inter-apertural-distance (I.A.D.) is measured between the centres of apertures which are adjacent in a single longitudinal row of a branch. It is closely correlated with the length of zooecial chambers and is likely to be a useful parameter for specific determinations.

Inter-nodal-distance (I.N.D.) is measured between the centres of nodes which are adjacent in a single longitudinal row of a branch.

Apertural diameter (A.D.) is measured between the inner rims of an autozooecial aperture. If an aperture is not circular the longer

and shorter dimensions are given.

Zooecial chamber base parallel to length (Z.B.L.) is the maximum dimension of the zooecial chamber base parallel to the length of a branch. This can be measured in tangential thin sections and in specimens in cast preservations.

Zooecial chamber base perpendicular to length (Z.B.W.) is the maximum width of the zooecial chamber base perpendicular to the length of a branch.

The number of apertures per fenestrule is given in descriptions, for the convenience of comparison with the work of other authors, although it is a character made redundant by the presence of both inter-apertural-distance and fenestrule length together in the description. The micrometric formula is also given for the above reason, in spite of its redundancy.

Thin sections are prepared in specific orientations:- Tangential, along the length of branches, transverse, perpendicular to the length of branches and longitudinal, along the length of one branch (see fig. 16). The various elements visible in thin section are described.

Genus Fenestella Lonsdale, 1839

Type Species

Fenestella subantiqua d'Orbigny, 1850 = F. antiqua Lonsdale 1839 [partim, non Gorgonia antiqua Goldfuss, 1829].

Diagnosis

Fenestellid with two rows of autozooecial apertures on branches. Branches connected at regular intervals by sterile dissepiments. Zooecial chamber bases triangular, trapezoidal or pentagonal. Carina with nodes variably developed. Reverse surface with longitudinal striae, nodes or pustules. Ovicells and nanate zooecia may occur.

Range

Silurian to Permian (Triassic?)

Generic Level Subdivision of Fenestella

Hall (1885) erected several new genera which were closely related to Fenestella, differing only in the nature of the keel and processes developed from the keel, e.g. Isotrypa and Unitrypa. The expansion of the keel and reduction of dissepiments characterised his genus Loculipora. In 1895 Simpson divided Fenestella into seven groups on the basis of different carinal morphologies. The genus Hemitrypa is widely recognised as being similar to Fenestella - it was erected by Phillips in 1841 and consists of a normal reticulate Fenestella meshwork surmounted by an anastomosing superstructure with hexagonal openings; each hexagonal opening lies directly above an autozooeal aperture, Bancroft (1984). The network is connected to the branches of the zoarium by regularly spaced carinal nodes. Hinganotrypa (Romantchuk and Kiseleva, 1968) is similar to Hemitrypa which is considered to be ancestral to Hinganotrypa by Romantchuk and Kiseleva (1968). It has a superstructure with double the number of openings of Hemitrypa - on average with two openings per autozooeal aperture. The genus Cervella was erected by Chronic (1949) for forms identical to Fenestella except for the extension of carinal nodes into asymmetrically stellate processes - these processes may be so well developed that they form an almost completely interlocking meshwork. In his generic diagnosis Chronic wrote "When well developed, these structures recall the form of the antlers of deer". It is apparent from his descriptions of species assigned to this genus that the development of the processes on the nodes is variable, e.g. "transversely elongate stellate processes" in Cervella cervoidea and

"erect spines which branch laterally one or more times near the top" in C. aspera. In the present study nodes have been found which branch laterally near their top in Fenestella retiformis. Other nodes have been found with lateral projections and others are simple straight spines. The variable occurrences throughout a zoarium of these highly developed nodes, may be a true representation of their original distribution, or it could be a preservational effect. In view of the variability described by Chronic in his own species of this genus and the analogous variability found in the morphology and distribution of nodes in Fenestella retiformis the generic status of Cervella is doubtful. Elias and Condra (1957) considered Cervella a subgenus because the characteristic nodes were not developed over the whole zoarium and because they believed similar developments occurred in more than one phyletic lineage of Fenestella in the Permian, Carboniferous and Devonian. Morozova (1974) denied the generic status of Cervella and stated that most authors now considered it a junior synonym of Fenestella. Popeko and Gorelova (1975) also considered it a junior synonym of Fenestella. Likharev (1926) described large nodes in F. retiformis from the Vologda region. They often showed lateral projections at their tops which, in some cases, were sutured with those from a neighbouring branch to produce a continuous superstructure. The fact that a superstructure of a morphology comparable to that found in Hemitrypa can be partly developed or not developed at all within one species militates against the feature having generic significance. However, evidence derived by analogy ought not to be considered more important than that derived empirically and Bancroft (pers. comm.) claims that the superstructure

of Hemitrypa is a constant feature and of generic significance.

Since Nekhoroshev (1932), a number of authors have expressed reservations about the homogeneity of the genus Fenestella and have cited features such as size of fenestrules and variation in the shape of zooecial chambers as reasons for grouping species together or creating new genera.

Nekhoroshev (1932) noted great differences in the internal structure of species of Fenestella but did not propose any subdivision of the genus. Elias (1937) suggested groupings of Carboniferous and Permian species on the basis of the number of apertures per fenestrule and the number of rows of carinal nodes. Trizna (1939) and Shulga-Nesterenko (1941) both suggested groupings of species based on morphological similarities and Shulga-Nesterenko (op. cit.) claimed her groups were phylogenetically distinct. Shulga-Nesterenko (1952) extended her work on separate lineages within the genus Fenestella and suggested distinct branches of Carboniferous and Permian species with their supposed phylogenies. While the details of her phylogenetic interpretation are bound to be somewhat speculative, the concept of grouping Fenestella species on the basis of morphology seems reasonable (the very large number of species of Fenestella, over 2000 at the present day, is often cited as a reason for generic subdivision, perhaps with some justification). Elias and Condra (1957) also attempted to group species together on morphological and phylogenetic grounds. They recognised thirteen groups on the basis of diverse characters:-

- (1) The number of zooecia per fenestrule.
- (2) The stability of the position of zooecial apertures relative to

dissepiments.

(3) The shape of the zooecial chamber, particularly its base.

(4) Whether one or two rows of carinal nodes occur.

(5) The existence of longer and shorter fenestrules in the same zoarium.

(6) Zoarial growth form, if stabilized.

However, the choice of characters which define the various groups appears to be inconsistent. In some cases the shape of the zooecial chamber base is supposed to be characteristic and in others it is the shape of the zoarium. A combination of supposedly group-distinctive characters within one species renders the classification unworkable. Any attempt to explain such occurrences as homeomorphies or examples of polyphyletic derivation of features is as unreasonable as the classification itself. The 13 groups are classified into 3 larger sections. These sections are not distinct; a continuum appears to exist between sections 'A' and 'C'. According to Elias and Condra (op. cit.) section 'A' consists of "groups with long fenestrules: 3 to 5 zooecia per fenestrule and a single row of nodes", section 'C' consists of "groups with short fenestrules: 2 to 3 zooecia per fenestrule, and a single row of nodes". By their own definition there is a continuum between these sections - but they also place their groups IV and V in section 'A', these groups are defined by having 2 to 3 zooecia per fenestrule. These sections obviously are not significant. Although better conceived, the 13 groups should be rejected because of inconsistencies in definition and because this work of Elias and Condra is superceded by more recent authors.

Miller (1961) erected the new genus Parafenestella for forms with

a node developed on the dissepiment. He cited, as his justification, the generic significance attributed to the double row of carinal nodes in Minilya by Crockford (1944 b). He also suggested that homology of these nodes with trepostome acanthopores (stylets, styles) favoured their generic taxonomic significance.

Termier and Termier (1971) subdivided Fenestella into 8 genera:- Fenestella (s.s.), Aequifenestella, Rhombofenestella, Alternifenestella, Spinofenestella, Rugofenestella, Fenestellina, and Mirandifenestella. Type species were designated for only five of these and thus Aequifenestella and Rugofenestella (without types) are invalid. The scheme is rendered unworkable because, in several cases, the morphological features which are supposed to characterise each new genus are not properly defined.

Morozova (1974) places species of Fenestella into 14 separate genera - she claimed that these were "natural groupings of species that are connected by common origin and developed independently in different stages of the Paleozoic." These groups were defined on features such as the shape of zooecial chambers, the nature of the carina and the diverse manifestations of polymorphism in species. The shape of fenestellid colonies was considered to be an adaptive feature largely dependent on abiotic and biotic factors. She retained the genera Alternifenestella and Spinofenestella of Termier and Termier (1971) as well as Archaeofenestella of Miller (1962) and erected ten new genera. Most of these new genera seem distinct and fairly consistent; the majority are defined by differences in the shape of the zooecial chamber. It is, however, regrettable that Morozova usually describes the cross sectional shape of a zooecium without

stating the level at which it is seen in the branch. It has to be assumed that the zooecial chamber base shape is that which is given. Rectifenestella (Morozova n. gen.) is supposedly distinguished from Spinofenestella Termier and Termier (1971) by the shape of the zooecial chamber, it being pentagonal in the former and triangular in the latter. However, in her diagnosis of each genus she described the chamber shape as triangular - pentagonal before bifurcation. This alone is not enough to warrant doubting the distinct identity of these genera but she referred F. retiformis to Rectifenestella; F. retiformis has a triangular zooecial chamber base shape rather than pentagonal, so that either Morozova's concept of F. retiformis is wrong or there is intrageneric variability from triangular to pentagonal zooecial chamber base shape. In view of this uncertainty it is proposed to retain the genus Fenestella for F. retiformis in preference to Morozova's Rectifenestella. While accepting that there is justification for generic subdivision of Fenestella, Morozova's scheme, like those before it, is far from perfect, relying on variable combinations of characters to distinguish genera and phylogenetic interpretations which are bound to be circumspect.

Popeko and Gorelova (1975) make specific criticisms of Morozova's scheme, citing species which have combinations of supposedly generically distinct features. These species cannot therefore be assigned solely to one of Morozova's genera. They also comment on Morozova's grouping of species where the generic diagnosis contradicts the typical species morphology. They reject the phylogenetic approach because of its inherent uncertainties and propose a phenetic classification based on the shape of the zooecial chamber base, the

presence or absence of nodes on the peristome, the structure of the carina and the microstructure of the skeletal tissue. These characters are expressed as variables in a table which shows that 120 different combinations of these features are possible. They assign species to various combinations but do not consider there to be any generic groupings present in their system of 120 "classes", even though several "classes" remain unoccupied by known species (this conclusion depends on the potential of undiscovered species to fall into "classes" currently unoccupied). Since each "class" is considered equal in rank and prohibited combinations of characters are absent, then "class-level" discontinuities are not considered sufficient to warrant generic subdivision of Fenestella. This approach is essentially that of the numerical taxonomist but the absolute objectivity of any such grouping is illusory because an initial choice of characters for the system is made which does not represent the total sum of characters defining the genus and its species.

For the purpose of the present study the genus Fenestella is retained, not as a statement of belief in the homogeneity of the genus but because all attempts at subdivision have proved unsuccessful or inconsistent to varying degrees.

Fenestella retiformis Schlotheim, (1816-17)

Figs. 17-26, Pls 1-31

- 1816-17 Keratophytes retiformis Schlotheim p. 17, pl. 1, figs. I, II
- 1820 Escharites retiformis Schlotheim p. 342
- 1826-33 Gorgonia infundibuliformis Goldfuss p. 20, pl. X, fig. I
- 1846 Gorgonia retiformis Schlotheim; Geinitz p. 585
- 1848 Fenestella retiformis Schlotheim; Geinitz p. 17 pl. VII,
figs. 11 and 12 [partim - non fig. 13]
- 1848 Fenestella retiformis Schlotheim; King, p. 6
- 1850 Fenestella retiformis Schlotheim; King p. 35, pl. II, figs.
8-19
- 1861 Fenestella retiformis Schlotheim; Geinitz p. 116, pl. XXII,
fig. 1
- 1926 Fenestella retiformis Schlotheim; Likharev p. 1012-1027, pl.
14, figs. 1-5, 7, 8 and 10, pl. 15, figs. 2-4 and 6
- 1930 Fenestella retiformis Schlotheim; Korn p. 354, pl. I, figs.
1, 2, 4 [partim-non fig. 3]
- 1930 Fenestella minuta Korn p. 356, pl. I figs. 7, 8, 13, 14, pl.
III fig. 10
- 1936 Fenestella retiformis Schlotheim; Shulga-Nesterenko pp. 240,
271.
- 1941 Fenestella retiformis Schlotheim; Shulga-Nesterenko p. 77,
pl. X fig 3, ?pl. XI fig. 6
- 1948 Fenestella retiformis Schlotheim; Trizna.
- 1961 Fenestella retiformis Schlotheim; Dreyer p. 9-12, pl. I
figs. 1-5, pl. II, pl. III

- 1961 Fenestella cf. retiformis Schlotheim; Sakagami p.35, pl. 17,
 figs. 1-3
- 1968c Fenestella retiformis Schlotheim; Sakagami p. 57, pl. IX
 fig. 5
- 1970 Fenestella retiformis Schlotheim; Morozova p. 162, pl. XXX
 fig. 2, pl. XXXII fig. 1.

Types

The specimen (K20) from Schlotheim's collection which was described in the present study does not correspond to either of the specimens figured in Schlotheim's original description (1816/17, Tab. 1, figs. I and II). Schlotheim did not select any specimen as holotype. No later author has designated any specimen as neotype or lectotype.

Diagnosis

Fenestella with 2½-3 autozooecial apertures per fenestrule. Apertures fairly small and closely spaced. Straight, fairly narrow branches. Dissepiments fairly narrow. Fenestrules fairly short and rectangular. Median carina developed with regularly spaced nodes. Nodes may extend into processes which bifurcate, trifurcate or have lateral projections. Zooecial chamber bases triangular. Nanate zooecia may occur.

Description

External

Zoaria are infundibuliform. After initial fairly steeply erect growth the inverted cone often flattens to an almost horizontal zoarial lamina (see Pl. 1); the auto-zooecial apertures always open onto the inside of the cone. The lamina of the zoarium may be variably plicate; at its maximum development this plication leads to the formation of festoons - a common feature of this species (see Pl. 1, Pl. 2 fig. a), multilaminar growth sometimes results from this. Intra-colonial fusion of branches may occur, especially in areas of festoon development. Spines occur on the reverse surfaces of branches, in particular, close to the origin of the colony (see Pl. 2 fig. b).

Fenestrules are quite small and usually rectangular (rarely, almost square). The corners may be rounded to varying degrees rarely producing almost oval fenestrules. The sides of fenestrules may be sinuous with a bulge near their mid-point caused by the protruberance of an autozooecial apertural margin (see Fig. 17 and Pl. 7).

Branches are fairly thin and have sides which slope fairly steeply into the fenestrules and up into the median carina. The median carina is straight, angular and prominent, and has a single row of closely and regularly spaced nodes (see Pl. 8). These nodes may bifurcate or trifurcate at their apex or may show lateral projections. They may reach a height above the obverse surface of 0.475mm and their lateral projections may extend at right angles to the main stem of the node for up to 0.07mm. The bifurcations and trifurcations of the nodes show angular divergences up to about 80° (see 19 and Pl. 9). At

their bases, the nodes are fairly broad and elongate parallel to branch length, higher up they become more circular in cross-section and may become elongate perpendicular to branch length where they bifurcate (see Fig. 19). There are 2½-3 autozooecial apertures per fenestrule - often with one at the junction with each dissepiment and one at the mid-point of the fenestrule. They open on the sloping sides of the branch and have a thin peristome. The peristome is more elevated on the side of the aperture nearer the fenestrule so that the aperture is directed upwards rather than laterally into the fenestrule. A small node occurs on the proximal edge of the peristome. Apertures are fairly small, circular, and closely spaced. Nanate zooecia occur rarely (see Pl. 8). Branch width increases slightly for one to two fenestrules prior to bifurcation. In the angle of the bifurcation an extra zooecium is developed which may be larger than normal zooecia and of a different shape (see Pl. 10). (This is considered to be a Kenozooecium). The reverse surface is gently rounded and may show three, rarely more, longitudinal striae.

Dissepiments are thin and quite depressed relative to the obverse surface; they expand in width as they join the branches. They are much less depressed relative to the reverse surface. On the obverse surface they are gently rounded but are more steeply rounded on the reverse and do not expand in width at the branch junction to such an extent as on the obverse surface.

Internal form and Skeletal Microstructure

In cast preservation the zooecial chamber base has a triangular shape with gently rounded corners (see fig. 18).

In tangential section the zooecial chamber base is triangular - this becomes pentagonal (hemi-hexagonal) with rounded corners close to the zooecial chamber base then sub-reniform/oval and then circular as the vestibule is reached (see e.g. Pl. 10). The zooecial chambers interlock at the level of their bases - the interzooecial wall zig-zags between them for the length of the branch (see Pl. 11). The inner laminated skeleton is more thickly developed near the base of zooecial chambers than it is near the obverse surface. In tangential section 5 longitudinal striae can be seen, with the outer 2 tending to be situated more on the sides of branches. In transverse section up to 12 ridges can be seen which extend well up the sides of branches and close to the obverse surface (see Pls. 12, 13). The 'inner platy core' (Elias and Condra, 1957) of the longitudinal striae appears to remain in extinction in all orientations in some cases - it is fairly thin (see Pls. 14, 16). The outer component of the primary granular layer is variable in thickness, but is thicker than the 'inner platy core' (see Pls. 14, 16). The point of fusion of the two halves of a dissepiment is usually defined by a discontinuity in skeletal structure (see Pl. 12 fig. a). The boundary between the outer laminated layer and the primary granular layer is not very regular; there are often patches of primary granular layer contained within the outer laminated layer and 'wisps' of laminated material which pass laterally into primary granular material (see Pl. 17 fig. a). The thickness of the outer laminated layer is very variable but is thicker on the reverse than it is on the obverse surface. The outer laminated layer shows a deflection in its growth in places, where the laminae form a V-shape pointing towards the reverse surface

(see Pl. 17 fig. b). These minor perturbations of the laminated layer have no granular core and do not extend to the surface of the branch, but are otherwise similar in morphology to the disturbances caused in the outer laminated layer by skeletal rods; these are considered to be poorly developed skeletal rods. Rare and fairly irregularly distributed nodes may occur on the reverse surface (see Pl. 18). They have granular cores surrounded by concentric outer laminated skeleton. They are circular in tangential section and variable in size (see p. 96).

Measurements (Refer to fig. 15 for abbreviations)

These measurements do not include the specimens seen from Museum Collections in East Germany.

N = 128

	NM	Mn	Mx	S.D.	C.V.	$\bar{X}$
F.L.	1160	0.497	0.717	0.0516	8.46	0.61
F.W.	1100	0.40	0.572	0.0394	7.9	0.498
B.W.	850	0.143	0.308	0.032	14.4	0.222
D.W.	780	0.073	0.190	0.023	18.7	0.123
I.A.D.	600	0.208	0.293	0.0165	6.5	0.253
I.N.D.	220	0.18	0.34	0.03	11.6	0.258
Z.B.L.	200	0.183	0.246	0.016	7.5	0.214
Z.B.W.	200	0.10	0.15	0.012	9.4	0.127
A.D.	100	0.084	0.106	-	-	0.098

Micrometric Formula 18-25/14-20/17-24/15-28

Measurements on Schlotheim's Material

Only one specimen of Schlotheim's original material was available
- specimen number K20 (see Pl. 19).

	NM	Mn	Mx	$\bar{X}$
F.L.	15	0.55	0.65	0.605
F.W.	15	0.45	0.55	0.518
B.W.	15	0.14	0.21	0.175
D.W.	15	0.09	0.13	0.106
I.A.D.	15	0.24	0.26	0.251
Z.B.L.	9	0.16	0.22	0.202
Z.B.W.	9	0.10	0.13	0.115

Micrometric formula 21/18-19/20

These measurements (although probably fortuitously) correspond well with the average values for the whole sample from the reef in N.E. England.

Measurements on Korn's Material

These are the measurements on the specimens which were correctly assigned to F. retiformis by Korn - Taf. I fig. 1, 2 and Taf. I fig. 4 (see Pl. 20).

N = 2

	NM	Mn	Mx	$\bar{X}$
F.L.	19	0.54	0.66	0.593
F.W.	18	0.42	0.64	0.534
B.W.	18	0.19	0.28	0.245
D.W.	18	0.09	0.15	0.128
I.A.D.	3	-	-	0.25

Figures 20 and 21 show histograms of the colony average values for F.L., F.W., B.W., and I.A.D. In each case the modal value corresponds well with the mean calculated value (see above). I.A.D., B.W. and F.W. are all clearly unimodal with an approximately normal distribution. F.L. can also be considered unimodal although it does show a secondary peak at F.L. = 0.52-0.54 mm and a smaller peak at F.L. = 0.7-0.72 mm. These secondary peaks can probably be explained as sampling biases. The data from the other measured parameters were not plotted as histograms because of the low number of averages available or because of the small scale of the variation shown by the parameters. It is clear from these graphs that the data represent a single, homogeneous species.

The range of colony mean values of fenestrule length is quite large. It is of the same scale as that considered to warrant specific subdivision by some authors. The importance of a large sample size is demonstrated by this parameter whose end-members show no degree of overlap - fig. 22 shows a hypothetical histogram of a biased sample of nine specimens of F. retiformis. The bimodality of fenestrule length is caused by the small biased sample. Several authors erect new species on samples of this size and on the basis of a difference in one parameter - the dangers inherent in such a procedure are obvious.

Inter-locality variation

The measured parameters were studied by locality to try to ascertain whether any of their variability could be explained by environmental factors or by intra specific evolution (Elias (1937) described an evolutionary increase in fenestrule dimensions in

Carboniferous and Permian Fenestella - though his data base may not justify all his conclusions). The parameter which showed most variation in the present study was fenestrule length. Fig. 23 shows the average values for F.W. and F.L. at each locality, with the range of colony averages. There appears to be a weak correlation between the locality average values of F.L. and relative stratigraphic position in the reef - a standard statistical test of significance cannot be applied to these data since stratigraphic position in the reef cannot be quantified. Those localities near the top of the reef (SBC, BH, HM7, MP1, RH2) tend to have low locality mean values of F.L. whereas those nearer the base of the reef (RH1, RH4, HYR, MP5) tend to have higher values (see below).

	F.L. (mm)
SBC	0.575
BH	0.576
HM7	0.562
MP1	0.578
RH2	0.586
RH1	0.64
RH4	0.662
HYR	0.642
MP5	0.624

However, the data from localities HA and HM5 contradict this pattern - HA is stratigraphically above HM7 and the locality mean value of F.L. is 0.614 mm (cf. 0.562 mm at HM7) - HM5 is only just below HM7 stratigraphically but the locality mean value of F.L. is 0.62 mm.

It is generally accepted (e.g. Trechmann, 1913 and Smith, 1981) that the stratigraphically higher reef localities have reduced faunas as a consequence of increased environmental pressure - if conditions were significantly different between lower and higher parts of the reef then any systematic variation of fenestrule length could be explained as ecophenotypic variation; it would be impossible to prove the existence of a component of intraspecific evolution which effected fenestrule length.

Although the locality means of fenestrule length show quite large differences the spread of the colony means which comprise the data is also very large e.g. at locality RH2 the variation is from 0.526 mm to 0.686 mm, and at locality HYR from 0.55 to 0.716 mm. Both of these encompass almost the total variation found and thus the weak pattern observed in locality mean variation is likely to be insignificant.

Comparison of within and between colony coefficients of variation

Dissepiment width and zooecial chamber base measurements are not considered because of their small size. Inter-apertural-distance is not considered because it shows so little variation.

The table below compares the average value of intra-colony C.V. and inter-colony C.V. for a representative sample of the species - the number in parentheses is the C.V. for all specimens of F. retiformis.

	Intra	Inter	n
F.L.	4.72	10.5(8.46)	13
F.W.	7.11	8 (7.9)	13
B.W.	6.19	13.8(14.4)	10
I.N.D.	5.18	10.3(11.6)	7

The ranges of intra-colony C.V.s are shown on the histograms of fig. 24.

A simple visual comparison of the coefficients of variation suggests that the inter-colony component of variance adds significantly to the "total variance" in all of the measured parameters apart from fenestrule width. Schopf (1976) describes a method for evaluating the contributions to what he calls the "total variance" of the within and between colony components of variance. The "total variance" consists of the additive sum of the variances of the individual colonies ($\sum \sigma_w^2$), plus the between colony variance for n colonies ($n\sigma_b^2$). Then, using the F test described by Schopf and Dutton (1976) the significance of the between colony component of variance can be assessed using :-

$$F = \frac{\sum \sigma_w^2 + n\sigma_b^2}{\sum \sigma_w^2}$$

The significance of the within colony component of variance is assessed by:-

$$F = \frac{\sum \sigma_w^2 + n\sigma_b^2}{n\sigma_b^2}$$

The critical value of F is read from tables - the number of degrees of freedom of numerator and denominator is one less than the number of observations for each of the variances summed.

For fenestrule length, branch width and inter-nodal-distance the between colony component of variance was significant at the 1% level. The between colony component of variance of fenestrule width was not

significant at the 5% level - but was fairly close to significance. The within colony component of variance was not significant for any of these parameters at the 5% level, but fenestrule width came close to being significant.

The data for fenestrule width demonstrate that the within colony variance is as good an estimate of total variance as is the between colony variance. Since a bryozoan colony is a genetically homogeneous entity the within colony variance is a measure of microenvironmental influences and the natural variability of different stages in the development of the colony. The between colony variance includes these factors plus a component of intra-specific genetic variability and a component due to macroenvironmental influences. Thus, the macroenvironmental and genetic influences on fenestrule width appear to be similar in importance to those of microenvironment and colony development. The macroenvironmental and genetic influences on fenestrule length appear to be more significant than those of microenvironment and colony development. The same is true for branch width - this is a little surprising since branch width ought to be a very constant specific character but one which varies a great deal within a colony because of the thick accretion of outer laminated skeleton in more proximal parts - the results could be explained by the fact that almost no specimens are complete colonies, the large between colony variance could be reflecting the representation of different parts of colonies in the fragmentary specimens; alternatively, a thicker branch might be an adaptation for greater structural strength in a higher energy environment. Inter-nodal-

distance also shows a greater influence from macroenvironmental and genetic factors than from microenvironmental and developmental factors. Unfortunately, in as heterogeneous an environment as a reef, it is almost impossible to separate variability due to genetic differences from that due to macroenvironmental influences.

Measurements in Thin Section

Measurements of branch width demonstrate that much of the 'within-locality' variation in this parameter could probably be explained by the variable thickness of the outer laminated layer. This can be between $13\text{-}60\mu$ thick on one side of a branch - therefore its variability can account for a 94μ difference in the measured branch width.

The thickness of the inter-zooecial wall varies between $7\text{-}10\mu$ and is constant within a zoarium. The inner laminated layer which lines a zooecial chamber varies in thickness from $3\text{-}13\mu$ but is usually between $4\text{-}6\mu$ thick.

The longitudinal striae extend below the zooecial chamber bases for $17\text{-}35\mu$. The width of the longitudinal striae as defined by different extinction bands is $20\text{-}25\mu$.

Carinal nodes have widths from $33\text{-}106\mu$, measured near their base. Their length is greater than their width and may reach 132μ .

The diameter of the irregularly distributed reverse surface nodes (see p.89) is variable; in 12 nodes measured from one zoarium the diameter varied from $7 - 40\mu$.

Discussion

Fenestella retiformis is a very common species in the Zechstein reef - it was originally described from Glücksbrunn in the Thuringian district of Germany by Schlotheim (1816/17). He figured a specimen of F. retiformis in 1813 but simply referred to it as "Gorgonia". Since then, numerous authors have described the species from various parts of the world (see table 2).

Geinitz (1848) counted 7-9 fenestrules in a 5 mm line in specimens from the Zechstein reef in the Thuringian district of Germany.

King (1850) emphasised the variability of the species, drawing attention to the differences between proximal and distal parts of colonies. However, it seems likely that some of the variability he described was due to his inclusion of specimens of Fenestella geinitzi with F. retiformis e.g. B122B and B103A from the King Collection.

Likharev (1926) measured several parameters of the species (see table 2) and described its microstructure in detail. He remarked, in particular, on the nature of the carinal nodes which reached lengths up to 1 mm and had lateral projections. These lateral projections occasionally were sutured with those of a node from a neighbouring branch forming a sort of "protective grill".

The measurements of Korn (1930) on the species probably have to be treated with a degree of scepticism e.g. Branch width = 0.4 mm - these differ quite markedly from the present author's measurements of Korn's material (i.e. B.W. = 0.245 mm).

Measurements made on a photograph of F. retiformis from Shulgá-Nesterenko (1941) agree fairly well with the results from the present

study.

Dreyer's (1961) measurements on the species agree closely with the results from the present study.

The measurements and description of the species by Sakagami (1968c) agree fairly well with those of the present study, apart from fenestrule length which is larger in the specimens seen by Sakagami - 0.592-0.848 mm with an average of 0.691 mm. Branch width is also larger - 0.272-0.336 mm in Sakagami's specimens.

Morozova (1970) described F. retiformis - her measurements agree well with those of the present study apart from dissepiment width which varies from 0.22-0.36 mm.

TABLE 2

Author	B/10 (F.W.)	D/10 (F.L.)	A/5 (I.A.D.)	B.W.	D.W.	Comments Loc.
Geinitz 1848		14-18				U. Permian Germany.
King 1850						U. Permian England.
Likharev 1926	18-20	14	17-19	0.22-0.46 Ave. = 0.3	0.15-0.2	U. Permian Vologda
Korn 1930	18-19	14-15		0.4		U. Permian Germany
Shulga-Nesterenko 1936	18-21	15½	18-20	0.29-0.35	0.11-0.24	Permian N. Ural
Trizna 1939 = var. <u>tenuis</u>	19-20	13-14	17-18	0.2-0.22	0.11-0.15	U. Palaeozoic Bashkirian Urals.
Shulga-Nesterenko 1941	(19) 0.53	(15) 0.67	(19) 0.26	0.24	0.12	L. Permian Urals.
Trizna 1948	17-20	15-16	18-20	0.28-0.35	0.1-0.17	Permian Sulva river, USSR. (I.N.D. = 0.28- 0.35)
Dreyer 1961	19-21	15-17	20-22	0.24	0.12	U. Permian Germany.
Sakagami 1961 = <u>F. cf. retiformis</u>	17-18	15-16	22-23			Permian Kamiyatsuse, Japan.
Sakagami 1968 c	19-20	14-15	17-19	0.272-0.336	0.16-0.192	Permian Thailand
Morozova 1970	19-21	15-17	20-22	0.24-0.28	0.22-0.36	U. Permian USSR.
Present Study	18-25	14-20	17-24	0.143-0.308 Ave. = 0.222	0.073-0.190 Ave. = 0.123	U. Permian England.

Fenestella minuta Korn (1930) is regarded here as a subjective synonym of F. retiformis. The dimensions given for it by Korn are distinct from his dimensions for F. retiformis - the other differences he cites are the form of the zoarium (being more erect) and the presence of "roots" near the base of the zoarium. The dimensions given by Korn:- F.L. = 0.59 mm, F.W. = 0.417 mm, B.W. = 0.13-0.18 mm, and D.W. = 0.08-0.10 mm overlap with those of F. retiformis from the present study. Spines near the base of a zoarium and the erect form of the zoarium are intraspecifically variable characters - probably related to environment of growth. Measurements on Korn's original material gave these values for parameters:-

	Taf. I fig. 13 & 14 Taf III fig. 10	Taf. I fig. 8
F.L.	0.608	0.598
F.W.	0.448	0.44
B.W.	0.193	0.211
D.W.	0.106	0.102
I.A.D.	0.25	0.234
A.D.	0.08	0.08

On the basis of these data F. minuta is inseparable from F. retiformis.

Dreyer (1961) also comments on F. minuta - her measurements hardly differ from those given by Korn (1930). Thus, it must be concluded that F. minuta is a subjective synonym of F. retiformis

Fenestella geinitzi is a species which can be very similar to F. retiformis. Its zooecial chambers are more or less identical to those

of F. retiformis and all of the measured parameters show a large degree of overlap apart from fenestrule length. There is also some degree of overlap in fenestrule length, which can be the same, intra-colonially, for both species. In the present study it was believed initially that the specimens with longer fenestrules were ecophenotypic variants of the same species, but the occurrence, in the same hand specimens, of zoaria of Fenestella whose average values of fenestrule length were distinct and widely different led to the recognition of the separate species F. geinitzi. Fig. 25 shows a histogram of fenestrule length for both species of Fenestella - although there is a continuum, the graph is bimodal (the weakness of the bimodality is caused by the much rarer occurrence of F. geinitzi). The importance in taxonomy of large sample size is demonstrated by these species. In certain areas of a zoarium of F. geinitzi the fenestrule length may be as low as in F. retiformis (e.g. RH 4.1 has a fenestrule length of 0.7 mm over some areas of the zoarium but is generally 0.76 mm) - a small tangential section of the wrong area of a zoarium would make a correct specific assignment impossible. Although fenestrule width is generally larger in F. geinitzi than F. retiformis no convincing bimodality of data for the genus exists (see fig. 25).

Other species which are similar to F. retiformis include:- F. parviuscula Bassler (1929) which appears to differ only in having shorter and more square fenestrules (probably about 0.48 - 0.5 mm long); F. canthariformis Crockford (1941b) is identical to F. retiformis apart from its larger inter-apertural-distance of 0.29 mm (if this species was erected on the basis of a small sample size its validity may be in question); F. horologia Bretnall (1926) (in

Crockford 1944c) is similar apart from having a larger branch width of 0.31-0.37 mm; F. cacuminatis Crockford (1944b) differs from F. retiformis in having slightly larger fenestrules (approx. 0.7 mm) (it is difficult to tell whether or not it could be conspecific with F. retiformis because of the obviously inaccurate drawings of it and the lack of a photograph); F. nomatae Sakagami (1961) appears very similar to F. retiformis from the measurements given but has a slightly larger I.A.D. of 0.29 mm and appears (from Sakagami's figures) to have fenestrules which are too wide; F. tuberculifera Shulga-Nesterenko (1952) has dimensions which are almost identical to those of F. retiformis but has regularly distributed nodes on its reverse surface, F. vischerensis var. gamovica Trizna (1948) is similar in all respects apart from having a branch width which is larger (0.28-0.35 mm) and a fenestrule length which is smaller (0.56 mm) although it falls within the range of variation found in F. retiformis; F. accurata Trizna (1950) differs from F. retiformis in having a slightly larger fenestrule length (0.66-0.7 mm), a smaller I.A.D. (0.22 mm) and regularly distributed reverse surface nodes; F. veneriformis Trizna (1961) is similar to F. retiformis but has longer fenestrules (0.7 mm); F. perelegans Waagen and Pichl (1885) is similar to F. retiformis but has shorter fenestrules at 0.5 mm and branches which are probably wider; F. pseudostuckenbergi var. gansuensis Yang et Loo (1962) is very similar to F. retiformis but has a slightly larger branch width (0.25-0.3 mm), its zooecial chamber may have a slightly different shape but the figures of Yang and Loo neither deny or confirm this; F. gutayensis Shishova (1960) is very similar to F. retiformis but appears to have shorter and squarer fenestrules - in



spite of the zooecial chamber base shape being described as 5-sided in the text it is clearly triangular in plate V Fig 4; F. microaperturata Shulga-Nesterenko (1941) is indistinguishable from F. retiformis on the basis of any of its measurements (micrometric formula = 21-22/17/20-21), its zooecial chambers are also identical to those of F. retiformis, it is difficult to see any difference in microstructure from the figures and so it is very likely that this species belongs in synonymy with F. retiformis; F. superretiformis Romantchuk (in Morozova 1970) differs from F. retiformis only in its larger branch width (0.32-0.35 mm); F. pseudoretiformis Morozova (1970) differs significantly from F. retiformis only in its larger branch width (0.35-0.45 mm); F. quasipermulta Morozova (1970) is similar to F. retiformis but has branches which are slightly thicker (0.27 - 0.3 mm) and fenestrules which are marginally larger (0.67 mm); F. kubergandensis Gorjunova (1975) is very similar to F. retiformis but the zooecial chambers may be slightly more elongate at their base.

Thus, there are several species which are very close in morphology to F. retiformis of the present study. It is possible that some of these species are truly synonymous with F. retiformis.

Material

RH1.3* ¹ , RH1.3** ²	Locality RH1
HM7* ¹ , -7* ² , -7* ³ , -7* ⁴	Locality HM7
HM5.8, HM2 HM5.15, HM5.3	Locality HM5
HA3, -20 HAW1, -42, -76 -55* ¹ , -55* ² , -47 -26, -61, -54,	Locality HA

HAG2.1, -2.4, -2.21, -2.24, -2.27, -2.26, -2.25, -2.20, -2.19, -2.16, -2.9, -2.2, -2.1#1, HAG2, HAG4#2, HAG6 to HAG12, HAG1, HAG5, HAG4#1 HAG3	
BH1 to BH4	Locality BH
MP1.63, -1.51, -1.41, -1.36, -1.32, -1.31, -1.28, -1.25, -1.3	Locality MP1
RH2.21a to d, RH2.22 to 2.26 RH2.43	Locality RH2
HYR3 to HYR10	Locality HYR
MP4.2, MP4.3	Locality MP4
MP5.7 to MP5.11 MP5.2/1, MP5.2	Locality MP5
MP5/1 to MP5/8 MP5F10, MP5F1, MP5F2, MP5.50, MP5.52a, MP5.49, MP5.29, MP5.48, MP5.62, MP5 TS 1	Thin section from locality MP5
MP5.57 (1) to (7)	Serial peels, from locality MP5
GLF1	Thin section, from locality GLT
RH4.2, RH4.13 to 4.17, RH4.19, RH4.20, RH4.21#a, RH4.23 to 4.26	Locality RH4
RH4F6, RH4F1, RH4F4	Thin sections, locality RH4
SBC1, SBC2	Locality SBC
HYRF3, HYRF2	Thin sections, locality HYR
HM5, HM5.3	Thin sections, locality HM5

Kirkby-Howse Collection

G3.55.1

Humbledon Hill

Phillips Collection

717F

Non. loc.

King Collection

B28, B105B, B33, B34,
B122A, B105C, B105A,
B103B, B104C, B104B,
B104A, B35A, B35B

Humbledon Hill

B102E, B102D, B102C,
B102B, B102A, B120

Tunstall Hills

B27

Humbledon figured by
King (1850) - Plate II
fig. 18

B121

Humbledon figured by
King - Plate II fig.8a

B42

Humbledon figured by
King - Plate II fig. 8

Schlotheim Collection

K20

Germany, Glücksbrunn -
reef facies. A specimen
from Schlotheim's
collection which is not
figured.
Reverse surface.

Korn Collection

Taf. I fig. 4

Oepitz - reef facies

Taf.I figs. 1, 2

Oepitz - reef facies

Taf. I figs. 13 and 14, and
Taf. III fig. 10

"Productus kalk" at
Gosswitz. Back-reef
environment. Labelled
as Fenestella minuta.

Taf. I fig. 8

Lower Zechstein at
Wartberg. Labelled as
Fenestella minuta.

Stratigraphical Range

Permian

Occurrence

Middle Magnesium Limestone, Upper Permian of N.E. England (see p. for detailed occurrence). Zechstein of Germany. Southern Spitsbergen, Malecki (1977). The Upper and Lower Permian of the U.S.S.R. (Vologda, the Urals and the Sulva river area). The Permian of Peninsular Thailand (Khao Ta Mong Rai). The Permian (Kamiyatsuse) of Japan - from the Miyagi prefecture.

Varieties of *Fenestella retiformis*

Trizna (1939) erected *Fenestella retiformis* var. *tenuis*. Its distinguishing features were its "thinner branches, wider fenestrules, more distinctly triangular zooecia and the presence of capillaries on the keel", according to Trizna. Of these features, only the capillaries on the keel could be said to differentiate the variety from the normal *F. retiformis* seen in the present study.

F. retiformis var. *lunaris* was erected by Shulga-Nesterenko in 1941 (p. 79, plate XI) for forms whose apertures had a lunarium with a tubercle. The fenestrule length of this variety is given as 0.87 mm which falls well beyond the range found for fenestrule length of *F. retiformis* in the present study. In view of this it is felt that this variety ought to be assigned to another species - it is fairly similar to *F. geinitzi* in its measurements but has an inter-apertural-distance which is slightly too large.

Dreyer (1961) removed Korn's (1930) variety *F. geinitzi* var.

thuringiaca from F. geinitzi to F. retiformis var. thuringiaca, a decision which was confirmed as correct by study of Korn's type material - specimens of F. geinitzi var. thuringiaca are identical to F. retiformis apart from the very distinctive tubercles on the reverse surface (see Pl. 22). Measurements made on Korn's figured specimen of F. geinitzi var. thuringiaca (Taf. I fig. 5) are given below.

	Mx	Mn	Ave
F.L.	0.68	0.60	0.65
F.W.	0.6	0.52	0.541
B.W.	0.24	0.22	0.228
D.W.	0.18	0.13	0.153

Aspects of the Morphology of Fenestella retiformis

Zoarial Growth and Fusion

The basically infundibuliform shape of the zoarium in F. retiformis can be modified by various complications in its growth. Sulcation of the zoarial lamina can lead to crowding of branches and a consequent reduction of fenestrule width; at its more extreme development branches may fuse with others of the same colony and, rarely, multi-laminar growth may occur with one zoarial lamina inside another (see Pl. 2 figs, c, a, Pl. 1 figs, b, c). In some specimens several branches bifurcate at the same level in the zoarium (see Pl. 4 fig. a). This results often in the crowding of branches and may cause a constriction of fenestrules. Such a sudden expansion of the zoarium (which would presumably have been detrimental to feeding zooids in parts of the colony) may have occurred because the colony had acquired space into which it could expand or that its food supply had increased, encouraging rapid growth. Areas of lateral rather than distal expansion of zoaria occur quite commonly with new branches arising at high angles to a parent branch (see Pl. 4 figs. b, d) - asymmetrical expansion of the zoarium often serves to unite the opposite ends of the zoarial lamina into a cone-shape in proximal parts of zoaria (see Pl. 4 fig. c).

Examples of fusion of zoarial laminae are common - many of these may be intra-colonial fusion (see Pl. 3 fig. b), however, there are some unequivocal cases of inter-colonial fusion where the two distinct zoarial origins can be seen (see Pl. 5). The fusion of several

branches is clearly visible but it is impossible to say whether or not they then grew together as one. The poor preservation of these specimens renders thin sectioning impracticable and so it is impossible to prove, through an examination of the microstructure, that the epithelia of the two colonies had fused. The external relationships suggest that this was probably the case rather than that the branches merely abut against one another. McKinney (1981) used examples of inter-colony fusion to suggest the occurrence of polyembryony in Permian species of Septopora, Polypora and Hemitrypa. Specimens of Septopora which had origins very close together and which had reached roughly the same size (within 5%) showed homosyndrome in several cases. Specimens of unequal size, therefore probably of different age, did not show homosyndrome where they came into contact. McKinney uses this fact to suggest that homozygosity at a particular gene locus was not responsible for the fusion in Septopora, because, if this had been the case, all contacting colonies should have shown homosyndrome. McKinney dismissed the possibility that the fusion in Septopora was between fragmented clones of the same colony by considering only specimens in which an obvious point of larval attachment could be seen. He used the fact that fusing colonies were of the same size and had points of origin very close together to suggest that they developed from larvae which settled close together and at the same time and therefore were likely to have been siblings. He used the probable existence of histoimmunological systems in these taxa to go further and suggest that the degree of genetic similarity encountered in the fusing colonies of Septopora was perhaps even greater than that in sibling colonies and therefore that they may have

been produced by polyembryony rather than from larvae developed from different eggs.

It is impossible to say if the specimens of F. retiformis described above show true homosyndrome, but, even if they do it is very doubtful whether their fusion can be seen as evidence of polyembryony in the species. The two colony origins have a fairly large separation (approx. 55 mm) and there is a 20-25% discrepancy in their sizes which suggests that they are of different ages and thus different pulses of larval settlement. An alternative is that the fusion of the specimens could represent isogenic fusion of fragmented clones from the same colony. Better preserved material is necessary to establish the occurrence of homosyndrome in F. retiformis with certainty.

Spines and other processes

Spines are quite commonly developed near the origins of zoaria - particularly if the zoarium forms a flat-lying expanse. They have a variable diameter but average about 0.6 mm in width (see Pl. 2 fig. b) and presumably performed a supportive function. Spines may also be developed more distally in a zoarium; Pl. 6 fig. a shows two zoarial laminae with numerous spines joining them - if the laminae are from separate colonies a defensive function for the spines seems likely. Where multilaminar growth occurs, spines may extend from one zoarial lamina to another (see Pl. 6 fig. 6). In this example a number of spines curve from the reverse surface to the obverse surface of the next zoarial lamina, they are closely spaced and numerous. Elias and Condra (1957) comment on similar developments in Fenestella

parviuscula var. libellus and Fenestella archimediterranea. They agree with the standard interpretation of spines as supportive or as mechanically strengthening the zoarium but find it hard to explain their distribution in terms of these functions. In order to explain their often random distribution and extremely dense spacing in some areas of a zoarium they suggested that their growth was induced by symbiotic algae. A similar, often dense, and apparently haphazard spacing of spines has been seen in F. retiformis in the present study - an algal origin for their growth must be rejected but a simple structural strengthening function may not adequately explain their great abundance in some places. They may have performed a dual function of strengthening the zoarium and defence against predators but their distribution remains, in several cases, enigmatic.

Irregularly stellate processes, associated with carinal nodes, have been seen in one transverse section of F. retiformis. These consist of a primary granular core surrounded by outer laminated skeleton of identical type to that found in branches of Fenestella. These structures are thus almost certainly bryozoan in origin. In each case these processes are developed around a node and in one case the process links two nodes which are adjacent along a branch (see Pls. 23, 24). The microstructural elements of the nodes and the processes are not in continuity. The nodes consist of primary granular skeleton which is enveloped by either primary granular skeleton of the processes, in a different optical orientation, or by laminated skeleton of the processes (see Pl. 25). The stellate form of these processes is fairly irregularly developed with between 5 and 8 projections parallel to the plane of the branch (see Pls. 23, 27,

28); these projections are not all of equal length - they consist of a primary granular core (of the order of $20-40\mu$ thick) surrounded by outer laminated skeleton which varies from about $15-70\mu$ in thickness. In one of the processes, two of the lateral projections extend down to the neighbouring branch (see Pls. 23, 24). The granular core of these projections abuts against the outer laminated layer of the branch - in one case it extends distally along the branch for a short distance before thinning out; it follows the contours of the branch accurately. The outer laminated layer of the projection also extends along the branch for a short distance. The more proximal of the two projections appears to extend at a high angle across the end of a broken dissepiment (see Pl. 26) - it is possible, however, that this effect is merely an artefact of the oblique plane of section and the projection simply extends to the reverse side of the dissepiment.

The relationships between the microstructural elements of the projections and those of the branches show that the projections grew down onto the branches after a fairly thick outer laminated layer had been deposited. Therefore, growth of these projections is unlikely to have been taking place contemporaneously with growth in the immediately adjacent branch.

The nature and origin of these processes is problematical. They may have originated from some level in the nodes not seen in the plane of the transverse section and are thus a very elaborate form of superstructure. A more plausible alternative is that these processes represent the distal ends of spines developed from the reverse surface of another zoarial lamina (either within the same colony or from another colony of the same species) which have grown to meet the

obverse surface of a zoarial lamina at a different level. Spines of this type have been described by Elias and Condra (1957); in Fenestella archimediiformis and Fenestella parviuscula var. libellus spines project from the reverse surface to the obverse surface of another lamina in the same zoarium. These spines may spread out palmately where they make contact with the obverse surface. The stellate shape of the processes, seen in Fenestella retiformis, could well represent a transverse section through the palmate tip of such a spine. It is, however, peculiar that in each case the processes of F. retiformis are centred around a carinal node; this fact may militate against a deterministic explanation for their distribution and may suggest a close physiological control on growth and a specific function for these structures. The processes and their projections which extend to the obverse surface would certainly interfere with the normal feeding behaviour of autozooids; thus this could be an example of the subjugation of the needs of the individual in favour of those of the colony. Alternatively, these spines could be from another colony for which they performed a defensive function - in this case, having to regard the growth of each spine around a node as a chance occurrence is difficult to accept.

Similar elaborate spinose structures, though more extensively developed, have been seen on the reverse surface of a zoarium of Fenestella ivanovi by Bancroft (pers. comm).

These structures, attached to the obverse of Fenestella retiformis, recall quite strongly the aspect of 'Palaeocoryne', which was the subject of some controversy in the last century. Vine (1879) believed it to be an appendage of Fenestella as did Young and Young

(1874) who figured a specimen of 'Palaeocoryne' from the Permian (though they did not say exactly where it came from); they considered it to be just one type of appendage that could be developed from Fenestella. Their interpretations are almost certainly correct, unlike those of Duncan (1873) who believed it to be a type of hydrozoan.

Polymorphs

Nanate Zooecia

Autozooecial apertures which are closed by a calcareous plate with a minute perforation in its centre have been seen in one zoarium. Such closed chambers probably housed secondary nanozoids (see Pl. 8 and p.50). Although their abundance is too low to allow a significant statistical analysis of their distribution there appears to be a preferential occurrence of nanate zooecia at points of branch bifurcation - areas in a zoarium where it is likely that not all zooids could have fed effectively. This would have been an advantageous place for a polymorphic non-feeding zooid. The width of the branch is greater at a bifurcation point providing a larger surface area for encrustation by foreign organisms - a secondary nanozoid in this position could have discouraged such encrustation.

Kenozooecia

Abnormally large zooecia with atypical morphologies may occur in branches prior to bifurcation points (see Pl. 10). Their size and morphology suggest that they acted merely as 'space fillers' in branches - their shape being dictated by the geometrical constraints of bifurcation. It is unlikely that a zoecium of this sort would

have housed a normal feeding zooid - it may have had no aperture and no functional soft parts and consequently can be considered a kenozoecium.

Similar kenozoecia have been observed in Fenestella geinitzi (see p.120).

Accessory Pores

True accessory pores of the type described by Morozova (1973) have not been seen in Fenestella retiformis. However, structures resembling accessory pores may occur on the reverse surface of branches of the species. Externally, they appear identical to accessory pores but transverse section reveals them to be secondary features. The two 'pores' in Pl. 12 are 0.1 mm in diameter and circular; they cut through the longitudinal striae on the reverse of the branch, proving that they are not an integral part of the bryozoan colony but probably the work of some boring organism.

Colony Origins

Colony origins of F. retiformis are only very rarely preserved, and in most cases thin sectioning of these is impossible.

Pl. 29 figs. c, d, show a specimen before serial sectioning. The zooecial apertures open onto the inside of the cone-shaped zoarium - this cone-shape is established after only a few zooecia have been budded. It is not possible to determine the budding sequence or the substrate of attachment. Spines are developed from the reverse surface and project to below the level of the ancestrula. These spines are longitudinally striate and may have a fairly thick covering

of secondary laminated skeleton.

In Pl. 29 figs. a, b, the origin appears to consist of an almost complete circle of zooecial chambers. The branches arise in a spiral and bifurcate rapidly forming a cone-shaped zoarium with apertures opening onto the inside of the cone.

Abnormal Zooecia

Deflection of the wall of a zooecium towards a dissepiment may occur rarely (see Pl. 30). This phenomenon was described by Tavener-Smith (1969a) who attributed great importance to it in his growth model for fenestellids. The drag of the soft parts into the dissepiments and the consequent bulging of zooecial walls towards them was used by Tavener-Smith (op. cit.) as evidence in favour of the complete soft-part development of a zooid prior to any calcification. However, the same degree of deflection of zooecial walls could occur if the budded zooid were only partly formed when calcification commenced.

There is a single occurrence of abnormal growth of the primary granular layer to form a 'partition' at the distal end of the base of a zooecial chamber (see Pl. 11 fig. a). This 'partition' completely separates the distalmost third of the zooecial chamber from the proximal part at this level of the tangential section. It is unlikely to be a structure characteristic of a particular type of polymorph. It is more likely to be an aberrant growth, and one which would have modified the disposition of the zooidal soft parts to some extent.

Bioimmuration

A sub-triangular cavity occurs at the branch margin in a tangential section of Fenestella retiformis. It has a maximum length of 40μ and is up to 20μ wide (see Pl. 31). This cavity is almost surrounded by laminated skeleton which is similar in character to the weakly laminated component of the primary granular layer. This laminated skeleton is not easily traceable at the innermost edge of the cavity where it appears to be more amorphous. Outside this lined cavity, on the branch margin, is a layer of laminated skeleton, 75μ thick - this is of the same character as normal outer laminated skeleton and extends well beyond where the branch margin would have been; consequently, it occludes a large part of the fenestrule. This structure may represent an example of bioimmuration. The size of the cavity is quite comparable with the size of algae or worm-tubes in the same lithology. A number of worm-tubes are attached to the obverse surface of this zoarium of Fenestella retiformis, it is possible that a worm became incorporated into the branch wall of the colony.

The detailed mechanism by which an organism could be incorporated into the wall structure of a bryozoan is difficult to envisage. It is necessary for the organism to be almost completely surrounded by the hypostegal epithelium in order that the laminated skeleton be deposited in its observed configuration. The most likely way in which such a configuration could be achieved may be by the rupturing of both the eustegal and hypostegal epithelia and then their regrowth and fusion around the foreign organism (see fig. 26). The organism must have been growing slightly away from the branch at the plane of the section because skeletal material has been deposited at the inner edge

of the cavity. Presumably, the organism was initially attached to the branch at some place out of the plane of the section. Initially, deposition of laminated skeleton was immediately adjacent to the foreign organism, then the epithelia withdrew from the organism depositing laminated skeleton as they did so. Deposition continued beyond normal branch limits causing the fenestrule to become largely occluded by outer laminated skeleton.

Fenestella geinitzi, d'Orbigny (1850)

Figs. 27-29, Pls. 32-34

1829 Gorgonia antiqua Goldfuss; p. 99 pl. 36 fig. 3

1848 Fenestella antiqua Goldfuss; Geinitz p. 18, pl. VII, figs. 14, 15

1848 Fenestella antiqua Goldfuss; Howse pp. 261-262

1850 Fenestrella geinitzii [sic] d'Orbigny p. 168

1861 Fenestella geinitzi d'Orbigny; Geinitz p. 116, pl. XXII fig. 2

1930 Fenestella geinitzi d'Orbigny; Korn p. 355, pl. 1 fig 6, ^{text} fig. 1.

1930 Fenestella retiformis Schlotheim ; Korn p. 354 [partim - pl. 1
fig. 3]

1961 Fenestella geinitzi d'Orbigny; Dreyer p. 13, pl. IV figs. 2, 3

Types

The specimens figured by Goldfuss (1829) were untraceable. The specimen figured by Korn (1930) is missing. The specimen of Fenestella geinitzi var. thuringiaca Korn (1930, pl. 1 fig. 5) was studied and considered synonymous with Fenestella retiformis (see p. 105).

Diagnosis

Fenestella with $3\frac{1}{2}$ -4 autozooecial apertures per fenestrule. Apertures fairly small and closely spaced. Branches fairly narrow, parallel-sided and straight or gently zig-zag. Dissepiments fairly narrow. Fenestrules of moderate length, rectangular or 'barrel-shaped'. Median carina slightly rounded at its apex, surmounted by fairly weakly developed nodes. Zooecial chamber bases triangular. Nanate zooecia may occur.

Description

External

Zoaria are probably infundibuliform. Areas of rapid lateral expansion may occur. Spines may occur on the reverse surface of branches (see Pl. 32 fig. a).

Fenestrules are of moderate length and rectangular (often with rounded corners) or 'barrel-shaped'. The latter shape occurs quite often and is produced when the dissepiments from neighbouring fenestrules join the branches at or close to the mid-point of the fenestrule causing the branches to bow outwards at this point (see fig. 28). The sides of fenestrules are not sinuous.

Branches are fairly narrow with sides which slope fairly steeply into the fenestrules and up to the median carina. The median carina is straight, fairly prominent and tends to be slightly rounded; it has a single row of fairly closely spaced nodes (see fig. 27). These nodes may be regularly or irregularly spaced and are fairly weakly developed (see measurements p120). They are slightly elongate parallel to branch length near their base and circular in cross-section higher up. There are $3\frac{1}{2}$ -4 autozooeal apertures per fenestrule. They open on the sloping sides of the branch and have a thin peristome. The peristome appears to be more elevated on the side of the aperture nearer the fenestrule. Apertures are fairly small, circular, and closely spaced and are rarely nanate. Branch width increases for one to two fenestrules prior to bifurcation - in such areas a kenozoecium may be developed (see Pl. 34 fig. a).

The reverse surface of branches is fairly gently rounded and may be longitudinally striate.

Dissepiments are narrow and well depressed relative to the obverse surface; they expand in width as they join the branches. They are much less depressed relative to the reverse surface and appear not to expand in width at the branch junction to such an extent as on the obverse surface. Dissepiments are fairly steeply rounded on both obverse and reverse surfaces.

Internal Form and Microstructure

In cast preservation the zooecial chamber base has a triangular shape, often with gently rounded corners (see Pl. 34 fig. b).

In tangential section the zooecial chamber base is triangular - this then becomes pentagonal (hemi-hexagonal) then sub-reniform/oval and finally circular as the obverse surface is reached; 5 longitudinal striae can be seen. Zooecial chambers have a thin lining of inner laminated skeleton. Outer laminated skeleton is of variable thickness around branches, nodes and dissepiments. Skeletal rods have not been seen in this species in the present study.

Measurements

N = 29

	NM	Mn	Mx	S.D.	C.V.	$\bar{X}$
F.L.	324	0.74	0.906	0.04	4.9	0.818
F.W.	312	0.48	0.667	0.043	7.5	0.573
B.W.	152	0.18	0.265	0.019	8.1	0.236
D.W.	144	0.099	0.16	0.0146	12.0	0.122

I.A.D.	105	0.239	0.261	5.64×10^{-3}	2.2	0.249
I.N.D.	50	0.244	0.386	0.05	16.3	0.306
Z.B.L.	24	0.188	0.223	-	-	0.202
Z.B.W.	24	0.091	0.148	-	-	0.112
A.D.	40	0.09	0.10	-	-	0.098

Micrometric formula:- 15-20/11-13 /19-21/13-21

Measurements on Korn's Material

N=1. This specimen (Taf. 1 fig. 3) (see Pl. 34 fig. c) is referred to Fenestella retiformis by Korn (1930) but is assigned here to F. geinitzi because of its larger fenestrules and more rounded median carina.

	NM	Mn	Mx	$\bar{X}$
F.L.	9	0.74	0.78	0.754
F.W.	9	0.53	0.60	0.567
B.W.	9	0.26	0.30	0.278
D.W.	9	0.14	0.19	0.169
I.A.D.	9	0.24	0.26	0.25
I.N.D.	3	0.28	0.30	0.29
A.D.	2	-	-	0.1

Histograms of F.L., F.W., B.W. and I.A.D. are shown in fig. 29. There is a large spread of values for F.L. and F.W., but in neither case is there any convincing bimodality of the data, sufficient to doubt the homogeneity of the species.

Measurements in thin section

The outer laminated layer may reach 30μ in thickness. The thickness of the inter-zooecial wall varies between $7-10\mu$. The inner laminated layer is between $3-8\mu$ thick near the base of a zooecial chamber. The longitudinal striae, as defined by different extinction bands, are approximately 20μ wide. Carinal nodes, near their base, are 60μ long and 33μ wide. Higher up, where they are circular in cross-section, they have a diameter of 33μ .

Discussion

Goldfuss (1829) was the first to note the existence of two distinct species of Fenestella in the Zechstein of Germany. He referred one to Gorgonia infundibuliformis (Fenestella retiformis) and the other to Gorgonia antiqua (Fenestella geinitzi). His descriptions do not make clear the distinction between the two species. His figure of Gorgonia infundibuliformis shows a keel with nodes which is typical of that which occurs in Fenestella retiformis but has four apertures per fenestrule (a feature characteristic of Fenestella geinitzi). The figure of Gorgonia antiqua is inaccurately drawn, showing variable inter-apertural-distances and fenestrule lengths. Geinitz (1848) referred Gorgonia antiqua to Fenestella antiqua - his description of the species corresponds well with the Fenestella geinitzi of the present study. d'Orbigny (1855) is cited as the author of Fenestella geinitzi in all later publications, including Geinitz (1861). The date of d'Orbigny's publication is in fact (1850) and the name of the taxon is given there as "Fenestrella geinitzii". d'Orbigny gives 1848 as the date of the species-name and himself as the author - however,

no relevant publication by d'Orbigny can be found for that date - it is assumed that he was recognizing priority of usage rather than priority of publication in giving the date of "Fenestrella geinitzii" as 1848. All later authors have referred to the species as 'geinitzi' rather than 'geinitzii' - this procedure will be followed in the present study (the change from a double 'i' to a single 'i' at the end of a number of species names appears to have occurred for several taxa). d'Orbigny (1850) gives no reason for rejecting the earlier name of Gorgonia antiqua, Goldfuss (1829) - Goldfuss (op. cit.) described the species from both the Eifel (Devonian in age) and from Glücksbrunn (which is Permian) and so his concept of Gorgonia antiqua was almost certainly one which embraced two different species. Lonsdale (1839) erected the Silurian species Fenestella antiqua and suggested, though only tentatively, that Gorgonia antiqua from the Eifel was synonymous with it. Lonsdale's figure of the species shows 6 or 7 apertures per fenestrule and is thus distinct from the forms figured by Goldfuss (op. cit.). Lonsdale was therefore wrong to use the name "F. antiqua" for his Silurian species. Because of the uncertainty over the original definition, Geinitz (1848) was incorrect to retain the name "F. antiqua" for the Permian species and d'Orbigny (1850) was therefore probably justified in rejecting Goldfuss's species and in establishing "Fenestrella geinitzii" for the Permian material.

Fenestella geinitzi can be very similar to Fenestella retiformis (see p. 98). It is distinguished from that species by its larger fenestrules, more rounded and more weakly developed keel and smaller nodes which have a larger separation.

Fenestella ruidacarinata Crockford (1944b) is similar to F. geinitzi but its branch width is too great at 0.33-0.38 mm and its inter-nodal-distance is too small at 0.13-0.22 mm. Fenestella teres Trizna (1961) only differs from F. geinitzi in having zooecial chamber bases which are more pentagonal than triangular. Fenestella aequabilis Trizna (1961) only differs from F. geinitzi in having slightly shorter fenestrules (0.7 mm).

Material

RH4.1, RH4.3	From locality RH4
RH4.4, RH4.5,	
RH4.12, RH4.21Eb,	
RH4.22, RH4.26a,	
RH4.27, RH4.28	
HM5.20/1, HM5.32	From locality HM5
HYR1, HYR2	From locality HYR
HM7.6, HM7.6+1,	From locality HM7
HM7.6+2, HM7.6+3,	
HM7.6+4, HM7.6+5,	
HM7.6+6, HM7.6+8,	
HM7.6+9, HM7.6+11	
HM5/1	Locality HM5 - Thin Section
RH4.3, RH4.7,	Locality RH4 - Thin
RH4.10, RH4.12,	Section
RH4F5	

King Collection

B103A, B122B	Humbledon Hill

Korn Collection

Taf.1 fig. 3	Labelled as <u>Fenestella</u> <u>retiformis</u> . Reef at Pössneck

Stratigraphical Range

Upper Permian.

Occurrence

Middle Magnesium Limestone, Upper Permian of N.E. England.
Zechstein of Germany.

Family Polyporidae Vine, 1883

Type Genus

Polypora McCoy, 1844

Diagnosis

Fenestrata with dichotomous, pinnate or reticulate zoaria. In reticulate zoaria branches may anastomose or be connected by dissepiments. Dissepiments sterile or with zooecia. Zooecia open onto the obverse surface in two or more rows. Nodes and longitudinal ridges may occur on the obverse surface. Reverse surfaces smooth, longitudinally striate, pustulose or nodose. Ovicells and nanate zooecia may occur.

Range

Ordovician to Permian.

Subfamily Reteporidrinae Dunaeva and Morozova, 1975

Emended Diagnosis

Polyporidae with reticulate colonies. Branches anastomosing or connected by wide short dissepiments. Branches and dissepiments both with two or more rows of zooecia. ?Ovicells may occur.

Range

Devonian-Permian.

Genus Kingopora Morozova, 1970

Type Species

Gorgonia ehrenbergii, Geinitz, 1846

Diagnosis

Polyporidae with basically infundibuliform zoaria. Substantial holdfasts often developed. Branches and dissepiments have two or three rows of apertures. Nodes may occur on the obverse and reverse surfaces. Dissepiments may be distinct or formed by the anastomosis of branches. Reverse surfaces are smooth, longitudinally striate, pustulose or nodose. Zooecial chamber bases are polygonal. Zooecial chambers extend normal to the reverse and obverse surfaces. Autozooecial apertures open onto the outside of the zoarium. Nanate zooecia and ? ovicells may occur.

Discussion

King erected the genus Phyllopora in 1849 with Gorgonia ehrenbergii Geinitz (1846) as type species. The distinctive characters of Phyllopora, according to King's description, were the occurrence of the apertures on the outside of the infundibuliform zoarium, with zooecial chambers normal to the obverse and reverse surfaces.

Several authors referred species to this genus but in so doing often broadened the initial concept of the genus and in some cases actually contradicted it e.g. Waagen and Pichl (1885) described Phyllopora cribellum Koninck (1863) with apertures opening onto the

inside of the zoarium. A number of species with several rows of apertures on branches and dissepiments were referred to Phyllopora e.g. P. jabiensis Waagen and Pichl (1885) - while this assignment does not contradict the generic diagnosis of King (1849), where no mention is made of the number of rows of apertures, it is inconsistent with the type species, described by King (1850) as having 2 to 3 rows of apertures.

De Koninck (1877) erected the genus Protoretepora for forms which were fairly similar to Phyllopora but with apertures opening onto the inside of the infundibuliform zoarium and zooecia "less closely packed, and more regularly arranged in lines". This genus has not been accepted by all, and in particular by Russian workers, e.g. Morozova (1970), who suggested that it might be congeneric with Polypora. The main reason for this confusion is de Koninck's choice of Fenestella ampla Lonsdale (1844) as the type species of the genus Protoretepora. Lonsdale's (1844) description of Fenestella ampla strongly suggests that he was looking in part at a species of Polypora - the dissepiments are described only as "sometimes cellular" and he described a longitudinal ridge on the obverse surface; zooecial chambers are arranged obliquely. Morozova (1970) points out that apertures may encroach occasionally onto dissepiments in some species of Polypora. Crockford (1941a) claims that Lonsdale's (op. cit.) figures of Fenestella ampla show two species:- one possibly identical with Polypora montuosa Laseyron and the other similar to Phyllopora cribellum de Koninck and Phyllopora jabiensis Waagen and Pichl. She retained the genus Protoretepora, which she distinguished from Phyllopora by having more than 2 rows of chambers on branches. This

distinction is difficult to follow since the type species of Phyllopora has both 2 and 3 rows of chambers on branches.

Termier and Termier (1971) and Simonsen and Cuffey (1980) have used the genus Protoretepora for species which fit de Koninck's (op. cit.) diagnosis of the genus but Morozova (1970) used the genus Reteporidra Nickles and Bassler (1900) for similar forms. Until a detailed study of type specimens can be undertaken the genera Protoretepora and Reteporidra must be used with caution.

Phyllopora can be considered generically distinct from Protoretepora (cf. Bassler 1953) on the basis of de Koninck's original reasoning, i.e. that the apertures open onto the outside of the zoarium in Phyllopora in contrast to Protoretepora in which they open onto the inside of the zoarium. The difference in the number of rows of apertures may be significant also but a study of type material is needed to confirm this.

Morozova (1970) rejected the generic name Phyllopora since it was preoccupied as a name used for a Mesozoic foraminiferan (Ehrenberg 1837) and she established the genus Kingopora in its place with Gorgonia ehrenbergi as type species.

Range

Upper Permian.

Taxonomic Procedure

The taxonomic procedure for the genus Kingopora is essentially the same as that described for the Fenestellidae. Measurements on the fenestrate meshwork are slightly different, see fig. 30.

Branch Width (B.W.) is measured perpendicular to branch length at its narrowest part adjacent to each fenestrule.

Dissepiment Width (D.W.) is measured at the narrowest point across the dissepiment between two fenestrules which are longitudinally adjacent.

Fenestrule Length (F.L.) is the greatest dimension measured between the edges of longitudinally adjacent dissepiments. (This is not measured between the centres of adjacent dissepiments, as in the Fenestellidae, because of the difficulty in locating the exact centre of the dissepiment caused by the relative irregularity of the meshwork in Kingopora).

Fenestrule Width (F.W.) is the greatest dimension measured between the edges of laterally adjacent branches. (This is not measured from the centres of adjacent branches for the same reason as given in the measurement of fenestrule length).

Inter-apertural-distance (I.A.D.) is measured between the centres of apertures which are longitudinally adjacent in a row. (Care must be taken to avoid measuring inter-apertural-distances between apertures which are adjacent but not in the same longitudinal row).

Inter-nodal-distance (I.N.D.) is measured between the centres of nodes which are longitudinally adjacent.

Apertural diameter (A.D.) is measured as in the Fenestellidae.

The micrometric formula is quoted.

Thin sections are prepared in specific orientations:- Tangential, longitudinal and transverse. Measurements of zooecial chamber bases are made in tangential section - zooecial chamber base length and width are given; though this simplistic quantification of zooecial chamber base is not an accurate expression of its shape it is of use as an approximate measure of size.

Kingopora ehrenbergi Geinitz, 1846

Figs. 30-34, Pls. 35-53

- 1846 Gorgonia ehrenbergii[sic] Geinitz, p. 585, pl. XXIIIa fig. 12
- 1848 Retepora lonsdalii Howse, p. 263
- 1848 Fenestella ehrenbergi Geinitz; Geinitz, p. 18, pl. VII figs. 16-18
- 1850 Phyllopora ehrenbergi Geinitz; King, p. 43, pl. V figs. 1-6
- 1861 Phyllopora ehrenbergi Geinitz; Geinitz, p. 117
- 1930 Phyllopora ehrenbergi Geinitz; Korn, p. 362, pl. III, figs. 6-9, pl. IV figs. 4, 5
- 1930 Phyllopora solida Korn, p. 363, pl. III figs. 11-14, pl. IV figs. 1-3, 20
- 1961 Protoretepora ehrenbergi Geinitz; Dreyer, p. 15, pl. V figs 4-6, pl. VI
- 1961 Protoretepora solida Korn; Dreyer, p. 17, pl. VII fig. 4
- 1961 Protoretepora solida atuberculata Dreyer, p. 18, pl. VII fig. 4
- 1970 Kingopora ehrenbergi Geinitz; Morozova, p. 236, pl. LVII figs. 2, 4

Types

The specimen originally figured by Geinitz (1846) was destroyed during the bombing of Dresden in World War II. The specimens of Phyllopora solida figured by Korn (1930) (including the lectotype, Taf. IV fig. 3, selected by Dreyer (1961)) have been studied and are placed in synonymy with Kingopora ehrenbergi (see Discussion, p. 138). It was not possible to locate Dreyer's (1961) figured specimens.

Diagnosis

Kingopora with 2 or 3 rows of apertures on branches and dissepiments. Substantial holdfasts, spines, and much extrazoooidal skeleton developed. Dissepiments distinct or formed by the anastomosis of branches. Fairly well-developed nodes may occur on the obverse surface. Less well-developed nodes may occur on the reverse surface. Reverse surfaces may show longitudinal striae or be pustulose. Zooecial chamber bases are polygonal and varied in shape. Zooecial chambers extend normal to the reverse and obverse surfaces. Nanate zooecia and ? Ovicells may occur.

Description

External

Zoaria are infundibuliform and nearly always steeply erect; they may be plicate and laterally compressed (see Pl. 35). Autozooecial apertures always open onto the outside of the zoarium. A substantial holdfast is developed with a thick accretion of skeleton over the inside and outside of proximal parts of zoaria (see Pls. 36, 37). Spines may be developed near zoarial origins, spreading out horizontally, or vertically up the inside of the zoarium (see Pl. 37, fig. d, Pl. 46).

Fenestrules are quite small and oval, rarely almost circular (see Figs. 31, 32, Pls. 38, 39). Autozooecial apertural margins occasionally may protrude slightly from the edge of a branch into the fenestrule.

Branches are fairly thin and have sides which slope fairly gently into fenestrules. The obverse surface is fairly flat but the reverse

may show a more marked curvature. Branches are variably zig-zag - where this feature is well-developed the dissepiments are usually defined by the anastomosis of the branches but where it is more weakly developed a distinct dissepiment occurs. Autozooecial apertures occur in two or three rows and are fairly small and usually circular though they may be elongate parallel to branch length. Nanate zooecia occur rarely. The outer rows of apertures tend to open on the sloping sides of branches. Nodes occur in a row along the centre of a branch and also rarely at the inner edge of autozooecial apertures which are on the edge of a branch. They are fairly broad, prominent, closely and regularly spaced, and may be elongate parallel to branch length or roughly circular in cross-section. The reverse surface of a branch may be pustulose or show between 6 and 8 longitudinal striae. Rarely, the reverse surface of a branch may be sharply angular along its centre. Nodes may occur on the reverse surface of branches at the base of dissepiments; their distribution is very regular but their occurrence may be limited to only some parts of a zoarium (see Pl. 39 fig. c).

Dissepiments are of variable thickness but are generally thicker when they are defined by anastomosis of the branches.

? Ovicells may occur (see p.147).

Internal form and Skeletal Microstructure

Zooecial chamber bases have a very variable polygonal shape (see Pls. 40, 41). They are usually 5-sided but may also be 4 and 3-sided. Nearer the obverse surface the zooecial chambers become oval in tangential section and then approximately circular as the obverse surface is reached (see Pl. 41). They extend normal to both obverse

and reverse surfaces. 'Vestibules' may reach considerable lengths in the proximal parts of colonies and may have undulatory walls (see p.145).

The primary granular layer is quite thick - no 'inner platy core' has been observed.

There are between 7 and 10 longitudinal striae visible in tangential section and up to 14 visible in transverse section where they may be observed well up the sides of branches close to the obverse surface (see fig. Pl. 42 fig. a).

Minute skeletal rods may occur in the primary granular layer (see Pl. 42).

A large amount of extrazoooidal skeleton may be developed, particularly in the proximal parts of zoaria. This may be vesicular in nature or may be striated skeleton which is similar in nature to the primary granular layer (see p.145). Thin extrazoooidal walls may extend into fenestrules forming 'chambers' of comparable size to auto-zooecial chambers (see Pl. 52).

Measurements

N = 36

	NM	Mn	Mx	S.D.	C.V.	$\bar{X}$
F.L.	350	0.50	0.68	0.0475	8.2	0.576
F.W.	350	0.309	0.498	0.042	10.2	0.411
B.W.	300	0.328	0.53	0.051	12.8	0.397
D.W.	280	0.396	0.70	0.074	13.8	0.537
I.A.D.	150	0.231	0.283	0.012	4.7	0.253
I.N.D.	20	0.256	0.33	-	-	0.293

Z.B.L.	27	0.203	0.236	-	-	0.224
Z.B.W.	27	0.115	0.138	-	-	0.125
A.D.	25	0.086	0.107	-	-	0.10

Micrometric Formula:- 10-15/8-11/18-20

Measurements on Korn's Material

Specimens Taf. IV fig. 20, Taf. IV fig. 1; Taf. IV fig. 3, Taf. IV fig. 2, Taf. III fig. 14, Taf. III fig. 12 referred to Phyllopora solida by Korn.

N = 6

	NM	Mn	Mx	$\bar{X}$
F.L.	65	0.535	0.745	0.606
F.W.	65	0.278	0.450	0.316
B.W.	44	0.345	0.45	0.371
D.W.	27	0.4	0.477	0.433
I.A.D.	24	0.236	0.258	0.246
I.N.D.	11	0.31	0.42	0.356

Specimens Taf. III fig. 7, Taf. IV fig. 4, Taf. III fig. 8, Taf. III fig. 6, referred to Phyllopora ehrenbergi by Korn.

N = 4

	NM	Mn	Mx	$\bar{X}$
F.L.	37	0.542	0.587	0.565
F.W.	37	0.36	0.40	0.38
B.W.	29	0.311	0.39	0.356
D.W.	27	0.33	0.504	0.44
I.A.D.	15	0.243	0.257	0.25

Figs. 33 and 34 show histograms of the colony average values for various measured parameters (excluding Korn's material). F.L. and F.W. have fairly broad distributions but the data are not bimodal. I.A.D. is clearly unimodal, with a normal distribution. D.W. shows a very broad distribution - this probably reflects the different modes of development of a dissepiment which occur intraspecifically (i.e. by anastomosis of branches or not). B.W. has a fairly unimodal normal distribution apart from two values above 0.5 mm which are not considered significant here since one represents measurement in the proximal part of a colony and the other is considered to be an aberrant form with 3 rows of apertures (see discussion).

Measurements in thin section

The primary granular layer beneath zooecial chambers varies from 46μ to 90μ thick. The outer laminated layer is very variable in thickness. The inner laminated layer may reach 26μ in thickness - it is thicker at the base of zooecial chambers than it is in the 'vestibule' nearer the obverse surface (see Pl. 43).

The inter-zooecial wall is from $6-10\mu$ thick. Longitudinal striae, as defined by extinction bands, average 20μ in width; they may extend below zooecial chambers for 75μ (see Pl. 42).

Zooecial chambers exceptionally may reach 1.02 mm in length in proximal parts of zoaria (see Pl. 48).

Discussion

Kingopora ehrenbergi is a rare species in the Middle Magnesian Limestone. The species was erected in 1846 by Geinitz, as Gorgonia

ehrenbergii, which he distinguished from Fenestella retiformis by its thicker zig-zag branches and larger, often rhombic zooecial chambers arranged in irregular rows.

Howse (1848) drew attention to the fact that the apertures open onto the outside of the zoarium and that the zooecial chambers extend normal to both the obverse and reverse surfaces.

King (1850) noted the occurrence of both two and three rows of apertures on branches.

Korn (1930) established the species Phyllopora solida which he differentiated from Phyllopora ehrenbergi by its more steeply erect zoarium, the anastomosis of branches to form a dissepiment rather than the production of a distinct dissepiment, its more elongate fenestrules, the occurrence of obverse surface nodes and its smaller autozooecial apertural diameter. The degree of erectness of the zoarium has no specific taxonomic significance. The anastomosis of branches to form dissepiments is a feature which may be variably developed within one zoarium. It may occur in a zoarium in combination with features which are specifically characteristic of Kingopora ehrenbergi. Korn himself was obviously confused about the species since he assigned specimen Taf. III fig. 7 to Phyllopora ehrenbergi (see Pl. 44 fig. a) but this specimen has numerous dissepiments defined by anastomosis of branches and a row of nodes on the obverse surface (these are features supposedly characteristic of Phyllopora solida). The degree of elongation of fenestrules does not serve to distinguish the species (the measurements given by Korn are only slightly different:- F.L. = 0.6-0.75, F.W. = 0.4-0.6 in Phyllopora ehrenbergi and F.L. = 0.6-0.7, F.W. = 0.3-0.38 in

Phyllopora solida). Measurements on specimen Taf. III fig. 12, assigned to P. solida by Korn (see Pl. 44, fig. b), gave an average fenestrule width of 0.45 mm and an average fenestrule length of 0.59 mm. These dimensions show complete overlap with those of specimens referred to P. ehrenbergi by Korn. The smaller autozooecial apertural diameter (0.045 mm), supposedly characteristic of P. solida, does not occur in most of the specimens assigned to that species by Korn. Smaller apertures occur together with normal autozooecial apertures in one specimen (Taf. IV fig. 3). Some of these are simply mineralogically overgrown, others appear to be partly closed by skeletal material and may have housed polymorphs (the occurrence of nanate zooecia in the same specimen may support this interpretation).

Dreyer (1961) retained both Protoretepora ehrenbergi and Protoretepora solida but erected a new subspecies, Protoretepora solida atuberculata. She established this subspecies on the basis of Korn's specimen Taf. IV fig. 1 (assigned to P. solida by him) which she believed had no obverse surface nodes. The present study has confirmed that this specimen does in fact have nodes on the obverse surface. The other feature which she considered to distinguish this subspecies from the normal P. solida was the smaller size of its fenestrules - although the fenestrules of specimen Taf. IV fig. 1 are smaller than average they are not sufficiently distinct to warrant the erection of a subspecies.

On the basis of the material seen from Korn's collection and from the Permian in N.E. England the species Phyllopora solida Korn and the subspecies Protoretepora solida atuberculata Dreyer must be considered subjective synonyms of the morphologically variable species Kingopora

ehrenbergi Geinitz.

A single specimen (GLT 14) shows regularly distributed nodes on the reverse surface; 3 occur per fenestrule, on each branch. These nodes are very characteristic but can be seen only in certain parts of the specimen (see Pl. 39 fig. c). Two other specimens show very weakly developed nodes on the reverse surface :- 2 nodes can be seen in specimen GLT4, 1-3 nodes can be seen in specimen GLQ12. These occupy comparable positions to the well-developed nodes of specimen GLT14; though their scarcity may be a function of differential preservation it seems more likely that they were not developed over an entire zoarium. No reverse surface nodes have been seen in any thin sections of this species. Features similar to these nodes are often used as specific or subspecific taxonomic characters in many genera of the Fenestrata, but, in the above case, this practice will not be followed because of the probability that the development of regular reverse surface nodes is an intraspecifically variable feature.

Some specimens develop 3 rows of autozooecial chambers over most of the observable zoarium (see Pl. 41 fig. a). While this is in quite marked contrast to the 2 rows of chambers in most specimens and might be considered a feature of specific, or even generic taxonomic significance by many authors, there exist a number of specimens which have both 2 and 3 rows of chambers developed within the same zoarium. Although one condition is usually dominant, the variability of this feature precludes its use for taxonomic subdivision in this case.

Phyllopora aspera Ulrich (1890) is a species which appears very similar to Kingopora ehrenbergi; fenestrule width may be slightly smaller in Ulrich's species. Kingopora parvifenestrata Morozova

(1970) is similar to K. ehrenbergi but has smaller fenestrules.

Material

MP1.76	Locality MP1
MP5.1, MP5.4, MP5.5, MP5.12a, MP5.12b, MP5-3/2, MP5-3/3, MP5-3/4	Locality MP5
MP5-3/1, MP5-6, MP5.2, MP5-13	Thin Sections, Locality MP5
MP5.6 (1)-(4)	Serial Acetate Peels Locality MP5
HA7, HAG6, HAG7	Locality HA
NH1	? Humbledon Hill
GLT3, GLT3a-3b-3c, GLT4-4a-4b, GLT5, GLT9, GLT10, GLT10a, GLT11-GLT14	Locality GLT
GLT2	Thin Section, Locality GLT
GLQ1, GLQ11, GLQ12, GLQ15, GLQ18, GLQ20-GLQ23, GLQ27	Locality GLQ
GLQ2-GLQ4, GLQ6-GLQ9 GLQ13-GLQ15, GLQ17, GLQ18, GLQ25, GLQ26	Thin Sections, Locality GLQ
GLQ2(1), GLQ4(1)-(5) GLQ5(1)-(4), GLQ6(1)-(4)	Serial Acetate Peels Locality GLQ

King Collection

B52A	Silksworth, Pl. 5 Fig. 1 of King (1850)
B52B	Silksworth. Pl. 5 Fig. 2 of King (op. cit.)
B52C	Silksworth

B108A-B108D

Tunstall Hills

B108F-B108G

Tunstall Hills

Korn Collection

Taf. IV fig. 4

Labelled Phyllopora
ehrenbergi in Korn
(1930), from Oepitz.

Taf. III fig. 6

P. ehrenbergi from
Glücksbrunn

Taf. III fig. 7

P. ehrenbergi from
Kochsberg bei Alten-
burg

Taf. III fig. 8

P. ehrenbergi "Aus
tieferen Niveau des
Krolpauer Riffs".

Taf. III fig. 12

Labelled Phyllopora
solida in Korn
(1930), from Oepitz.

Taf. III fig. 14

P. solida,
Spitziger Stein bei
Thal

Taf. IV fig. 1

P. solida,
Kochsberg bei
Altenburg

Taf. IV fig. 2

P. solida, Oepitz

Taf. IV fig. 3

P. solida,
Kochsberg bei
Altenburg

Taf. IV fig. 20

P. solida, Roschitz
bei Gera

Stratigraphical Range

Upper Permian

Occurrence

Kingopora ehrenbergi is a rare species at German and English reef localities (see p.323 for details of distribution). Its only other documented occurrence is in the U. Permian of the Russian platform, Morozova (1970).

Aspects of the Morphology of Kingopora ehrenbergi

Colony Origins

The holdfast of this species is strikingly robust - the base of the zoarium may reach a diameter of 12 mm and extrazoooidal skeleton may extend for up to 15 mm above the substrate of attachment, covering apertures and fenestrules (see Pl. 36). Extrazoooidal skeleton is developed on both the inside and outside of the zoarium and may reach a great thickness. Fine longitudinal striae may be visible in this skeleton - they are 20 μ wide and their length is parallel to colony growth direction. The proximal part of the inside of infundibuliform zoaria may be completely infilled by massive skeleton similar in nature to the primary granular skeleton (see Pl. 47). Vesicular skeleton may be developed in this region (see Pl. 45). Vesicles are variable in size but generally between 0.1-0.15 mm in diameter. It is assumed that the disposition of soft parts relative to this skeleton was as in the *Fistuliporina*, i.e. the space in a vesicle contained no soft parts, Utgaard (1973). Similar vesicular extrazoooidal skeleton is described by Tavener-Smith and Williams (1972) in Semicoscium rhombicum. The vesicles of Kingopora ehrenbergi tend to be

rectangular in shape, in this respect they differ from those in the majority of fistuliporid species and in Seminicoscinium which are more blister-like and more strongly curved. As with most fistuliporids these vesicles do not have compound walls. Utgaard (1973) describes the extrazoooidal skeleton of fistuliporids as buttressing the colony in between autozooecia; the vesicular skeleton close to the colony origin in K. ehrenbergi may be analogous to this in strengthening the zoarium.

Spines near colony origins may also have functioned to maintain the strength and stability of the colony (see Pl. 46). They may reach a diameter of 2.3 mm and usually extend normal to the obverse surface, occasionally bifurcating or growing more nearly vertically. They may also grow vertically up the inside of the zoarium 'encrusting' the reverse surface of branches and dissepiments and obscuring fenestrules (see Pl. 37 fig. d).

In thin section the extrazoooidal skeleton developed around a colony origin has a very characteristic striated appearance (see Pl. 47). The striation is defined by skeletal bands showing alternate extinction - they have an average width of 20μ and presumably correspond to the striae visible in hand specimens. Discontinuities, perpendicular to the length of the striae, may occur in this skeleton (see Pl. 47); the orientation of the striae changes slightly across these discontinuities and there appears to be a concentration of iron-rich material at the boundary. It is possible that these discontinuities represent temporal breaks in deposition of the skeleton.

Zooecial chambers close to colony origins may reach considerable

lengths (up to at least 1.02 mm) - well in excess of that of a normal autozooecial chamber in a mature part of a zoarium (see Pl. 48). The fact that the zooecial chamber has not been sealed by the secondary laminated skeleton, which is deposited in great thicknesses all around it, suggests that some form of zooid was functioning in the chamber during the deposition of that skeleton. A normal autozooid is very unlikely to have reached 1.02 mm in length; unless a specific polymorph was developed, it may be that the polypide only occupied the more distal part of the chamber - having achieved this position by some degeneration - regeneration process. There is no basal diaphragm developed in the chamber, which would support this interpretation, but the possibility exists of a soft-part, analogous in function to a calcified basal diaphragm, being developed in the chamber at some level closer to the aperture. Utgaard (1973) cites the occurrence of ontogenetic elongation of autozooecia in the oral direction as evidence in favour of the existence of degeneration - regeneration cycles in Cystoporates.

A 'supplementary lateral lamina' is developed in one specimen (see Pl. 49). It occurs on one side of the zoarium, 14mm above the zoarial origin and consists of a thin (approx. 10 μ) layer of skeleton which extends at right angles to the direction of colony growth for 5.2mm. It tapers away from the zoarium and is slightly undulatory.

Geinitz (1861) described "Dingeria depressa" as a coral. Korn (1930) suggested that it was part of the holdfast of Kingopora ehrenbergi. Korn's text fig. 6a may well be part of a holdfast but fig. 6b could be of a transverse section of a trepostome in cast preservation (see fig. 32). Specimens similar to Korn's fig. 6b have

been found in the present study (see Pl. 50), most of these appear to be trepostomes in cast preservation.

Polymorphs

Nanate zooecia occur rarely.

In one zoarium inflated mound-like structures occur on the obverse surface; they are developed on branches and extend laterally to cover fenestrules. They may be roughly circular or may form a narrow prominent band (see Pl. 51) and are superficially similar to the maculae of some trepostomes. Apertures occur on their surface and have the same size and I.A.D. as autozooecial apertures. They are not regularly distributed in the zoarium, so they are not likely to be analogous to the maculae of some trepostomes whose function is probably to aid the production of excurrent water chimneys, Banta, McKinney and Zimmer, (1974). The proposed water-current model for K. ehrenbergi (see ^{p. 365}) excludes an excurrent chimney interpretation for these structures. A polished section of one of these areas revealed thin walls which partitioned what would have been the fenestrule (unfortunately a thin section of this was destroyed during preparation). Pl. 52 shows a zoarium in which thin skeletal walls are developed in a fenestrule of the species. This may represent a stage in the development of the feature described above.

Without thin sections it is difficult to interpret these structures with certainty, but their inflated mound-like shape suggests an analogy with the gonozooids of some cyclostomes might be appropriate. Their distribution may contradict this interpretation to some extent - they do not occur in zones in a zoarium, unlike

structures considered to be ovicells in other Palaeozoic Stenolaemates (e.g. Utgaard 1973). The possibility that they are merely some pathological feature is suggested by the fact that they have been seen in only one specimen, though their occurrence in several parts of the zoarium decreases the likelihood of such an explanation being correct.

Subfamily Acanthocladiinae Zittel, 1880

Diagnosis

Polyporidae with pinnate, dichotomous or reticulate zoaria.
Branches and dissepiments with autozooea.

Range

Devonian - Permian.

Genus Synocladia King, 1849

Type Species

Retepora virgulacea Sedgwick, 1829

Diagnosis

Polyporidae with irregularly shaped fenestrules. Dissepiments V-shaped, of variable length, straight or oblique to branches. Branches straight, with 3 or more rows of apertures; one or more rows of apertures on dissepiments. Nodes and longitudinal ridges may occur on the obverse surface. Fine longitudinal striae may occur on the reverse surface. Zooecial chambers curve obliquely from the reverse to the obverse surface. Zooecial chamber bases rhomboidal to elongate hexagonal. Ovicells may occur. Nanate zooecia may occur. ? Accessory pores may occur.

Range

Permian

Taxonomic Procedure

The procedure in the present study is basically the same as that used for the Fenestellidae (see p 72). Fenestrule dimensions are not considered to have the same taxonomic significance in Synocladia virgulacea as in species of Fenestella.

Fig. 35 shows measured parameters. Fenestrule length is measured at the point of contact of a dissepiment with a branch, parallel to

branch length, from centre to centre of longitudinally adjacent dissepiments which arise from the same branch.

Fenestrule width is measured perpendicular to branch length between the centres of adjacent branches.

Branch width is measured perpendicular to branch length, away from points of bifurcation.

Dissepiment width is measured perpendicular to dissepiment length at its narrowest point.

Inter-Apertural-Distance is measured between the centres of apertures which are longitudinally adjacent on a branch.

Inter-Nodal-Distance is measured between the centres of nodes which are longitudinally adjacent on a branch. Apertural diameter is measured between the inner edges of the aperture.

Thin sections are prepared in three orientations, as in the Fenestellidae:- Tangential, Longitudinal and Transverse. Zooecial chamber base length and zooecial chamber base width are measured in tangential section. Z.B.L. is the maximum dimension of the chamber base parallel to branch length. Z.B.W. is the maximum dimension of the chamber base perpendicular to branch length.

Synocladia virgulacea Sedgwick, 1829

Figs. 35-39, Pls. 54-70

- 1820 Keratophytes dubius Schlottheim, p. 340-341 [partim].
- 1826 Gorgonia dubia Goldfuss, p. 18-19, pl. VII fig. 1 ? [partim].
- 1829 Retepora virgulacea Sedgwick, p. 120, pl. 12 fig. 6.
- 1848 Fenestella virgulacea Phillips; Howse, p. 262-263 .
- 1850 Synocladia virgulacea Phillips; King, p. 39-40, pl. III fig.14,
pl. IV figs. 1-8 .
- 1861 Synocladia virgulacea Phillips; Geinitz, p. 118, pl. XXII figs. 3
and 4 .
- 1885 Synocladia virgulacea Phillips; Waagen and Pichl, p. 802-804,
pls. XCII fig. 4, XCIII figs. 1 and 2.
- 1930 Synocladia virgulacea Phillips, ; Korn, p. 357-359, pl. II figs.
2-4, pl. I fig. 9 , text fig. 3 .
- 1930 Synocladia weigelti Korn, p. 359-360, pl. I figs. 10 and 11, pl.
II fig. 1.
- 1930 Synocladia dux Korn, p. 360, pl. II figs. 5 and 6.
- 1961 Synocladia virgulacea Phillips; Dreyer, p. 24, pl. XI, figs. 1
and 2.

Type material

Schlottheim (1820) figured no specimen and designated no specimen as type for the species Keratophytes dubius. Goldfuss's (1826) figured specimen of Gorgonia dubia could not be traced. The type specimen of Retepora virgulacea which was figured by Sedgwick (1829)

could not be located and is presumed lost. Korn's (1930) type material for Synocladia dux and Synocladia weigelti was studied and placed in synonymy with Synocladia virgulacea (see p. 151 for discussion).

Diagnosis

Synocladia with variably shaped fenestrules. Branches narrow to fairly robust with 3-5 rows of apertures. Dissepiments with 1-3 rows of apertures, fairly narrow, V-shaped, oblique or at right angles to branches. Secondary branches may be developed from dissepiments. Apertures circular, arranged in quincunx. Nodes may occur in 2 rows on the obverse surface of branches and 1 row on dissepiments. Two weakly developed longitudinal ridges may occur on the obverse surface. Reverse surface may show fine longitudinal striae. Zooecial chamber bases elongate hexagonal. Ovicells may be common. Nanate zooecia may occur.

Description

External

The zoarium is basically infundibuliform, often forming a flat expanse after initial fairly steeply erect growth (see Pl. 54 fig. a). Autozooecial apertures open onto the inside of the zoarium. Multilaminar growth occurs (see Pl. 63). Intra-zoarial fusion of branches is common. Spines may occur throughout a zoarium but tend to be concentrated near the zoarial origin (see Pl. 55 fig. b).

Fenestrules are very variable in shape and size (see fig. 37) but tend to be rectangular.

Branches are straight and fairly flat at the obverse surface; 3-5

rows of circular (rarely slightly elongate parallel to branch length) autozooeal apertures may be developed quincunxially; 3 rows is the norm. Narrow branches which only extend a short distance may rarely have only 2 rows of apertures (see Pl. 55 fig. c). Nodes are variably developed throughout a zoarium but usually form two longitudinal rows either side of the central row of apertures; occasionally they appear to be situated at the apex of a weakly developed longitudinal ridge. They occur also on dissepiments, isolated or in a single row (see fig. 36). They are elongate parallel to branch length near their base and circular in cross-section higher up. They are quite regularly spaced. Dissepiments are not usually depressed relative to the obverse surface. The reverse surface of a branch may be gently to steeply curved. From 6-8 longitudinal striae may be visible. Dissepiments are usually well-depressed relative to the reverse surface.

Dissepiments may be at right angles or oblique to branches or may form a distally-pointing V. 2-3 rows of apertures may occur (rarely, only 1 row), arranged in quincunx. Branches may arise at the point of fusion of two halves of a dissepiment - these are often narrower than normal branches. Short, minor secondary branches may occur at a high angle to dissepiments - these are usually developed only when fenestrules are particularly wide (see Pl. 56 figs. a, b)

Ovicells may be common. Nanate zooecia may occur.

Internal Form and Skeletal Microstructure

Zooeal chamber bases are elongate hexagonal (see Pl. 56 fig. c, Pl. 57 fig. a). Their shape in tangential section becomes oval and

then circular as the obverse surface is approached (see Pl. 57 fig. 9). Zooecial chambers curve obliquely from the reverse to the obverse surface (see Pl. 58 figs. b, c).

The primary granular layer is quite thick - the 'inner platy core' is not clearly defined.

Between 6 and 8 longitudinal striae are visible in tangential section.

A large amount of extrazoooidal skeleton may be developed in the proximal parts of zoaria. This may be outer laminated skeleton, and/or primary granular layer which may have laminae in a chevron-like arrangement.

Narrow skeletal rods are visible in tangential section (see Pl. 58 fig. a).

Only poorly-developed inner laminated layer has been seen in this species in the present study.

The outer laminated layer is of a variable thickness; its boundary with the primary granular layer is often irregular (e.g. see Pl. 65). Concentric laminae are developed around apertures.

The fusion of the two halves of dissepiments is often irregular with growth in slightly different planes c f. Fenestella retiformis (see Pl. 57 fig. a).

Measurements

N = 96

	NM	Mn	Mx	S.D.	C.V.	$\bar{X}$
F.L.	820	0.761	1.81	0.196	17.9	1.096
F.W.	830	0.761	1.85	0.207	17.8	1.165

B.W.	830	0.397	0.849	0.088	15.4	0.573
D.W.	800	0.214	0.518	0.062	17.4	0.35
I.A.D.	600	0.243	0.307	0.015	5.3	0.279
I.N.D	65	0.293	0.347	0.021	6.5	0.319
Z.B.L.	45	0.281	0.306	-	-	0.296
Z.B.W.	45	0.102	0.112	-	-	0.108
A.D.	50	0.09	0.12	-	-	0.098

Measurements on Korn's Material

Specimens Taf. II fig. 2, Taf. II fig 4 and Taf. I fig. 9, referred to Synocladia virgulaca by Korn (1930).

N = 2

	NM	Mn	Mx	$\bar{X}$
F.L.	18	1.14	1.32	1.23
F.W.	18	1.9	2.0	1.95
B.W.	18	0.633	0.647	0.64
D.W.	18	0.329	0.338	0.334
I.A.D.	8	(0.30)	(0.34)	0.323

Specimen Taf. II fig. 6, referred to Synocladia dux Korn, by Korn (1930).

N = 1

	NM	Mn	Mx	$\bar{X}$
F.L.	9	1.3	1.6	1.47
F.W.	-	-	-	-
B.W.	9	0.54	0.66	0.589
D.W.	9	0.3	0.4	0.36
I.A.D.	10	0.32	0.36	0.328

Fenestrule width was so variable on this specimen that its measurement was impractical.

Specimen Taf. I fig. 10, Taf. II fig. 1, referred to Synocladia weigelti Korn, by Korn (op. cit.).

N = 1

	NM	Mn	Mx	$\bar{X}$
F.L.	-	-	-	-
F.W.	-	-	-	-
B.W.	10	0.38	0.54	0.43
D.W.	9	0.3	0.34	0.313
I.A.D.	9	0.28	0.33	0.30
A.D.	3	0.10	0.10	0.10

Fenestrule dimensions were so variable on this specimen that measurement was impractical.

Figs. 38 and 39 show histograms of colony average values of various parameters. D.W. and B.W. show fairly broad, normal distributions; the modal value corresponds well with the calculated sample mean in both cases. F.L. and F.W. are fairly weakly positively skewed. This is not considered significant enough to warrant taxonomic subdivision of these specimens; it reflects a bias of specimens with larger fenestrule dimensions (this variation is considered to be ecophenotypic, or due to intraspecific genetic differences or different intra-colonial developmental phases, or a combination of all three). The reason for the lack of specimens with small fenestrules, which would 'balance' those with larger

fenestrules, giving a normal distribution, may be that there is a definite minimum size to a fenestrule below which the functional efficiency of feeding zooids is likely to be impaired. Such a stringent constraint is unlikely to apply to the maximum size of fenestrules.

Measurements in Thin Section

The primary granular layer beneath zooecial chambers varies in thickness from $65-115\mu$. The outer laminated layer is very variable in thickness. The inner laminated layer may reach 4μ in thickness.

The inter-zooecial wall is from $8-10\mu$ thick. Longitudinal striae, as defined by extinction bands, average 25μ in width.

Vestibule lengths average about $150-180\mu$. Zooecial chamber lengths average about 0.7mm .

Skeletal rods are 3μ in diameter and have a nearest-neighbour separation, centre to centre, of 12μ .

Intra-zoarial variation

Measurements were made on one specimen (HN9) (see Pl. 59 fig. a) which showed a striking dichotomy of morphology between proximal and distal parts of the zoarium.

Proximal:

	NM	Mn	Mx	$\bar{X}$
F.L.	13	1.6	2.88	2.22
F.W.	9	0.9	1.4	1.17
B.W.	9	0.48	0.66	0.582

D.W.	9	0.24	0.44	0.324

Distal:

	NM	Mn	Mx	$\bar{X}$
F.L.	14	1.0	1.5	1.25
F.W.	10	0.9	1.4	1.03
B.W.	9	0.44	0.54	0.491
D.W.	9	0.38	0.5	0.428

Fenestrules are markedly shorter in the more distal part of the zoarium. Dissepiments are broader and branches are narrower. The distal part of the zoarium has a distinct boundary with the proximal part and represents a 'sub-colony' (in 'The Treatise' this term is used to described a grouping of zooids, the function of which is related to the production of excurrent water outlets - its use here is for a part of a colony which develops from a point on a branch, expanding rapidly out of the plane of growth of the more proximal parts and consequently having an aspect similar to that of a colony origin). Such features are quite commonly developed in this species (see also p.166). The distinct 'sub-colony' morphology in the example above could be the result of different developmental phases of the colony or environmental influences or a combination of the two.

Discussion

Specimens K45.1, K45.2, C20 and K40 (2 specimens), from Schlotheim's collection, labelled as Keratophytes dubius, were studied and were, without exception, found to be Synocladia virgulacea. This raises the question of the suitability of the retention of

Keratophytes dubius as type for the species Thamniscus dubius. However, Schlotheim's material of Keratophytes dubius is very extensive and probably includes specimens which would be referred to the Thamniscus dubius of the present study - Korn examined Schlotheim's material in greater detail and referred part of Keratophytes dubius to Thamniscus dubius and to Thamniscus geometricus. Since only a small part of Schlotheim's collection was seen in the present study, Korn's (1930) conclusions are accepted and Keratophytes dubius is retained as the type for Thamniscus dubius, not Synocladia virgulacea, in order to minimize systematic upset.

The figure of Gorgonia dubia in Goldfuss (1826) appears to be of Synocladia virgulacea, however the description of the species is such that Acanthocladia may have been included in Goldfuss's concept of the species. None of Goldfuss's specimens have been seen and so Gorgonia dubia is only tentatively placed in synonymy with Synocladia virgulacea.

The species 'Retepora virgulacea' has been attributed, without exception, to Phillips (1829). However, no such publication exists. The reference which is cited is in fact Sedgwick (1829). In this publication, Sedgwick adopts the trivial name 'virgulacea' from a manuscript catalogue of Phillips and is thus the true author of 'Retepora virgulacea'.

King (1850), and Waagen and Pichl (1885), in detailed descriptions of the species, emphasised the variability of its zoarium and in particular of its fenestrules and dissepiments.

Korn (1930) produced an incomplete description of Synocladia virgulacea. Unfortunately, his understanding of the genus was

inadequate and he established two new species - Synocladia weigelti and Synocladia dux; both of these are here placed in synonymy with S. virgulacea.

The distinguishing specific characteristic of S. weigelti, according to Korn (op. cit.), is the presence of two rows of circular apertures and two rows of longer, oval apertures on a branch. Korn has clearly mistaken the moulds of nodes for apertures. Study of Korn's type specimen (Taf. I, fig. 10, Taf. II, fig. 1) (see Pl. 60 fig. a) has shown that it has three rows of apertures and 1 or 2 rows of nodes. Korn gives the apertural diameter in this species as 0.2 mm - the present author's measurements gave a value of 0.1 mm. Branch width of Korn's type specimen is very narrow (0.43 mm), but this falls just within the range of values found in S. virgulacea. The very delicate branches and the sparse occurrence of dissepiments are not typical of S. virgulacea but it is doubtful whether they are characters which warrant establishing a new species. Dissepiment spacing may be very variable within a specimen (see Pl. 59 fig. a) and as such is difficult to use as a specific taxonomic character. Branch width varies continuously, and although the end-member specimens in the series of the present study look strikingly different (see Pl. 61), no significant discontinuity exists such that a new species could be defined by a difference in this parameter. Synocladia weigelti Korn (1930) is thus considered synonymous with Synocladia virgulacea in the present study.

In his description of Synocladia dux, Korn does not state clearly the distinguishing characteristics of the new species. From his figure (Taf. II fig. 6), the specific characteristic would appear to

be the great divergence of branches and the consequently large fenestrules (see Pl. 60 fig. b). This zoarial habit is strongly homeomorphic with that of Acanthocladia but obverse surface details of Korn's type specimen confirm its generic assignment to Synocladia. Measurements of B.W., D.W., F.L. and I.A.D., made on the specimen all agree well with values for S. virgulacea (see above), though I.A.D. is slightly larger. Specimens with a comparable zoarial morphology have been found in the present study (see Pl. 60 fig. c) and are considered to be distal parts of zoaria of S. virgulacea where rapid expansion has taken place without the production of the normal number of new branches. Synocladia dux Korn (1930) is thus here regarded as synonymous with Synocladia virgulacea.

The concept of S. virgulacea in this study embraces a considerable range of morphology. Intra-zoarial analysis of measured parameters demonstrates the scale of variation which may be encountered in a single specimen (see p.158). In some cases, different zoarial morphologies appear to be correlated with growth in particular environments (see p.315).

It was initially thought that a new species of Synocladia was represented by three specimens collected in the present study (RH 1.70, MP 1.23, MP 1.83) (see pl. 61). They have almost identical morphologies - branch widths and dissepiment widths are at the minimum end of the scale considered characteristic of the limits of variation of S. virgulacea; this gives the zoarium a very delicate aspect. However, specimen MP1.83 has a more robust distal margin where it is more characteristic of the typical S. virgulacea. This can be interpreted as homeomorphy with S. virgulacea by a different species

or as evidence in favour of the specimen's true identity as S. virgulacea. In view of the great variation in morphology encountered in S. virgulacea it is felt that these three specimens should be assigned to that species.

Synocladia pyriformis Yang and Loo (1962) is virtually indistinguishable from Synocladia virgulacea on the basis of Yang and Loo's measurements and figure, though average I.A.D. appears to be slightly lower. Synocladia irregularis Yang and Loo (1962) is comparable in dimensions with S. virgulacea but its zooecial chamber shape may be slightly different (Yang and Loo's figures are not clear with respect to this feature). Synocladia rigida Morozova (1965) is similar to S. virgulacea but has zooecial chamber bases which are more rhomboidal.

Material

RH1.17, RH1.54-RH1.56 RH1.70	Locality RH1
MP1.2, MP1.14, MP1.14b, MP1.7-MP1.9, MP1.10a-MP1.10c, M1.16-MP1.19, MP1.21-MP1.24, MP1.35, MP1.44, MP1.47-MP1.49, MP1.54, MP1.55, MP1.65, MP1.66-MP1.71, MP1.73#1, MP1.73#2, MP1.74#1, MP1.74#2, MP1.77-MP1.84, MP1.100	Locality MP1
MP1.a, MP1.b, MP1#1-MP1#7	Thin Sections Locality MP1
MP3.3	Locality MP3
MP4.5	Locality MP4
HM5.1, HM5.4, HM5.5, HM5.8, HM5.10, HM5.11, HM5.23, HM5.24, HM5.28	Locality HM5
HM5.5 tang, HM5.5 tran	Thin Sections Locality HM5
HAG2.3, HAG2.11	Locality HAG

RH2.1-RH2.10	Locality RH2
RH2.36	Thin Section, RH2
BH5-BH9	Locality BH
SBC3-SBC5	Locality SBC
SBC3a, SBC4a, SBC5a	Thin Sections Locality SBC
HN1-HN14	Locality HN
HYQ11, HYQ12	Locality HYQ
MP5.14-MP5.18, MP5.19a, MP5.19b	Locality MP5
MP5.20, MP5.22-MP5.26 MP5.27b, MP5.28, MP5.56	Thin Sections Locality MP5

Kirkby-Howse, Collection, Hancock Museum

No no.	Non loc.

Oxford Museum

F299	Non loc.

Phillips Collection, York Museum

690F, 697F	Non loc.

King collection

B43A	Humbledon, figured Pl. IV, fig. 3 (King, 1850)
B93	Figured, Pl. IV fig. 10, labelled as <u>Thamniscus</u> <u>dubius</u> by King
B29A	Humbledon, figured Pl. IV, fig. 1
B100	Humbledon, figured ? Pl. IV fig. 2

B45	Humbledon, figured Pl. III fig. 14
B30	Cast of a specimen, figured Pl. IV fig. 7
B29B, B32A, B32B, B43B, B44, B46, B99, B124	Humbledon
B31, B101, B125A	Tunstall Hills

Korn Collection

Taf. I fig. 9	Altenburg near Pössneck
Taf. II fig. 2?	Altenburg near Pössneck
Taf. II fig. 4	Altenburg near Pössneck
Taf. I fig. 10, Taf. II fig. 1	Specimen labelled as <u>Synocladia weigelti</u> by Korn. Altenburg near Pössneck.

Schlotheim Collection

K45.1, K45.2, C20, K40, K40	Labelled as ' <u>Keratophytes dubius</u> '

Stratigraphical Range

Permian

Occurrence

Common in the Middle Magnesium Limestone of N.E. England. Rare in the Zechstein of Germany. Common in the Middle and Upper parts of the Productus-limestone (Permian) of the Salt Range, Pakistan, Waagen and Pichl (1885).

Aspects of the Morphology of *Synocladia virgulacea*

Zoarial Morphology

The basically infundibuliform zoarium of *S. virgulacea* may be variably modified. The zoarium may expand to form an approximately horizontal zoarial lamina, this may be weakly plicate (see Pl. 62 fig. a); this feature is not developed to the same extent as in *Fenestella retiformis*. Intra-zoarial fusion of branches is common, particularly in areas of branch crowding (see Pl. 55 fig. a, Pl. 62 fig. c). Lateral expansion of the zoarium may occur, with new branches arising at right angles to the growth direction of their parent branch (see Pl. 62 figs. b, d) - the significance of such a growth aberration, which is repeated in several different specimens (and therefore unlikely to be functionally insignificant), is not known.

Multi-laminar growth is not uncommon in this species, often resulting from the asymmetrical expansion of a zoarial lamina which may lead to a spiral growth of the zoarium (see Pl. 63). McKinney (1980a) described spiral growth in *Archimedes* and the living *Bugula turrita*, and then later attempted a computer simulation of spiral growth, McKinney and Raup (1982). The type of spiral growth encountered in *Synocladia virgulacea* is not comparable to that modelled by McKinney and Raup (op. cit.), being essentially the product of asymmetrical branch bifurcations rather than the development of branches, successively obliquely offset, from a central helix. Although the mode of development of the spiral in *S. virgulacea* is different, the end product is analogous in its gross morphology to the zoaria produced in McKinney and Raup's (op. cit.)

modelling when the rate of climb of the central helical margin has a value close to zero. Hypothesised water flow patterns through colonies of S. virgulacea may be effected by the development of this spiral morphology (see p.379). Flat-lying zoaria with multi-laminar and spiral growth patterns are much commoner at specific localities - a correlation of zoarial morphology with environment is suggested (see p.325).

'Sub-colonies' may be developed inside the main funnel-shaped zoarium (see Pl. 59 figs. b, c). They arise from a point on a branch and expand rapidly to form a fan shape - it is not known whether the opposite ends of the fan ever unite to form a cone.

Polymorphs

Ovicells are a distinctive and common feature of this species (see p.53 for a full discussion of their morphology and distribution). They may be absent from a zoarium, or very abundant.

Nanate zooecia (see p.50) occur. In some cases (see Pl. 64) large areas of a zoarium may possess such zooecia to the exclusion of normal autozooecia; these are not necessarily the most proximal parts of zoaria. A possible explanation for such a distribution may be that they occur preferentially on branches forming part of a lower (more proximal) spiral zoarial lamina. Refiltration of water after it had passed through a higher (more distal) zoarial lamina would probably be inefficient - a concentration of nanozoids in the lower lamina would avoid this (see p.379 for further discussion).

Colony Origins

Colony origins of Synocladia virgulacea are almost never preserved because of their extreme frailty. Pl. 65 shows a thin section of a preserved zoarial origin. The ancestrula and the earliest zooecial chambers are not visible. The basal layer has a diameter of 3.4 mm; it has a very irregular lower surface and appears to have almost 'flowed' around irregularities of the substrate (see Pl. 66 fig. a). Ductility of the cuticle at the growing edge of encrusting cheilostomes has been described by Soule and Soule (1974) (Ryland, 1976). Analogously, the cuticle of S. virgulacea at the base of the colony may have been ductile. Most of the holdfast skeleton consists of the laminated component of the primary granular layer, though there is a minor amount of outer laminated skeleton. It is a roughly dome-shaped structure with tapering margins - within this, the microstructural elements are quite complex. 'Chevron-like' folds with a wavelength of 35μ are developed in the primary granular layer - they radiate distally but extend only part of the way across the 'dome' (see Pl. 66). They stop at a discontinuity which is defined by a thin layer of less translucent material. Distal to this, the laminations in the primary granular layer are roughly parallel to the surface of the 'dome' but may be crinkled in places. The height of the 'dome' is 1.2 mm - its apex is defined by a change in orientation of the microstructural elements. Distal to this point, a number of spines can be seen in transverse section - they originate at the reverse surface of the zoarium and have a primary granular core surrounded by outer laminated skeleton (see Pl. 67 fig. a). Spines are often numerous near colony origins of S. virgulacea where they

would have provided valuable support, compensating to some extent for the weakness of the holdfast.

Genus Thamniscus King, 1849

Type Species

Keratophytes dubius Schlotheim, 1820

Diagnosis

Acanthocladiid with a zoarium which expands solely by the bifurcation of branches. Sterile dissepiments may occur very rarely but lateral branches and pinnae never occur. The obverse surface has three or more rows of apertures, and nodes which are usually irregularly disposed. The reverse surface may be longitudinally striate. Ovicells may occur.

Stratigraphic Range

(?) Silurian-Permian.

Taxonomic Procedure in Thamniscus

The basic principles are the same as those followed in the Fenestellidae (see p.72).

Branch width (B.W.) is measured transverse to growth direction away from points of bifurcation (see fig. 40).

Branch thickness (B.T.) is the maximum thickness of a branch, measured perpendicular to its width. It is rare that more than one or two measurements of this character can be made for a specimen and usually these have a low degree of accuracy. The taxonomic value of this character is thus reduced.

Inter-apertural distance (I.A.D.), apertural diameter (A.D.) and inter-nodal distance (I.N.D.) are all measured as in the Fenestellidae.

Zooecial chamber base length (Z.B.L.) is measured as in the Fenestellidae - the accuracy of measurement is often impaired by the variable degree of curvature of the chamber base.

Zooecial chamber base width (Z.B.W.) is measured as in the Fenestellidae - the same constraints apply to the accuracy of this measurement as apply to measurements of Z.B.L.

Bifurcation angle (α) is the initial angle of divergence of branches (see fig. 40) - this method of measurement differs from that used by Harmelin (1973) where the angle is determined by theoretical axes joining a proximal bifurcation point to the two succeeding distal points. The method used in the present study is considered to be preferable since Harmelin's measurement includes components of variation other than those of the angle of bifurcation (i.e. distance between successive bifurcations and angle of divergence of branches).

The nature of bifurcation

Since the distinction between the genera Thamniscus and Acanthocladia relies essentially on the difference between a bifurcated branch and a main branch with a lateral branch, it is worth considering this difference in more detail; several features could be significant in this respect:-

- i. Branch Width - bifurcated branches are usually, but not invariably, of roughly equal width, a lateral branch is usually narrower than a main branch.
- ii. Angle between branches - the angle of a bifurcation is usually lower than the angle of divergence of a lateral branch from a main branch.
- iii. The occurrence of lateral branches, regularly spaced, on both sides of a main branch is distinctive but they do not always occur on both sides of a main branch and their spacing may not be regular in all cases (e.g. in Acanthocladia diffusus).
- iv. Attempts were made to differentiate a bifurcated branch from a lateral branch on the basis of budding patterns of autozoecia. These proved inconclusive and would be impossible to apply to most specimens.

All the above features may be taken into account when trying to distinguish between lateral and bifurcated branches. If a number of branches arise successively from a single parent branch then these are considered to be lateral branches - this may be the simplest and most consistent way of distinguishing between branch types.

Thamniscus dubius Schlotheim, 1820

Figs. 40-43, Pls. 71-79

- 1820 Keratophytes dubius Schlotheim, p. 340-341 [partim].
- 1826 [non] Gorgonia dubia Goldfuss, p. 18-19, pl. VII fig. 1.
- 1850 Thamniscus dubius Schlotheim; King p. 44-47, pl. V figs. 7, 8, 9, 11 and 12. [partim-non fig. 10].
- 1861 Acanthocladia dubia Schlotheim; Geinitz p. 119, pl. XXII fig. 5, [partim-non fig. 6].
- 1882 Thamniscus dubius King; Shrubsole, p. 343-344.
- 1885 Thamniscus dubius Schlotheim; Waagen and Pichl p. 808-810, pl. XCIII fig. 4.
- 1929 Thamniscus dubius (?Schlotheim) Waagen and Pichl; Bassler p. 80, pl. CCXLV fig. 12.
- 1930 Thamniscus dubius Schlotheim; Korn, p. 366, Taf. III fig. 1, ? Taf. II figs. 8-11, [partim-non Taf. II fig. 7].
- 1930 Thamniscus geometricus Korn, p. 366-367 [partim]Taf III fig. 2
- 1961 Thamniscus cf.dubius Schlotheim; Sakagami, p. 42, pl. 22, fig. 1.
- 1961 [non] Thamniscus dubius Schlotheim; Dreyer, p. 19, Taf. VII fig. 5.

Type material

No type specimen has been formally designated (see discussion).

Diagnosis

Thamniscus forming small colonies consisting of robust bifurcating branches. Branches roughly circular in cross-section but with flattened obverse and reverse surfaces. Apertures fairly large,

circular to slightly oval, well-spaced longitudinally and arranged in 4-6 rows. Peristomes quite well-developed. Nodes developed on the obverse surface, in isolation or forming a single imperfect row. Reverse surface with well-developed papillate longitudinal striae. Zooecial chamber bases elongate rhombic, or very occasionally elongate hexagonal. Nanate zooecia ? may be present.

Description

No zoarial origin has been seen in the present study but it is likely that the colony was fairly small and essentially bush-shaped; branches often extend sub-horizontally, a short distance from the substrate above which they were supported by spines which originate from the reverse surface of branches (see fig. 42 + Pl. 71 fig. c). These spines may be robust and quite numerous. The zoarium expands solely by the bifurcation of branches -this takes place at an angle of 45-60°. Where branches are subjected to a space constraint within the zoarium they may be of below average width or may terminate within a relatively short distance.

Branches are wide, thick, usually straight between points of bifurcation, with an approximately circular transverse section slightly flattened on the obverse and reverse surfaces. Branch margins may have a weakly serrated appearance, caused by the protruberance of the peristomes of the outermost row of apertures, these apertures tend to encroach some way onto the sides of branches. There are 4-6 rows of apertures (6 rows occur only rarely), arranged quincunxially. They are circular to oval, of fairly great longitudinal separation, fairly large, often with quite well-developed

peristomes. Two small nodes are occasionally visible, one on the inner and one on the outer margin of a peristome. Fairly stout nodes may occur on the obverse surface, isolated, or in a poorly defined row (see Fig. 41).

Nanate zooecia ? may be present.

Internal Form and Skeletal Microstructure

The zooecial chamber base is elongate rhombic (diamond-shaped) but may be rarely elongate hexagonal. The chamber curves gently towards the obverse surface, becoming oval in tangential section a short distance from the reverse surface and then circular to slightly elongate as the long tubular distal part of the zooecium is reached (see Pl. 73 fig. c, Pl. 74 figs. a, b, Pl. 77 fig. b).

The detailed microstructure of this species was mostly not preserved in the material available. In tangential sections, close to the obverse surface, sinuous traces are visible, defined by an alternation of light and dark bands (see fig. Pl. 77 fig. b) - these curve round apertures and appear to represent either a compositional difference or a difference in orientation of elements of the outer laminated layer.

Measurements

N = 30 (see fig. 43)

	NM	Mn	Mx	S.D.	C.V.	$\bar{X}$
B.W.	145	0.804	1.31	0.117	11.9	0.978
B.T.	16	0.68	0.94	0.085	10.4	0.819
I.A.D.	135	0.357	0.454	0.0221	5.7	0.391
A.D.	15	0.135	0.155	8.06×10^{-3}	5.5	0.147
(Z.B.L.	3	0.28	0.32	-	-	0.3)
(Z.B.W.	3	0.12	0.12	-	-	0.12)

Specimen RH 4.38a is not included in the statistics of B.W. for which it has a particularly low value (0.68 mm), it is a very small specimen only preserved as a mould and therefore of uncertain taxonomic position. The colony average maximum of I.A.D. may be unreasonably high - it represents a single measurement in thin section and ought not to be considered of great significance. Specimens MP4.4 and GLQ37 are not included in the statistics of A.D. - they both have low average values for this parameter (0.11 and 0.088 mm respectively) and may not be truly referrable to Thamniscus dubius (see discussion p.177). Measurements of Z.B.L. and Z.B.W. were possible only on one specimen.

Measurements of Korn's Material

These specimens (Taf. III fig. 2, Taf. III fig. 1 and Taf. II fig. 8) (see Pl. 79) are assigned tentatively to Thamniscus dubius.

N = 3

	Nm	Mn	Mx	$\bar{X}$
B.W.	17	0.617	1.12	0.936
I.A.D.	29	0.343	0.349	0.346

Specimen Taf. III fig. 2, assigned to Thamniscus geometricus by Korn (1930) is considered here to be Thamniscus dubius on the basis of its I.A.D. (0.349 mm), though its B.W. (0.617 mm) and its mode of branching are atypical of the species and leave some doubt about the true taxonomic position of this specimen. Specimens Taf. II fig. 1 and Taf. II fig. 8 are probably part of the same zoarium - their taxonomic position is also uncertain because of their poor state of preservation.

Discussion

Thamniscus dubius is a very rare but characteristic species of the Middle Magnesian Limestone. Its large I.A.D., relatively large A.D., robust branches and mode of zoarial growth, exclusively by bifurcation, serve to distinguish it.

Earliest descriptions of the species relied mostly on the mode of growth of the zoarium to separate it from Acanthocladia anceps e.g. King (1850). This distinction is beset by problems of homeomorphy. Branches in Acanthocladia anceps may bifurcate over quite large areas of a zoarium, which usually show lateral branching e.g. see fig. 52 - the bifurcated area of this specimen would be considered of sufficient size for taxonomic work by most authors, without knowledge of its I.A.D. or the form of the rest of the zoarium (confirming it to be A. anceps) it could be erroneously assigned to Thamniscus dubius on the

basis of its zoarial morphology.

The validity of retaining Keratophytes dubius Schlotheim (1820) as the type of Thamniscus dubius^{sensu King} must be questioned. All of Schlotheim's specimens of the species which have been examined in the present study are in fact Synocladia virgulacea. Korn (1930) recognised this in referring part of Keratophytes dubius to his new species Synocladia weigelti, but he also referred part to Thamniscus dubius and to Thamniscus geometricus. All of Schlotheim's collection was not seen so it is reasonable to accept Korn's (1930) conclusion that Keratophytes dubius includes both Synocladia and Thamniscus dubius. The retention of Keratophytes dubius Schlotheim (1820) as the type of Thamniscus dubius^{sensu King} is thus justified because of this and because there is nothing in Schlotheim's original description to contradict significantly the present concept of the species.

King (1850) considered T. dubius to have a very variable morphology - this was due largely to his inclusion of specimens of Synocladia virgulacea in the species, e.g. no. B93 (Plate V fig 10 of King (1850)). He also described specimens which demonstrated a tendency towards the zoarial habit of Acanthocladia - it is likely that these were in fact Acanthocladia. Specimen B92A (Pl. V fig. 7 of King) has pores in its reverse surface (see Pl. 74 fig. c), they are all circular, of the same diameter (0.1-0.11 mm), and irregularly arranged (cf. King's figure which shows them regularly arranged). The pores bear a superficial resemblance to the type of accessory pores described by Morozova (1973), however, they are of variable depth and appear to truncate the longitudinal striae of the reverse surface - these features suggest that the pores result from the activity of some

boring organism (cf. in Fenestella retiformis, p. 114) rather than being an integral part of the bryozoan colony. The longitudinal striae in specimen B92A - Plate V fig. 7 of King (1850) are not 'waved' as King describes them but are straight and parallel to branch length.

Shrubsole (1882) drew attention to some of the inaccuracies of King's (1850) description of the species. He pointed out that the "gemmuliferous vesicles", which King considered characteristic of the species, were merely weathered obverse surface nodes. He also noted that specimens of Synocladia virgulacea had been attributed to Thamniscus dubius by King, thus partly explaining King's mistaken belief that the taxon had a very variable morphology.

The specimens attributed to Thamniscus dubius by Korn (1930) conform fairly well to the concept of that species in the present study, but the specimen Taf. II fig. 7 is closer in morphology to Acanthocladia diffusus. Specimen Taf. III fig. 2, assigned to Thamniscus geometricus by Korn, is tentatively placed in synonymy with T. dubius here - it has an I.A.D. at the minimum end of the scale of variation for the species and an uncharacteristically low branch width.

Material

RH4.26c, RH4.30,
RH4.31, ?RH4.32,
RH4.33, RH4.36,
?RH4.38a, ?RH4.43,
?RH4.38b

Locality RH4

RH4.3, RH4.10
RH4.39, RH4.39a
RH4.32a, RH4.42

Thin Sections
Locality RH4

HM5.1a, HM5.101	Locality HM5
?MP4.4	Locality MP4
?GLQ37	Locality GLQ
?GLT19	Locality GLT

King Collection

B92A	Humbledon Hill, figured (Pl.V fig. 7) by King (1850).
B92B	Humbledon Hill
B92C	Non loc
B92D	Humbledon Hill
B90A	Humbledon Hill
B90B	Humbledon Hill

Korn

?Taf. III fig. 2	Labelled as <u>Thamniscus</u> <u>geometricus</u> by Korn (1930). From Jüdewein.
?Taf. III fig. 1	Oepitz
?Taf. II fig. 8	Oepitz

York Museum

710F-713F	Non loc.

Stratigraphical Range

Permian.

Occurrence

Rare in the Tunstall Member of N.E. England (see p.339 for detailed occurrence), probably rare in the Zechstein of Germany, ? the Productus Limestone of the Salt Range, Pakistan, Waagen and Pichl (1885), ? rare at Noil Baun in the Permian of Timor, Bassler (1929), Kamiyatsuse in the Miyagi prefecture of Japan, Sakagami (1961).

Thamniscus geometricus Korn, 1930

Figs. 44, 45, Pls. 80, 81

1930 Thamniscus geometricus Korn, pp. 366-367, pl. II figs. 17, 18,
pl. III figs. 3-5. [? non fig. 2.], text fig. 8.

1961 Thamniscus geometricus Korn; Dreyer, p. 20, pl. VIII figs. 5, 6.

Type Material

Korn's material was studied. The lectotype (Taf. III fig. 2) is here assigned to Thamniscus dubius and Korn's specimen Taf. II fig. 17 is now designated neotype.

Diagnosis

Thamniscus with a zoarium forming an approximately sub-horizontal cone. Branches bifurcate regularly at short intervals. Branches quite narrow, fairly thick and with a flattened circular cross-section. Apertures quite small, circular to oval, quite closely-spaced in 3-5 quincunxially developed rows. Peristomes fairly well-developed. Small nodes are irregularly distributed over the obverse surface. The reverse surface may show weak longitudinal striae. Zooecial chamber base elongate hexagonal. Ovicells may occur.

Description

The zoarium is an approximately sub-horizontal cone, comprising branches which bifurcate at an angle of from 45-60° at regular distances of usually 1-2 mm. Distally, bifurcations may be more infrequent. Narrow, sterile dissepiments occur very occasionally (see Pl. 80 fig. a).

Branches are quite narrow and fairly thick with a flattened circular cross-section. Narrower branches may occur; they terminate within a relatively short distance - probably because of a space constraint on their growth. There are 3-5 rows (five only rarely) of circular to oval, quite small, quite closely spaced, quincunxially developed apertures - these often extend well onto the sides of branches. A fairly well-developed peristome may be visible - it is better developed in the rows of apertures on the edges of a branch. Small nodes may occur irregularly distributed over the obverse surface.

The reverse surface may show weak longitudinal striae.

The zooecial chamber base is elongate hexagonal. Zooecial chambers curve obliquely from the reverse to the obverse surface.

Ovicells may occur.

Measurements

N = 6

	NM	Mn	Mx	S.D.	C.V.	$\bar{X}$
B.W.	45	0.48	0.787	0.105	15.4	0.682
I.A.D.	42	0.28	0.302	7.34×10^{-3}	2.5	0.293
A.D.	11	0.084	0.1	-	-	0.095
B.T.	5	0.525	0.66	-	-	0.593

Measurements on Korn's material

N = 4

	NM	Mn	Mx	$\bar{X}$
B.W.	28	0.608	0.68	0.636
I.A.D.	28	0.288	0.308	0.296
A.D.	10	0.08	0.1	0.09

The material from the present study agrees closely with that in the Korn collection, except for specimen MP1.26 which has an atypically low value of B.W. (0.48 mm).

Discussion

Korn (1930) assigned this species to Thamniscus, emphasising its differences from T. dubius as its smaller dimensions and the growth of its zoarium as a "flat cone" (cf. the bushy growth he considered characteristic of T. dubius). The form of the zoarium in T. geometricus is not considered here to be particularly distinctive but the smaller value of I.A.D. is considered significant enough to warrant the retention of Korn's taxon.

Dreyer's (1961) choice of specimen Taf. III fig. 2 as lectotype is unfortunate - it has an atypically large I.A.D., of 0.349 mm, which suggests an assignment to T. dubius would be more appropriate, but is typical of T. geometricus in other respects. Although this specimen could be considered an aberrant form of T. geometricus, it is here tentatively referred to T. dubius, Korn's specimen Taf. II fig. 17, (Pl. 81 fig. c) being more typical of the taxon, is proposed as a neotype in place of the lectotype chosen by Dreyer (op. cit.).

Fairly large parts of some zoaria of Acanthocladia anceps may consist solely of bifurcated branches (see fig. 52). Such areas may be of a size considered sufficient for taxonomic work by many authors - the similarity in I.A.D. and the number of rows of apertures in A. anceps and T. geometricus means that small, imperfectly preserved specimens of the two species may be virtually indistinguishable in some cases. Korn's small specimens Taf. III fig. 4 and Taf. III fig. 5 (see Pl. 80 figs. a, c) could represent the bifurcated parts of zoaria of A. anceps, though the tendency for the outer rows of apertures to occur on the sides of branches is more typical of T. geometricus. In spite of these problems, T. geometricus is considered referable to the genus Thamniscus because of the expansion of its zoarium solely by the dichotomy of branches.

The distinction between a lateral and a bifurcated branch is not always easily made (see p.171- in specimen Taf. II fig. 17 (see Pl. 81 fig. c) there are branches which diverge from both sides of a main branch (and may thus be considered lateral branches), though at a low angle (close to that of bifurcation) and they are of comparable width to their parent branch. Branches that are distinctly narrower than normal may occur in this taxon, these are not lateral but are simply bifurcated branches that appear to have suffered a space constraint during growth which has prevented them attaining normal width.

The distalmost parts of specimen HAW63 (see Pl. 81 fig. a) are practically indistinguishable from specimens which are assigned to Thamniscus siccus Dreyer (1961). It is possible that Dreyer's taxon is truly synonymous with T. geometricus, of which it represents a distal margin (see p.189).

Material

MP1.26, ?MP1.64	Locality MP1
HAW63, ?HAW54a	Locality HAW
RH2.73a	Locality RH2
MP5.59	Locality MP5

Korn Collection

Taf. II fig. 17	Pössneck
Taf. III fig. 3	Oepitz
Taf. III fig. 4	Pössneck
Taf. III fig. 5	Oepitz

Stratigraphical Range

Upper Permian.

Occurrence

Thamniscus geometricus is very rare in the Tunstall Member of N.E. England, but, according to Korn (1930), is commoner in the Zechstein reef of Germany.

Thamniscus siccus Dreyer, 1961

Pl. 82

1961 Thamniscus siccus Dreyer, p. 20, pl. VIII figs. 1-4.

Type Material

Dreyer's type material could not be located.

Diagnosis

Thamniscus with a simple main branch with widely spaced bifurcations. Branches straight, quite narrow but relatively thick. Usually with four rows of quite small, circular, fairly closely-spaced apertures. Small obverse surface nodes may occur in two irregular, discontinuous rows. The reverse surface may show fine longitudinal striae. Zooecial chamber bases elongate hexagonal.

Description

The complete form of the zoarium is not known, but, according to Dreyer (1961), it consists of simple bifurcating branches in a "tuft-like" arrangement.

Branches are quite narrow and quite thick with a flattened circular cross-section. They bifurcate at an angle of 50-60° at intervals of 5-15 mm, according to Dreyer (1961), and are straight between bifurcations. Branch margins have a serrated appearance caused by the protruberance of apertural margins.

Apertures are quite small, circular, and quite closely-spaced in usually four quincunxially developed rows - these may extend some way

onto the sides of branches. According to Dreyer (1961), five rows of apertures may occur rarely and three rows may be present after bifurcation. A fairly well-developed peristome occurs. There are two irregular and discontinuous rows of small nodes on the obverse surface; they are approximately circular in cross-section and tend to be developed at the edge of an aperture.

The reverse surface may show fine longitudinal striae.

Zooecial chamber bases are elongate hexagonal.

Measurements

N = 3

	NM	Mn	Mx	$\bar{X}$
B.W.	14	0.558	0.775	0.688
I.A.D.	24	0.303	0.354	0.32
A.D.	7	0.08	0.09	0.085

Accurate measurement was possible on only three specimens. Two of these were very similar, the third had a lower value of B.W. and a higher value of I.A.D. - it was not possible to attribute any significance to these differences because of the small number of specimens of the taxon examined in the present study.

Discussion

The specimens from the present study which have been assigned to Thamniscus siccus agree closely with Dreyer's (1961) description of the taxon, except in the measurement of apertural diameter (0.085 mm here and 0.13 mm according to Dreyer) - this is not considered significant since such a discrepancy could be caused by different

methods of measurement and Dreyer (op. cit.) gives no indication of her methods.

Specimen BH10c (see Pl. 82 fig. c) has a larger value of I.A.D. than the other two specimens measured (0.354 mm $\sqrt$ 0.304 mm) - this difference is quite large but its significance cannot be assessed without a greater sample size. There is uncertainty about the correct taxonomic assignment of small specimens - the main branch of T. siccus differs little from a lateral branch of Acanthocladia anceps with four rows of apertures; the presence of bifurcations is the only feature which could confirm a specimen to be T. siccus.

T. siccus appears to differ from Thamniscus geometricus only in the form of the zoarium and the greater distance between bifurcations. However, bifurcations may be more widely separated in the distal parts of T. geometricus which are thus practically indistinguishable from parts of T. siccus. Although these two species are thus not very clearly differentiated in the material of the present study, they are not placed in synonymy because of the small number of specimens seen and because Dreyer's type material could not be examined.

Material

RH1.18	Locality RH1
HAG2.46	Locality HAG
BH10c	Locality BH
HYR23, HYR23a	Locality HYR - HYR23a is a cavity slide, part of specimen HYR 23

Stratigraphical Range

Upper Permian.

Occurrence

Very rare in the Tunstall Member of N.E. England. Rare in the Zechstein reef of Germany.

Genus Acanthocladia King, 1849

Type Species

Keratophytes anceps Schlotheim, 1820

Diagnosis

Acanthocladiid with main branches from which diverge lateral branches and/or pinnae. Lateral branches may be pinnate. Main branches have three or more rows of apertures and often two rows of nodes. Lateral branches have two or more rows of apertures. Fusion may occur, rarely producing fenestrules. Reverse surfaces may be longitudinally striate or pustulose. Ovicells and nanate zooecia may occur.

Stratigraphical Range

? Carboniferous-Permian.

Taxonomic Procedure in Acanthocladia

The basic principles are the same as those followed in the Fenestellidae. The measurement scheme described by Olaloye (1974) for Carboniferous species of Penniretepora is essentially that followed here (see fig. 46).

The width of the main branch (W.M.B.) is measured transverse to growth direction away from points of bifurcation and the origins of lateral branches where the thickness of the main branch may be significantly increased.

The width of a lateral branch (W.L.B.) is measured transverse to growth direction where its width is stabilized, close to the main branch (this is in contrast to Olaloye's (1974) procedure - she measures across the base of a lateral branch; an extra zooecium is often intercalated here in Acanthocladia, causing a significant increase in width). Bancroft (1984) separated the lateral branches of Penniretepora into 2:1 primary branches (these are developed from a main branch and have branches along their length), 1:2 minor branches (these are relatively short and regularly spaced along a main branch, they have no further branches along their length) and 2:2 minor branches (these are short and thin and are the lateral offsets of 2:1 primary branches). An attempt was made to apply a similar branch classification system to species of Acanthocladia - this was found to be possible only in large, nearly complete specimens. Bancroft (1984) described a grading of zoarial and zooecial dimensions in branches of decreasing order; this feature is inconsistently developed in Acanthocladia and the trend towards smaller dimensions in narrower

branches may be reversed for some characters. Any distinction between branches of different orders on the basis of their width tends to be obscured by the large range of intraspecific variation found in populations from the present study. Because of these problems, and because most specimens are fragmented it was impossible to apply Bancroft's branch classification scheme consistently. A distinction is made between pinnae and lateral branches where possible (e.g. in Acanthocladia magna sp. nov.) but breakage of lateral branches may render this distinction unclear (e.g. often in Acanthocladia anceps).

The spacing of lateral branches (S.L.B.) is measured between the mid-points of longitudinally adjacent branches close to their origins on the main branch. The spacing of pinnae is usually the same as that of lateral branches so no attempt is made to distinguish the two.

The angle of divergence of a lateral branch from the main branch (α) is the initial angle between the two. The bifurcation angle is measured as in Thamniscus (see p.171).

Branch thickness (B.T.) is the maximum dimension perpendicular to branch width.

The number of rows of apertures on branches is stated.

Inter-apertural distance (I.A.D.), apertural diameter (A.D.) and inter-nodal distance (I.N.D.) are measured as in the Fenestellidae.

Zooecial chamber base length (Z.B.L.) is the maximum dimension parallel or sub-parallel to branch length - the accuracy of this measurement is often impaired by the variable degree of curvature of the chamber base.

Zooecial chamber base width (Z.B.W.) is the maximum dimension parallel or sub-parallel to branch length - the accuracy of this

measurement is often impaired by the variable degree of curvature of the chamber base.

Zooecial chamber base width (Z.B.W.) is the maximum dimension transverse to chamber base length - the same constraints apply to the accuracy of this measurement as apply to the measurement of Z.B.L.

'Vestibule' length (V.L.) is the length of the distal tubular part of the zooecial chamber, measured at its proximal edge.

Zooecial chamber length (Z.C.L.) is the total length of the base and distal edge of a zooecial chamber (see fig. 46) - this is measurable only in longitudinal thin sections and cannot be made very accurately.

Acanthocladia anceps Schlotheim, 1820

Figs. 46-54, Pls. 83-91

- 1820 Keratophytes anceps Schlotheim, pp. 341-342.
- 1829 Gorgonia anceps Scholtheim; Goldfuss p. 98, pl. XXXVI figs. 1a-1d
- 1846 Gorgonia anceps Schlotheim; Geinitz, p. 586.
- 1848 Fenestella anceps Schlotheim; Geinitz, p. 18 [partim - non figs. 19-21], pl. VII, figs. 22, 23.
- 1848 Fenestella anceps Schlotheim; Howse, p. 261.
- 1850 Acanthocladia anceps Schlotheim; King, pp. 48-49 [? partim], pl. V figs. 13-18.
- 1861 Acanthocladia anceps Schlotheim; Geinitz, pp. 119-120, [? partim - non fig. 8], pl. XXII fig. 7.
- 1885 Acanthocladia anceps Schlotheim; Waagen and Pichl, pp. 812-814, [?partim], pl. XCIV figs. 1, 2, 3.
- 1930 Acanthocladia anceps Schlotheim; Korn, pp. 369-370, pl. IV figs. 8, 9.
- 1961 Acanthocladia anceps Schlotheim; Dreyer, pp. 21-22, pl. IX figs. 2-5.
- 1970 Acanthocladia anceps Schlotheim; Morozova, p. 240, pl. LVII figs. 2, 3.

Type Material

No types have been designated for this taxon. Specimens K57.1, K57.2, K57.3 from Schlotheim's collection were studied.

Diagnosis

Acanthocladia with three (rarely four) rows of quite small, circular to oval apertures on the main branch and two to four rows on lateral branches. Peristomes and ? fossulae may be developed. Two rows of obverse surface nodes may be developed. Main branches quite narrow to fairly broad and straight. Lateral branches fairly narrow, regularly and quite closely spaced, diverging from the main branch at an angle of usually 70° . Lateral branches may be pinnate. The reverse surface may be longitudinally striate. Zooecial chamber bases are elongate hexagonal. Nanate zooecia may occur. Ovicells may occur.

Description

The form of the colony origin is not known with certainty but the zoarium often forms a sub-horizontal expansion (up to at least 4.5 x 5 cm in size) which may develop from an initial, single, erect branch (see fig. 50 + Pl. 84). It is also possible that the colony origin consists of a circle of radiating branches (see fig. 49, though this specimen could be truly referable to Acanthocladia laxa). Reverse surface spines are quite common and may be robust, their occurrence often coinciding with growth of the zoarium in a sub-horizontal plane. Main branches are always free and may or may not grow in the same plane. Lateral branches and pinnae may fuse with one another, especially in the more proximal parts of zoaria.

Main branches are usually straight but may develop some degree of torsion or occasionally may zig-zag where lateral branches are developed alternately instead of opposite one another. They may be

quite narrow or fairly broad and vary from fairly thin to quite thick. The bifurcation angle is normally 45° but may be as low as 30° , or rarely as high as 60° . Both the obverse and reverse surfaces are flat to weakly convex, the sides of branches are more steeply curved.

Lateral branches are fairly narrow, regularly and quite closely spaced along a main branch, from which they diverge at an angle of 60° - 85° (usually 70°). They may be exactly opposite one another on either side of the main branch or offset to varying degrees. Their length is variable - longer, more robust lateral branches may extend to become main branches. They tend to be more rounded in transverse section than main branches. Short pinnae may be developed on lateral branches.

Pinnae are quite closely and regularly spaced along a lateral branch, or occasionally along a main branch. They are generally shorter and less robust than lateral branches, but are not always distinct from them.

Apertures are quite small, circular to oval, closely-spaced and arranged quincunxially in three rows on a main branch (rarely in four rows and rarely, for short distances, in two rows). A well-developed peristome may be visible and may have a (?) fossula at its proximal edge. Two discontinuous rows of nodes may be developed. They are situated on either side of the central row of apertures and are often at the inner edge of the outer row of apertures. They are elongate parallel to branch length at their base and circular in transverse section higher up. They may be fairly robust and may reach a height of 0.26 mm. A weak median carina is developed where there are only two rows of apertures (see fig. 51 + Pl. 86 fig. c).

Lateral branches have three or four rows of apertures and may

have two rows of nodes. Pinnae have two or three rows of apertures.

The reverse surface may show 6-10 longitudinal striae where the outermost skeleton has been removed. Tubercles of diameter $20-30\mu$ and with a nearest neighbour spacing of $80-120\mu$ occur rarely, forming six or seven slightly irregular rows.

Ovicells and nanate zooecia may occur.

Internal Form and Skeletal Microstructure

The zooecial chamber base is elongate hexagonal in the central row of chambers but tends to be hemi-hexagonal in the outer rows. In tangential section the zooecial chambers become oval and then circular towards the obverse surface. In longitudinal section the shape of the zooecial chamber varies from almost tubular to basically rhombic with a fairly long 'vestibule' - it curves obliquely from the reverse to obverse surface (see Pl. 87, Pl. 89 figs. c,d).

The primary granular layer is of variable thickness. The 'inner platy core' is up to 16μ thick. The inter-zooecial wall is from $10-16\mu$ thick. The inner laminated layer may reach 10μ in thickness. The outer laminated layer is from $60-110\mu$ thick. Skeletal rods extend at right angles to the reverse surface and are $2-3\mu$ in diameter with a nearest neighbour spacing of 15μ . Less densely and regularly spaced skeletal rods with a diameter of $4-6\mu$ may protrude slightly at the obverse surface. Longitudinal striae are approximately 30μ wide.

Measurements

N = 125

	NM	Mn	Mx	S.D.	C.V.	$\bar{X}$
W.M.B.	815	0.56	0.993	0.0999	13.1	0.762
W.L.B.	820	0.353	0.65	0.0753	14.9	0.492
S.L.B.	700	0.8	1.47	0.12	10.7	1.12
B.T.	60	0.4	0.765	0.0871	16.1	0.54
I.A.D.	510	0.267	0.338	0.0135	4.6	0.295
A.D.	80	0.085	0.108	6.89×10^{-3}	7.3	0.095
I.N.D.	46	0.313	0.42	0.052	14.1	0.368
Z.B.L.	10	0.3	0.306	-	-	0.303
Z.B.W.	10	0.094	0.102	-	-	0.098
V.L.	15	0.157	0.212	-	-	0.184
Z.C.L.	12	0.688	0.78	-	-	0.728

Measurements on Schlotheim's Material

N = 3

	NM	Mn	Mx	$\bar{X}$
W.M.B.	30	0.728	0.772	0.744
W.L.B.	30	0.438	0.45	0.442
S.L.B.	30	0.896	1.08	0.992
I.A.D.	30	0.291	0.298	0.294

These measurements correspond well with the average values for the whole sample from N.E. England.

Measurements on Korn's material

N = 2 - specimens Taf. IV fig. 9 and Taf. IV fig. 10.

	NM	MN	Mx	$\bar{X}$
W.M.B.	15	0.731	0.78	0.756
W.L.B.	15	0.433	0.489	0.461
S.L.B.	12	1.23	1.44	1.34
I.A.D.	17	0.32	0.34	0.33

The measurements of I.A.D. and S.L.B. are both higher than the average values for the whole sample from N.E. England, but not significantly so.

The histogram of W.M.B. (see fig. 53) shows a fairly good normal distribution, the model value corresponds well with the calculated sample mean. The histogram of W.L.B. does not show a very good normal distribution, but has a weak positive skewness. Its shape is a reflection of the fact that two distinct sizes of lateral branch may occur - it is not always possible to make this distinction between narrower pinnae and relatively broad lateral branches in small incomplete specimens (see p.192) and the two have thus been grouped together in the statistics for W.L.B. The range of variation of S.L.B. is fairly large but the histogram approximates a normal distribution. Branch thickness has an almost normal distribution, a slight positive skewness probably reflects the variable thicknesses of outer laminated skeleton which may be developed around branches - the upper limit of this character is not subject to as strict a control as the lower limit (which has a definite minimum value related to the shape and size of zooecial chambers). The maximum and minimum values of I.A.D. may not be truly representative. The maximum value of 0.338 mm represents measurement in thin section and may incorporate some spuriously high values. The minimum of 0.267 mm is from a specimen

with only two rows of apertures on the main branch in places (see p.202).

Discussion

Schlotheim (1816/17) figured a specimen of Acanthocladia anceps (pl. II fig. VII) but simply referred to it as some kind of "Keratophyten". He established the species Keratophytes anceps in 1820 for forms consisting of a main branch with lateral branches on either side. Measurements on three specimens from Schlotheim's collection (see Pl. 90) gave average values for all characters which are closely comparable to those of the present study though spacing of lateral branches is slightly lower and they tend to diverge from the main branch at a higher angle.

Goldfuss's (1829) figures show three rows of apertures on the obverse surface of the taxon.

Geinitz (1848) considered the taxon to have from 2-4 rows of apertures on the obverse surface of the main branch. His belief that the taxon could have only two rows of apertures was a result of his inclusion of specimens of Penniretepora in Fenestella anceps (i.e. pl. VI figs. 19-21).

King (1850) described Acanthocladia anceps with three rows of apertures usually but claimed that there were rarely up to six rows present; such specimens may be truly referable to Acanthocladia magna sp. nov., though no such specimen was seen in the King collection.

Pl. XXII fig. 8 of Geinitz (1861) shows Acanthocladia anceps with five rows of apertures on the main branch - this feature suggests that the specimen is referable to Acanthocladia magna, but the form of the zoarium is more characteristic of A. anceps.

Waagen and Pichl (1885) considered A. anceps to have up to six rows of apertures on the main branch.

The broad range of morphologies previously encompassed by A. anceps was narrowed considerably by Korn in 1930 when he established two new species of Acanthocladia and restricted A. anceps to forms with three rows of apertures on the main branch and two on lateral branches. However, Korn's observations were often inaccurate - specimens Taf. IV fig. 10 and Taf. IV fig. 9 (both assigned to A. anceps by Korn) have three rows of apertures on lateral branches. The present author's measurements on Korn's material differ in several respects from those quoted by Korn (1930) - lateral branches diverge from the main branch at angles of 60-70°, not 48-53°, main branches are narrower (0.78 mm. and 0.731 mm ~ 0.85-0.9 mm), lateral branches are narrower (0.489 mm and 0.433 mm ~ 0.55 mm), the oval apertures described by Korn (length 0.14 mm and width 0.1 mm) were almost certainly observed in weathered specimens at a level below that of the obverse surface.

Dreyer's (1961) description of A. anceps differed little from that of Korn though she noted the higher angle of divergence (68-70°) of lateral branches from the main branch. She informally separated A. anceps into two forms:- Acanthocladia anceps A and Acanthocladia anceps B. A. anceps A differs from the typical A. anceps in having two rows of chambers on the main branch in places; a median keel separates the two rows of apertures (see fig. 51). Specimens HAW26a and HAW 32 of the present study show a similar feature (though HAW 32 is very poorly preserved and may be truly referable to Kalvariella - in spite of poor preservation it is clear that the development of two

rows of apertures only takes place for a short distance along the main branch. There is no other significant difference from A. anceps s.s., apart from a slightly small inter-apertural-distance (this value of 0.267 mm may be unreasonably low since a few values of 0.35 mm were excluded from the statistics because they appear abnormally large, their inclusion would raise the value of I.A.D. closer to the average for A. anceps). The occurrence of the median keel coincides with the development of only two rows of apertures. The rarity of specimens which show this feature, and its development along only part of a main branch suggest that it can be considered merely a growth aberration and not of any taxonomic significance. Acanthocladia biserialis, Chronic (1949) appears similar to this form but, according to Chronic (op. cit.), normally has two rows of apertures on the main branch with rarely a third or even a fourth row developed near the base of a lateral branch or pinna. If Chronic's description is accurate and A. biserialis has two rows of apertures on the main branch with four rows on lateral branches, then his taxon may be truly referable to the genus Kalvariella, Morozova (1970) (see p.25). Dreyer (1961) considered Acanthocladia anceps B to be similar to her subspecies Acanthocladia anceps laxa in dimensions and in having three or four rows of apertures on the main branch with three on lateral branches, but referred the form to A. anceps because of its uncharacteristically regular morphology. A row of tubercles occurs on the reverse surface of the main branch of this form. Apart from the row of tubercles on the reverse surface (which could be considered of subspecific taxonomic significance), this form does not differ from the A. anceps of the present study.

Morozova's (1970) concept of A. anceps differs little from that of the present study. She claims that lateral branches diverge from the main branch at an angle of 45-50° - examination of her figures suggests an angle of 60-65° would be more accurate. She describes reverse surface tubercles which are 30-40 μ in diameter. Similar, regularly disposed tubercles have been seen in the present study, they occur in only 7 specimens (from one locality) and have a diameter of 20-30 μ with a nearest neighbour spacing, centre to centre, of 80-120 μ . These have been seen only in mould preservation and probably represent the protruberant tips of skeletal rods. If this is the case then they are strikingly different from the skeletal rods, of diameter 2-3 μ , which have been seen in thin section. The few specimens which show the tubercles do not differ significantly from the normal Acanthocladia anceps in any other respect. A feature such as this could be considered of subspecific or even specific taxonomic significance, however, no attempt will be made to establish a separate taxon for these forms because of their poor preservation and because their distinguishing characteristic is probably unobservable in most specimens.

In the present study it has been found that A. anceps is not always easily distinguishable from A. laxa, A. minor, or A. magna n.sp. For a discussion of the comparisons between these taxa see p.239

The more proximal and/or morphologically less stabilized parts of a zoarium may bifurcate over a fairly large area (e.g. HAW7, see fig. 52). If such an area were the only part of a zoarium available for taxonomic work, it might be wrongly assigned to the genus Thamniscus on the basis of its expansion solely by bifurcation (see p.244 for

further discussion).

Material

HAW1, HAW3a-c, HAW6, HAW7, HAW10 HAW12, HAW13a, HAW14, HAW15, HAW20, HAW26a, HAW32, HAW35, HAW41, ?HAW53, HAW54b, HAW67, HAW78, HAG2.5, HAG2.12, HAG2.23, HAG2.29, HAG2.32, HAG2.35, HAG2.36a, HAG2.36b, HAG2.47, HM7.1, HM7.4a, HM7.4b, HM7.12	Humbleton Hill
HYR19-HYR22, HYR24, HYR25	Locality HYR
RH2.30a, RH2.40b, ?RH2.44, RH2.45, RH2.48a, RH2.49, RH2.50, RH2.51, RH2.54, RH2.57, RH2.64b, RH2.66, RH2.68, ?RH2.72	Locality RH2
BH4a, BH10a, BH11c, BH13	Locality BH
SBC6-SBC8	Locality SBC
RH4.35, RH4.40, RH4.45, RH4.46, RH4.53	Locality RH4
MP5.30a, MP5.30b, MP5.31, ?MP5.33, MP5.34, MP5.36, MP5.37, MP5.38b, MP5.39, MP5.40, ?MP5.41, MP5.30c	Locality MP5 Cavity slide
RH1.50, RH1.51, RH1.53	Locality RH1
MP1.5, MP1.11, ?MP1.15, MP1.28, MP1.29, MP1.32, MP1.37, MP1.38, MP1.45, MP1.56, MP1.57a, MP1.57b, MP1.58, MP1.59, MP1.60a, MP1.60b, MP1.61-MP1.63, ?MP1.72, MP1.101, MP1.102	Locality MP1
MP3.1a, MP3.1b, MP3.3, MP3.4	Locality MP3
?MP4.1, MP4.6, MP4.9, MP4.10	Locality MP4
GLQ32, GLQ32a, ?GLQ33, GLQ38	Locality GLQ
GLQ30, GLQ31	Thin Sections Locality GLQ

RH4.50-RH4.52

Thin Sections,
Locality RH4

MP5.46, MP5.65, MP5.80
MP5.81, MP5.150, MP5T10

Thin Sections,
Locality MP5

Phillips Collection - York Museum

698F, 700F, 701F, 714F

Non loc.

King Collection

B78A

Humbledon, figured
by King (1850), pl.
5 fig. 13.

B91B

Humbledon, figured
by King (1850), pl.
5 fig. 14.

B94

Humbledon, figured
by King (1850), pl.
5 fig. 15

B78B, B96, B126B, B127

Humbledon

B83B

Tunstall Hills

?B91A

Non loc.

Korn Collection

Taf. IV fig. 9

Oepitz

Taf. IV fig. 10

Oepitz

Schlotheim Collection

K57.1, K57.2, K57.3

Non loc.

Stratigraphical Range

Upper Permian.

Occurrence

Acanthocladia anceps is a common element of the fauna of the Zechstein reef in Britain and Germany (see p.339 for detailed distribution). Waagen and Pichl (1885) recorded the taxon from the Middle Productus Limestone of the Salt Range, Pakistan, and Morozova (1970) recorded it from the U. Permian of the Urals. Schaumberg (1979) recorded A. anceps from the Marl Slate of Germany, though his specimens may be truly referable to Acanthocladia laxa

Acanthocladia minor Korn, 1930

Figs. 55-57, Pl. 108

1930 Acanthocladia minor Korn, pp. 370-371, pl. IV, figs. 11-13.

1961 Acanthocladia minor Korn; Dreyer, p. 23, pl. X figs. 2, 3.

Type material

Dreyer (1961) chose Korn's specimen Taf. IV fig. 12 as lectotype for the taxon. This was examined in the present study, as was specimen Taf. IV fig. 13.

Diagnosis

Acanthocladia with straight, pinnate, quite narrow, relatively thick main branches. Pinnae very narrow and short, diverging from the main branch at an angle of 80-90°. Main branches bifurcate at 35-45° and continue to diverge at a constant angle. Quite small, circular to weakly elongate apertures are arranged quincunxially in three rows on the obverse surface. Pinnae have two, rarely three rows of apertures. A thin peristome with a small notch (?fossula) may be developed. Two rows of small nodes may be developed on the obverse surface. The reverse surface may show 5-6 longitudinal striae. The zooecial chamber base is elongate hexagonal. ? Ovicells and nanate zooecia may occur.

Description

External

The form of the complete zoarium is not known. The more proximal parts of a zoarium may consist of irregularly bifurcated branches with

reverse surface spines but distally, the characteristic form of the species is established with main branches diverging widely at a constant angle; the angle of bifurcation being 45° .

The main branch is narrow and quite thick with a flattened circular cross-section. It is usually straight but may develop a small degree of torsion. Short, narrow pinnae are closely and evenly spaced along its length, diverging from the main branch at an angle of $80-90^{\circ}$. Pinnae tend to be more nearly circular in cross-section.

The obverse surface of the main branch has three quincunxially arranged rows of apertures; occasionally a fourth aperture is developed on the edge of the branch. Apertures are quite small, closely-spaced and oval (slightly elongate parallel to branch length) or circular. A peristome is weakly developed but may be quite high at the outer edge of apertures which are on the margin of a branch. The peristome may be incomplete at its proximal side where a small notch (? fossula) is developed. Two rows of small nodes occur on either side of the central row of apertures - they are often at the inner margin of an aperture which is in the outer row. They are roughly circular in cross-section or slightly elongate parallel to branch length.

The reverse surface is quite flat and may show five or six longitudinal striae.

Pinnae usually have two (rarely three) rows of apertures. They reach a length of only 0.6-0.7 mm but may be longer where they have three rows of apertures.

Nanate zooecia and ovicells may occur.

Internal Form and Skeletal Microstructure

The zooecial chamber is elongate hexagonal in tangential section at its base, this becomes oval and then circular towards the obverse surface.

The outer laminated layer is from 60-80 μ thick on the sides of the main branch.

Measurements

N = 8

	NM	Mn	Mx	S.D.	C.V.	$\bar{X}$
W.M.B.	60	0.58	0.717	0.0416	6.6	0.63
W.P.	60	0.323	0.42	0.0263	7.2	0.367
S.L.B.	63	0.944	1.06	0.0355	3.6	0.991
B.T.	2	0.56	0.6	-	-	0.58
I.A.D.	33	0.283	0.324	0.0142	4.8	0.299
A.D.(L)	11	0.087	0.09	-	-	0.089
A.D.(W)	11	0.08	0.08	-	-	0.08
I.N.D.	6	0.35	0.373	-	-	0.362

Measurements on Korn's Material

N = 2 - Specimens Taf. IV fig. 12 and Taf. IV fig. 13.

	NM	Mn	Mx	$\bar{X}$
W.M.B.	11	0.67	0.74	0.705
W.L.B.	16	0.331	0.334	0.333
S.L.B.	14	0.869	0.874	0.872

The material from N.E. England is comparable to the lectotype from Korn's collection - only S.L.B. is slightly larger.

Discussion

Korn (1930) established this taxon for Acanthocladia with branches and pinnae that were narrower than those of Acanthocladia anceps. The divergence of short pinnae from the main branch at an angle of 80-90° was considered by Korn to be the most characteristic feature of the species. He also noted that the zoarium expands only by the bifurcation of the main branch, at an angle of 30°.

Korn's measurements of branch width show no significant difference between Acanthocladia minor and A. anceps (0.7-0.9 mm in A. minor and 0.85-0.9 mm in A. anceps). The present author's measurement of Korn's material (see Pl. 108 fig. a) gave values of 0.67 mm and 0.74 mm for this character, and a bifurcation angle of 35-45° (cf. 30° according to Korn). Korn's specimens of A. minor are distinct from those of A. anceps with respect to the width and separation of pinnae.

The clear dichotomy between Korn's specimens of A. minor and A. anceps is not so well-defined in the large suite of specimens seen in the present study. The separate consideration of each morphological character shows that a degree of overlap exists in each case.

Width of Main Branch

The average value of W.M.B. in A. minor is lower than that in A. anceps (0.63-0.762) but the range in A. anceps (from 0.993 to 0.56 mm) encompasses that found in A. minor (from 0.717 to 0.58 mm)

Width of Pinnae/Lateral Branches

Although the average values are different (0.367-0.492mm) there is an overlap between the minimum value for A. anceps (0.353 mm) and the maximum value for A. minor (0.42 mm). Fig. 57 is a graph of W.L.B. W.M.B. for A. anceps and A. minor and shows that specimens referred to A. minor can be regarded as the minimum end of a continuous scale of variation of these characters in A. anceps.

Spacing of Lateral Branches/Pinnae

The large range of values found in A. anceps (1.47-0.8 mm) completely encompasses that of A. minor (1.06-0.944 mm).

Inter-apertural distance

There are very few measurements of I.A.D. for A. minor but these are practically indistinguishable from any in A. anceps.

Branch Thickness

The few measurements of B.T. show no significant difference between the two species.

Angle of Pinnae/Lateral Branches

The characteristically high angle between pinnae and the main branch in A. minor (80-90°) also occurs in some specimens of A. anceps. It is very rare that a whole specimen has lateral branches in the range 80-90°, but 25% of all specimens of A. anceps have some lateral branches at this angle.

Length of Pinnae/Lateral Branches

The distinction between a broken secondary branch and a short pinna is not always easily made, but 12% of specimens referred to A.

anceps appear to have some lateral branches of comparable length to those of A. minor.

Rows of apertures

The number of rows of apertures on the main branch is the same in both species. A. minor usually has two rows on pinnae but rarely has three. A. anceps usually has three or four rows on lateral branches but very occasionally has only two rows.

None of the above characters, considered in isolation, clearly and consistently distinguishes A. minor from A. anceps. There is a large inequality between the number of specimens of A. anceps and A. minor. However, if an n-dimensional matrix is considered, where the n dimensions represent n morphological characters of the two species, then the space of that matrix would be filled almost completely by the characters of specimens from the present study. The lack of any significant discontinuities in that space could be considered evidence in favour of the synonymy of A. minor with A. anceps. However, the retention of Acanthocladia minor Korn is felt to be justified on the basis of the combination of characters found in the species and because no individual specimen combines all the characters which are unequivocally typical of both A. anceps and A. minor.

Specimens HAW13b and HAW8 are only tentatively assigned to A. minor. They are both in a poor state of preservation and may represent the proximal parts of zoaria. Distally, they are almost identical to the typical A. minor but have a relatively high proportion of pinnae with three rows of apertures. The occurrence of two rows of apertures on pinnae, their narrow width, short length, and

the high angle at which they diverge from the main branch are considered to be the characters which best define A. minor; if specimens HAW13b and HAW8 are correctly assigned to that species then its definition becomes less clear, if they belong truly in A. anceps, parts of zoaria of that species can be strongly homeomorphic with A. minor.

Material

?HAW8, ?HAW13b	Locality HAW
RH1.15, RH1.16, RH1.28, RH1.80	Locality RH1
RH2.55, RH2.56a, RH2.74	Locality RH2

Korn's Material

Taf. IV fig. 12	Lectotype from Pössneck
Taf. IV fig. 13	Paralectotype from Pössneck

Stratigraphical Range

Upper Permian.

Occurrence

Rare at English reef localities but more common at German localities, according to Korn (1930).

Acanthocladia magna sp. nov.

Fig. 58, Pls. 109, 110

1850 Acanthocladia anceps Schlotheim; King, pp. 48-49 [partim]?

1861 Acanthocladia anceps Schlotheim; Geinitz, pp. 119-120 [partim]?
pl. XXII fig. 8.

1885 Acanthocladia anceps Schlotheim; Waagen and Pichl, pp. 812,814
[partim]?

Derivation of name

The trivial name is descriptive of the taxon's relatively robust zoarium.

Type Material

Specimen RH2.43 is designated holotype for the taxon, RH2.52a, RH2.67, RH2.73b, RH2.70a, RH2.46 are paratypes.

Diagnosis

Acanthocladia with a broad, quite thick, pinnate main branch. Lateral branches are broad and pinnate. Pinnae and lateral branches diverge from the main branch at an angle of 70-80°. Pinnae are quite broad. Apertures are quite small, circular to weakly elongate, closely-spaced and arranged in five rows on main and lateral branches, three rows on pinnae. A well-developed peristome with a (?) fossula may occur. Nanate zooecia may occur.

Description

External

The form of the complete zoarium is not known. The main branch is broad and quite thick with a fairly rounded cross-section. Pinnae are regularly and quite closely-spaced along its length, they are quite broad, with three rows of apertures, and diverge from the main branch at an angle of 70-80°. Both pinnae and lateral branches have a fairly rounded cross-section.

The obverse surface of the main branch has five rows of apertures, though the fifth row is not always perfectly developed. The central three rows are arranged in quincunx, the outer two rows tend not to be diagonally offset from the nearest row and tend to be situated on the sides of the branch. Apertures are quite small, circular to slightly oval and closely-spaced. They have a well-developed peristome with a small notch (? fossula) at the proximal edge. No nodes have been seen in the species. The obverse surface (?) may be covered with fine tubercles of diameter 15 μ .

The nature of the reverse surface is not known.

Nanate zooecia may occur.

Internal form and skeletal microstructure

This is based on thin section GLQ16, which is only tentatively assigned to Acanthocladia magna sp. nov. (see Pl. 110).

The zooecial chamber base is elongate hexagonal to diamond-shaped in the central row and hemi-hexagonal in the outer rows. Its shape, in tangential section, becomes oval then circular as the obverse surface is approached.

Measurements

N = 6

	NM	Mn	Mx	S.D.	C.V.	$\bar{X}$
W.M.B.	27	0.88	1.09	0.0787	7.9	0.993
W.L.B.	11	0.907	1.0	-	-	0.954
S.L.B.	8	1.14	1.2	-	-	1.18
W.P.	10	0.6	0.72	0.0457	7.0	0.654
B.T.	5	0.64	0.76	0.0427	6.1	0.696
I.A.D.	45	0.294	0.339	0.0155	5.0	0.313
A.D.	12	0.101	0.104	-	-	0.103

Discussion

In spite of its rarity a new species name is suggested for this form which is characterized by a robust main branch with five rows of apertures. Comparison of various characters shows there to be a small degree of overlap with Acanthocladia anceps.

Width of Main Branch

The main branch width of Acanthocladia magna has a higher average value than A. anceps (0.993 ~ 0.762 mm) but the maximum value in A. anceps (0.993 mm) falls within the range found in A. magna.

Lateral Branches

Lateral branches, with an average width of 0.954 mm, are developed rarely in this species - they are practically indistinguishable from the main branch and are a distinctive feature of the taxon.

Pinnae

The average value of pinna width in A. magna is higher than the average W.L.B. in A. anceps but the minimum is 0.6 mm in A. magna and the maximum is 0.65 mm in A. anceps.

Spacing of Lateral Branches

There is no significant difference in this parameter.

Inter-apertural distance

This is only slightly higher in A. magna (0.313-0.295 mm).

Apertural Diameter

The average apertural diameter is slightly larger in A. magna but cannot be considered significantly different.

Branch Thickness

Branch thickness has a high coefficient of variation in A. anceps (16.1), representing a range from 0.4-0.765 mm, average values for A. magna all lie within this range.

Rows of Apertures

The occurrence of five rows of apertures on the main branch is considered to be the most characteristic feature of the species. However, the fifth row is not always perfectly developed. Some specimens which are referred to A. anceps have four rows of apertures on the main branch - thus a distinction between the two species on the basis of the number of rows of apertures on the main branch is not

invariably evident.

It is believed that the combination of fairly small differences and characters which are rarely inconstant is significant enough to warrant the establishment of a new species. Palaeoecological evidence may be considered to support this view; specimens which are assigned with certainty to Acanthocladia magna occur only at one locality (see p.323). The faunal diversity at this locality is one of the greatest of any studied - the area of outcrop is very small and no distinct, diverse, ecological niches could be identified, so the variation between species of Acanthocladia is unlikely to be ecophenotypic; there is no overlap between A. magna and A. anceps in several of their measured characters at this locality. It is unlikely that specimens have been transported any distance since delicate morphological features are well-preserved.

Thin section GLQ16 is assigned to Acanthocladia magna because it has five rows of zooecial chambers for most of the main branch. It appears to have only four rows for part of the branch but this may be a function of the plane of section - the specimen was not seen prior to sectioning to confirm its taxonomic position.

King (1850) considered the normal condition of A. anceps to be with three rows of apertures on the main branch but claimed that up to six rows could occur. If this is so then part of King's A. anceps may be synonymous with A. magna - none of the specimens studied from the King collection were considered synonymous with A. magna.

Geinitz (1861) described A. anceps with from 2-5 rows of apertures on the main branch. He figured (pl. XXII fig. 8) a specimen with five rows of apertures - this specimen is not similar to A. magna in any

other respect and may simply be inaccurately drawn.

A. anceps described by Waagen and Pichl (1885) may be partly synonymous with A. magna - they considered it to have up to six rows of apertures.

Acanthocladia (?) pampinosa Trizna (1950) is similar to A. magna but has more widely separated lateral branches (as opposed to pinnae), and a broader main branch.

Acanthocladia tumulosa Morozova (1970) is similar to A. magna but has broader and more widely separated lateral branches (as opposed to pinnae) and a zooecial chamber base shape which may be more rectangular.

Material

RH2.43, RH2.46, RH.2.52a
RH2.67, RH2.70a, RH2.73b

Locality RH2

? GLQ16

Thin Section
Locality GLQ

Stratigraphical Range

Upper Permian.

Occurrence

Very rare in the Tunstall Member of N.E. England (see p.220 for detailed distribution). The taxon may also occur (?) at German reef localities and in the Salt Range of Pakistan, Waagen and Pichl (1885).

Acanthocladia laxa Korn, 1930

Fig. 59, Pls. 92-97

1930 Acanthocladia laxa Korn, p. 371, pl. IV figs. 6, 7.

1961 Acanthocladia anceps laxa Korn; Dreyer pp. 22-23, pl. X fig. 1.

1970 Acanthocladia laxa Korn; Morozova, p. 241, pl. LVIII fig. 4.

Type Material

Dreyer (1961) chose Korn's (1930) figured specimen, Taf. IV fig. 7 as lectotype for the species. This specimen was studied, as was Taf. IV fig. 6 of Korn.

Diagnosis

Acanthocladia with a fairly irregular zoarial morphology. Fusion of branches is quite common. Main branches usually have four, but rarely three rows of quite small, circular apertures. Two rows of obverse surface nodes may be developed. Main branches are thin and quite broad. Lateral branches are quite narrow to fairly broad and usually diverge from the main branch at 70°. Zooecial chamber bases are irregular rhombic to elongate hexagonal. The reverse surface may show fine longitudinal striae.

Description

The zoarium probably consisted of a bush-shaped expansion of branches - the largest known specimens reach a height of 3 cm and consist of main branches which may expand in approximately the same plane but also often grow out of this plane. Lateral branches are

often recurved out of this plane towards the obverse surface. Fusion of lateral branches may be quite common. Reverse surface spines may occur.

Main branches are usually straight but often show some torsion and may be recurved from a single plane, they may zig-zag weakly. They bifurcate at angles from 30-60°, are quite narrow to fairly broad and are quite thin. The main branch usually expands in width prior to the development of a lateral branch.

Lateral branches are usually closely and fairly regularly spaced. They diverge from the main branch at an angle of 50-80° (average 70°) and are of variable length. Occasionally, a lateral branch may extend to become a main branch. Fusion of lateral branches is common, often producing irregular fenestrules (see e.g. Pl. 94 fig. b). Lateral branches often flare away from a main branch.

The obverse surface of the main branch is flat to weakly concave. Apertures are quite small, circular and closely-spaced in four (more rarely three) quincunxially developed rows. These rows tend to be slightly oblique to the length of a branch. A thin low peristome may be developed. Nodes are rarely visible in two longitudinally discontinuous rows. They are fairly robust and roughly circular in transverse section. Lateral branches have three rows of apertures.

The reverse surface is gently convex to almost flat and may show 10-20 fine longitudinal striae where the outermost layers of skeleton have been removed.

Internal Form and Skeletal Microstructure

The zooecial chamber base is irregularly rhombic to roughly

elongate hexagonal. Closer to the obverse surface it is rhombic/oval in tangential section, then oval and finally circular. In longitudinal section the chamber consists of a roughly rhomb-shaped proximal part with a distal tubular 'vestibule' of variable length. The lower edge of the rhomb may be sub-parallel to the reverse surface or curve at a shallow angle into the distal edge of the 'vestibule' (see Pl. 96). The most proximal part of the chamber may extend into a small 'toe' (see Pl. 97 figs. a, b).

The primary granular layer beneath a zooecial chamber is from 80-200 μ thick, the 'inner platy core' is only rarely discernible and may be from 6-10 μ thick. The interzooecial wall is 16 μ thick. The inner laminated layer reaches about 10 μ in thickness. Narrow skeletal rods extend perpendicular to the reverse surface and the obverse surface - they have a diameter of 2-3 μ and a 'nearest neighbour spacing' of 13 μ . Longitudinal striae, as defined by extinction bands, are 20-24 μ wide, with new striae often intercalated distally. The outer laminated layer is usually very poorly developed but may reach 100 μ in thickness on the reverse surface and 80 μ on the obverse surface.

Measurements

N = 31

	NM	Mn	Mx	S.D.	C.V.	$\bar{X}$
W.M.B.	190	0.722	1.16	0.125	14.0	0.892
W.L.B.	170	0.42	0.75	0.083	14.8	0.56
S.L.B.	110	0.93	1.43	0.14	12.4	1.13
B.T.	70	0.272	0.6	0.079	18.9	0.42

I.A.D.	75	0.247	0.306	0.017	6.2	0.275
A.D.	20	0.083	0.092	3.31×10^{-3}	3.8	0.087
I.N.D.	4	0.255	0.315	-	-	0.287
Z.B.L.	4	0.272	0.306	-	-	0.293
Z.B.W.	3	0.085	0.119	-	-	0.102
V.L.	40	0.084	0.182	0.028	23.3	0.12
Z.C.L.	40	0.391	0.731	0.097	17.8	0.542

Measurements on Korn's Material

N = 2 - specimens Taf. IV fig. 6 and Taf. IV fig. 7

	NM	Mn	Mx	$\bar{X}$
W.M.B.	10	0.728	0.812	0.77
W.L.B.	17	0.389	0.404	0.397
S.L.B.	8	1.01	1.03	1.02
I.A.D.	4	(0.26)	(0.28)	0.273

W.L.B. from Korn's material is lower than the sample average for specimens from N.E. England; but this difference is not considered significant. Histograms of the data from the present study show very broad distributions for all characters apart from I.A.D. This is partly a function of sample size but also shows how poorly defined this taxon is with respect to these measured parameters.

Discussion

Korn established the species Acanthocladia laxa in 1930. It differed from Acanthocladia anceps in its more irregular zoarium, more flattened branches, broader, and often short lateral branches, the

expansion in width of the main branch prior to the development of a lateral branch, its finer longitudinal striae and the occurrence of four rows of apertures on the main branch with three on lateral branches.

Dreyer (1961) reduced Korn's taxon to a subspecies - Acanthocladia anceps laxa but gave no reason for this step and changed nothing from Korn's original description.

Morozova (1970) maintained Acanthocladia laxa as a species; she considered it to differ significantly from A. anceps only in the number of rows of apertures on the main branch (four versus three).

The study of a large suite of specimens has shown that some of the distinctive characters of A. laxa (according to Korn (1930)) may occur in various combinations in specimens which are assigned to A. anceps or Acanthocladia diffusus on the basis of other criteria. Several specimens can be referred to A. laxa only very tentatively. The possible synonymy of either or both A. anceps and A. diffusus is discussed further on p.239 The separate consideration of each morphological character shows how poorly defined this species is:-

Main Branch

The main branch of A. laxa is wider than that of A. anceps but the range of variation in the two species overlaps to a large extent (see fig. 53). The expansion in width of the main branch prior to the development of a lateral branch is a quite characteristic difference between A. laxa and A. anceps, though not all specimens of A. laxa show this feature, e.g. GLQ34a and b, GLQ35 - referred to A. laxa because they have four rows of apertures on the main branch and an irregular zoarium. Some specimens show this feature in only parts of

a zoarium, e.g. RH1.1b, BH14. The main branch of A. diffusus is usually narrower than that of A. laxa but shows a significant increase in width prior to the development of a lateral branch.

Lateral Branches

The lateral branches of A. laxa are only slightly broader than those of A. anceps; they are usually shorter and tend to flare away from the main branch. However, the lengths and widths of lateral branches in the two species show considerable overlap (see fig. 54) and not all lateral branches of A. laxa flare away from the main branch. Lateral branches of A. diffusus are similar to those of A. laxa but are much more irregularly distributed.

Branch Cross-Section

The more flattened branches which Korn (1930) thought to be characteristic of A. laxa differ only slightly from those of A. anceps and A. diffusus. A. laxa can be considered intermediate in morphology between A. anceps (biconvex) and A. diffusus (concavo-convex) with regard to this feature.

A histogram of B.T. (fig. 53) shows that this feature is not particularly distinct for the three species.

Longitudinal Striae

The longitudinal striae of A. laxa differ only slightly from those of A. anceps - they are narrower ($23\mu \sim 30\mu$), more numerous on a branch (10-20 $\sim$ 6-10) and tend to be intercalated rather than parallel. The differences in size and number of the longitudinal striae are not very great and the degree of intercalation of striae may be increased in A. anceps close to bifurcation points.

Rows of Apertures

The supposed dichotomy between A. laxa and A. anceps on the basis of the number of rows of apertures on the main branch (i.e. 4~3) is not well-defined. Dreyer's (1961) choice of lectotype for A. laxa (Taf. IV fig. 7 of Korn) is unfortunate since it is a specimen with both three and four rows of apertures on the main branch. Several specimens from the present study have both three and four rows developed along the same branch e.g. GLQ32a, HYR25, GLQ33 (these are all assigned to A. anceps and RH1.7 (assigned to A. laxa). Specimen B94 (see Pl. 87) has four rows of apertures but is assigned to A. anceps on the basis of all other criteria. RH1.1b has three (rarely four) rows of apertures and is assigned to A. laxa. A fourth aperture, not part of a row, is developed on the edge of a branch in many specimens. A discontinuous fourth row may be budded for several zooecia prior to the formation of a lateral branch e.g. GLQ33.

Apertural Diameter and Inter-apertural distance

A.D. and I.A.D. in A. laxa are both slightly lower than in A. anceps and slightly higher than in A. diffusus. The differences are only small though and there is some overlap between the species (see measurements).

Zooecial Chamber Shape and Size

Zooecial chambers are smaller in A. laxa than in A. anceps ('vestibule' length 0.12 mm~0.184mm and 'length' of zooecial chamber 0.542 mm~0.728 mm) and the zooecial chamber base in A. laxa has a more rhombic shape in tangential section. Zooecial chambers in A. diffusus are smaller than those of A. laxa ('vestibule' length 0.094 mm~0.12 mm and 'length of zooecial chamber 0.428 mm~0.542 mm) and

tend to be more recumbent (see Pls. 97, 104). However, these differences are not very pronounced - large variations in shape and size of chambers may occur within one specimen such that a distinction between these species solely on that basis is not always possible.

Morphology of the Zoarium

The zoarium of A. laxa is more irregular than that of A. anceps and less irregular than that of A. diffusus. The simplest way to compare such a character is by outline drawings of specimens; figs. 60 and 61 show this - the distinction between A. anceps, A. laxa and

A. diffusus is far from clear. The more proximal, morphologically irregular part of a zoarium of A. anceps is practically indistinguishable from a zoarium of A. laxa.

Thus it is clear that A. laxa is often only poorly differentiated from A. anceps and A. diffusus - the taxon is not placed in synonymy with these species because of the great range of intraspecific morphology which would result and because of the combination of characters which exists in most specimens here referred to A. laxa.

Material

?HAW4, HM7.13	Humbledon Hill
BH14, BH17	Locality BH
MP5.38a	Locality MP5
?GLQ35, CLQ36, GLQ34a and b	Locality GLQ
RH2.58, RH2.59, RH2.64a	Locality RH2
HDN12, HDN10, ?HDN8 ?HDN9, ?HDN19, ?HDN7	Locality HDN
HDN1-HDN6, HDN11, HDN13-HDN19b HDN22, HDN23, HDN26	Thin Sections Locality HDN

?RH1.4, ?RH1.2, RH1.23
 RH1.1a, RH1.1b, RH1.14, ?RH1.7,
 ?RH1.8b, RH1.8a, ?RH1.49,
 RH1.11, RH1.13, ?RH1.20

Locality RH1

?RH1.9a-RH1.9e

Thin Sections
 Locality RH1

?RH2.65a-RH2.65c, RH2.65e

Thin Sections,
 Locality RH2

Korn's Material

Taf. IV fig. 6

Pössneck, Paralectotype

Taf. IV fig. 7

Lectotype from Pössneck

Stratigraphical Range

Upper Permian.

Occurrence

Acanthocladia laxa is quite common in the Tunstall Member of N.E. England but less common in the reef in Germany, Korn (1930) (see p. 331 for detailed distribution). Its only other documented occurrence is in the Upper Permian of the Urals, Morozova (1970).

Acanthocladia diffusus (Korn, 1930)

Figs. 62, 63, Pls. 98-107

1930 Thamniscus diffusus Korn, pp. 367-368, pl. I fig. 12, pl. II figs. 12-16.

1930 Thamniscus dubius Schlotheim; Korn, p. 366 [partim], only ? pl. II fig. 7.

1961 Thamniscus diffusus Korn; Dreyer, pp. 20-21, pl. IX fig. 1.

Type Material

Dreyer (1961) chose Korn's specimen Taf. II fig. 13 as lectotype for the species. Unfortunately, this is missing from the collection at Halle. Korn's figured specimens Taf. II fig. 15 and Taf. II fig. 16 were studied - Taf. II fig. 15 is chosen from the available paralectotypes as neotype for the taxon. Korn's Taf. II fig. 7, which he referred to Thamniscus dubius, is here tentatively placed in synonymy with Acanthocladia diffusus.

Diagnosis

Acanthocladia with a very irregular zoarial morphology. Fusion is widespread. Branches bifurcate frequently. Lateral branches are developed irregularly. Apertures small, circular and closely-spaced in three quicunxial rows on main branches, three or two rows on lateral branches. Two rows of obverse surface nodes may be developed. Branches quite narrow, very thin and concavo-convex in cross-section. The reverse surface may show weakly developed longitudinal striae. Narrow spines may link neighbouring branches. Zooecial chamber bases

irregularly rhombic to roughly elongate hexagonal. Ovicells may occur. Nanate zooecia may occur.

Description

The zoarium often consists of approximately coplanar branches in a multilaminar arrangement, but may also be bush-shaped, reaching a height of 3-4 cm. Main branches do not always extend in closely-spaced sub-parallel planes but may be more irregularly disposed. Short lateral branches may link main branches within or between these planes (see fig. 63). Narrow spines may link the obverse surface of one 'lamina' with the reverse surface of the next - in most cases they appear to originate from the reverse surface (see Pl. 107 fig. c) but some are probably extended obverse surface nodes (see Pl. 106 fig. b). The obverse surfaces of all branches of a zoarium face in approximately the same direction (see Pl. 98).

Main branches are straight for only short distances, they bifurcate frequently and often zig-zag, they are quite narrow and very thin. Their growth may not be restricted to a single plane. Branches bifurcate at an angle of 40-60°. Fusion of branches is common, sometimes producing areas of greatly increased branch width.

When uniting adjacent main branches, lateral branches are short; they diverge from the main branch at an angle of 60-90° and produce irregular fenestrules which may be a common feature of the taxon. The main branch may show a significant increase in width prior to the development of a lateral branch. Longer lateral branches tend to diverge from the main branch at a lower angle of 60°, they may be free, but show fusion more commonly. They may become sub-parallel to

the main branch and may be of comparable width to it - in such cases the distinction between a bifurcated branch and a lateral branch is not very clear (see p. 172).

The obverse surface is flat to weakly concave and bears three rows of small, circular, closely-spaced apertures which are arranged quincunxially. These rows may be slightly oblique to the length of a branch. A thin low peristome may be visible. Two rows of nodes are developed, one on either side of the central row of apertures - these rows are often discontinuous. They are fairly robust, tend to be elongate parallel to branch length at their base and circular in cross-section higher up, and may reach great lengths (greater than 0.255 mm).

The reverse surface is weakly convex but may show small-scale irregularities. Between 6-12 fine longitudinal striae may be visible where the outermost skeleton has been removed.

Ovicells may occur. Nanate zooecia may be common.

Internal Form and Skeletal Microstructure

The zooecial chamber base varies in shape from roughly elongate hexagonal to irregularly rounded rhombic (see Pl. 102 figs. a, c, Pl. 105 figs. b, c). Closer to the obverse surface its shape becomes rectangular/oval in tangential section, then oval, and finally circular. In longitudinal section, the zooecial chamber is basically rhomb-shaped with slightly rounded corners, the lower edge of the rhomb is parallel to the reverse surface and the distal edge curves gently up into a very short 'vestibule'.

All thin sections studied are from poorly preserved material so

that no detailed observations on the nature of the microstructure have been possible. However, the thickness of the primary granular layer beneath zooecial chambers varies from 25-45 μ , it is 16 μ thick in inter-zooecial walls and from 25-65 μ thick above a zooecial chamber. The outer laminated layer is very thin - not more than 40 μ thick on the reverse surface and from 30-80 μ thick on the obverse surface.

Measurements

N = 30						
	NM	Mn	Mx	S.D.	C.V.	$\bar{X}$
W.M.B.	210	0.472	0.784	0.078	12.9	0.609
W.L.B.	90	0.325	0.6	0.085	17.2	0.494
S.L.B.	14	1.0	1.4	0.156	13.5	1.152
B.T.	50	0.221	0.391	0.0395	13.9	0.285
I.A.D.	140	0.249	0.289	0.0106	4.0	0.265
A.D.	65	0.076	0.09	3.87x10 ⁻³	4.6	0.0835
I.N.D.	30	0.262	0.357	0.031	9.8	0.318
(Z.B.L.	1	-	-	-	-	0.255)
(Z.B.W.	1	-	-	-	-	0.136)
V.L.	24	0.0396	0.115	0.027	28.7	0.094
Z.C.L.	20	0.34	0.51	0.056	13.0	0.428

Measurements of Korn's Material

N = 2 - Specimens Taf. II fig. 15 and Taf. II fig. 16.

	NM	Mn	Mx	$\bar{X}$
W.M.B.	18	0.655	0.684	0.67
B.T.	2	-	-	0.3
I.A.D.	3	0.24	0.25	0.247

N = 1 - Specimen Taf. II fig. 7 assigned to Thamniscus dubius by Korn.

	NM	Mn	Mx	$\bar{X}$
W.M.B.	7	0.7	0.88	0.803
I.A.D.	7	0.26	0.3	0.285

The measurements of Korn's specimens which were assigned to Thamniscus diffusus by him differ little from the sample averages for N.E. England. Specimen Taf. II fig. 7, assigned to Thamniscus dubius by Korn (1930) is here only tentatively placed in Acanthocladia diffusus on the basis of its general morphology - its measurements of W.M.B. and I.A.D. are atypical of the taxon.

Histograms of B.T. and W.M.B. show approximately normal distributions for the data from N.E. England, though the spread of the data for W.M.B. is quite large (see fig. 53).

The minimum value of W.M.B. may be exceptionally low since it relates to measurement of a very poorly preserved specimen. The maximum value of 0.784 mm was made on a specimen which may be truly referable to Acanthocladia laxa. The minimum value of W.L.B. may not be representative because the difficulty in distinguishing lateral branches from main branches may have led to the omission of some measurements of broader lateral branches, thus lowering the average value for W.L.B. The irregular development of lateral branches allows only a small amount of reliable data for this parameter. The I.A.D. maximum of 0.289 mm represents a single measurement in thin section and may thus not be of particular significance.

Discussion

Korn (1930) established the taxon Thamniscus diffusus for a characteristically irregular form - he suggested that instead, it may be referable to the genus Polypora but this is obviously not the case since it lacks any of the diagnostic features of that genus. Korn described a marked convergence of morphology between Acanthocladia laxa and Thamniscus diffusus - a feature which has been confirmed in the present study and which leads to the suggestion that the two species may be synonymous (see p.239).

The characters which define T. diffusus - according to Korn (1930) are :- a small zoarium (several zoaria often grow one inside another), nearly all branches anastomose or are fused with neighbouring branches, they are flat and 0.7-0.85 mm wide, the reverse surface is not longitudinally striate, there are 2-4 rows of apertures on the obverse surface with the third and fourth rows often imperfectly developed.

In the present study, the taxon is referred to Acanthocladia rather than Thamniscus. Although the distinction between a bifurcated branch and a lateral branch is not always clear (see p.172,) bona fide lateral branches occur in the species; the zoarium does not expand solely by bifurcation as Korn suggested. The possibility of Acanthocladia laxa and Acanthocladia diffusus being synonymous also supports the generic assignment to Acanthocladia. The morphological differences between A. diffusus and Thamniscus dubius (the type species of the genus Thamniscus) are greater than those between A. diffusus and Acanthocladia anceps (the type species of the genus Acanthocladia). The establishment of a new monotypic genus for this

species is not suggested in spite of the fact that it contradicts one aspect of King's generic diagnosis for Acanthocladia i.e. it is not "... rarely bifurcating ...". Thus, Thamniscus diffusus Korn (1930) is referred here to the genus Acanthocladia.

A few of the aspects of Korn's description of the taxon are considered here to be inaccurate. Measurement of his material gave average values for branch width of 0.684 mm and 0.655 mm (c.f. 0.7-0.85 mm). Where the outermost layers of skeleton have been removed it is possible to see that there are in fact fine longitudinal striae on the reverse surface. Apertures are not arranged in two rows with another two only developed in parts, as Korn described, but in three rows which are not always clearly defined because of the irregularity and fusion of branches and because they are often oblique to branch length. Zoaria do not usually grow one inside another.

Acanthocladia diffusus is often not morphologically distinct from Acanthocladia laxa. A dense bush-like growth is characteristic of A. diffusus and different from the more simple arrangement of A. laxa, though this is often in part an effect caused by the close proximity of several zoaria. Zoarial irregularity may not invariably distinguish the two species (see discussion of A. laxa, p.224). A consideration of other characters shows how similar these species are:-

Main Branch

There is only a small amount of overlap in W.M.B. but no particularly significant discontinuity serves to distinguish these species solely on that basis (see fig. 53).

Lateral Branches

Lateral branches are less regularly arranged in A. diffusus than they are in A. laxa but are otherwise quite similar.

Branch Cross-Section

The obverse surface of A. diffusus is more strongly concave than that of A. laxa. A histogram of branch thickness (see fig. 53) shows that this character does not clearly distinguish the two species.

Longitudinal Striae

These are more numerous in A. laxa than in A. diffusus (10-20_v6-12) but this difference is likely to be, at least in part, a reflection of the different branch widths of the two taxa.

Rows of Apertures

A. laxa usually has four and A. diffusus three rows of apertures on a main branch, but, as shown on p.224, rarely, A. laxa may have only three rows in places.

Apertural diameter, inter-apertural distance and zooecial chamber shape and size are compared in the discussion of A. laxa (p.224).

Although differences in individual characters between these two species are often small and may be inconstant it is felt that a subdivision is justified on the basis of the total combination of characters found in most specimens.

Material

MP5.58	Locality MP5
HTQ1, ?HTQ2, HTQ3, HTQ4	Locality HTQ
HYR16-HYR18, HYR25	Locality HYR
BH12, BH16a, BH16b	Locality BH

HM7.11, HM7.14-HM7.19	Locality HM7
?RH4.41	Locality RH4
RH1.27, RH1.30, ?RH1.35, RH1.36, RH1.37, ?RH1.38, RH1.39, ?RH1.41, RH1.43, RH1.47, RH1.48.	Locality RH1
HYR13, HYR13a, HYR14, HYR14a HYR15, HYR15a, HYR20-HYR23	Thin Sections Locality HYR

Korn's Material

Taf. II fig. 15	Oepitz, designated neotype
Taf. II fig. 16	Oepitz
? Taf. II fig. 7	Assigned to <u>Thamnisucs</u> <u>dubius</u> by Korn. Oepitz

Stratigraphical Range

Upper Permian

Occurrence

Acanthocladia diffusus is quite common at English and German reef localities (see p. 339 for detailed distribution). It has not been recorded from anywhere else in the world.

Discussion of the possibility that species of Acanthocladia and
Thamniscus are synonymous

Species of Acanthocladia anceps, Acanthocladia laxa and Acanthocladia diffusus may be very similar in several of their morphological characters. The possibility that these species are truly synonymous and that the variation between them is largely a result of environmental influences will be discussed below. The same possibility will be considered with reference to Thamniscus dubius, Thamniscus geometricus and Thamniscus siccus.

Values of I.A.D., A.D., B.T. and Z.C.L. are greater for A. anceps than A. laxa and greater for A. laxa than A. diffusus. These differences are quite small and there is some overlap between the three species. These measurements are probably an accurate reflection of zooecial chamber size which is almost certainly closely related to polypide size e.g. McKinney (1980a), McKinney and Boardman (1985)(in press) Jebram (1973, 1979) described intraspecific variability of polypide size which he attributed to variations in the quantity and quality of nourishment available to a colony. The better nourished the colony the larger the newly budded polypides, up to a genetically controlled maximum size.

A. diffusus, which is interpreted as having the smallest polypides of the three species, is always part (on the very local scale) of a low diversity community of usually small individuals. It may occur in almost monospecific patches and is abundant at localities where the reduced fauna has been interpreted as resulting from

increased salinity, e.g. Trechmann (1925). There is evidence to suggest that it often grew in recesses or cavities within the reef framework (see p.323). Therefore A. diffusus appears to be generally restricted to environments where adverse factors may have limited community diversity - one of these factors may have been a reduced food supply. While increased salinity is unlikely to have had a direct effect on the size of polypides it may have affected the distribution of a planktonic food source and thus, indirectly, the size of polypides of Acanthocladia. A. anceps does not occur in close association with A. diffusus and is generally most abundant at localities where it is part of a diverse community with numerous large individuals. The optimum conditions for the support of a diverse fauna may have included a plentiful supply of the ideal food species for A. anceps (hence its larger polypide size). A. laxa, which is considered to have polypides intermediate in size between those of A. anceps and A. diffusus, is usually part of a low diversity community. Thus, there may be a correlation between polypide size (reflected in skeletal morphology) and amount of nourishment in Acanthocladia - it is possible that the variability between species of Acanthocladia is truly intraspecific and is a result of diverse environmental influences. The fact that a combination of values for measured characters related to polypide size in the three phenotypes of Acanthocladia does not form a normal distribution could be explained as a function of incomparable sample sizes for the three phenotypes or as being a reflection of discontinuities in the environmental influences (i.e. availability of food). Jebram's (1973, 1975, 1979) work may not be truly applicable to the above case though, since his

experiments were performed on gymnolaemate bryozoans with much larger polypides than those of Acanthocladia, which is a stenolaemate - the range of intraspecific variation possible in Acanthocladia is likely to be much less than that found by Jebram (op. cit.).

The regularity of the zoarium decreases from A. anceps through A. laxa to A. diffusus. Harmelin (1973) correlated variations in the morphology of the cyclostome "Idmonea" atlantica with microhabitat (in 1975 he suggested similar correlations for other cyclostomes) - colonies growing in nooks or sheltered recesses had narrower branches and bifurcated less frequently and less regularly than those in the precoralligenous bioceonosis. Though "Idmonea" atlantica has only a few similarities with Acanthocladia there may be an analogous influence of habitat on colony form in Acanthocladia - the irregularity of the zoarium of A. diffusus could be partly controlled by the growth of colonies in recesses or cavities (see p.323). Several zoaria of this species often grow in very close proximity, forming dense patches with zoaria possibly intertwined - this situation may be comparable to that described from Bermuda reefs by Cuffey and Foerster (1975) where numerous colonies of Crisia eburnea may become intertwined while growing in a recess.

"Idmonea" atlantica is probably a better analogue for Thamniscus than for Acanthocladia. As discussed on p.185 the distal margin of a zoarium of Thamniscus geometricus may bifurcate less frequently than the more proximal parts - such a margin of T. geometricus may be practically indistinguishable from T. siccus. Thus, it is possible that T. siccus is merely an environmentally controlled variant of T. geometricus - T. siccus being the poorly branched form typical of

growth in an obscure recess whereas T. geometricus has a more regularly branched morphology typical of growth in a more open environment, (see fig. 64). However, there is no palaeocological evidence in favour of such a partitioning of environments for T. siccus and T. geometricus. Without such evidence the placing in synonymy of these two species would be unreasonable.

T. dubius differs from T. geometricus in its larger I.A.D., larger A.D., greater B.W. and usually greater number of rows of apertures. As discussed above, the size of polypide, and thus probably I.A.D., may be controlled to some extent by the nourishment of the colony. However, the large difference between T. dubius and T. geometricus with respect to this character is unlikely to be attributable to environmental influences. There may be a correlation between the depth at which a colony grows and its branch width. Schopf et al. (1980) measured branch diameters of the cyclostome Heteropora pacifica at several depths and in areas of different current strengths and levels of suspended organic matter. They found that branch diameter did not appear to be related to current strength or level of organic matter but appeared to decrease with increasing depth. The factors, related to depth, which were controlling branch diameter were unclear. Heteropora pacifica may not be a very good analogue for Thamniscus though - Schopf et al. (op. cit.) cited Rhombopora and Rhinidictya as Palaeozoic analogues. Brood (1972, p. 119) correlated an increase in apertural diameter and size of zooecium with a habitat of decreased water depth for Upper Cretaceous cyclostomes. Thus B.W., I.A.D. and A.D. in Thamniscus may vary to some extent with the depth at which a colony grew.

However, T. dubius and T. geometricus are not considered synonymous because there is no good palaeoecological evidence relating to relative depths of habitat and because there is no continuum between the two species in measured morphological characters.

There is evidence, from analogy with recent forms, that some of the characters considered useful in taxonomy in Acanthocladia and Thamniscus may be affected to some extent by environmental factors. However, the correlation of a particular factor with variation in a morphological character of a taxon is practically impossible to achieve. A. anceps, A. laxa and A. diffusus are thus not considered synonymous. The fact that these phenotypes never occur in close association could be considered as evidence in favour of the variability between them being environmentally controlled. The principle of competitive exclusion offers an alternative explanation for this fact. Similar species competing for the same resources may effectively exclude one another, or the three species of Acanthocladia may have subtly different environmental preferences which would explain their mutually exclusive occurrence.

Comparison of the genera *Thamniscus* King and *Acanthocladia* King

King (1849) established both *Thamniscus* and *Acanthocladia*. *Thamniscus* was characterized by its frequent, irregular bifurcations and "Gemmuliferous vesicles ..." (nodes) "... overlying the cellule-apertures". *Acanthocladia* was defined as symmetrically and bilaterally branched, rarely bifurcating with "(?) Gemmuliferous vesicles on the dividing ridges". King (op. cit.) considered the differences between *Acanthocladia* and *Thamniscus* to be "... its mode of branching and some other characters". "... some other characters" probably includes the disposition of obverse surface nodes; this may not serve to distinguish the genera - an examination of type specimens for the type species of the genus *Acanthocladia* revealed no "dividing ridges".

King (op. cit.) chose *Keratophytes dubius* Schlotheim as type for *Thamniscus* and *Keratophytes anceps* Schlotheim as type for *Acanthocladia*. His choice of *Keratophytes dubius* may have been responsible for much of the later confusion over the characteristics of the taxon, e.g. Goldfuss (1826) - Schlotheim's collection of the species includes several specimens of *Synocladia virgulacea*. The retention of *Keratophytes dubius* Schlotheim as type species for the genus *Thamniscus* is, however, probably justified (see p.177).

Shrubsole (1882), after an investigation of Permian, Carboniferous and Silurian species of *Thamniscus*, modified King's diagnosis so that the genus was characterized only by its regular bifurcation. All later authors have applied this definition when assigning species to the genus *Thamniscus*.

Geinitz (1861) and Zittel (1880) believed Thamniscus and Acanthocladia to be synonymous; Waagen and Pichl (1885) refuted this and the two genera have been maintained separate by later authors e.g. Ulrich (1890), Bassler (1953), Morozova (1970). Confusion over these genera has been compounded by some authors' specific assignments which are probably incorrect e.g. Thamniscus pinnatus Condra (1902) which is pinnate and therefore ought to be referred to the genus Acanthocladia.

Thamniscus dubius and Acanthocladia anceps of the present study have a number of morphological differences considered significant enough to warrant the retention of the two genera. The larger I.A.D., A.D. and expansion of the zoarium solely by bifurcation distinguish T. dubius from A. anceps; the most reliable of these characters may be the higher value of I.A.D. in T. dubius since quite large areas of a zoarium of A. anceps may consist solely of bifurcations (see p.204). However, I.A.D. alone cannot be considered of generic level taxonomic significance since other species assigned to the genus Thamniscus (on the basis of their growth by bifurcation) have lower values for that character e.g. Thamniscus geometricus; several species of Acanthocladia have relatively high values (see table 3). Thus the expansion of the zoarium by bifurcation rather than the production of lateral branches is the only criterion which can be used for distinguishing Thamniscus from Acanthocladia.

The difference between a bifurcated branch and a lateral branch may not always be clear (see p.172) e.g. in the case of Acanthocladia diffusus. A. diffusus was originally assigned by Korn (1930) to the genus Thamniscus because he considered it to expand solely by bifurcation. The taxon is referred to Acanthocladia in the present

study because, although a large part of the zoarium consists of bifurcated branches, bona fide lateral branches also occur; the fact that the zooecial chambers of A. diffusus are closer in size to those of A. anceps (the type species of Acanthocladia) than those of T. dubius (the type species of Thamniscus) was also taken into account when considering its generic position.

The assignment of A. diffusus to the genus Acanthocladia renders the morphological boundary between Acanthocladia and Thamniscus less distinct; in fact, A. diffusus contradicts an aspect of King's original generic diagnosis, i.e. it is not "...rarely bifurcating...". Since this aspect is not considered particularly significant it is felt that the establishment of a new monotypic genus for A. diffusus would be unjustified. A case such as this highlights the greater artificiality of the genus concept as opposed to the species concept in palaeontology. The consistent application of taxonomic criteria to species with a unique combination of morphological characters, which cannot be the same combination as exists in the type species, necessitates the choice of usually one character as that typical of the genus - such a choice ignores the combination of characters in a species and is often arbitrarily made. If the type species of a genus is only poorly differentiated from a species referred to another genus or the original diagnosis is not clear, then the use of the higher taxonomic category is beset with problems.

The case of T. dubius demonstrates the incompatibility of an 'evolutionary' approach to taxonomy with the concept of a type species for a genus. Since the type species, T. dubius, is Permian in age it presumably represents the end product of an evolutionary lineage of

the genus extending from the Silurian (this is assuming that there has been no iterative evolution of species with the generic characteristics of Thamniscus). To be truly consistent with the 'evolutionary' approach to taxonomy the species representing the central concept of a genus ought to be the earliest known form, from which all other species of that genus have evolved. However, the application of a more consistent philosophy is impractical, and unrealistic in view of the uncertainties which surround phylogenetic relationships.

Although the type species of Acanthocladia and Thamniscus are clearly distinct, and the differences between them can be considered significant at the generic taxonomic level (King's generic diagnoses can be easily applied in most cases), other species from different stratigraphical systems which have been referred to these genera need to be studied and incorrect assignments noted before their complete morphological limits are understood and any serious attempt at a classification based on phylogeny can be undertaken.

Table 3, comparing some of the morphological characters of species of
Thamniscus and Acanthocladia

	A.D.	I.A.D.	B.W.	Comments
<u>T. pustulata</u> Etheridge jun., 1877				Carboniferous
<u>T. crassus</u> Shrubsole, 1882				Silurian
<u>T. serialis</u> Waagen & Pichl, 1885			2.0	Permian
<u>T. divaricans</u> Ulrich, 1890	0.1		1-1.5	?May be partly <u>Polypora</u> Carboniferous

<u>T. sculptilis</u> Ulrich, 1890	0.07	0.3	0.4-0.8	Carboniferous
<u>T. furcillatus</u> Ulrich, 1890	0.08	0.3	0.5-0.7	Carboniferous
<u>T. ramulosus</u> Ulrich, 1890	0.08	0.25	0.3-0.5	Carboniferous <u>?Polypora</u>
<u>T. octonarius</u> Ulrich, 1890	0.07	0.32		Carboniferous
<u>T. poritidus</u> Stuckenberg, 1895				
<u>T. timanicus</u> Stuckenberg, 1895				Not <u>Thamniscus</u> zoarium a meshwork
<u>T. uralicus</u> Stuckenberg, 1895				
<u>T. pinnatus</u> Condra, 1902	0.07	0.33	1.0-2.0	Pinnate, therefore not <u>Thamniscus</u>
<u>T. palmatus</u> Condra, 1902		0.385	0.65	Carboniferous
<u>T. orientalis</u> Reed, 1927		0.385	2.5	Permo- Carboniferous
<u>T. gracilis</u> Bassler, 1929		0.4	0.65	Permian
<u>T. megastoma</u> Bassler, 1929	0.2	0.8	1.0	Permian
<u>T. humilis</u> Bassler, 1929		0.45		Permian
<u>T. geometricus</u> Korn, 1930	0.095	0.293	0.682	Permian
<u>?T. unilateralis</u> Fritz, 1932		0.36	0.75	? only 2 rows of apertures Permian
<u>T. erectus</u> Elias, 1957		0.33	0.5	Carboniferous
<u>T. raribifurcatus</u> Burckle, 1960	0.09	0.3	0.78	Carboniferous
<u>T. ?problematicus</u> Sakagami, 1961		0.5	1.5	Shows anastomosis Permian
<u>T. siccus</u> Dreyer, 1961	0.085	0.32	0.688	Permian
<u>T. indubius</u> Morozova, 1970	0.1	0.35	0.7-0.85	Permian
<u>T. dubius</u> King, 1850 (present study)	0.147	0.391	0.978	Permian

<u>A. carbonica</u> Stuckenberg, 1895				
<u>A. regularis</u> Bassler, 1929		0.8		Permian
<u>A. rectifurcata</u> Bassler, 1929				Permian
<u>A. acuticosta</u> Bassler, 1929		0.5		Permian
<u>A. simplex</u> Moore, 1929	0.1	0.28	0.6-0.85	May have 2 rows of apertures on main branch, therefore = <u>Penniretepora</u> Carboniferous
<u>A. ciscoensis</u> Moore, 1929	0.12	0.25	0.67	?Could be <u>Penniretepora</u> Carboniferous
<u>A. ciscoensis</u> var. <u>granulosa</u> Moore, 1929		0.31		? <u>Penniretepora</u> Carboniferous
<u>A. ciscoensis</u> var. <u>irregularis</u> Moore, 1929				? <u>Penniretepora</u> Carboniferous
<u>A. laxa</u> Korn, 1930	0.087	0.273	0.77	Permian
<u>A. minor</u> Korn, 1930	0.089x0.08	0.299	0.705	Permian
<u>A. diffusus</u> Korn, 1930	0.0835	0.247	0.67	Very irregular zoarium Permian.
<u>A. multipora</u> Fritz, 1932		0.33	1.75	Permian
<u>A. crebriramosa</u> Trizna, 1939	0.15x0.1	0.28		Permian
<u>A. sparsifurcata</u> Shulga-Nesterenko, 1941	0.12x0.1	0.365	1.25	Permian
<u>A. biserialis</u> Chronic, 1949	0.11	0.3	1.05	? <u>Kalvariella</u> Permian
<u>A. macer</u> Trizna, 1950	0.12x0.1	>0.4	0.84	Permian
<u>A. robusta</u> Yang and Loo, 1962		0.32		Permian
<u>A. thaiensis</u> Sakagami, 1968a		0.33	1.8	Permian

<u>A. tumulosa</u> Morozova, 1970	0.13-0.12	0.33	1.13	Permian
<u>A. guadalupensis</u> Girty, 1908 (Simonsen and Cuffey, 1980)		0.31	0.98	Permian

Genus Kalvariella Morozova, 1970

Type Species

Kalvariella typica Morozova, 1970

Diagnosis

Acanthocladiid with a pinnate or bipinnate zoarium. Apertures in two rows on the main branch, usually in three or four rows on lateral branches but rarely only two rows. Pinnae usually have two rows of apertures but may have three or four. Nodes occur at the inner or proximal edge of each aperture. Ovicells may occur. Nanate zooecia ? may occur.

Range

Lower Permian to Upper Permian.

Discussion

Morozova (1970) established this genus for forms similar to Penniretepora but with three or four rows of apertures on lateral branches. There may be problems associated with the identification of this generic characteristic in small specimens - BH10b (see Pl. III), assigned to Kalvariella typica, has three rows of apertures on lateral branches, but this decreases along a given branch to two rows. The decrease in the number of rows of apertures appears to coincide with the development of pinnae. Small fragments of such a specimen may be indistinguishable from Penniretepora (this is only if the characteristic disposition of nodes is not discernable). In spite of this, the genus Kalvariella is maintained here for a number of

reasons:- (i) the assignment of these forms to the genus Penniretepora would entail a significant contradiction of its generic diagnosis, (ii) the genus appears not to be monotypic and may be geographically widespread - Morozova (1970) mentions (though does not formally describe) two new species of it from the Lower Permian of S.W. Mongolia, some species which have been referred to Penniretepora or Acanthocladia may be truly referable to Kalvariella e.g. Penniretepora peculiaris Sakagami (1970a) has three rows of apertures on lateral branches and two on the main branch, Acanthocladia biserialis Chronic (1949) from the Lower Permian of Peru has two rows of apertures on the main branch and four on lateral branches (these four rows decrease distally along a branch to two, cf. specimen BH10b p.254), Acanthocladia ciscoensis Moore (1929), from the Pennsylvanian of central Texas is described as having two (locally three) rows of apertures on its main branch with three, rarely two on pinnae.

Taxonomic Procedure in Kalvariella

This is the same as for the genus Penniretepora (see p.257).

Kalvariella typica Morozova, 1970

Fig. 65, Pls. 111, 112

1930 Pinnatopora waltheri Korn, pp. 372-373 [partim], pl. IV fig. 18.

1970 Kalvariella typica Morozova, pp. 242-243, pl. LVIII fig. 6.

Type Material

Morozova's type material was not examined.

Diagnosis

Kalvariella with a bipinnate zoarium. Main branches quite narrow and moderately thin. Lateral branches quite narrow, regularly and fairly closely spaced, diverging from the main branch at 45-55°. Pinnae narrow and thin, diverging from lateral branches at 45-55°, rarely fused with neighbouring branches. Apertures quite small, circular, and arranged in two rows on main branches, three or four (more rarely two) on lateral branches, two or three (more rarely four) on pinnae. Peristomes well-developed, often incomplete at their proximal margins. Nodes occur at the inner or proximal edge of each aperture. Ovicells may occur. Nanate zooecia ? may occur.

Description

The zoarium is bipinnate (it may also be pinnate, if specimen RH2.61 is correctly assigned to this species). The main branch is straight, quite narrow and moderately thin with a slightly flattened circular cross-section. It bifurcates rarely at an angle of 30°. Lateral branches are regularly and quite closely spaced along both sides of the main branch, from which they diverge at an angle of 45-

55°. They may be opposite one another or offset to varying degrees. They are straight, quite narrow, fairly thin and flattened circular in cross-section. Pinnae are narrow and thin, they may or may not occur, regularly and quite closely-spaced, along both sides of a lateral branch from which they diverge at an angle of 45-55°. Lateral branches tend to be free of pinnae until they have grown at least 2mm from the main branch. Pinnae may fuse with their neighbours or may be joined by short, narrow, sterile dissepiments.

The main branch has two alternate rows of quite small, fairly closely-spaced, circular apertures. Peristomes are quite well-developed. Nodes occur at the inner margin of each aperture. There does not appear to be a median carina.

Three (more rarely four) rows of apertures are developed quincunxially on lateral branches - distally, along a single lateral branch, this may reduce to two rows (this change appears to coincide with the development of pinnae). The outer rows of apertures protrude quite markedly at branch margins. The well-developed peristome is incomplete at its proximal margin (this ? may have been the position of a small fossula) and may extend into a small node at its outer edge. A fairly prominent node is developed at the inner edge of each aperture in the outer rows of a branch and also usually at the proximal margin of an aperture in the central row.

Apertures on pinnae are as those of the lateral branches but are usually arranged in two (more rarely three, very rarely four) rows.

Ovicells may be common. Nanate zooecia ? may occur.

No specimen showing the reverse surface was seen.

Measurements

N = 3

	NM	Mn	Mx	$\bar{X}$
W.M.B.	10	0.54	0.58	0.558
W.L.B.	14	0.425	0.54	0.506
W.P.	12	0.35	0.363	0.357
S.L.B.	11	1.07	1.2	1.16
I.A.D.	37	0.291	0.297	0.295
A.D.	12	0.08	0.083	0.081

These measurements differ only slightly from those given by Morozova (1970) for the taxon. W.M.B. above is larger (0.558 mm $\sim$ 0.35-0.4 mm) and so is W.L.B. (0.506 mm $\sim$ 0.4 mm). Apertural diameter is smaller (0.081 mm $\sim$ 0.09-0.1 mm). There are no other clear differences.

Discussion

Specimen RH2.61 (see Pl. 112fig. b) is here only tentatively assigned to Kalvariella typica. Because of its poor state of preservation there is some uncertainty over the number of rows of apertures on lateral branches - there are undoubtedly some lateral branches with only two rows. Its measured parameters are characteristic of K. typica, not Penniretepora waltheri or P. waltheri nodata - if the specimen is truly referable to Penniretepora it may represent a new species of that genus. The apparent absence of a median keel supports an assignment to K. typica though this feature may be obscured by a fairly thick accretion of dolomite. The possibility that this specimen is merely an aberrant form of P.

waltheri remains.

Material

BH10b

Locality BH

RH2.52b

Locality RH2

?RH2.61

Stratigraphical Range

Upper Permian.

Occurrence

Very rare in the Tunstall member of N.E. England, very rare in the German Zechstein. Rare in the U. Permian of the Urals.

Genus Penniretepora D'Orbigny, 1849

Type Species

Retepora pluma Phillips, 1836

Diagnosis

Acanthocladiid with pinnate or bipinnate zoaria with a straight to sinuous main branch from which two rows of regularly spaced lateral branches diverge at acute angles, more or less in the same plane. Obverse surfaces have a median carina, with or without a row of nodes. Lateral branches may be pinnate - fusion of pinnae serves rarely to connect adjacent lateral branches. Obverse surfaces are granular, pustulose or nodose. Autozooecial apertures are arranged in two alternate rows on branches of every status. Ovicells and nanate zooecia may occur.

Range

? Silurian-Permian.

Taxonomic Procedure in Penniretepora

This is the same as for the genus Acanthocladia (see p.192). The grading of zoarial and zooecial dimensions in branches of different status as described by Bancroft (1984) is too inconsistently developed in specimens studied here to allow discrimination between some of the characters of different branch types.

Penniretepora waltheri Korn, 1930

Fig. 66, Pls. 113, 114

1848 Fenestella anceps Schlotheim; Geinitz, p. 18 [partim], pl. VII
figs. 19-21.

1930 Pinnatopora waltheri Korn, pp. 372-373 [partim - non fig. 18],
pl. IV figs. 14-17, 19.

1961 Penniretepora waltheri Korn; Dreyer, pp. 23-24, pl. X figs. 4-6.

Type Material

The lectotype, specimen Taf. IV fig. 14, 15 from the Korn collection, was studied as was specimen Taf. IV fig. 16, a paralectotype.

Diagnosis

Penniretepora with a pinnate or bipinnate zoarium. Main branches narrow and quite thin. Lateral branches, narrow, pinnate, quite closely-spaced, diverging from the main branch at 50-60°. Pinnae short, narrow and quite closely spaced. Apertures fairly small, circular and quite closely spaced, their rows separated by a prominent median carina with nodes at its apex. The reverse surface has three longitudinal striae and is free of nodes.

Description

The zoarium may be pinnate or bipinnate. It is possible that the zoarium expands as a sub-horizontal fan composed of radiating branches (if specimen HYR 28 is correctly assigned to P. waltheri)(see Pl. 113). Three or more main branches may diverge from the origin of the

zoarium. Regularly spaced lateral branches occur on both sides of a main branch and are usually pinnate.

The main branch is narrow, straight and quite thin with a flattened circular/sub-triangular cross-section; rarely, it bifurcates at an angle of 30° . Two rows of quite closely-spaced, fairly small circular apertures occur on the obverse surface - they are separated by a prominent median carina with a single row of fairly closely spaced nodes. These nodes are roughly circular in cross-section. The reverse surface has three fairly prominent longitudinal striae.

Lateral branches are straight and only very slightly narrower than main branches, from which they diverge at an angle of $50-60^{\circ}$. They are regularly and quite closely spaced along both sides of a main branch. They may be opposite one another or diagonally offset to some degree. There is a tendency for the main branch to show a slight expansion in width prior to the development of a lateral branch. Fusion of branches may occur.

Pinnae are regularly and quite closely spaced along lateral branches - they are short and narrow and diverge from a lateral branch at an angle of $50-70^{\circ}$. Fusion of pinnae with neighbouring branches is quite common. Occasionally a pinna may consist of only one zooecial chamber.

? Ovicells may occur.

Measurements

N = 2

	NM	Mn	Mx	$\bar{X}$
W.M.B.	11	0.336	0.36	0.348

W.L.B.	15	0.293	0.31	0.302
W.P.	12	(0.20)	(0.24)	0.218
S.L.B.	15	0.988	1.04	1.01
I.A.D.	5	(0.28)	(0.3)	0.292

Measurements on Korn's Material

N = 2 Specimens Taf. IV fig. 16, Taf. IV fig., 14, 15

	NM	Mn	Mx	$\bar{X}$
W.M.B.	15	0.368	0.394	0.381
W.L.B.	14	0.271	0.297	0.284
S.L.B.	12	0.949	0.988	0.969
I.A.D.	7	(0.28)	(0.34)	0.307

The measurements of Korn's material are closely comparable with those of the specimens from N.E. England.

Discussion

Korn established this taxon in 1930. Most of his description is accurate but he described a groove at the apex of the median carina; this was not observable in any specimens from the Korn collection.

A number of specimens from the present study are very similar to Penniretepora waltheri but have a large distinctive node on the reverse surface. Korn did not describe such a node in his material and none was observed by the present author. It is unlikely that this character would be affected by preservation. The fact that this character is constant and occurs in combination with a slightly lower value of S.L.B. suggests it is appropriate that a new subspecies is established for these specimens (see p.263). Apart from the small

difference in S.L.B. there are no observable differences on the obverse surfaces between these forms.

The specimen HYR 28 (see Pl. 113), assigned here to P. waltheri, has a zoarial morphology which is atypical of the taxon. The radiation of main branches around an arc and the fusion of lateral branches and pinnae were not observed in Korn's specimens. However, this difference is not considered significant since specimen HYR 28 probably represents the most proximal part of a colony - fragments of the distal parts of colonies may consist of a single main branch with free lateral branches and pinnae e.g. specimen Taf. of IV fig. 16 (see Pl. 114).

Dreyer (1961) described, as Penniretepora waltheri A, a form which differed from P. waltheri s.s. in its larger branch width (0.4-0.5 mm), larger S.L.B. (1 mm) and the angle of 90° between pinnae and the main branch.

Material

HYR28, HYR29

Locality HYR

Korn Collection

Taf. IV figs. 14, 15

Lectotype from Oepitz

Taf. IV fig. 16

Oepitz, paralectotype

Stratigraphical Range

Upper Permian.

Occurrence

Very rare in the Tunstall Member of N.E. England. Rare in the Zechstein of Germany.

Penniretepora waltheri nodata subsp. nov.

Figs. 67, 68, Pls. 115-118

Type Material

Specimen RH2.42 is chosen as holotype, the specimens listed in 'Material' below are paratypes.

Diagnosis

Penniretepora waltheri with a prominent reverse surface node developed usually opposite the junction between a lateral branch and the main branch. Lateral branches are relatively closely spaced.

Description

External

The zoarium may be pinnate or bipinnate. The complete form of the zoarium is not known since only small specimens have been found. The main branch is straight, narrow and quite thin with a roughly sub-triangular/circular cross-section. It may bifurcate at an angle of 30°. Lateral branches are closely and regularly spaced along its length, they may be directly opposite one another on either side of the main branch or offset to varying degrees. There may be a very slight flaring of the main branch prior to the development of a lateral branch.

Lateral branches are narrow, straight, and may be pinnate; they diverge from the main branch at an angle of 55-70° and are roughly circular in cross-section.

Pinnae are very narrow, short and roughly circular in cross-

section.

The obverse surface has two alternating rows of fairly small, circular (occasionally slightly elongate parallel to branch length), closely-spaced apertures. A thin complete peristome is developed - it is higher on the edge of the branch than in the centre. The outer edge of the peristome may extend into a small node (see Pl. 117 fig. b). The median carina is quite prominent and sharp with a single row of nodes which may be circular in cross-section or slightly elongate parallel to branch length. They are quite large and may be irregularly distributed but often occur in closely-spaced longitudinal pairs - the distance between the nodes of a pair is less than the distance between successive pairs (see Pl. 116 fig. b). They may also be close to the inner edge of an aperture and weakly directed away from the median carina.

The reverse surface is flat to gently curved and has a characteristic, prominent node which is usually developed opposite the junction between a lateral branch and the main branch; it is elongate parallel to branch length (0.08-0.15 mm long and 0.06-0.12 mm wide) (see Pl. 115, figs. a-e). Where the outermost skeleton has been removed three longitudinal striae may be visible.

Ovicells may occur.

Internal Form and Skeletal Microstructure

The zooecial chamber base is rhombic/oval, at the mid-point of the branch the chamber is oval/hemi-hexagonal in tangential section. Zooecial chambers in lateral branches tend to have a better developed hemi-hexagonal shape in tangential section.

The inter-zooecial wall is 20-23 μ thick. The 'inner platy core' is 10 μ thick - it zig-zags weakly between zooecial chambers close to their base but becomes straight nearer the obverse surface. No inner laminated layer or skeletal rods have been observed in thin sections.

Measurements

	N = 17					
	NM	Mn	Mx	S.D.	C.V.	$\bar{X}$
W.M.B.	49	0.28	0.54	0.0652	17.6	0.378
W.L.B.	72	0.24	0.42	0.051	17.5	0.292
W.P.	8	0.21	0.287	-	-	0.249
S.L.B.	63	0.64	0.913	0.086	11.8	0.731
I.A.D.	41	0.265	0.317	0.02	7.1	0.283
I.N.D.	12	(0.14)	(0.36)	-	-	0.244
A.D.	10	0.08	0.088	-	-	0.084
Z.B.L.	2	-	-	-	-	0.255
Z.B.W.	2	-	-	-	-	0.085

The high coefficients of variation for W.M.B. and W.L.B. may reflect, in part, the uncertainty over the branch status of very small specimens - some specimens considered to be main branches may be truly lateral branches. There is some degree of bimodality in the measurements of I.N.D. - this is because of the spacing of nodes with two close together within a pair and a larger space between successive pairs.

Discussion

This rare form is considered to have subspecific status because of its very characteristic, prominent, reverse surface node. Penniretepora waltheri nodata n. subsp. is otherwise very similar to Penniretepora waltheri - this leads to problems in the correct assignment of specimens which show only the obverse surface. The spacing of lateral branches in P. waltheri is slightly larger than in P. waltheri nodata but the difference is so small that some uncertainty remains over the true identity of specimens in which the characteristic reverse surface node is concealed. Thin section MP5.60 (see Pl. 118) is assigned to P. waltheri nodata because of its relatively low value of S.L.B., in spite of the fact that no reverse surface node is visible.

Specimen RH2.1a (see Pl. 116, figs. d, e, Pl. 117) is considered to be a slightly aberrant form. It has one lateral branch with three rows of apertures (though this is visible for a distance of only 0.5 mm), all its other lateral branches have two rows of apertures. Though the occurrence of three or four rows of apertures on lateral branches is a character typical of the genus Kalvariella, this specimen is not assigned to that genus; the extra row of apertures is considered to be merely a growth aberration.

Material

RH2.1a, RH2.1b
RH2.70b, RH2.42
RH2.31, RH2.33a,
RH2.33b, RH2.38,
RH2.36, RH2.34,
RH2.29, RH2.41,
RH2.32, RH2.10,
RH2.28, RH2.56b.

Locality RH2

RH2a	Thin Section, locality RH2
BH11b	Locality BH
MP5.60 ?MP5.27a	Thin Sections, Locality MP5

Stratigraphical Range

Upper Permian.

Occurrence

Penniretepora waltheri nodata is quite rare in the Tunstall Member of N.E. England (see p.339 for detailed occurrence) - it has not been recorded from the German Zechstein.

Genus Ryhopora gen.nov. (?)

Type Species

Ryhopora delicata sp. nov. (?)

Derivation of Name

After the locality Ryhope, where it was first found.

Diagnosis

Acanthocladiid with a zoarium which expands solely by bifurcation. Apertures in two alternate rows, sometimes increasing to three for a short distance prior to bifurcation. A node occurs at the inner edge of each aperture.

Discussion

See discussion of Ryhopora delicata below.

Taxonomic Procedure in Ryhopora

This is the same as for the genus Thamniscus

Ryhopora delicata gen. nov., sp. nov.

Fig. 69, Pls. 119, 120

Type Material

Specimen RH2.30b is chosen as holotype, RH2.27 and MP5.100a are paratypes.

Derivation of name

The trivial name is descriptive of the delicate branches of the taxon.

Diagnosis

Ryhopora with narrow thin branches which bifurcate regularly at short intervals. Rarely, branches may be linked by a lateral zooecium. Apertures are small, closely-spaced and circular to oval with a well-developed peristome. They are arranged in two alternate rows. Nodes occur at the inner, proximal edge of each aperture. The zooecial chamber base is elongate oval/irregularly rhombic. ? Heterozooecia may occur.

Description

External

The form of the complete zoarium is not known since only a few small specimens have been found - these expand solely by the bifurcation of branches. Bifurcations are closely spaced, every 0.4-1.0 mm, and occur at an angle of 60-80°. Adjacent branches are rarely linked by a single, lateral zooecium.

Branches are narrow and thin with a flattened circular cross-

section, their sides are fairly steeply curved. They are straight in between bifurcations. Occasionally, fusion may occur between neighbouring branches.

Apertures are small, closely spaced and circular to oval with a well-developed peristome - they are arranged in two alternate rows with margins which protrude to varying degrees at branch edges. A third row of apertures may occur for a short distance prior to bifurcation. In the angle of a bifurcation there is often an abnormally small aperture (of diameter 0.04-0.06 mm) - this may be the aperture of some type of heterozooecium. Nodes are developed at the inner, proximal edge of each aperture - they are quite long, slightly elongate at their base (length = 0.06-0.08 mm) and more circular in cross-section higher up (diameter = 0.03-0.05 mm).

The reverse surface was not seen.

Internal Form and Skeletal Microstructure

The zooecial chamber base is elongate/oval/irregularly rhombic. The inter-zooecial wall is 10-15 μ thick, the 'inner platy core' comprises 7-10 μ of this. The outer laminated layer is thinly developed.

Measurements

N = 3

	NM	Mn	Mx	$\bar{X}$
B.W.	10	0.343	0.4	0.375
I.A.D.	19	0.244	0.255	0.25
A.D. (L)	5	0.08	0.09	0.085

A.D. (W)	5	0.06	0.08	0.07
B.T.	1	-	-	0.25

Discussion

A new species is tentatively suggested for this delicate form with a zoarium which expands solely by bifurcation. The similarity of its dimensions to those of Penniretepora waltheri or Penniretepora waltheri nodata suggests that it might represent the bifurcated proximal part of a zoarium of one of those species. However, there is no proof that this is the case and the inter-apertural distance of Ryhopora delicata is smaller than in the species of Penniretepora (0.25mm~0.283 and 0.292 mm). The slight difference in the disposition of obverse surface nodes may also be significant in this respect. The thin section MP5.100a (see Pl. 120) may not be truly referable to R. delicata since it appears to have a narrow lateral branch - if this is the case then this specimen probably represents the proximal part of a zoarium of Penniretepora. The small size of this specimen prevents a conclusion with regard to this feature.

Material

RH2.30b, RH2.27

Locality RH2

?MP5.100a

Thin Section,
Locality MP5

Stratigraphical Range

Upper Permian.

Occurrence

Ryhopora delicata is very rare in the Tunstall Member of N.E. England - it has not been recorded from anywhere else.

Diagnosis

Stenolaemata with adnate or erect ramose cylindrical zoaria. Autozooecia are long and tubular, they are budded from a thin basal layer in adnate forms. In erect forms they are budded in a thin-walled endozone where chambers are sub-parallel to branch length. Autozooecia bend fairly sharply into a thicker-walled exozone; they meet the zoarial surface at a high angle, often perpendicularly. Autozooecial apertures are usually circular to oval and quite large. Autozooecial walls are composed of sub-parallel laminae and are compound. Skeletal laminae are parallel to autozooecial walls in the endozone but are orally convex in the exozone where they may or may not be continuous between adjacent zooecia. Exozone walls may be of uniform width, club-shaped, undulatory or moniliform. Autozooecia tend to be rectangular to polygonal in cross-section in the endozone but are more rounded in the exozone. Basal diaphragms, terminal diaphragms, hemiphragms, cystiphragms and ring septa may occur in autozooecia. Mesozooecia and exilazooecia are common, occurring as scattered individuals or forming monticules. Acanthostyles, aktinotostyles and paurostyles are abundant. Secondary overgrowths may occur.

Range

Ordovician to Triassic.

Zoarial Morphology and Budding of Zooecia

Zoaria may be erect and ramose, developing from a small initial encrustation, or adnate where a thin layer of zooecia encrusts a relatively large area of substratum. Several authors consider these different growth habits to have taxonomic significance e.g. Astrova (1978). However, both types may occur within single specimens of Dyscritella columnaris (see Pl. 128 fig. a) and Jackson (1979) suggested that the growth form of sessile animals may be controlled to some extent by exogenous factors.

Erect zoaria are considered to consist of distinct zones - the endozone, where inter-zooecial walls are thin and tend to be sub-parallel to branch growth direction and the exozone, external to the endozone and with thicker inter-zooecial walls at a high angle to branch growth direction. Autozooecia are budded interzooecially in the endozone - bifurcation of proximal interzooecial walls creates the distal space which expands rapidly to achieve the diameter of a normal autozooecial chamber; this remains approximately constant for the length of the chamber. In the endozone autozooecia curve at a low angle towards the zoarial surface but this angle increases, often sharply, at the exozone and autozooecia usually meet the zoarial surface at a high angle, close to 90°. The curvature of zooecia towards the zoarial surface allows the branch diameter to remain constant in spite of the intercalation of new zooecia.

Autozooecial Chambers and Apertures

Autozooecial chambers reach great lengths in the Trepostomata, the endozone usually comprises the greater part of this length but in some species the endozone and exozone may be of more comparable dimensions (e.g. Dyscritella columnaris). The boundary between the thin-walled endozone and the thick-walled exozone is usually sharply defined - the nature of the exozone wall is variable and is considered of taxonomic significance. Walls may be of uniform width e.g. in Dyscritella, club-shaped (increasing in width towards the zoarial surface) or moniliform e.g. in Stenopora, Tabulipora. Moniliform walls consist of bilaterally symmetrical thickenings separated by thin-walled portions, the relative lengths of these parts may be quite variable. The shapes, in cross-section, of autozooecia tend to vary from the endozone to the exozone. In the endozone they are usually well-faceted and triangular, square, pentagonal or hexagonal. In the exozone they are more rounded.

Autozooecial apertures are usually quite closely spaced at the zoarial surface, their spacing depends, to a large extent, on the abundance and disposition of mesozooecia. They are usually circular to oval but may be more polygonal in shape.

Mesozooecia

Mesozooecia are chambers, usually budded in the exozone, which are distinctly smaller than autozooecia. They are often polygonal in cross-section and have apertures which may be polygonal, circular or oval to sub-triangular. They have imperforate diaphragms which are usually closely spaced and often occur very close to the distal ends

of chambers. Astrova (1978) claims a fundamental distinction between mesozooecia and the exilazooecia of Dunaeva and Morozova (1967). Exilazooecia are more typical of late Palaeozoic genera and have no diaphragms whereas mesozooecia are characteristic of early Palaeozoic forms and have diaphragms. Astrova (op. cit.) considers the two types to be mutually exclusive in trepostome zoaria and characteristic of widely divergent evolutionary stocks. It is believed here that a distinction between mesozooecia and exilazooecia is best based solely on morphological criteria, i.e. the presence or absence of diaphragms. Dyscritella columnaris (which has mesozooecia) is here referred to the genus Dyscritella and the family Dyscritellidae, Dunaeva and Morozova (1967) although Astrova (op. cit.) considers both the genus and the family to be characterized by exilazooecia rather than mesozooecia. In her diagnosis of Pseudobatostomella Morozova (1960), Astrova (op. cit.) allows the occurrence of diaphragms in exilazooecia - this genus is referred to the family Dyscritellidae. Morozova (1970) described diaphragms in the exilazooecia of Dyscritella vjushkovi. Thus it is apparent that a clear morphological distinction between mesozooecia and exilazooecia is not made by some authors - because of this it is felt that the higher taxonomic significance of such characters is reduced and there is justification for considering D. columnaris to have mesozooecia but to be referable still to the genus Dyscritella and the family Dyscritellidae.

Mesozooecia tend to occur singly between the autozooecia of D. columnaris; they are more rarely clustered into small groups of three or four. Their function, in D. columnaris, is uncertain - the close proximity of the distalmost diaphragm to the aperture of a

mesozooecium suggests that there was no space in the chamber for a functional polymorph analogous to those known from Recent stenolaemates. However, Boardman and Cheetham (1973) suggested that exilazooecia may have housed some form of unknown polymorph - if the distalmost diaphragm in a mesozooecium of D. columnaris is merely a terminal diaphragm secreted during some phase of degeneration then these chambers may have been large enough to have housed a polymorph. Boardman and Cheetham (1969) considered mesozooecia to be simply space fillers between autozooecia, improving the structural strength of the colony; this interpretation may well be applicable to the mesozooecia of D. columnaris. Mesozooecia and exilazooecia may occur in clusters, excluding normal autozooecia; they are raised up above the general surface of the zoarium. Such areas are called monticules - they occur quite commonly throughout the Trepostomata and have been interpreted as the possible loci of excurrent water outlet, Banta, McKinney and Zimmer (1974). Banta, McKinney and Zimmer observed loci of excurrent water outlet in Recent encrusting species of Membranipora and suggested that similar water current patterns may have existed in Palaeozoic trepostomes - regularly arranged areas without feeding zooids would have facilitated the expulsion from the zoarium of already filtered water. A number of observations of monticules support such an interpretation :-

- i) They are commonly developed in a wide variety of taxa with both adnate and erect colonies.
- ii) Distances between monticules are relatively constant.
- iii) Monticules are arranged in a rhombic or hexagonal pattern in most taxa possessing them.

- iv) The sizes of monticules remain fairly constant within, and even across taxa, Bancroft (1984).
- v) Delicate colonies, where water can be expelled from the zoarium more easily, tend not to develop monticules.

Anstey and Delmet (1972) interpreted monticules as budding centres in erect trepostomes - this interpretation is not mutually exclusive of that suggested by Banta, McKinney and Zimmer (op. cit.)

Microstructure and Growth

Walls in both the endozone and exozone consist of laminated skeleton. In the thin-walled endozone laminae are parallel to chamber length but they become more thickly developed and convex orally in the exozone. Laminae curve at a shallow angle into the edge of the zooecial cavity but become sub-parallel to the zoarial surface near the mid-point of the interzooecial wall (see fig. 70). At the proximal end of the exozone interzooecial wall there may be a discontinuity between the laminae at the zooecial boundary - this disappears distally and laminae are continuous across interzooecial walls. Boardman and Cheetham (1969) interpret this phenomenon as merely a function of the angle of intersection of laminae with the zooecial boundary - proximally the laminae intersect this boundary at a high angle whereas distally the angle is shallower.

In longitudinal and transverse sections laminae of the interzooecial wall can be seen to flex distally around acanthostyles, curving to become sub-parallel with them (see fig. 71 and Pl. 172 fig. c). In tangential section this appears as a central granular core surrounded by concentric laminae (see Pl. 126 fig. b).

In shallow tangential section interzooecial walls often appear to have a narrow granular cone flanked on either side by laminated skeleton. Armstrong (1970) drew attention to the fact that this is probably a function of the plane of section - close to the edge of the interzooecial wall the laminae are roughly perpendicular to a transverse section whereas close to the centre of the interzooecial wall the laminae are sub-parallel to such a section (see fig. 70).

Tavener-Smith (1969b) and Boardman and Cheetham (1969) considered the disposition of epithelia and the mode of growth of trepostomes to be comparable to that described by Borg (1933) for heteroporids (see fig. 72). A number of lines of evidence support this interpretation:-

- i) Assuming that each lamina was deposited successively by a closely associated epithelium the continuity of laminae across interzooecial walls suggests that the depositing epithelium was continuous between adjacent zooids.
- ii) Interzooecial structures such as mesozooecia (interpreted not to have housed a functional polypide) have walls and diaphragms which were probably formed by a colony-wide epithelium.
- iii) The equal extent of distal growth of all types of zooecia to form a regular zoarial surface is better explained by colony-wide control of skeletal deposition than the autonomous action of individual polypides.
- iv) The interzooecial walls of trepostomes have been shown to be non-porous, any inter-zooidal transfer of nutrients must then have taken place via a colony-wide coelomic space.

Evidence for such a transfer of nutrients comes from the inference of degeneration-regeneration cycles in trepostomes - basal

diaphragms in autozooecia are considered to represent the successive positions of the floor of the living chamber, thus several cycles of regeneration are often represented in zoaria.

It is a reasonable assumption that laminae were deposited parallel to the surface of the secreting epithelium in trepostomes, Boardman and Cheetham (1969), and thus that the laminae can be considered as growth surfaces. However, Boardman and Cheetham (op. cit.) note some possible exceptions. Some Recent heteroporids have zooecial wall laminae which are oblique orally (see fig. 70) - if the depositing epithelium lines zooecial chambers then skeletal growth can only take place by edgewise enlargement of laminae (electron micrographs reveal calcite seed crystals at the edges of earlier formed crystals rather than on the surfaces, suggesting that edgewise growth is indeed taking place). Laminae roughly parallel to the depositing epithelium of some heteroporids may also show edgewise growth - thus the relationship between skeletal laminae orientation and growth may be complex. Armstrong (1970) considered the walls of Stenopora crinita Lonsdale to grow both by the successive addition of laminae and by edgewise enlargement, though he could envisage no simple mechanism to explain the occurrence of both types of growth in a single colony.

Acanthostyles

Acanthostyles are narrow, cylindrical structures developed in zooecial walls and projecting, as spines, above the level of apertures at the surface of the zoarium. They consist of a core of granular calcite the length of which is parallel to the length of the zooecial wall. The core is surrounded by usually sub-parallel sheath laminae

which are strongly deflected into the structure. The terms acanthopore, stylet and style have been used previously to describe such structures.

Blake (1973) described three morphological types of acanthopore in rhabdomesids, he referred to them as A, B and C types and later (1975) suggested the terms acanthostyle, aktinostyle and heterostyle respectively for these types. Bancroft (1984) applied Blake's work to trepostomes and suggested that three types of stylet could be recognized, A, B and C. Type A-stylets (comparable to acanthostyles here), according to Bancroft (op. cit.), consist of a well defined homogeneous granular calcite core varying in diameter from 0.005 to 0.025 mm - the core diameter remains fairly constant for its length but fairly great intrazooarial variation may occur. The core often shows uniform extinction under crossed polars. The surrounding sheath laminae are continuous with the wall laminae and do not continue into the core, with which they are sub-parallel. They are usually regularly developed. Bancroft's type B-stylets differ from type A in having a more poorly defined core which may be crossed at irregular intervals by skeletal laminae. Wall laminae tend to terminate against the core, which has a diameter of 0.002-0.01 mm. Bancroft's type C-stylets are morphologically comparable to the type A variants (paurostyles) and the type C acanthopores of Blake (1973, 1975). They are composed of tightly packed orally flexed nests of skeletal laminae with no clearly differentiated core, though occasionally small lenses of granular calcite may occur. The laminae are continuous with those of the zooecial wall. They are only developed in middle and upper exozone regions and are quite variable in morphology and distribution.

Blake (1973) stated that the different types of acanthopore were probably only convenient end-members of a morphological continuum. It is felt here that the type A (= Acanthostyles) and type B (= Aktinotostyles) stylets of Bancroft (1984) may not be always clearly differentiated but a morphological distinction will be maintained here, in keeping with the procedure of 'The Treatise'.

Acanthostyles were believed, for a long time, to have been the hollow chambers of polymorphic zooids in trepostomes e.g. Ulrich (1890), Bassler (1953), Elias and Condra (1957), Boardman (1960) and Cuffey (1967) - they were compared to the basal parts of cheilostome avicularia by Elias and Condra (op. cit.). However, work by Tavener-Smith (1969b) and Armstrong (1970) has demonstrated that acanthostyles were solid structures during the life of a trepostome colony - this was suggested as early as 1886 by Waagen and Wentzel. Astrova (1978) described "acanthozooecia" as hollow structures, claiming the presence of small detrital clasts within a calcitic matrix - she distinguished these from "acanthopores" which she considered to be solid. It is likely that her "acanthozooecia" correspond to the acanthostyles described here, in which case it is unlikely that they were originally hollow. The evidence in favour of acanthostyles being originally solid structures is:-

- i) Acanthostyles are localized modifications of zooecial wall laminae in Leioclema asperum, the boundary between the axial core and the surrounding sheath laminae is seen to be ragged and irregular in electron micrographs - if they were originally hollow this would probably not be the case, Tavener-Smith (1969b).

- ii) Growth lines, defined by skeletal laminae, can sometimes be traced across the axial core of acanthostyles - this would not be the case if they had been hollow, Tavener-Smith (op. cit.).
- iii) Acanthostyles do not have a laminated skeletal lining, unlike autozooecia and mesozooecia, the laminae surrounding them dip away from the core rather than into it, which would be expected if they had been hollow chambers, Tavener-Smith (op. cit.).
- iv) Armstrong (1970) found calcite, ferroan calcite and ferroan dolomite infilling zooecia of Stenopora ovata and S. crinita but only calcite in acanthostyles, suggesting that the mineralogy of the acanthostyles is not diagenetic in origin.
- v) Detrital particles have not been seen in acanthostyles in the present study, but may occur in autozooecia. Bancroft (1984) found this to be true of Carboniferous trepostomes.

According to Tavener-Smith (1969b) acanthostyles arise within the exozone by a differentiation of growth rates - where the growth rate increases the axial core of the acanthostyle is initiated by oral flexure of laminae; a gradual increase in the differential growth rate leads to the deposition of a core of continuous calcite surrounded by laminated skeleton. Bancroft (1984) considered this to be the mode of development of acanthostyles in Carboniferous trepostomes. Armstrong (1970) believed acanthostyles to be produced by relatively rapid continuous deposition by areas of specialised zooidal epithelium. Acanthostyles have not been observed to originate from gradually increasing oral flexures of zooecial wall laminae in the present study - it may be that they have a more discrete origin in Dyscritella columnaris but no detailed observations of this feature were possible.

Assuming that acanthostyles were not originally hollow their function would probably have been related to the attachment of soft parts. Tavener-Smith (1969b) considered them to have been the locus of attachment for epithelial tissues and suggested that they may also have performed a defensive function. Armstrong (1970) suggested, by analogy with brachiopod pseudopunctae, that acanthostyles were the attachment points of small tendons or tonofibrils.

Diaphragms

Diaphragms are thin skeletal structures which form transverse partitions of autozooecia and mesozooecia. They may be complete, or perforate, with a central foramen - such perforate diaphragms are termed ring septa, Gautier (1970). Hemiphragms are similar features which extend transversely, part of the way across a zooecial chamber, arising alternately from the proximal and distal edge of the chamber - they were calcified from both sides, Boardman (1971). Only imperforate diaphragms occur in Dyscritella columnaris - they consist of laminae, parallel to the diaphragm's length and continuous orally with laminae lining the zooecial chamber and forming the interzooecial wall (see fig. 71). This fact requires the depositing zooidal epithelium to be orally situated with respect to a diaphragm and supports Boardman's (1960, 1971) interpretation of diaphragms as the floors of living chambers. The occurrence of several diaphragms in a single autozooecial chamber and their frequent interzooecial alignment have led to the suggestion that they represent the successive positions of the floor of the living chamber and thus that several cycles of degeneration and regeneration may be represented in a

chamber e.g. Boardman (1960, 1971). The occurrence of material, possibly representing brown bodies, in each abandoned chamber of a Devonian trepostome may be considered further evidence in support of this idea, Boardman (1971).

Diaphragms in autozooeal chambers of Dyscritella columnaris may occur very close to the aperture - as close as one half of the zooeal chamber diameter (see e.g. Pl. 130 fig. a). This is in contrast to the situation described by Boardman (1971) where the nearest to the aperture they occur is one and a half times the chamber diameter. If the last formed diaphragm in a chamber of D. columnaris is truly a basal diaphragm then little space is left for the accommodation of the polypide. It is suggested that these are in fact terminal diaphragms, though it is possible that some of the exozone wall suffered resorption thus increasing the apparent closeness of a diaphragm to the aperture. Boardman (1960) and Cuffey (1967) describe cyclic resorption of exozone walls in trepostomes. Terminal diaphragms appear to effectively seal an autozooeal chamber - their functional significance is uncertain.

Diaphragms are widely used as taxonomic characters at the level of species and genus. There is considered to be a fairly large range in the abundance of diaphragms in chambers of D. columnaris but no taxonomic significance has been attributed to this. The number of diaphragms in a zooeal chamber may be a function of ontogenetic stage - Boardman (1960) correlated the number of diaphragms with width of the exozone in some Devonian trepostomes and drew attention to the importance for taxonomic work of recognizing ontogeny. Boardman (1971) also described the occurrence of membranous diaphragms in

Devonian trepostomes, suggesting that the lack of calcification of such features may lead to some taxonomic confusion where this is not recognised.

Taxonomic Procedure in the Trepostomata

The procedure followed in the present study is basically the same as that described by Cuffey (1967) for Tabulipora carbonaria Worthen. Cuffey considered 22 characters to be of significance in his taxonomic work but only ten of these are used in the present study.

Measurements are made on the external surface (see fig. 73) and qualitative descriptions of several characters are given:- a simple shape description is given for autozooecial apertures (Fourier analysis of zooecial shapes, as described by Anstey and Delmet (1973), was not considered necessary for the limited amount of material in the present study), the shapes and dispositions of mesozooecia and acanthostyles are described.

Measurements are made, and characters are described from thin sections in different orientations (transverse, longitudinal and shallow tangential) (see fig. 73, + Pls. 123, 124, 126). The shapes of autozooecial chambers and mesozooecia, the nature of the wall structure, the structure and type of styles and the distribution and type of diaphragms are all described.

Z1 is the number of autozooecial apertures in one square millimetre - if over half the area of an aperture falls within the square it is counted as one, if less than half falls within the square it is counted as nought. This can be measured in external or shallow tangential section.

Z2 is the number of autozooecial apertures intersecting or adjacent to a 2 mm line, parallel to colony growth direction and starting at the mid-point of an interzooecial wall. This is usually

measured externally.

A.D. is the autozooecial apertural diameter; because of the variability of aperture shape only the maximum dimension is given, measured between the inner rims of interapertural walls. This is most accurately measured externally but may be measured in shallow tangential sections.

Inter-apertural wall thickness (I.W.T.) is usually measured externally and is the minimum thickness between adjacent autozooecial apertures. Measurements in thin section are less accurate because of slight uncertainties about the plane of section.

Mesozooecium apertural diameter (M.Z.D.) is the maximum dimension of the aperture, measured between the inner edges of its walls. It may be measured externally or in shallow tangential section.

Acanthostyle diameter (A.C.D.) is measured in thin section and is the maximum width, transverse to length, of the granular core of an acanthostyle.

The diameter of the zoarium (Z.D.) is measured in thin section and is the maximum diameter transverse to growth direction. It is not measured in hand specimen where it is usually difficult to detect the presence of layers of secondary overgrowth. Overgrowths are not included in the measurement of zoarial diameter.

The width of the exozone (EX.W.) is the distance, measured transverse to growth direction, from the base of the exozone to the surface of the zoarium (not including any layers of secondary overgrowth). It is measured in longitudinal sections.

The axial ratio (AX.R.) is the diameter of the axial region (endozone) divided by the total diameter of the branch, not including

layers of overgrowth.

The number of diaphragms in an autozooecial chamber (N.D.) is quoted as the range found in a specimen - the total number of diaphragms was not divided by the number of autozooecial chambers to give an average because of the practical difficulty of such a procedure. No distinction is made between basal diaphragms and terminal diaphragms because this is not always clear, and no distinction is made between diaphragms in the endozone and those in the exozone because the boundary between the two zones is not always well-defined in Dyscritella columnaris.

Family Dyscritellidae Dunaeva and Morozova, 1967

Type Genus

Dyscritella Girty, 1910

Diagnosis

Trepostomata with erect ramose, more rarely adnate zoaria. Endozone walls are very thin, exozone walls tend to be of uniform width. Skeletal laminae are continuous between adjacent autozooecia in the exozone. Autozooecial apertures are circular to oval and usually quite closely spaced. Diaphragms may be absent or quite common. Exilazooecia may be abundant and monticules developed. Mesozooecia may occur. Acanthostyles, aktinotostyles and paurostyles may occur.

Stratigraphical Range

Carboniferous to Triassic (e.g. Sakagami and Sakai (1979)).

Genus Dyscritella Girty, 1910

Type Species

Dyscritella robusta Girty, 1910

Diagnosis

Dyscritellid with erect ramose or adnate zoaria. Endozone walls very thin, exozone walls fairly thin and of uniform width. Skeletal laminae continuous between adjacent autozooecia in the exozone. Autozooecial apertures usually quite small and circular to oval. Exilazooecia may be abundant, mesozooecia may occur. Diaphragms are usually uncommon. Acanthostyles, aktinotostyles and pautostyles may occur and are often abundant.

Stratigraphical Range

Carboniferous - Triassic (e.g. Sakagami and Sakai (1979)).

Discussion

See discussion of Dyscritella columnaris

Dyscritella columnaris Schlotheim, 1813

Figs. 70-74, Pls. 121-132

1813 Coralliolithes columnaris Schlotheim, p. 59

?1829 Calamopora spongites Goldfuss, p. 82

1846 Calamopora mackrothii Geinitz, p. 582

1848 Stenopora crassa Lonsdale; Howse, p. 260

1848 Stenopora mackrothi Geinitz; Geinitz, p. 17, pl. VII, figs. 8-10

1848 Coscinium dubium Geinitz, p. 19, pl. VII figs. 24-27

1848 Alveolites producti Geinitz, p. 19, pl. VII figs. 28-31

1850 Calamopora mackrothii Geinitz; King, pp. 26-28, pl. III figs. 3-6

1850 Stenopora columnaris Schlotheim; King, pp. 28-29, pl. III figs.
7-9

?1850 Alveolites buchiana King, p. 30, pl. III figs. 10-12

1861 Stenopora columnaris var. incrustans Geinitz, p. 114, pl. XXI
figs. 1-6, 8, 19

1861 Stenopora columnaris var. ramosa Geinitz, pp. 114-115, pl. XXI,
figs. 9, 11-18

1861 Stenopora columnaris var. tuberosa Geinitz, p. 115, pl. XXI figs.
10, 20.

1886 Geinitzella columnaris var. incrustans Geinitz; Waagen and
Wentzel, p. 883, pl. CVI figs. 5-6

1886 Geinitzella columnaris var. ramosa sparsigemmata Waagen and
Wentzel, p. 883, pl. CXII figs. 1a, 1c, 4; pl. CXIII figs. 1a,
1c, 1d

?1961 Stenopora columnaris ramosa Geinitz; Dreyer, p. 25, pl. XI
fig. 3

- 1961 Stenopora columnaris incrustans Geinitz; Dreyer, pl. 26, pl. XI
fig. 4
- ?1977 Batostomella columnaris buchiana King; Pattison, p. 36
- 1977 Batostomella crassa Lonsdale; Pattison, p. 36
- 1977 Batostomella columnaris Schlotheim; Pattison, p. 36

Type Material

None of Schlotheim's specimens of "Coralliolites columnaris" were available for study. Geinitz's material was destroyed during World War II. King's only specimen of "Alveolites buchiana" was examined and is tentatively placed in synonymy with Dyscritella columnaris (see discussion).

Diagnosis

Dyscritella with adnate or erect ramose zoaria. Branches of erect zoaria narrow, but their width often increased by several layers of secondary overgrowth. Autozooecial apertures of moderate size and oval to circular or rounded polygonal. Mesozooecia not very abundant, their apertures small and circular, sub-triangular, oval or polygonal. They may occur isolated or in small groups. Acanthostyles quite abundant and narrow, five or six occur around one autozooecial aperture. Endozone walls thin, often weakly crenulated. Exozone walls fairly thin and of uniform width. Diaphragms are usually quite common but may be absent from autozooecia. Acanthostyles quite narrow, of uniform width with their origin usually in the exozone, more rarely the endozone. Mesozooecia originate in the exozone and have usually two or three diaphragms. Secondary overgrowths very

common, without an endozone.

Description

External

Erect ramose zoaria consist of narrow cylindrical branches. Their thickness may be increased locally or over most of a zoarium by layers of secondary overgrowth (up to seven may occur). Zoaria may reach a length of 4-5 cm and may show no substantial thickening of branches in this distance (see Pl. 121 fig. f). Bifurcation occurs at angles from 60-90° (with the majority at 80°) and usually at irregular intervals. Branches of the same zoaria may fuse (see Pl. 121 fig. d). Zoaria are often adnate, forming 0.5 mm thick sheets which are usually of limited areal extent, developing erect branches in places (see Pl. 121 fig. a). Rarely, adnate zoaria may be quite extensive, covering an area of substrate up to approximately 26 x 17 mm (see Pl. 122 fig. a).

Autozooeal apertures are of moderate size, closely spaced and usually oval in shape but may be rounded, polygonal or circular. Inter-apertural walls are thin but may be thicker in areas of a zoarium where mesozooecia have increased abundance.

Mesozooecia are small (approximately one quarter of the size of autozooeal apertures) and circular, sub-triangular, oval or polygonal in shape. They are not very abundant throughout a zoarium. They occur singly, or rarely in pairs at interapertural angles. They may also be clustered into groups of three or four.

Acanthostyles are quite abundant and narrow, reaching a diameter of 0.02 mm where they project (up to at least 0.1 mm) above the level

of autozooecial apertures. There are usually five, occasionally six, quite evenly spaced around an autozooecial aperture and three or four around a mesozooecium.

Internal

Autozooecial chambers are budded in the endozone and extend sub-parallel to the longitudinal axis of the branch for only a short distance, after which they curve gently towards the surface of the zoarium, meeting it at an angle of 80-90°. The endozone and exozone are of approximately equal widths - the boundary between them is not very sharply defined.

Interzooecial walls are thin in the endozone, averaging 6-7 μ . They tend to be crenulated on a fine scale. Laminae are orientated parallel to the direction of growth and may enclose the axial core of an acanthostyle. Autozooecial chambers are polygonal/circular to oval or sub-triangular in cross-section.

Exozone walls are thin and of approximately uniform width. Their laminated skeleton is thicker and orally convex - it is continuous across inter-zooecial walls. The laminae curve into sub-parallelism with acanthostyles. Autozooecial chambers are polygonal/circular to oval in cross-section in the exozone.

Diaphragms may be relatively common or may be absent from zooecial chambers (they appear to be more abundant in specimens which show secondary overgrowths). They may occur rarely in the upper endozone, where they are widely spaced, but are more common in the exozone. Their spacing tends to decrease into the exozone (where it is usually 0.1-0.15 mm) - the diaphragms which are nearest the aperture are usually more closely spaced (approximately 0.05 mm).

Diaphragms deeper in autozooecial chambers tend to be thicker than those close to the aperture. They are composed of parallel laminae which are continuous with those of the inter-zooecial wall, however, the laminae are not observable in most cases. Diaphragms may extend obliquely across autozooecial chambers but are usually weakly concave orally. There may be some poorly defined interzooecial alignment of diaphragms, but numbers of diaphragms may be very different between adjacent autozooecia of some specimens. The distalmost diaphragm in a chamber is often very close to the aperture (approximately 0.05 mm) and may thus be a terminal as opposed to a basal diaphragm.

Acanthostyles occur quite abundantly. They are fairly narrow and only rarely do they show much variation in size. They usually originate at the base of the exozone but may originate in the endozone. They have well-defined straight boundaries between an axial core and the laminated skeleton of the interzooecial wall. This boundary may be irregular on the very small scale.

Mesozooecia are developed in the exozone, usually with their origins 0.25 mm from the surface of the zoarium. Their proximal shape is rounded to angular, this becomes circular/polygonal as their width stabilizes just below the zoarial surface. They are narrow and have usually two quite closely spaced diaphragms. Acanthostyles occur in mesozooecial walls.

Secondary overgrowths are very commonly developed. They consist of a layer approximately 0.5 mm thick which is almost identical to the exozone below. Autozooecial chambers tend to be directed proximally. No endozone is developed. The basal lamina of the overgrowth may follow closely the topographic irregularities of the zoarium below but

often grows some distance above the zoarial surface. Most cases of overgrowth are probably intrazoarial (see p.305 for further discussion).

Adnate zoaria do not differ significantly from erect ramose zoaria in their internal morphological details; they frequently develop erectly growing branches (see Pl. 128 fig. a).

Measurements

N = 72

	NM	Mn	Mx	S.D.	C.V.	$\bar{X}$
Z1	30	13	20	1.96	12.6	15.6
Z2	35	6	10	1.17	13.9	8.4
A.D.	600	0.145	0.223	0.0187	10.9	0.172
I.W.T.	500	0.03	0.081	0.011	22	0.05
M.Z.D.	120	0.05	0.085	0.01	15.4	0.067
AC.D.	180	0.008	0.02	2.85×10^{-3}	24.5	0.0116
Z.D.	15	1.3	2.2	0.181	10.4	1.74
EX.W.	18	0.425	0.68	0.064	12.3	0.521
AX.R.	13	0.138	0.52	0.097	24.3	0.4
N.D.	24	0	8	-	-	-

Discussion

The generic assignment of this species presents considerable problems. There are a number of genera to which it has been referred or with which it has a number of morphological characters in common.

Dreyer (1961) referred the taxon to the genus Stenopora Lonsdale (1844) on the basis of its external morphology. This assignment is incorrect since Stenopora is characterized by moniliform walls - a

feature lacking in any of the thin sections of the species examined in the present study.

Ross (1979) suggested tentatively that the taxon be referred to Pseudobatostomella Morozova (1960). According to Astrova (1978), Pseudobatostomella is very similar to Dyscritella but differs in its development, in all cases, of rare diaphragms, less exilazooecia, and styles of usually only one type. Compared to Dyscritella diaphragms are more widespread in Pseudobatostomella which suggests that this genus may be more appropriate for D. columnaris. However, Pseudobatostomella salairiensis Morozova (1961) has a much thicker inter-zooecial wall than D. columnaris and diaphragms which are essentially restricted to the endozone. Thus, it has fewer morphological similarities with D. columnaris than several other species referred to the genus Dyscritella e.g. Dyscritella vjushkovi Morozova (1970). The occurrence of exilazooecia rather than mesozooecia suggests that Pseudobatostomella may not be appropriate for D. columnaris, however, the distinction between these two types of zooecia is not always clearly made - the "exilazooecia" of the type species for Pseudobatostomella, Batostomella spinulosa Ulrich (1890), may have diaphragms and thus may be truly mesozooecia. Pseudobatostomella awahensis Sakagami (1973a) has a much wider zoarium than D. columnaris and a characteristically different disposition of diaphragms; they occur in the endozone and are well-spaced. Astrova (1978) considers Pseudobatostomella to form exclusively erect zoaria - if this is an accurate observation and a character of taxonomic significance then D. columnaris, which often forms adnate zoaria, ought not to be referred to Pseudobatostomella. Thus, while the

diagnosis given for Pseudobatostomella by Astrova (op. cit.) suggests that the genus may be appropriate for D. columnaris, species which have been assigned to the genus by later authors appear morphologically further removed from D. columnaris than do species which have been referred to Dyscritella.

The genus Geinitzella was established in 1886 by Waagen and Wentzel - they assigned two species, one of which was "Geinitzella columnaris", to this genus. The retention of this genus for the taxon described above would save broadening the generic concept of Dyscritella. However, Geinitzella is poorly defined, apparently characterized by "transverse wrinkling" of zooecial chambers. This feature may not be of great taxonomic significance and is variably developed in specimens of the present study. The description and figures of Geinitzella columnaris in Waagen and Wentzel (1886) show diaphragms to be very rare or nearly absent suggesting the species could be referred to Dyscritella. The use of the genus by later authors has served to increase confusion - Astrova (1978) places species of Geinitzella in synonymy with Tabulipora, Stenodiscus, Stenopora and Rhombotrypella and rejects its validity. However, Sakagami and Sugimura (1981) maintained the genus for Geinitzella cf. columnaris. It is not used in the present study because it is so poorly defined and because some of the material upon which it was based has not been seen.

Girty (1910) established Dyscritella as a subgenus, with D. robusta as type species. It was characterized by its complete lack of diaphragms, fairly numerous styles (of two distinct sizes) and mesozooecia. Lee (1912) emended the diagnosis to include forms with

rare diaphragms. Most species which have been referred to this genus by later authors have no diaphragms in autozooecial chambers e.g. Dyscritella adnascens Bassler (1929), Dyscritella spinulosa Bassler (1929), Dyscritella phetchabunensis Sakagami (1975) but diaphragms may be rare in some species e.g. Dyscritella tubulosa Morozova (1970) and Dyscritella vjushkovi Morozova (1970). In Dyscritella miliaria Nicholson, basal diaphragms may be quite common (up to five in a chamber) but they tend to occur in the endozone, Bancroft (1984). Several species referred to the genus have only one type of style. In her diagnosis of the genus Astrova (1978) considers exilazooecia to be often numerous. The presence of diaphragms in mesozooecia (not exilazooecia of D. columnaris) may be an important departure from Astrova's concept of the genus, but Morozova (1970) describes rare diaphragms in the 'exilapores' of D. vjushkovi. D. columnaris is very tentatively assigned here to the genus Dyscritella because of its similarity in most morphological characters to several species which are referred to that genus and in spite of the necessity of broadening the generic concept to include forms with relatively abundant diaphragms in both autozooecia and mesozooecia.

Geinitz (1848) considered there to be three distinct trepostome species in the reef. "Stenopora mackrothi" was an erect ramose form which he differentiated from "Alveolites producti" - an encrusting form. This appears to have been the only distinguishing characteristic and is a feature considered here to have no taxonomic significance in specimens of Dyscritella columnaris, which often show both growth forms in a single zoarium (see Pl. 128 fig. a). Geinitz's third species, "Coscinium dubium", was differentiated from "Stenopora

mackrothi" only by the greater width of its zoarium - this is likely to be a function of the number of secondary overgrowths present and is not considered here to be of taxonomic significance (see p.305).

King (1850) maintained two separate species largely on the basis of their growth form, but correlated this difference with other morphological characters. He considered the ramose form, "Calamopora mackrothii" to have diaphragms and the encrusting form, "Stenopora columnaris" to lack diaphragms and to have a thicker inter-zooecial wall. This correlation of characters does not occur in specimens of the present study. King (op. cit.) describes a specimen of "Stenopora columnaris" which produces an erect branch; he dismisses this as simply the growth of a zoarium of "Calamopora mackrothii" on the surface of "Stenopora columnaris". "Alveolites buchiana" King (1850) was established on the basis of a single encrusting specimen which had virtually no mesozooecia. The specimen was examined in the present study (see Pl. 122 fig. a,b) and appears to have very few mesozooecia. This feature may be of taxonomic significance but "Alveolites buchiana" is only tentatively placed in synonymy with Dyscritella columnaris because it is very poorly preserved (thickly encrusted by dolomite) and because it has not been possible to observe any morphological features in thin section.

Geinitz (1861) established three varieties of "Stenopora columnaris" Schlotheim - "S. columnaris var. incrustans" which was exclusively adnate and which Geinitz considered to be morphologically quite variable, particularly with regard to the spacing of zooecial chambers, "S. columnaris var. ramosa" which was erect but otherwise did not differ significantly from "S. columnaris var. incrustans", and

"S. columnaris var. tuberosa" which is more robust than "S. columnaris var. ramosa", probably consisting of several layers of secondary overgrowth. These varieties are here placed in synonymy with D. columnaris.

Waagen and Wentzel (1886) recognized two distinct forms within the ramose variety of Geinitz (1861) - "Geinitzella columnaris var. ramosa sparsigemmata" which is synonymised with D. columnaris and "G. columnaris var. ramosa multigemmata" which has very abundant mesozooecia and appears sufficiently distinct to warrant its retention as a separate form.

The description of "Stenopora columnaris ramosa" by Dreyer (1961), is not detailed but seems to be of a different form from anything seen in the present study. She claims that inter-zooecial wall thickness is 0.18-0.36 mm and that 13-15 acanthostyles occur around an aperture. This is certainly not comparable to D. columnaris, but Dreyer's description may be inaccurate.

The specimens assigned to D. columnaris in the present study encompass a fairly large range of morphological variation. Mesozooecia have a variable abundance, reflected to some extent in the quite large range of values for Z1 (13-20) and Z2 (6-10), but there is no significant discontinuity in this character, such as was described by Waagen and Wentzel (1886). Diaphragms may be absent from the autozooecial chambers of some zoaria but usually number from two to four; very rarely an autozooecial chamber has up to eight diaphragms. These differences are not considered significant because intra-zoarial variation in the number of diaphragms is often as great as that found inter-zoariaally and the number of diaphragms in an autozooecial

chamber may relate to the ontogenetic stage of the specimen (see p.284).

Material

MP5.200-MP5.209	Thin Sections, locality MP5
MP5.211-MP5.214, MP5.53, MP5.68, MP5.70-MP5.72 MP5T1, MP5T2, MP5T4, MP5T5, MP5T7, MP5T10	
MP5.43, MP5.45	Hand Specimens, locality MP5
HDN50-HDN52 HDN20-HDN25, HDN28-HDN30	Thin Sections, locality HDN
RH2.4, RH2.6 RH2.13-RH2.20, RH2.43	Locality RH2
RH1.57	Locality RH1
MP4.11	Locality MP4
HAW38, HAW29, HAW28, HAW18	Thin Sections, locality HAW
HAW45, HAW39, HAW61, HAW70, HAW72, HAW33, HAW31	Hand Specimens, locality HAW
GLQ100	Thin Section, locality GLQ

Phillips Collection, York Museum

693F, 694F	Loc. unknown

King Collection

B117A-B117I, B117M	Tunstall Hills
B118	" <u>Alveolites buchiana</u> " of King (1850), pl. III figs. 10-12
B119	Figured by King (1850), pl. III fig. 9. From Humbledon Hill
B119B	No loc.
B119C	Humbledon Hill

Stratigraphical Range

Upper Permian.

Occurrence

Very common in the Tunstall Member, N.E. England, common in the Zechstein of Germany. The species also occurs in the *Productus*-Limestone of the Salt Range, Pakistan, Waagen and Wentzel (1886), and may ? occur in the Akiyoshi limestone group of Japan, Sakagami and Sugimura (1981).

Secondary Overgrowths in *Dyscritella columnaris*

In the present study, secondary overgrowths have been observed in the majority of specimens of *D. columnaris* - they often consist of a single layer of zooecia but up to seven layers may occur.

The overgrowth is very similar in character to the exozone below and develops no endozone - Bigey (1981) described a similar overgrowth morphology in a Devonian leioclemid but Bancroft (1984) found a reduced endozone to be present in some Carboniferous examples. In some cases the origin of the overgrowth is visible and it can be seen clearly as intrazoarial - it originates from a point distally in the zoarium where the exozone may be significantly wider than usual. Zooecia extend proximally along the older core of the zoarium, they are recumbent and orientated in the opposite direction from those of the exozone below. Bigey (1981) cited the reversal of zooecial orientation in an overgrowth as evidence against it being intrazoarially developed - she considered such overgrowths to be of a new colony using the earlier colony as a substrate. This interpretation is clearly unjustified.

Budding of zooecia in an overgrowth appears to take place interzooecially, though Bigey (1981) describes intrazooecial fission in a Devonian leptotrypelliid. A thin (5-10 μ) basal lamina is developed as the base of the overgrowth - it may be draped over the topographic irregularities of the zoarial surface below e.g. acanthostyles (see Pl. 130 fig. a) and may extend into zooecial chambers (see Pl. 127 fig. b). However, the basal lamina is often not in contact with the zoarium below (e.g. see Pl. 127 fig. b, Pl. 129

figs. a, b, c) - the raising of the lamina above the zoarial surface may be caused by the presence of sediment in chambers and on the surface of the zoarium (see Pl. 127 fig. b, Pl. 129 fig. b) but in some cases it bends sharply and grows at a relatively large distance from the zoarium (see Pl. 129 fig. a). Such growth irregularities are often caused by the incorporation of foreign bodies into the overgrowth but in several examples of D. columnaris no such body is apparent. The cause of such irregularities is thus a matter for some speculation. Pl. 129 fig b shows encrusting algae or worm tubes which have been incorporated within an intrazoarial overgrowth, they are attached to a terminal diaphragm and thus must have settled while the relevant zooids were in a degenerated state. The overgrowth in this case may have developed as a response to exogenous factors, i.e. the settlement of foreign bodies on the zoarial surface; Bigey (1981) considers localised overgrowths to develop as a response to exogenous factors in some Devonian trepostomes, though she considers overgrowths of greater extent to be controlled by endogenous factors, i.e. degeneration-regeneration processes. In the above case, as well as incorporating a foreign body, the intrazoarial overgrowth extends for the whole width of the zoarium - thus it may not be possible to make a clear distinction between endogenous and exogenous factors as those responsible for the development of overgrowths.

In GLQ101 (see fig. 74) the basal lamina of the overgrowth is everywhere raised above the level of the zoarium beneath. This probably represents overgrowth of a colony which had already been partially enclosed in sediment (probably micrite (which would have been lithified) but another possibility is the occurrence of a high-Mg

calcite fringing cement - details of the sediment are obliterated by later dolomitisation) - it may be intracolony or intercolony and its development may have proceeded by the proximal extension of the overgrowth over an earlier part of the colony which was buried in sediment and in life position (see fig. 74).

The distinction between intra and inter-colony overgrowth is not easily made, though the recognition of an ancestrula in an overgrowth is unequivocal proof of its intercolony. The majority of secondary overgrowths in D. columnaris are considered to be intracolony because of the frequency of their occurrence (in well over half the specimens examined), if each overgrowth represents a new colony developed from an ancestrula then the larva of D. columnaris must have been exhibiting an extreme degree of substrate preference (though the larvae of modern stenotopic bryozoans may show a very marked preference for a particular substratum e.g. Eggleston (1972) in Ryland (1976)). It is believed here that most of the secondary overgrowths in D. columnaris were related to degeneration-regeneration cycles but may also have been influenced to some extent by exogenous factors. Their growth towards the proximal part of a colony may have had a strengthening function - the continued distal extension of narrow branches which are not substantially thickened secondarily (as in the Fenestrata) is likely to lead to relative structural weakness, the development of a layer of overgrowth, particularly near the origin would have increased colony robustness.

CHAPTER 6

ORDER CYCLOSTOMATA Busk, 1852

($\equiv$ ORDER TUBULIPORATA Johnston, 1847)

Diagnosis

Stenolaemata with adnate or erect zoaria. Autozooecia tubular and often quite long, often with well-developed peristomes. Calcified frontal walls usually with pseudopores. Interzooecial walls regularly developed, usually with pores. Large brood chambers often occur in the form of gonozooecia or extrazooecial chambers.

Stratigraphical Range

Lower Ordovician-Recent.

Discussion

The Order Cyclostomata, Busk (1852) has been, and still is, widely used, but its replacement by the Order Tubuliporata, Johnston (1847) is recommended in the "Treatise". They adapt this name from the Tubuliporina of Johnston (op. cit.) and consider the name Cyclostomata to be a junior homonym. This step is partly justified because Duméril (1806) earlier used the name Cyclostomata in a classification of fishes. However, some confusion may arise because of the similarity of 'Tubuliporata' to the name Tubuloporina, Milne-Edwards (1838) which is used for a Sub-order of Mesozoic cyclostomes. The Order Cyclostomata, Busk (1852) has been used here because of its generally wider recognition at the present time.

Suborder Paleotubuloporina Brood, 1973

Diagnosis

Single-walled Cyclostomata lacking pseudopores. Zooecia₁ ^{may or may not be} in communication via pore-like or canal-like structures. Adapertural parts of zooecia relatively long. Gonozooecia probably absent.

Stratigraphical Range

Lower Ordovician-Upper Permian.

Discussion

In his original description of the Suborder, Brood (1973) considered it to be characterized by a lack of interzoooidal pores. However, Dzik (1981) and Taylor (1985) have shown species of the Suborder to possess interzoooidal pores.

Family Corynotrypidae Dzik, 1981

Diagnosis

Cyclostomata with non-pseudoporous frontal walls. Zooecia more or less pyriform in shape. Aperture close to the distal margin of a zooecium. The interior of mature zooecia is frequently constricted by adapertural hemiphragms or longitudinal ribs separating longitudinal canals.

Range

Lower Ordovician-Upper Permian.

Discussion

The diagnosis given above is essentially that given by Dzik (1981) - the importance of "hemiphragms" and "longitudinal ribs" as familial characters is uncertain because of the lack of clarity in Dzik's descriptions.

Genus Corynotrypa Bassler, 1911

Type Species

Hippothoa delicatula James, 1878

Diagnosis

Corynotrypid with encrusting zoaria which consist of uniserial branches with lateral branches. Zooecia are narrow proximally but broaden distally. Calcified interior walls lacking.

Range

Middle Ordovician-Upper Permian.

Taxonomic Procedure in the genus Corynotrypa

There are relatively few morphological characters observable in Corynotrypa voigtiana (see fig. 75).

Apertural diameter (A.D.) is the maximum dimension measured between the inner rims of the aperture in a direction parallel to the length of a zooecium. It is only rarely possible to measure this with any accuracy in the specimens of the present study.

Zooecium length (Z.L.) is the maximum length of a zooecium. This character is not affected by encrustations of dolomite.

Zooecium width (Z.W.) is the maximum width of a zooecium transverse to its length. This may be significantly increased by later diagenetic effects, the recognition of which is thus important.

Zoarium average values are calculated for these characters, minima and maxima are stated. The standard deviation, coefficient of variation and average are quoted for the whole sample of zoarium

averages.

No observations were possible in thin section.

Corynotrypa voigtiana King, 1850

Figs. 75-78, Pls. 133-135

- 1848 Stomatopora (Aulopora) dichotoma Lamouroux; King, p. 6
- 1850 Aulopora voigtiana King, pp. 31-32, pl. III fig. 13
- 1857 Hippothoa voigtiana King; Kirkby, pp. 217-218, pl. VII figs. 14,
15
- 1861 Hippothoa voigtiana King; Geinitz, p. 120, pl. XX figs. 24, 25
- 1977 Hippothoa ? voigtiana King; Pattison, p. 36
- 1980 Stomatopora voigtiana King; Taylor, pp. 621-626
- 1985 Corynotrypa voigtiana King; Taylor, pp. 359-372, figs. 4-8

Type Material

The specimen B132, from the King collection, was designated lectotype by Taylor (1980) - this was examined in the present study.

Diagnosis

Corynotrypa with uniserial branches; lateral branches frequently developed, arising from the distal end of a parent zooecium and diverging from the parent branch at an angle of usually 90°. Zooecia small and elongate pyriform. Frontal walls transversely wrinkled and without pseudopores. Zooecial apertures small and circular to transversely elongate.

Description

Zoaria appear to be quite small, they consist of encrusting branches which are composed of uniserially arranged zooecia. Branches are straight, or curved to various degrees, but never sharply.

Lateral branches arise from the distal ends of zooecia in a parent branch - they diverge from the parent branch mostly at an angle of 90° but more rarely at lower angles (as low as 60°). Occasionally the angle of divergence may be higher (see Pl. 133, fig. b) - and may ? be as high as 120° (see discussion). Lateral branches are developed quite frequently and may show a weak tendency to be paired on either side of a parent branch - their development, in some cases, may be affected by the nature of the substratum (see discussion).

Zooecia are small and elongate pyriform. The proximal third of a zooecium is narrow and often of fairly even width, this may increase gradually or more suddenly to the widest part of the zooecium which occurs approximately two thirds of the way along its length. Zooecia narrow slightly at their distal end which is usually bluntly rounded. They are often curved and asymmetrical; the degree of curvature is usually greater in the proximal part of a zooecium, and may be related to the nature of the substratum (see discussion). The first zooecium of a lateral branch tends to be longer than average. Very short zooecia without apertures may occur, these are probably kenozooecia, Taylor (1985). Frontal walls are transversely wrinkled and have no pseudopores, Taylor (op. cit.). Zooecial apertures are small, terminal and circular to transversely elongate. A low peristome ? may be developed.

Measurements

N = 9

	NM	Mn	Mx	S.D.	C.V.	$\bar{X}$
Z.L.	48	0.4	0.53	0.033	6.9	0.478
Z.W.	30	0.139	0.167	8.4×10^{-3}	5.5	0.152
A.D.	1	-	-	-	-	0.06

Discussion

King established the taxon in 1850 but remained uncertain of its true affinities, largely because of the few specimens available to him and their poor state of preservation.

Taylor (1980) assigned the taxon to the genus Stomatopora Bronn (1825) but he was misled in this generic assignment because the only available specimen was thickly encrusted by dolomite. Taylor (1985) referred the taxon to Corynotrypa when better preserved material was discovered.

The material examined in the present study is generally poorly preserved, only one specimen shows a clearly developed zooecial aperture. Thus some aspects of the description above are based on the work of Taylor (1985) e.g. the nature of the frontal wall. Taylor (op. cit.) did not observe any peristome in his specimens but it is tentatively suggested here that a low peristome may occur rarely.

A single specimen encrusting the reverse surface of Acanthocladia appears to develop a lateral branch at an angle of 120° . This higher angle is characteristic of the angle of divergence of zooecia which are regenerated in a proximal direction from a damaged zoarium, Taylor (1985) - because of the small number of zooecia preserved in this case

it is not possible to identify this with certainty as regeneration and it is suggested that it may represent an unusually high angle of divergence of a lateral branch. Unequivocal lateral branches may diverge at angles greater than 90° (see Pl. 133, dif. b) (cf. Taylor (1985)). Specimen RH2.26 (see Pl. 134) encrusts the reverse surface of Fenestella retiformis - the strict spatial constraints imposed on the colony of C. voigtiana by this substratum may have affected some aspects of its growth. Lateral branches may be restricted in their development by the fenestrate meshwork, they may only develop along dissepiments or branches. A number of zooecia are more strongly curved than is normal, particularly in their proximal parts - this may be caused by their growth around fenestrules and on narrow branches (e.g. see Pl. 134, fig. b)

The specimens RH4.29a and RH4.29b, encrusting the same Horridonia shell may not be distinct zoaria but could be fragmented clones as described by Taylor (1985). However, in the statistical analysis of measured parameters they are considered as separate zoaria.

Material

RH2.1a, RH2.1b, RH2.26 RH2.54	Locality RH2
RH3.1	Locality RH3
RH4.29a, RH4.29b	Locality RH4

King Collection

B132	Lectotype, from Humbledon Hill

Korn Collection

Taf. I fig. 5

Two zooecia encrusting
the reverse surface of
a specimen of Fenestella

Stratigraphical Range

Upper Permian.

Occurrence

Rare in the Tunstall Member of N.E. England. Rare in the
Zechstein of Germany.

CHAPTER 7

PALAEOECOLOGY

Introduction

Palaeoecology is basically the study of the interaction of organisms with their environment in the geological past. Ager (1963) separates the environment into three components:- Physical, Chemical and Biological, which can in turn be subdivided into various factors - in the present study, it is possible to suggest the influences of only a small proportion of the possible factors e.g. Water depth, current strength, substratum type, salinity and biotic interactions.

The keys to palaeoecological interpretation lie in the description and interpretation of sediments enclosing fossils and of the fossil assemblages themselves. A number of difficulties arise - the sediment enclosing a fossil assemblage provides clues about the physical and chemical environment pertaining to deposition of that sediment, these need not be the same conditions as existed during the life of the organisms (e.g. if the organisms have suffered post-mortem transportation or if there are significant hiatuses in deposition) - an assemblage of fossils may have few similarities, in terms of species composition, with an original community (biocoenosis) which it may be supposed to represent. It is important to make the distinction between an assemblage which does not contain most of the preservable elements of an original community and one which does. Several lines of evidence can be used to eliminate obviously unrepresentative assemblages e.g. Boucot (1953) distinguished bivalve

life assemblages (biocoenoses) from death assemblages (thanatocoenoses) by an analysis of valve size frequency distributions and the ratio of right to left valves present in the assemblage. In a life assemblage right and left valves ought to be equal in number, inequality suggests post-mortem transportation of shells. Similar criteria have been applied in the present analysis of faunas. The recognition of bryozoans in life position may be used as evidence of a life assemblage. Even where all elements of a community with hard parts are preserved, the deduced composition, trophic structure and biotic interactions may be very different from those of the original biocoenosis; this is largely because of the lack of preservation of the soft-bodied fauna. In some environments trace fossils provide evidence of this fauna; no such fossils are known from the Permian reef. Another problem, which is particularly acute in a fossil reef, is the delineation of the stratigraphic and spatial boundaries of a community. A community can be defined at a variety of levels, e.g. the cryptic community in a small reef crevice or the complete community of a patch-reef, the choice of level lies with the author. An essential requirement for the definition of a community is considered to be that the component species interact - this definition obviously leaves considerable scope for interpretation. The poor stratigraphical controls in a fossil reef mean that individuals or groups of individuals which are now adjacent may have been originally separated by tens or even hundreds of years, and thus were not part of the same biocoenosis. The localities analysed below almost certainly represent more than a single biocoenosis in each case, however, analysis at this level is justified because it allows description of

the relationships (albeit evolving) between the fauna and different reef sub-environments.

Recently, there has been an increasing emphasis on the quantification of palaeoecological data. Various statistical methods have been employed in the analysis of diversity in community comparisons e.g. Koch's (1957) "index of biotal dispersity", Brillouins, (1962) index was used to measure diversity by Brondos and Kaesler (1976). In the present study an attempt was made at a thorough quantitative analysis of assemblages but this procedure was abandoned for several reasons:-

(i) Whereas individual components of the shelly fauna can usually be enumerated, bryozoan zoaria are nearly always preserved in a fragmented state; counting each fragment would give a biased view of the number of individuals originally present. Alternatively, the relative surface areas of species in a polished block could be calculated - this procedure is very time-consuming and particularly sensitive to the lateral and vertical faunal heterogeneities which occur through most of the reef. Volumetric analysis of the fauna by water-displacement techniques is obviously impractical with the material of the present study which is mostly inseparable from the matrix.

(ii) As discussed above, there are considerable difficulties in collecting an assemblage which represents an original biocoenosis; thus the justification for a high degree of accuracy in calculations of species abundances is reduced.

(iii) The lateral and vertical inhomogeneities in faunal assemblages accentuate the inaccuracies generated by sampling bias thus reducing

the significance of a detailed quantitative analysis.

Thus, a semi-quantitative approach has been used in the comparison of species diversities. Seven increasing abundance categories are defined and have been plotted on histograms (see figs. 82-96).

1. Occurs (only 1 or 2 individuals)
2. Rare
3. Quite rare
4. Quite common
5. Common
6. Very common
7. Extremely common

Whereas bryozoans are identified at species level elements of the shelly fauna are named only to genus level. Although this is inconsistent and a source of inaccuracy it is felt that the observed general patterns of variability are not significantly affected.

Interpretation of the broad general patterns which emerge is difficult. Some gross ecological effect may be detected through changes in diversity but the assessment of the importance of particular factors is often only circumspect.

It is worth noting that inhomogeneities in faunal distributions and abundances need not be caused by inhomogeneities of their environment; factors such as larval dispersal and chance may be quite important determinants of distribution (e.g. the larval stage of Palaeozoic stenolaemates was probably very short lived with a limited dispersal potential - Nielsen (1970) described the larval stage of

Crisia eburnea as lasting only 15 minutes).

Cuffey (1985) recently proposed an expanded classification scheme for reef-rock types, largely to accommodate the diverse morphologies of bryozoans. This scheme has been used in part but the more general terminology of James (1983) is usually employed because of its greater flexibility.

Locality Descriptions and Faunal Lists

MP5

Location: NZ390544. Just below Tunstall Hills Cottage at the North end of Tunstall Hills.

Position in reef: Reef base.

The outcrop is limited in extent but consists of two distinct parts, separated by a fault (probably the High Barnes fault of Smith (1978)). The lithology which appears to have been downthrown was not considered in the description or the faunal analysis.

A well-preserved, undolomitized fauna occurs in a rudstone/floatstone. Skeletal grains are cemented by pseudospar or neomorphic spar which has been interpreted by Tucker and Hollingworth (1986, in press) to be the product of calcitization of an original aragonite fan cement. Thick crusts of calcitized aragonite also occur on skeletal grains. Tucker and Hollingworth (op. cit.) also described isopachous layers of acicular calcite crystals on bioclasts or on botryoids of an earlier cement - they interpreted them as original high-Mg calcite precipitates, which are a feature of modern reefs (e.g. James (1983)). Calcite fan crystals also occur as a cement type; they form large squat crystals with fanning subcrystals, Tucker and Hollingworth (op. cit.). The order of precipitation of these cements is not always the same though the calcite fan crystals are usually latest and the isopachous acicular calcite is usually earliest. These marine cements are quite voluminous and would have been an important factor contributing to the creation of a rigid framework in the earliest stages of reef growth; bryozoans are quite often cemented in

life position.

The high concentration of a shelly fauna and its proximity to the base of the reef suggest that this locality represents the reef basal coquina of Smith (1958). The distribution of the fauna is not uniform, even over the small scale of the outcrop (approx. 2 m vertically). The stratigraphically lower part is dominated by bivalves, particularly Pseudomonotis which often reaches a large size, bryozoans are rare - only Dyscritella occurs in any abundance (bivalves and brachiopods provide substrata for the attachment of colonies). Brachiopods become more abundant and bryozoans more diverse in the higher parts of the outcrop. Some colonies of Acanthocladia may have grown in small cavities within the developing reef framework (see Pl. 84), though the identification of such fossil cavities is circumspect (the criteria for their recognition described by Scoffin (1972) were not observed). Zoaria of Synocladia and Kingopora often appear to be preserved in life position.

Overall, the fauna is diverse and very abundant (see fig. 82).

HYR

Location: NZ 359588. Road Cut at Hylton Castle. (see Pls. 140-142).

Position in reef: Reef base and immediately above.

The outcrop is 40 m long and inhomogeneous lithologically and with respect to faunal composition. The stratigraphically lowest part of the outcrop consists almost entirely of algal mounds (see Pl. 141 fig b). Acanthocladia diffusus is only locally abundant above this, forming dense almost monospecific patches about 1/2 m² in extent - the boundaries of these patches are fairly sharp, leading to the

suggestion that these patches ? may represent cavities in the reef structure. The fauna is more diverse and abundant at the stratigraphically highest parts of the locality where Fenestella retiformis and Synocladia virgulacea are dominant elements and often in life position. Acanthocladia anceps is locally abundant. Thin (cm-scale) lensoid beds of comminuted bryozoan and shelly material occur within algal laminites (see Pl. 141 fig. c), this material may have been transported in by relatively high energy currents, bringing in elements of a normal, diverse reef biota which existed contemporaneously with the algae in an adjacent part of the reef. If this is the case then it serves to illustrate the difficulties of recognizing chronostratigraphic horizons in the context of a reef where lithologies of strikingly different characteristics may exist contemporaneously.

Clasts of lithified reef rock may be incorporated into algal laminites, this suggests that early marine cementation had taken place. The complete dolomitization at this locality renders the recognition of such cements impossible.

HYQ

Location: NZ 358589. Quarry at Hylton Castle.

Position in reef: Just above the reef base.

The fauna at this locality is essentially the same as that for locality HYR, though algal laminites are absent. In one part of the quarry colonies of Synocladia virgulacea appear to be growing from a near vertical rock wall (see Pl. 142 fig. b) - there is no evidence that this is a boulder of biolithite and the colonies have clearly not

suffered post-mortem transportation; therefore it must be assumed that they are preserved in life position (this can be compared to the 'Branchstone' of Cuffey (1985)). The zoarial morphology of such specimens of S. virgulacea is atypical of the taxon (see Pl. 63) but almost identical to that found in zoaria from locality HN which also appear to have been attached to a near vertical rock wall during life. Consequently, it is suggested that there may be some correlation between zoarial morphology and habitat.

RH4

Location: NZ 395538. Old Railway cutting at Ryhope, South end of
Tunstall Hills.

Position in reef: Lower reef and lower reef slope.

This locality consists of dolomite boundstone in reef talus, Smith (1981). Blocks of boundstone may have quite different faunal compositions from the lithologies around them e.g. consisting almost entirely of Acanthocladia diffusus - such blocks are presumably derived from higher in the reef structure. The fauna around the blocks is both very diverse and very abundant - the most noticeable element of the fauna is Fenestella retiformis which is only rarely in life position. Synocladia virgulacea is more commonly in life position. Kingopora ehrenbergi is notably absent from the fauna. Brachiopods are numerically a more important element of the fauna than are bivalves - a great range of sizes of individuals occurs. Cyathocrinus is relatively abundant at this locality.

RH1

Location: NZ 394539. Small Quarry, half way up the hill, south end of Tunstall hills.

Position in reef: Lower reef core/lower slope.

There are two distinct lithologies in this quarry - a dark brown Fe-rich dolomite in the ? downthrown part and, south of the fault, a white lithology dominated by dolospar. Only the lithology south of the fault was considered in the faunal analysis. The fauna is abundant and fairly diverse, dominated by bryozoans; much of it may be in life position - Strophalosia is often found with its delicate spines intact and Synocladia virgulacea may be preserved in life position. Acanthocladia diffusus occurs only in an isolated, almost monotypic patch of closely-spaced zoaria. There is a range of sizes represented in the shelly fauna but in some 'pockets' only small similar sized individuals occur - these are probably all juveniles, and since they show no signs of transportation some catastrophic mortality process may be envisaged.

RH2

Location: NZ 395540. Large quarry at the top of the hill, South end of Tunstall hills.

Position in reef: Reef Core/Upper Slope.

Most of the quarry is unfossiliferous but its eastern side contains a very abundant and diverse fauna - bryozoans are the most conspicuous element of the fauna. The lithology is an orange/brown dolomite which may show a botryoidal structure in thin section - this

structure is typical of the calcitized aragonite fan cements described from locality MP5; such cements may have been present originally in this lithology. Most of the fauna appears to be preserved in or close to life position since very delicate morphological features are usually well-preserved on bryozoan zoaria. Several pinnate bryozoans occur in cavities - these may have been original cavities in which the bryozoan grew.

MP1

Location: NZ 391548. The north end of Tunstall hills, adjacent to the electricity sub-station.

Position in reef: Top of reef core/back of upper slope.

(possibly only reef slope - D.B. Smith (pers. comm)).

The lithology is a bright yellow dolomite with an abundant and fairly diverse fauna. One of the most abundant elements of the fauna is Synocladia virgulacea which often occurs in life position.

MP2-MP4

Location: NZ 392547. The top of the north end of Tunstall Hills.

Position in reef: Top of reef core/reef flat to upper slope.

Histograms of species abundances were not plotted for these localities because most of the fauna occurs in pockets of comminuted debris and appears to have been derived from elsewhere. The fauna in life position is dominated by algae.

Location: NZ 442454. Beacon hill railway cutting.

Position in reef: Reef slope (mostly upper).

The fauna is diverse and abundant with both lateral and vertical inhomogeneities in the distributions of taxa. Acanthocladia diffusus and A. laxa are restricted to the lowest part of the outcrop (probably lower reef slope) while Synocladia virgulacea is abundant at the highest parts (upper slope) and often occurs in life position. Delicate pinnate bryozoans such as Kalvariella typica and Penniretepora waltheri nodata occur locally in the lower part of the outcrop - they have not suffered post-mortem transportation because very delicate morphological features are preserved; they occur in association with numerous specimens of Strophalosia which are in life position with their spines intact.

HM5 and HM7

Location: NZ 381552. The lower part of Humbledon Hill - an old quarry face. (Pl. 143)

Position in reef: Reef Core.

The fauna is very abundant and very diverse at this locality but community compositions show clear changes in a vertical succession (these can be compared, on a small scale, with those described by Walker and Alberstadt (1975)). The lowest part of the succession consists of bedded dolomites which are probably reef-equivalent in age, they are unfossiliferous and structureless, above this lies massive reef rock with a fauna characterized by Horridonia,

Cyathocrinus and Fenestella retiformis, faunal diversity increases above this, F. retiformis and brachiopods being the dominant elements. Close to the top of the outcrop Synocladia virgulacea becomes relatively abundant and often occurs in life position. Some areas are relatively unfossiliferous containing only rare Acanthocladia anceps. At the top of the outcrop Acanthocladia diffusus is dominant, occurring as closely-spaced zoaria in patches with a low faunal diversity.

HAW, HAG and HA

Location: NZ 380551. Top of Humbledon Hill, building works in 'Alpine Way'.

Position in reef: Reef core (approaching reef flat).

The lithology is a white porous dolomite with a very abundant but not very diverse fauna. The faunal diversity is reduced relative to lower parts of Humbledon Hill. Fenestella retiformis often occurs in life position, Acanthocladia anceps does so less commonly. Bivalves and brachiopods are often, but not always, small in size. Horridonia and Cyathocrinus are notably absent from the fauna. Numerous colonies of A. anceps occur in closely-spaced 'thickets' - their growth often appears to be in a sub-horizontal plane.

SBC

Location: NZ 418473. Cold Hesledon, railway cutting (Stony bank cut). (Pl. 144)

Position in reef: Reef flat and upper reef slope.

This locality provides a section from the reef flat (in the west) through to the upper reef slope (in the east). At no point is the diversity great; the faunal abundance is generally low. The reef flat consists of planar algal stromatolites which dip gently eastwards (Smith, (1981) considers this to be a primary depositional dip). These pass eastwards into fossiliferous dolomites which contain a high proportion of laminar algal encrustations - the exact zone of transition is not exposed. A characteristic association of A. anceps or A. laxa and Dyscritella columnaris, Bakevella and Dielasma occurs in patches. At the easternmost end of the railway cutting algal stromatolites and Synocladia virgulacea are dominant. Smith (1981) claimed that fenestrates here are smaller than in earlier parts of the reef, this was not found to be the case for S. virgulacea, though the rare zoaria of Fenestella retiformis never achieve large dimensions. S. virgulacea is often overgrown by algal laminae - in some cases colonies appear to grow downwards from the edges of algal mounds.

Most of the shelly fauna at this locality is small in size though rare large individuals occur.

HD

Location: NZ 434438. Townfield Quarry, Easington Colliery. (Pl. 145)

Position in reef: Reef flat close to top of Upper reef slope.

The fauna at this locality has a low diversity, but may be fairly abundant in patches. Acanthocladia laxa and Dyscritella columnaris occur together in a characteristic association with subordinate Dielasma and Bakevella. Pockets of shelly material occur, mostly consisting of Bakevella and Dielasma, individuals are nearly all

small in size. Most specimens of Acanthocladia are heavily encrusted by worm tubes or algae. Dyscritella columnaris commonly encrusts lithified substrata which appear to be widespread at this locality (though in some cases such hard substrata may simply be derived clasts). Algal stromatolites occur in beds at the top of the quarry - they have a pronounced dip eastwards; their angle of dip also increases in that direction.

The lithology in the quarry is often calcite-rich rather than dolomitic. Gypsum (with minor anhydrite) may occur in cavities - it is not known whether it is an early or late diagenetic mineral.

HTQ

Location: NZ 437463. Hawthorn Quarry. (Pl. 146)

Position in reef: Reef flat and upper reef slope passing up into the Hesleden Dene stromatolite biostrome (Smith, 1981)

The lowest parts of the quarry contain rare Fenestella retiformis, bivalves and Dielasma. The fauna becomes even more restricted at the top of the reef where Acanthocladia laxa occurs, Bakevellia and Dielasma are rare and A. diffusus and Dyscritella columnaris constitute by far the greatest proportion of the fauna. Small individuals of Diel^aasma may be concentrated in pockets. The uppermost parts of the quarry are composed of algal laminites and stromatolites which are considered to be part of the Hesleden Dene stromatolite biostrome, Smith (op. cit.).

GLT

Location: NZ 378 538. Temporary exposure in a builders' trench at
Gilley Law.

Position in reef: ? Patch reef in back-reef environment.

The trench exposed two different lithologies - a white fairly porous dolomite and a grey/green saccharoidal dolomite. There were no significant faunal differences between the lithologies. The most striking aspect of the fauna is the great abundance of Horridonia and Strophalosia in life position. They appear to form a shell bank which serves as a substratum for the attachment of zoaria of Kingopora ehrenbergi - this species occurs in great abundance (see fig. 94). Shells of Horridonia may also serve as a substratum for colonies of the rarer Fenestella retiformis. The lateral and vertical extent of this 'patch reef' is not known because of the geometry of the trench - it is possible that the outcrop represents no more than a shell bank rather than a patch reef; a distinction between the two is not easily made.

GLQ

Location: NZ 376537. Gilley Law Quarry, Silksworth.

Position in reef: Patch reef in back-reef environment (this ? maybe equivalent to the "Flachwasserriff" of Kerkmann (1969) which is simply a landward extension of the main reef).

The lower part of the quarry exposes thinly-bedded unfossiliferous dolomites of the back-reef; these are overlain by

massive dolomite (with some calcite) of the patch reef. The faunal distribution is variable with different elements dominant in different parts - Dyscritella columnaris is locally abundant as is Kingopora ehrenbergi, these are usually heavily encrusted by laminae of presumed algal origin. The shelly fauna has a relatively reduced diversity.

HN

Location: NZ 385538. Railway Cutting at High Newport. (Pl. 147).

Position in reef: ? Back reef environment.

Most of the cutting is unfossiliferous but very abundant Synocladia virgulacea and Dyscritella columnaris occur at one point. Colonies of S. virgulacea are in life position and appear to be growing from a near vertical rock wall, they are stacked one on top of another for a thickness of about half a metre forming a branchstone, Cuffey (1985). Their zoarial morphology is atypical and is similar to that found at locality HYQ - it is possible that the development of this zoarial morphology may be correlated with growth in this particular environment. Zoaria of S. virgulacea are heavily encrusted by D. columnaris and may also have served for the attachment of the relatively rare bivalves and brachiopods at this locality.

Interpretation of Diversity Patterns

Diversity is considered here to be simply the number of different species present in an assemblage or community - this definition is generally accepted by many authors but there are those who consider a component of the distribution of individuals in the various species to be essential to a measure of diversity, e.g. Margalef (1968) (i.e. an even distribution of individuals amongst species would represent a lower diversity than an uneven distribution amongst the same number of species).

The most obvious general pattern of diversity variation is a marked reduction at the highest reef localities compared to the base and core of the reef (e.g. 10 species at HD, 11 species at HTQ and 27 at MP5, 29 at RH4). This upward faunal impoverishment was noted as long ago as 1913, by Trechmann, who later (1925) suggested four divisions of the reef based on characteristic faunal assemblages. These four divisions of Trechmann (labelled a-d) do not represent simply vertical changes in the reef fauna but include the lateral variability across the reef.

There may be several causes of the upward decrease in faunal diversity - the relative importance of the possible factors is difficult to assess but their likely effects can be suggested. Smith (1981) pointed out that Trechmann considered increasing salinity to be the main factor responsible for the decrease in diversity but also suggested tentatively that decreasing water depth and autogenic succession, Odum (1971) may have been factors.

A significant increase in salinity would undoubtedly serve to

exclude stenohaline species from the reef in its later stages of growth. Cyathocrinus probably had a narrow salinity tolerance; it is absent from highest reef communities but more abundant at the base and core. Trechmann (1913, 1925) placed a strong emphasis on the occurrence of smaller individuals of the shelly fauna at the top of the reef relative to lower in the reef. This has generally been interpreted as the phenomenon of stunting, caused by an increase in salinity. However, the relationship between size of organisms and salinity is not a simple one, Reymont (1971) e.g. Gilchrist (1960) showed that the abdomen of the brine shrimp, Artemia salina (L) is longer in animals which have grown in water with a higher salinity. In several parts of the reef a large number of small individuals of Dielasma or Bakevellia predominate but occasionally a larger specimen occurs - an increase in salinity may not necessarily be the correct explanation for the large number of individuals with a relatively small size, some other factor may be causing a high rate of juvenile mortality. There are no lines of evidence, apart from that of faunal diversity, which support the hypothesis of an increase in salinity at higher reef levels. However, it is felt that such an increase may have occurred and may have been at least partly responsible for the observed faunal impoverishment.

Valentine (1971) related species diversity to food resource levels. He considered the resource level unpredictability to be a limiting factor more than simply the relative abundance of a food supply. Such unpredictability may be partly responsible for the decrease in diversity observed in the reef but the complete lack of preservation of nearly all food resources renders such interpretations

speculative.

Walker and Alberstadt (1975) described general patterns of community evolution in reefs - they recognised different stages within Palaeozoic reefs; succession of the communities in the earliest stages was largely autogenic (i.e. controlled by the community) but the later stages of reef growth tended to be characterized by allogenic succession (i.e. controlled by changes in the physical environment). However, they also suggested that a component of autogenic succession may have been partly responsible for community changes in the later stages of reefs. In the present study, the community changes observed towards the top of the reef are considered to be largely allogenic but autogenic succession cannot be ruled out as a factor.

Smith (1981) cites evidence in favour of shallowing in the later phases of reef growth (e.g. the higher proportions of algae and the contemporaneous erosion of lithified rock clasts). Smith (1970a) also suggested that sea level may have been declining during the later stages of reef growth. The approach of the reef to wave base may have been a significant factor in the reduction of faunal diversity, particularly of bryozoan species. The greater turbulence and more unpredictable energy levels could have been limiting factors on the occurrence of more delicate fenestrate bryozoans such as Fenestella and Penniretepora (absent from highest reef localities), even if they occupied cryptic habitats. Schopf (1969) analysed the ecology of some modern bryozoans and found a significant increase in the proportion of erect versus encrusting forms with an increase in water depth; flexible forms (jointed or lightly calcified) were relatively abundant in shallower water environments. Dyscritella columnaris is a dominant

element of the fauna at the top of the reef where it often has an encrusting form, it also grows erectly - this relatively robust erect zoarium may have been resistant to higher energy conditions. The other common bryozoans at the top of the reef are Acanthocladia laxa and A. diffusus whose small compact zoaria, the growth of which was often in dense patches, may have been relatively well-suited to survival in higher energy conditions.

Distribution of bryozoan species through the reef

Trechmann (1913, 1925) and Kerkmann (1967, 1969) have both documented the distribution of bryozoans in the reef to an extent but not in any detail and using taxonomic identifications which may be suspect. Each species will be considered in turn below. Fig. 81 shows the most characteristic bryozoan species of various reef sub-environments.

Fenestella retiformis

F. retiformis has been considered by many authors to be the characteristic reef bryozoan; it is, however, neither the most abundant or most widely distributed. It is very common in the reef core, often reaching a large size and rarely occurring in life position. It is quite common close to the reef base, fairly often in life position, less common in the lower slope and quite uncommon in the upper slope. It is either completely absent from or very rare in the reef flat but may be quite common in patch reefs. The rare zoaria from the upper reef slope are markedly smaller in size than those from the reef core - this suggests that conditions for their growth were not ideal in this environment.

Fenestella geinitzi

F. geinitzi is rare, restricted to the lower and middle parts of the reef core. It may be locally quite common. A similar distribution for the species was noted in German parts of the reef by Liebe (1884) and Korn (1930).

Kingopora ehrenbergi

There is a striking dichotomy between the abundance of K. ehrenbergi in patch-reefs of the back reef environment and its rarity in the main reef - it is quite uncommon at the reef base, very rare in the core and absent from all other parts of the reef. It appears that, as the resistant reef framework was developed, K. ehrenbergi became restricted to the back-reef environment. Such a distribution is difficult to interpret and may be related to a complex variety of factors; however, it is suggested that K. ehrenbergi was unable to compete in areas with relatively high energy ambient currents (see p. 345) - its steeply erect zoarium may have been more prone to damage in a high energy environment than that of Fenestella retiformis which often has a low sub-horizontally expanding zoarium.

Synocladia virgulacea

S. virgulacea occurs throughout the reef, apart from in the reef flat. It is generally quite common, but less common than F. retiformis, however, this pattern is reversed for the upper reef slope where S. virgulacea is very common. Kerkmann (1969) considered the taxon to be characteristic of this environment (which he described as having higher energy conditions). The energy of the environment may be a reason for the replacement of F. retiformis by S. virgulacea as the dominant bryozoan with a fenestrate morphology - S. virgulacea is more robust than F. retiformis and presumably better able to withstand higher bending stresses imposed by water turbulence.

Acanthocladia anceps

A. anceps is common throughout the reef but appears to be absent from the reef flat. It is difficult to assess the factors which may be limiting its distribution.

Acanthocladia magna and A. minor

Both these species are rare in the reef core, occurring in diverse communities.

Acanthocladia laxa

A. laxa occurs quite commonly throughout the reef (though some of the documented occurrences, e.g. at RH4, are in blocks which are probably derived from higher in the reef), it is very common in the reef flat. Its dominance in the reef flat environment may be the result of eurytopism with respect to one or several factors (A. laxa has been documented from the Marl Slate, Schaumberg (1979) and thus is probably able to tolerate environmental extremes).

Acanthocladia diffusus

A. diffusus occurs in local dense patches throughout the reef but is commonest in the reef flat. Its occurrence in almost monospecific patches and at the reef flat suggest it is a relatively eurytopic form.

Thamniscus dubius

T. dubius occurs only in diverse communities of the reef core.

Thamniscus geometricus

T. geometricus is very rare at the reef base and rare in the reef core.

Thamniscus siccus

T. siccus is very rare at the reef base, core and lower slope.

Kalvariella typica

K. typica is very rare in the reef core and lower slope and may be restricted to very low energy (? cryptic) sub-environments.

Penniretepora waltheri

P. waltheri is very rare at the reef base and lower reef slope.

Penniretepora waltheri nodata

P. waltheri nodata is rare at the reef base and quite rare in the reef core. As with P. waltheri, its distribution may be restricted by its delicate pinnate morphology.

Ryhopora delicata

R. delicata is very rare at ? the reef base and in the reef core.

Dyscritella columnaris

D. columnaris is abundant throughout the reef but is particularly dominant in the reef flat where its ability to encrust as well as to grow erectly may be an advantage in a higher energy environment.

Corynotrypa voigtiana

C. voigtiana is very rare, occurring only in the reef core as part of a diverse community. Its distribution is obviously limited by the availability of suitable substrata for encrustation.

The nature of substrata and evidence for contemporaneous lithification

The almost complete dolomitization of the reef has obliterated most of the evidence relating to sedimentation in the reef and the types of substrata which occurred. Different types of substratum can be identified but their relative importance in the reef cannot be assessed quantitatively.

The inferred mode of life of Horridonia supports the presence of soft sediment in the reef. A quasi-infaunal habit is generally accepted for productids with similar shell shapes and a spinose ventral valve e.g. Rudwick (1970). The generally limited distribution of Horridonia may suggest that soft sediment was largely restricted to local pockets within the reef structure. Horridonia is a common element of the fauna at the base of the Humbledon Hill locality (HM5), where the transition from bedded dolomites to reef core occurs (see Pl. 143) - colonization of a soft sediment substratum by numerous Horridonia may have provided the basis for the establishment of fenestellids (as is observed in the faunal succession) and then a normal reef fauna. N.T.J. Hollingworth (pers. comm. 1984) has analysed elements of the reef bivalve fauna in terms of their probable mode of life - he considers Schizodus to be infaunal, Permophorus to be endobyssate and the other, much commoner forms to be epibyssate. This could be taken as evidence in favour of a marked dominance of hard substrata over soft sediment as substratum type within the reef.

Tucker and Hollingworth (1986, in press) describe marine cementation during the early diagenesis of the reef basal coquina-

aragonite and high Mg calcite were precipitated on the sea floor. In several cases in situ bryozoans act as loci for the precipitation of such cements which are sufficiently voluminous to have formed substantial areas of hard substrata. There is, however, no direct evidence of substrate encrustation by bryozoans at this locality.

There is such evidence at several other localities (HDN, HYR and in blocks from the downthrown lithology at MP5). Dyscritella columnaris can be seen encrusting substrata (see Pl. 131 fig. c) which were presumably lithified since bryozoans appear to be unable to encrust soft mud. There is a possibility (because of their observation only in thin section) that some of these features are merely rock clasts which have been encrusted rather than laterally extensive lithified substrata. However, specimens MP5.3/1-MP5.3/5 (from loose blocks in the downthrown lithology of MP5) are an undoubted example which can be compared to lithified crusts of the type described by Shinn (1969). Polished slabs of the lithology (see Pls. 53, 136, fig. 97) reveal two marked discontinuities which it is proposed define the upper and lower boundaries of a lithified crust. Faunal evidence supports this interpretation and suggests a comparison can be made with the hardground and crevice faunas described from the Jurassic by Palmer and Fürsich (1974). The upper surface of the crust, a hardground, acts as substratum for algae, Dyscritella and Kingopora ehrenbergi (see fig. 97). The basal lamina of K. ehrenbergi follows exactly the small-scale (mm) topographic irregularities of the hardground (it also overgrows a colony of Dyscritella). Fürsich (1979) cites the presence of such encrustations as one of the lines of evidence which can be used for the recognition of a hardground.

Another criterion is the development of overhangs in the hardground surface - these are only rarely and weakly developed in the above example. The relatively abundant fauna above the hardground includes Acanthocladia, Dyscritella, Fenestella retiformis, Dielasma, ? Bivalves indet. and algae. XRD analysis of these three lithologies was undertaken, stable isotope work, which may have confirmed the interpretation of this feature, was not completed. XRD showed above the crust (labelled A in fig. 97) to be completely dolomite, the crust itself is composed of dolomite with minor calcite (B, in fig. 97) and the crevice filling (C, in fig. 97) is completely dolomite. The minor calcite present in the crust may be considered evidence in favour of some original sedimentological difference between the crust and the lithologies above and below it - any interpretation of this must be very speculative. The lithified crust has a low abundance fauna of algae, brachiopods and gastropods. Its thickness varies from 3.5 cm to 0.5 cm, averaging 2 cm, and its lower surface is very irregular - the microtopography of the surface is variable on the centimetre scale with re-entrant angles in places. The essential feature of this surface, which supports the interpretation as the underside of a lithified crust, is the nature of the algal laminae - these are clearly growing downwards from the surface (see fig. 97) and are themselves encrusted by ? worm tubes. Thus a space must have existed beneath the lithified crust - its size cannot be inferred from the available material but comparisons can be drawn with the type of crevice described by Palmer and Fürsich (1974) (these reached 5 cm from roof to floor). Palmer and Fürsich (op. cit.) noted a polarisation of the fauna into a hardground community and a crevice

community - it is difficult to interpret the small amount of material of the present study in this way but there appears to be some differentiation of the faunal elements. Above the crust, Kingopora Acanthocladia, Fenestella and Dyscritella are abundant as well as Dielasma, bivalves indet. and algae (it is considered probable that Acanthocladia, Fenestella and Dielasma were attached to the hard ground though this has not been observed directly), only algae and ? worm tubes occur attached to the crevice roof. Monty (1982) described the growth of algae in dark cavities, where interspecific competition was reduced.

The requirements for the formation of lithified crusts of this type are: carbonate-saturated sea-water, a low rate of sedimentation and high sediment stability, Shinn (1969). In order to form a crevice it is necessary for fine sediment beneath the crust to be winnowed out by currents, Palmer and Fürsich (1974) suggest such current winnowing as a possible mode of formation of their Jurassic example.

There is little evidence relating to the possible surface configuration of the reef. D.B. Smith (pers. comm., 1985) believes that up to 3 m local relief may have occurred and that overhangs and cavities may have existed. The growth of bryozoans provides some evidence of very small scale topographic irregularities - fig. 98 and Pl. 137 show Synocladia virgulacea in which the origin can be seen and one part of the zoarium grows 'below' the level of the origin for 14 mm. This may then have been the scale of the relief in a lithified part of the substratum.

Substrata for bryozoan attachment and Bryozoa as substrata

Since zoarial origins are rarely preserved, substrate attachment of fenestrate bryozoans can rarely be observed. Hard substrata are described above, these would have provided suitable surfaces for many bryozoans but in their absence colonies were probably attached to elements of the shelly fauna or other bryozoans. Pl. 65 shows a zoarium of Synocladia virgulacea attached to a fragment of Acanthocladia. Kingopora ehrenbergi is often attached to shells of Horridonia or Strophalosia (see Pl. 36). Corynotrypa voigtiana may exhibit a degree of substratum preference, though the small size of the sample examined reduces the significance of this - 50% of the specimens examined from N.E. England are on the brachiopod Horridonia, the other 50% are on various bryozoan zoaria (the much greater proportion of bryozoans examined is an obvious source of bias in favour of their identification as substrata for C. voigtiana). All elements of the shelly fauna were examined for zoaria of C. voigtiana but none was found on anything apart from Horridonia. The much larger available area of substratum on Horridonia may have been a factor inducing substratum choice by larvae of C. voigtiana (Ryland (1976) refers to Eggleston's (1972) work describing choice of substratum by bryozoan larvae). Larvae presumably settled after the shells of Horridonia had been exhumed since the colonies are attached to the valve which was probably within the sediment during life. However, specimens described by Taylor (1985) from E. Germany are all found encrusting crinoid columnals and a specimen described by Kirkby (1857) is encrusting Dielasma. Dyscritella columnaris occurs encrusting a variety of substrata, e.g. Dielasma (see Pl. 121 fig. c), Synocladia

virgulacea (see Pl. 121 fig. e) and crinoid columnals (see Pl. 121 fig. a). It may occur on almost any available surface. It is associated commonly with Acanthocladia laxa which often provides a substratum for its attachment (see Pl. 130 fig. b). However, in several cases, A. laxa appears to have been overgrown in life position (this has been interpreted from thin sections and is thus a little circumspect) - Pl. 131 fig. a may be an example of this. It is not possible to tell if D. columnaris ever overgrew A. laxa while the colony was still alive - interspecific aggression and overgrowth relationships are well documented for modern encrusting Bryozoa, e.g. Stebbing (1973), Jackson and Winston (1982). A. laxa and D. columnaris occur together in particularly dense growths and thus were probably spatial and resource competitors above the substratum.

Bryozoa served as a substratum for the attachment of other organisms both during life and post-mortem. Pl. 131 fig. b shows Dyscritella columnaris with either algae or worm tubes as epibiont which have then been overgrown by the colony of D. columnaris. Algae and ? worm tubes occur quite often on zoaria of D. columnaris but in most cases settlement probably took place after death of the bryozoan. Pl. 138 figs. b, c shows algae (or ? worm tubes) encrusting the surface of Acanthocladia and growing from a zooecial chamber onto the obverse surface - these were thus almost certainly not attached during the life of the colony. Pl. 138 fig. a, shows the obverse surface of Fenestella retiformis overgrown by algal filaments, obviously post-mortem. Synocladia, Fenestella and Acanthocladia all serve as substrata for Corynotrypa voigtiana. Concentric laminar encrustations (presumably algal in origin) are common around nearly all the

bryozoans of the reef.

Feeding Behaviour of Some Fenestrates

A detailed analysis of the possible mode of feeding of those taxa with fenestrate morphologies may suggest additional functions of certain skeletal features and may reveal a correlation between intraspecifically varying zoarial morphologies and the occupancy of different ecological niches in the reef. The fenestrate genera Fenestella, Kingopora and Synocladia are considered below.

These genera are referred to the Class Stenolaemata and thus analogy with modern cyclostomes is an obvious way of inferring the nature of soft parts and the type of feeding-currents which might have prevailed. However, analogy with the feeding behaviour of some cheilostomes (particularly reteporids) is justified and there may even be some justification for the interpretation of soft parts with reference to cheilostomes (the ovicells of Synocladia virgulacea have been compared to cheilostome ovicells rather than cyclostome gonozooids (see p.53)). A third alternative is to interpret soft parts and feeding with a non-actualistic model; this procedure is difficult to justify and is not used here but must be considered a possibility.

Within both of the Orders Cyclostomata and Cheilostomata there are a number of different types of lophophore with different modes of behaviour in relation to the generation of feeding-currents; there are also types of lophophore which occur across ordinal boundaries, e.g. the campylonemidan lophophore occurs in the encrusting cyclostome Lichenopora and the reteporid cheilostome Reteporellina evelinae (Winston, 1978). Fundamental research into the methods of feeding of bryozoans has only really taken place recently, though Borg (1926)

described the generation of water currents by the beating of the lateral cilia on tentacles. Water is drawn in through the top of the tentacle crown, passes downwards and then out between the tentacles (see fig. 99). Bullivant (1968) suggested that particles of food in the water current were thus thrown against the mouth - described as "impingement" feeding by him, but Strathmann (1973) later described the transport of food particles to the mouth by localized reversal of the direction of beat of the lateral cilia. The basic conclusion is that Bryozoa are active rather than passive filter-feeders and it is probably reasonable to assume that the three genera considered below were also active filter-feeders. An important consideration is the fate of the already filtered water - if only a relatively small percentage of the food particles is captured by passage through a single tentacle crown then refiltration by a second zooid is a possibility, this may be a rare occurrence though (Strathmann, (1973) reported 100% retention of particles by individuals but also stated that the fraction retained depended on how actively an individual was feeding and could fall as low as 0% in some cases). Thus, it would usually be desirable for the entire colony to ensure the removal of filtered water to an area where it was not likely to be drawn into the colony again. A number of morphological features have been suggested to have served just this purpose. Cowen and Rider (1972) attempted a functional analysis of fenestellids in terms of the filtering of water (see fig. 99). They proposed that zooids extended into the immediately adjacent fenestrule and that the expanded tentacle crowns effectively filled this space - a zooid-generated current was drawn through the fenestrule from the obverse side to the reverse thus

ensuring the removal of the filtered water beyond the reverse surface. They described features of the fenestellid skeleton which support this proposed direction of water flow, notably the presence of nodes along a median carina on the obverse surface which would help to divide the incoming flow so that it passed through the fenestrule more easily. This may not be such an important effect as they envisage since nodes are often fairly small features of low elevation and quite large longitudinal separation - their effect on incoming current is likely to be quite small. The general shape of the reverse surface in comparison to the obverse is considered to be advantageous to flow as they have described it - this would be a factor in favour of flow from the obverse to the reverse side. Cook (1977) described extrazoidal currents in living reteporids (which may be reasonable analogues of Palaeozoic fenestellids) where flow was always from the obverse side to the reverse. Cowen and Rider's analysis implies fairly strict constraints on tentacle size and behaviour - if the tentacle crown is expanding laterally into the fenestrule with no significant vertical component of expansion (as they appear to have figured on p. 154 (see. fig. 99)) then the size, or at least the degree of expansion of the tentacles would be equal to half the width of the fenestrule (assuming that the fenestrule is filled by tentacle crowns). In Permian specimens of Fenestella retiformis the nature of the peristome argues against a strictly lateral protrusion of the tentacle crown (see below).

Banta, McKinney and Zimmer (1974) described the monticules of Palaeozoic trepostomes as excurrent water outlets and compared them with exhalent chimneys formed by bending of tentacle sheaths in

Membranipora. Cook and Chimonides (1980) also described excurrent chimneys in Membranipora membranacea where they have no reflection in skeletal morphology, being formed by the tentacle sheaths 'leaning away' from the zone of water outlet. It is important to realise that colony-wide water current patterns may have no obvious reflection in skeletal morphology. However, in the analysis presented below, it is probably reasonable to rely on the hard parts for interpretive purposes - the fenestrate zoarial morphology is obviously and fundamentally different from that of an encrusting cheilostome and it is very unlikely that the protruded tentacle sheath in Fenestella and Kingopora was as long or as flexible as that in Membranipora membranacea (Borg (1926) described modern cyclostome lophophores as protruding only a short way from the aperture; Cook (1977) states that the tentacle sheath is not visible in feeding cyclostomes and that the proximal part of the tentacle crown may remain within the peristome; however, McKinney and Boardman (1985) point out that these observations were made on fixed-wall stenolaemates and that free-walled stenolaemates are able to completely evert their tentacle sheath, though without being able to bend significantly - an analogy with free-walled stenolaemates is probably appropriate for Fenestella, Kingopora and Synocladia. Cook (1977) described colony-wide water currents in thirteen species of cheilostome, cyclostome and ctenostome bryozoans. All her observations were made in a laboratory environment with still water - these conditions are probably appropriate to the forms she studied since they mostly inhabited quiet-water cryptic environments, however, in the analysis below it may be more important to try and take into account the effects of ambient water currents

impinging on zoaria. McKinney (1977) attempted an analysis of the way zooid-generated currents and prevailing currents might have interacted in the feeding process. His functional interpretation of lyre-shaped Bryozoa combined a uni-directional ambient flow with zooid-generated currents passing water through fenestrules to the open margin of the colony where the resulting pressure differential ensured the flow of filtered water away from the zoarium.

Winston (1978) related different types of lophophore and different zoarial morphologies to specific modes of feeding - current generation. Her category of Reteporellina-type meshwork in which polypides are separated but their orientation is controlled by colony structure may have some relevance to the discussion below, this category applies to cheilostomes with the obliquely truncate campylonemidan type of lophophore, which may have been developed to some degree in Palaeozoic fenestrates (see below).

In contrast to these studies of zooid-generated feeding currents, Stratton and Horowitz (1975) interpreted flabellate fans of Polypora in terms of an adaptive response to prevailing currents; the reverse surface of the zoarium was orientated facing into the current - the resulting flow through the fenestrules produced a low energy zone downcurrent in which they postulated the zooids could feed more easily. However, as pointed out by McKinney (1977), the zooids would then be pumping water through the fenestrules against the ambient current - a situation which would be energetically unsatisfactory.

Taylor (1979) stated that Bryozoa with the distal parts of autozooezia opening obliquely into fenestrules would probably have generated a unidirectional feeding - current through the fenestrule.

In the discussion of Fenestella retiformis below, this is assumed to be the case.

Fenestella retiformis

An assumption is that the colony-wide epithelial tissue in F. retiformis adhered closely in shape to the preserved hard parts and had no significant thickness such that it altered greatly the fenestrule and branch dimensions. Cowen and Rider (1972) suggested that the epithelial tissue around fenestrule margins might have been ciliated to enhance the flow of water through the fenestrule - this will not be accepted below.

The zoarial morphology of F. retiformis is fairly flexible - the early zooecia are usually added in a tight spiral to form a funnel-shaped zoarium early in the ontogeny of the colony; this basically infundibuliform zoarium may be variously modified as growth continues. The zoarium may become a fairly steep, erect, inverted cone which may be plicate or the zoarium may expand as an essentially horizontal lamina - again this may be variably plicate.

The feeding currents in F. retiformis can be considered in relation to zoarial morphology and also to smaller scale features such as carinal nodes.

Zoarial Morphology

It is assumed that F. retiformis fed by cilia-generated water currents rather than by passive filter-feeding in an ambient current - although passive feeding has not been observed in bryozoans and is unlikely to have occurred in Palaeozoic forms, it is not an impossibility. Winston (1979) comments on the observation of Crisp

and Southward (1961) that some barnacles may feed passively at high current speeds but actively generate currents at lower speeds. Winston also comments on the ability of some articulate brachiopods to augment ciliary currents with ambient flow by specific orientation of their shells.

The analogy between modern reteporids and the Palaeozoic fenestrates commented on here is an obvious one but it is important to be aware of the often striking difference in zoarial size between these forms - a straightforward analogy may thus be an oversimplification.

The apertures of F. retiformis are always on the inside of the infundibuliform zoarium. Thus, when the zoarium is an essentially horizontal lamina the apertures are on the upper surface (if the zoarium is growing up from a substrate) (see fig. 100). This is a fairly common zoarial morphology in F. retiformis and may have been an adaptation to growth in an environment of moderately high current velocities. If the colony had a steeply erect form then the passage of filtered water from the obverse side to the reverse, through the fenestrules, would have been disturbed by relatively high velocity currents impinging on the reverse surface. If, however, the zoarium formed an approximately horizontal lamina then the ambient currents would have been flowing over the obverse surface and a situation in which the zooid-generated currents were augmented by the prevailing flow could be imagined in a way superficially analogous to the situation described for lyre-shaped Bryozoa by McKinney (1977). The occurrence, on the obverse surface, of large regularly spaced nodes with lateral projections may argue against such an interpretation -

they may have served to create a relatively still water boundary layer from which zooid-generated currents were produced. A consequence of the zoarial morphology seen in fig. 100A may be that filtered water in the proximal part of the colony would be flowing in directions which cause the setting-up of eddies and thus the inefficient removal of filtered water - this would occur only if the most proximal zooids in the erect funnel-shaped part of the zoarium were feeding. It is probable that these most proximal zooids were not feeding actively. Bancroft (1984) described non-feeding secondary nanozooids in fenestellids and suggested that their abundance was greatest in the proximal parts of colonies. Cook (1977), in her observations of feeding currents in Bugula turrita noted that generally only the astogenetically younger six generations of zooids at the ends of branches were active feeders.

Zoarial plication, forming festoons, is a common feature of F. retiformis, though it is not always developed. Cowen and Rider (1972) mention this feature and state that it is unlikely to interfere with feeding currents; they suggest it provided more filtering zooids per unit volume and may also have strengthened the zoarium. Maximisation of the number of actively feeding zooids in a unit colony length is presumably advantageous - the development of festoons may be related to increased availability of food particles in the water surrounding a zoarium. If the density of food particles is not very high it would be advantageous for the colony to expand into a different microenvironment by maximum growth at the distal ends of branches. The formation of festoons, with consequent increase in the number of zooids per unit volume susceptible to zooid-generated currents, may

result in interzooidal, intrazoarial competition for a limited food supply - a situation usually avoided by organisms with a high degree of colonial integration such as bryozoans. Another factor which may explain the occurrence or non-occurrence of festoons is the unpredictability of ambient currents. Leversee (1972) relates plication of the zoarium of the gorgonian Leptogorgia to variability of ambient currents - while gorgonians are probably not good analogues for fenestrate Bryozoa, in terms of their mode of feeding, plication of the zoarium in Bryozoa could also be an advantage for feeding in variable currents. With zooids in various orientations any interruption to zooid - generated currents by unidirectional ambient currents would only be a local effect.

A conclusion which may be drawn is that there is some correlation between the degree of erectness of the zoarium in F. retiformis and the energy of the ambient currents impinging on that zoarium. Evidence to support this idea comes from the common occurrence of erect colonies in the quiet back-reef environment (localities GLT, GLQ). There are, of course, other factors which may effect the degree of erectness of a zoarium e.g. space constraints in a cryptic habitat.

Smaller scale features e.g. carinal nodes, may also have some bearing on the feeding behaviour of F. retiformis.

Carinal Nodes

A particularly striking zoarial feature in F. retiformis is a very large node with lateral projections. Likharev (1926) described such a node in the taxon and similar features have been described in some other species of Fenestella e.g. in F. bifida, Shulga-Nesterenko (1941, 1949), F. tenuiseptata, Shulga-Nesterenko (1941), Fenestrellina

(Fenestella) columnaris, Crockford (1944b). Chronic's (1949) genus Cervella has large nodes with processes (this genus was later referred to Fenestella by Elias and Condra (1957) because of the patchy distribution of the characteristic node throughout a zoarium and because they considered similar nodes to be developed in more than one phyletic lineage in the Permian). The low chances of preservation of such a delicate feature probably contribute to its poor record but it may also be of variable occurrence within a species. During the present study it has been observed in carefully prepared and orientated thin sections and in latex pulls.

In thin section GLF1 (see Pl. 9, fig. a) the node extends 0.475 mm above the obverse surface - the lateral projections occur at 0.19 mm above the obverse surface and extend for approximately 0.05-0.07 mm. In specimen HYRF5 (latex pull) it is difficult to measure the height of the node but the lateral projections are almost certainly at a comparable position to those in GLF1. Likharev (1926) described nodes up to 1 mm in length and nodes with lateral projections which may fuse with those from neighbouring branches to form a 'protective superstructure'. This protective superstructure is very similar to that developed in Hemitrypa hibernica.

The function of carinal nodes has been considered by many authors to be related to defence e.g. Cumings (1904), Tavener-Smith (1969a). This is likely to be their primary function in F. retiformis but it is also possible that they served to create turbulent lower energy flow from higher energy unidirectional ambient currents. 'High energy' here is considered relative to still-water and would probably not have been much greater than a Reynolds number of 10, certainly not as great

as $R = 100$, for reasons suggested below. The creation of a boundary layer of relatively still water is a necessity in the feeding process of bryozoans, enabling zooid-generated currents to be unperturbed by ambient flow, Winston (1978). The shape of the node in F. retiformis is particularly suited to the creation of a boundary layer above the obverse surface if the ambient flow is essentially parallel to the zoarial lamina. The node is cylindrical at its upper part and/or has lateral projections which are effectively flat discs, it is elongate parallel to branch length at its base (see fig. 19). At Reynolds numbers of approximately $R = 10$ standing eddies are produced on the lee-side of a cylindrical body (see fig. 101)- the same applies to a flat disc. Such standing eddies would have greatly facilitated the production of zooid-generated flow through fenestrules. When the Reynolds number becomes as great as $R = 100$ then the eddies become unsteady and the vortices separate from the rear of the body (Michell, 1970). It would be easier for a zooid to capture more food particles from an eddying current than from a high energy laminar current - the production and maintenance of these eddies needs energy, which is taken from the main stream and thus helps reduce the energy level of the main stream. The streamlined shape of the base of the node may have served to maintain laminar flow closer to the obverse surface. This may have been advantageous in preventing turbulence at a level where it could interfere with zooid-generated flow. However, such an effect would not have occurred in most cases - the angle of divergence of branches is such that ambient currents would be incident at the node at an acute angle which would result in the creation of a wake on the lee-side of the node. It is almost certainly wrong to consider

there to exist a dichotomy of flow regimes on the scale of a single node - it is much more likely that a turbulent boundary layer existed over a whole zoarial lamina, its thickness being roughly equal to the height of the nodes.

The size of the nodes can be considered to impose some constraints on the size (or at least the degree of eversion) of the tentacles in F. retiformis. It is assumed that the tentacles effectively filled the fenestrule - but with no degree of overlap. The tentacles of modern cheilostomes and cyclostomes do not overlap when protruded and feeding, if tentacles touch, retraction takes place. If the lateral projection on the node in F. retiformis served to create eddies in laminar ambient flow, where the zooid was then able to generate its own feeding current, then the tentacles would not have been protruded above the level of this projection (see fig. 102). It is not very likely that the tentacles extended laterally into a fenestrule, perpendicular to the branch, as Cowen and Rider (1972) appear to have figured (see fig. 99). The nature of the peristome and the arrangement of the apertures on the side of the median carina argue against this. The peristome forms a raised rim around the zooecial aperture, it has a greater elevation on the edge of the aperture closer to the fenestrule; this would tend to direct the tentacle sheath vertically rather than laterally. The generally poor preservation of the material studied is such that peristomes cannot often be observed - it may be that their development was variable and in consequence the degree of vertical versus lateral protrusion of tentacles was variable. The apertures are situated on the sides of the median carina and thus tend to be directed towards the fenestrule

but with a modification caused by the development of the peristome. As mentioned above, the flexibility of tentacles may be such that their orientation cannot be deduced with absolute certainty from skeletal features but in the above case the hindrance to lateral protrusion of the tentacles caused by the raised rim of the peristome suggests that there was a significant vertical component involved in tentacle eversion. In fig. 102 an attempt is made at suggesting a possible maximum size of tentacles in F. retiformis using the above constraints. Fenestrule width is taken as 0.5 mm, Branch width is 0.2 mm - these are average values for F. retiformis. If the lateral projections on the node are approximately 0.2 mm above the obverse surface then the maximum size geometrically possible, such that no overlap occurs in the fenestrule, is approximately 0.15 - 0.2 mm. Measurements of the length of the vestibule and the length of the zooecial chamber were made. According to McKinney and Boardman (1985) there is a constant relationship between tentacle sheath size, vestibule length and polypide length in free-walled stenolaemates; the vestibule length and tentacle sheath length are approximately equal with a tendency for the length of the tentacle sheath to be slightly greater. Palaeozoic fenestrates are considered by McKinney and Boardman (op. cit.) to be free-walled stenolaemates and so the above conclusions can be applied to F. retiformis. The maximum length of the vestibule in F. retiformis is 0.136 mm, the accuracy of measurement is a little doubtful because of the plane of section involved and the true value is likely to be a little greater. The length of zooecial chamber and therefore probable maximum length of the polypide is 0.255 mm. McKinney and Boardman (op. cit.) state that

there is a fairly constant ratio between tentacle length and polypide length - the tentacles making up about 55% of the entire length of the polypide - in this case then the length of the tentacles arrived at is 0.14 mm (55% of 0.255 mm) - this compares well with that derived by measurement of the vestibule alone. Both these measurements fit in well with the suggested maximum size of tentacles arrived at earlier by geometrical considerations.

In most of the species examined by Cook (1977) the length of normal tentacles is greater than about 0.15 mm, ranging from 0.24-0.7 mm in the cheilostomes but as low as 0.21 mm for some of the tentacles of the cyclostome Lichenopora. Winston (1978) looked at many more species and found mean tentacle lengths varying from 0.164 mm (in the cheilostome Synnoteum aegypticum) to 0.866 mm (in the cheilostome Trematooecia turrita).

In the simplest case the lophophore of F. retiformis would be equi-tentacled. However, the obliquely truncate type of lophophore which occurs in both cyclostomes and cheilostomes is a common feature of species in which the skeleton positions polypides so as to produce the maximum unidirectional flow, Winston (1978). The fenestrate skeleton can be considered to be of this type, thus it would not be unreasonable to suggest that the lophophores in F. retiformis were obliquely truncate to some degree.

A similar calculation to that given above was performed by McKinney (1980b) for the Devonian fenestrate Utropora Pořta.

Kingopora ehrenbergi

The same basic assumptions which were made in the discussion of F. retiformis apply also to K. ehrenbergi. This is a fenestrate species, similar to F. retiformis in some respects. It usually has two rows of apertures on branches, the branches are joined at regular intervals by dissepiments, though the regularity in Kingopora is not as great as in F. retiformis, and there are apertures on the dissepiments. There are differences though, which may be considered to have some influence on the relative distributions of the two species in the reef.

As described on p.339, K. ehrenbergi is particularly abundant in the low energy back-reef environment. It is a rare species in the main reef but where it occurs it is often in close proximity to steeply erect colonies of F. retiformis. The conclusion is that K. ehrenbergi is essentially restricted to environments in which the ambient currents have a low velocity. The likely pattern of feeding currents in the species can be seen as one possible explanation for its observed distribution.

K. ehrenbergi always has steeply erect zoaria - it appears not to expand horizontally, parallel to the substrate, as is often the case in F. retiformis. The apertures always open onto the outside of this steep inverted cone. Thus, if high energy currents were impinging on the surface of the zoarium they could perturb the zooid-generated currents passing water from the obverse side to the reverse side. Nodes appear to be features of relatively low elevation on the obverse surface and so would probably have had little baffling effect on high velocity ambient currents.

The basically infundibuliform zoarium is often modified by plications - this may have the effect of increasing the number of feeding zooids per unit volume of space occupied by the zoarium. This, in turn, could affect the exhalent current velocity. The zoarium also has the shape of a bilaterally compressed cone in many cases (see Pl. 35 fig. c). This could have significance in two particular respects. Firstly, the shape could be a response to bi-directional ambient currents which were, in fact, augmenting zooid-generated flow through the fenestrules; such currents would probably be of fairly low velocity. Secondly, and more probably, the shape could be an adaptation to increase the velocity of exhalent water such that it was ejected as far from the zoarium as possible, thus ensuring no refiltration. Bidder (1923) described constrictions at the open ends of sponges and showed that a constriction causes water passing through the open end to have an increased velocity. Considering two zoarial morphologies - one a perfect inverted cone, the other a bilaterally compressed cone, it is possible to calculate the relative areas of the open ends of the colonies. For a zoarium circumference of 30 cm the area of the open end of a perfectly infundibuliform zoarium is 71.36 cm^2 whereas that of a bilaminar zoarium (with a radius of curvature of $r = 0.955 \text{ cm}$ at either end of a straight lamina 12 cm in length) is 28.65 cm^2 (see fig. 103). Thus the open end of the bilaminar zoarium is considerably more constricted than that of a perfectly infundibuliform zoarium. In accordance with Bernoulli's theorem, if the same pressure head exists in each zoarium, as it does only if the same number of zooids are actively feeding in each zoarium, then the velocity of flow through the smaller area is

greater.

Only the size of fenestrules and measurements of likely polypide length can be used to estimate probable tentacle sheath lengths in K. ehrenbergi. The average space between apertures across a fenestrule varies from 0.36 - 0.55 mm and averages about 0.43 mm. Zooecial chamber length averages about 0.65 mm - therefore the maximum length of tentacle sheath in K. ehrenbergi could be assumed to be $0.65 \times 55\% = 0.358$ mm. It is unlikely that the tentacle sheath was fully protruded laterally into a fenestrule because there would have been overlap with the tentacles of the zooids of the neighbouring branch. Assuming the tentacles were always protruded 0.358 mm from the aperture and that the fenestrule was 0.43 mm wide, a simple geometrical calculation gives the height of the tentacles above the fenestrule as 0.286 mm.

Synocladia virgulacea

S. virgulacea is similar to F. retiformis in having a zoarium with varying degrees of erect growth; its apertures are on the inside of a basically infundibuliform zoarium. There are, however, three or four rows of apertures on branches and usually two to three rows on dissepiments. The regularity of the zoarium, which is so characteristic of F. retiformis, is not a feature of S. virgulacea; dissepiments may often be developed at various angles to the main branches. The spacing of zooecia on dissepiments may be variable where two halves of the dissepiment fuse at the mid-point of the fenestrule - thus, if all zooids were feeding it might imply that the orientation of their tentacles was not as strictly controlled in a regular pattern as in F. retiformis. An analogy with reteporids is

probably appropriate, with tentacles extended into the fenestrule and drawing a unidirectional current through it. If zooids were inflexible in their degree and direction of protrusion then the irregularity of the shape and size of fenestrule in S. virgulacea might suggest that it was not always completely filled by extended tentacle crowns. If zooids had some degree of orientation flexibility the complete filling of the fenestrule with tentacle crowns is likely. It is possible that zooids in the central row of a branch were extended vertically rather than in towards a fenestrule. The outer rows of apertures are on the sloping sides of branches and thus the zooidal tentacle crowns would have been naturally directed into the fenestrule. If all rows of zooids were actively feeding, the outer rows extending into the fenestrules, then there might have been a danger of the water filtered by the central row being refiltered by the outer row. A degree of vertical as well as lateral protrusion in zooids of the outer row could have served to diminish this possibility. Nodes in S. virgulacea have been observed only as low blunt projections - a function of current baffling, as suggested in F. retiformis, is thus unlikely.

There is a correlation between the development of dissepiments and fenestrule width in S. virgulacea (see p.153). If the fenestrule width becomes very large (e.g. 2.0 mm) then the dissepiments are well-developed at regular intervals. Thus the inability of the zooids on main branches to fill the fenestrule with their tentacle crowns is compensated by the zooids on dissepiments expanding their tentacle crowns into the space. Measurements of fenestrule size for several colonies of S. virgulacea show that the maximum extension of tentacles

needed to fill a fenestrule varies from about 0.25 - 0.35 mm and has a fairly constant average value of 0.3 mm. This is in spite of the general appearance of irregularity of the fenestrules. The inter-apertural distance of S. virgulacea averages approximately 0.3 mm - the dimension of the tentacle crown parallel to branch length is unlikely to have been greater than this. Assuming S. virgulacea to be a free-walled stenolaemate and using McKinney and Boardman's (1985) calculations of tentacle size in relation to polypide size gives a maximum value of approximately 0.38-0.44 mm for tentacle length (i.e. 55% of 0.7-0.8 mm). According to these calculations then the tentacle sheath is likely to have been between about 0.3-0.4 mm long - any value above 0.3 mm would require some vertical component of expansion of the zooids on a branch margin, which were directed into a fenestrule. The lophophore of S. virgulacea may have been obliquely truncate to some degree but there is no good evidence to suggest this type of lophophore occurred in preference to an equi-tentacled type.

There appears to be some correlation between zoarial morphology and environment of growth of S. virgulacea. In steeply erect zoaria, zooid-generated flow through fenestrules might have been perturbed by high energy ambient currents impinging on the reverse surface. If the ambient flow was unidirectional then this problem would only affect half the zooids of the colony, those of the other half would have been able to feed normally. In essentially horizontal colonies, high energy flow over the obverse surface may have perturbed zooid-generated currents, the lack of large nodes suggests that a turbulent boundary layer may not have been created. However, the extended tentacles themselves may have had the effect of creating such

a boundary layer (Okamura, pers. comm. (1985), who observed feeding of cheilostomes and ctenostomes in a flume tank, found that, at high current velocities, zooids upstream were unable to feed normally whereas those downstream could feed relatively successfully). Weak unidirectional currents probably had no detrimental effect on the feeding process. S. virgulacea from two localities is found with identical zoarial morphologies and in both cases appears to be growing from a near vertical rock wall. The adoption of this morphology may be a response to growth in this particular environment. This morphology is very similar to that observed in reteporid cheilostomes from the Enewetak Atoll by Cuffey and McKinney (1982). They suggest that the formation of a roughly horizontal zoarial lamina as opposed to an erect cone-shaped zoarium served to maximise the volume of nutrient-bearing water available to the feeding zooids. These reteporids were growing in a cryptic environment where, because of the weakness of ambient currents, the supply of nutrients is likely to have been limited. A relatively low concentration of nutrients in the water may have been the reason for the adoption of a roughly horizontal zoarial lamina in S. virgulacea.

In several cases the zoarium of S. virgulacea has an open spiral morphology (see p.166) with the consequence that one zoarial lamina occurs above another. The filtration of water through fenestrules may have resulted in the lower (more proximal) zoarial lamina being exposed to already filtered water - zooids in such a lamina may not have been able to feed efficiently. Nanate zooecia occur very frequently in such zoaria and may have been most abundant in lower zoarial laminae thus reducing feeding inefficiency.

'Sub-colonies' may be developed within the main body of the funnel-shaped zoarium of S. virgulacea (see p.166). It is unlikely that the feeding behaviour of zooids in such 'sub-colonies' was different from those of the rest of the colony.

Predators of the Bryozoa

The most important modern predators of Bryozoa are the pycnogonids and nudibranchs (Ryland, 1976). They feed on both erect and encrusting Bryozoa of various orders (Ctenostomata, Cyclostomata and Cheilostomata). However, they are not known to occur in the Permian. Other modern predators are echinoids, e.g. Echinus esculentus, L., Psammechinus miliaris Gmelin, Euechinus chloroticus Val. and Diadema setosum Leske, Omnivorous chitons, e.g. Cryptoconchus porosus Burrow and Notoplax violaceus Quoy and Gaimard, the flatworm Thysanozoan californicum Hyman and fish, e.g. grazing fish such as labrids.

Chitons are rare in the reef - six species are described by Kirkby (1859) who found that they were generally restricted to the locality at Tunstall Hills. In the present study a single poorly preserved specimen ? has been found from the Humbledon Hill locality also. Present day omnivorous chitons appear to consume only encrusting Bryozoa, Ryland (1976) - if the Permian chitons can be considered as analogues of the modern forms, then they would not have been serious predators on the largely erect forms of the reef. The most juvenile proximal parts of colonies, the rarely encrusting Dyscritella columnaris and the cyclostome Corynotrypa voigtiana may have been susceptible to predation.

Modern echinoids graze on encrusting Bryozoa but also feed on erect forms such as Crisia, Ryland (1976). Miocidaris keyserlingi Geinitz is found rarely in the reef but fragments of echinoderm which could be either echinoid or crinoid are often seen in thin section.

It is doubtful whether an echinoid would have been able to feed on the distal parts of the largest erect bryozoans such as Synocladia which may reach a height above the substrate of 15-20 cm, but could have been an effective predator in the more proximal parts of colonies or on juvenile specimens.

There is more direct evidence of the predation on the reef bryozoans by fish. Malzahn (1968) described fragments of Acanthocladia anceps (probably A. laxa, in fact) in the stomach of Janassa bituminosa (Schloth.) from the K pferschiefer of Germany. Schaumberg (1979) found Acanthocladia anceps (again, probably A. laxa) reaching 23 mm in length in the stomach of Janassa bituminosa. The bryozoan is unlikely to have been transported into the Kupferschiefer as its delicate form is well preserved. Schaumberg (op. cit.) is convinced that the bryozoan is actually in the stomach of the fish rather than merely fossilized with it - several secondary branches are found close to the largest fragment of Acanthocladia and appear to have been bitten by the fish. Janassa bituminosa was a benthonic fish which fed on brachiopods, Schaumberg (op. cit.) and probably other elements of the benthos - teeth attributed to Janassa bituminosa by J. Bell have been found in the reef by N.T.J. Hollingworth (pers. comm.) - Pl. 139 shows a tooth of Janassa and a tooth of Acrolepis (collected by the author) - Acropelis was an active predator (J. Bell, pers. comm. (1984)) but may not have fed on bryozoa. Pl. 139 Figs. a, b shows a specimen of Fenestella retiformis from the Phillips collection - the colony appears to have repaired damage to the zoarium by growing back across a hole in the meshwork (although it was not possible to confirm this by thin sectioning it was clear from the

external relationships that this was an example of colony repair to damage rather than an aberrant growth pattern). The hole was about 6.4 mm by 6.4 mm and may ? have been caused by fish predation.

CHAPTER 8

SUMMARY AND CONCLUSIONS

The taxonomy of Bryozoa from the Upper Permian Zechstein reef has been revised during a systematic study of type material and material from extensive field collection. Standard biometric procedures have been employed involving the qualitative and quantitative description of zoarial and zooecial characters. Calculations of coefficients of variation provide some indication of the relative taxonomic value of these characters which are also weighted in species-level subdivision to minimize the influence of ecophenotypic variation on classifications. The large sample size has allowed the limits of intraspecific morphological variability to be established.

Phyllopora solida Korn (1930) and Protoretetepora solida atuberculata Dreyer (1961) have been synonymised with Kingopora ehrenbergi Geinitz (1846). Fenestella minuta Korn (1930) has been synonymised with F. retiformis Schlotheim (1816/17); Synocladia weigelti Korn (1930) and S. dux Korn (1930) have been synonymised with the morphologically variable S. virgulacea Sedgwick (1829). Thin sections of Dyscritella columnaris Schlotheim (1813) have demonstrated both erect and adnate growth within a single zoarium and have shown substantial branch thickenings caused by the development of layers of secondary overgrowth - thus Geinitz's (1861) varieties Stenopora columnaris var. incrustans, S. columnaris var. ramosa and S. columnaris var. tuberosa are considered synonyms of D. columnaris.

Three new taxa have been described:- Ryhopora delicata gen. nov., sp. nov., Acanthocladia magna sp. nov. and Penniretetepora waltheri

nodata subsp. nov. The genera Penniretepora and Kalvariella have been described for the first time from the Permian reef in N.E. England.

The generic assignments of species have been reviewed; Thamniscus diffusus Korn (1930) has been referred to the genus Acanthocladia. The genera Thamniscus and Acanthocladia have been maintained in spite of problems arising from homeomorphy of zoarial morphology and in spite of difficulties over the type species of the genus Thamniscus (i.e. the few specimens seen from Schlotheim's extensive material of "Keratophytes dubius" are all truly referable to Synocladia virgulacea). Poor definition of Upper Palaeozoic trepostome genera, partly due to inconsistent skeletal nomenclature (e.g. the lack of clarity over the distinction between mesozooecia and exilazooecia) has resulted in uncertainties over the true generic assignment of Dyscritella columnaris.

Aspects of bryozoan palaeobiology have been inferred:- nanate zooecia are considered to have housed secondary nanozooids of the type described by Silén and Harmelin (1974); they occur in Fenestella, Kingopora, Synocladia, Acanthocladia, and ?Kalvariella. A new type of ovicell has been described in Synocladia, Acanthocladia, Thamniscus, ?Penniretepora and ?Kalvariella - it has been compared, across class boundaries, to the cheilostome type of ovicell rather than to the cyclostome gonozooid; any taxonomic significance of this character is considered to be above generic level. Vesicular extrazoooidal skeleton has been described in Kingopora ehrenbergi, it is morphologically distinct from the vesicular skeleton of cystoporates or that which occurs in the fenestrate Semicoscinium rhombicum but may be functionally comparable.

Intraspecifically varying zoarial morphologies of fenestrates may be correlatable with hydrodynamic regime and the restricted distribution of K. ehrenbergi may have been a result of its inability to compete in relatively high energy environments. Patterns of zooid-generated currents are suggested for taxa with a fenestrate morphology and approximate tentacle sizes are calculated.

The bryozoan species most characteristic of different reef sub-environments have been described and an impoverishment of taxa is noted at reef-flat localities. Allogenic community succession shows a general upward decrease in species diversities which confirms the observations of Trechmann (1913) and may be related to increasing salinity and decreasing water depth.

Evidence for the contemporaneous lithification of substrata is documented from some localities.

The present study has identified areas where further research is necessary or would be productive:-

1. Refinement of Morozova's (1974) attempts at subdivision of the genus "Fenestella".
2. A comparison of the genera Kingopora, Reteporidra and Protoretepora including an assessment of the species referred to them.
3. An examination of species which have been referred to the genera Thamniscus and Acanthocladia in order to identify incorrect assignments and elucidate phylogenetic relationships.
4. A study of Waagen and Wentzel's (1886) type specimens for the genus 'Geinitzella'.
5. A systematic study of morphological variability which may be

ecophenotypic, in areas where environmental parameters are well known.

6. A detailed assessment of the roles of bryozoans in Palaeozoic reefs and reefal mounds.

REFERENCES

- AGER, D.V. 1963. Principles of Paleoecology. 371 pp. McGraw-Hill, New York.
- ANSTEY, R.L. and DELMET, D.A. 1972. Genetic Meaning of Zooecial Chamber Shapes in Fossil Bryozoans: Fourier Analysis. Science vol. 177, p. 1000-1002.
- ANSTEY, R.L. and DELMET, D.A. 1973. Fourier analysis of zooecial shapes in fossil tubular bryozoans. Geol. Soc. Am. Bull., v. 84, p. 1753-1764.
- APLIN, G. 1981. Diagenesis of the Zechstein main reef complex, N.E. England. British Geological Survey, isotope geology unit. Stable isotope report no. 66, 16 pp.
- ARMSTRONG, J. 1970. Zoarial microstructures of two Permian species of the bryozoan genus Stenopora. Palaeontology, v. 13, p. 581-587.
- ASTROVA, G.G. 1978. The history of the development, system and phylogeny of the Bryozoa Order Trepostomata. Akademy Nauk CCCP, Trudy Paleontologicheskii Institut, vol. 169, 307 pp. [English Translation].
- ASTROVA, G.G. and MOROZOVA, I.P. 1956. K sistematike mshanok otryada Cryptostomata. Dokl. Akad. Nauk. SSSR, n. ser., v. 110, p. 661-664. [Systematics of Bryozoa of the Order Cryptostomata]. [In Russian]
- BANCROFT, A.J. 1984. Studies in Carboniferous Bryozoa. Unpubl. Ph.D. Thesis, University of Durham.
- BANCROFT, A.J. 1986. Ovicells in the Palaeozoic bryozoan order Fenestrata. Palaeontology (In press).

- BANCROFT, A.J. 1986. Secondary nanozooecia in some Upper Palaeozoic fenestrate Bryozoa. Palaeontology (In press).
- BANTA, W.C., MCKINNEY, F.K. and ZIMMER, R.L. 1974. Bryozoan monticules, excurrent water outlets. Science vol. 185 p. 783-784.
- BASSLER, R.S. 1911. Corynotrypa, a new genus of Tubuliporoid Bryozoa. Proc. U.S. Natn. Mus., Washington, 39, p. 497-527.
- BASSLER, R.S. 1929. The Permian Bryozoa of Timor. Paläontologie von Timor, Lief 16, no. 28, p. 37-89.
- BASSLER, R.S. 1953. Bryozoa, in R.C. Moore (Ed.), Treatise on Invertebrate Paleontology, Part G, 253 pp., Geological Society of America and University of Kansas Press, New York and Lawrence.
- BIDDER, G.P. 1923. The relation of the form of a sponge to its currents. Q. Jl. microsc. Sci., v. 67, p. 293-323.
- BIGEY, F. 1981. Overgrowths in Palaeozoic Bryozoa: examples from Devonian forms. pp. 7-17. In LARWOOD, G.P. and NIELSEN, C. (Eds) Recent and Fossil Bryozoa. 334 pp. Olsen and Olsen, Fredensborg.
- BLAKE, D.B. 1973. Acanthopore ultrastructure in the Palaeozoic bryozoan family Rhabdomesidae. pp. 221-229. In LARWOOD, G.P. (Ed.) Living and fossil Bryozoa. 634 pp. Academic Press, London.
- BLAKE, D.B. 1975. The Order Cryptostomata Resurrected. pp. 211-223. In S. Pouyet (ed.) "Bryozoa 1974" Docum. Lab. Géol. Fac. Sci. Lyon hors-série 3 (fasc. 1).
- BOARDMAN, R.S. 1960. Trepostomatous Bryozoa of the Hamilton Group of New York State. Geol. Surv. Prof. Paper, 340, p. 1-87.

- BOARDMAN, R.S. 1971. Mode of growth and functional morphology of autozooids in some Recent and Paleozoic tubular Bryozoa. Smithson. Contrib. Paleobiol., no. 8, 51 pp.
- BOARDMAN, R.S. 1973. Body walls and attachment organs in some Recent cyclostomes and Paleozoic trepostomes. pp. 231-246. In LARWOOD, G.P. (Ed.), Living and Fossil Bryozoa, 634 pp. Academic Press, London.
- BOARDMAN, R.S. and CHEETHAM, A.H. 1969. Skeletal growth, intracolony variation, and evolution in Bryozoa: a review. J. Paleont., v. 43, p. 205-233.
- BOARDMAN, R.S. and CHEETHAM, A.H. 1973. Degrees of colony dominance in stenolaemate and gymnolaemate Bryozoa, pp. 121-220. In Boardman, R.S., Cheetham, A.H. and Oliver, W.A. (eds.), Animal colonies, 603pp. Dowden, Hutchinson and Ross (Stroudsburg).
- BOARDMAN, R.S. and MCKINNEY, F.K. 1976. Skeletal architecture and preserved organs of four-sided zooids in convergent genera of Palaeozoic Trepostomata (Bryozoa). J. Paleont., v. 50, p. 25-78.
- BORG, F. 1926. Studies on Recent cyclostomatous Bryozoa. Zool. Bidr. Uppsala, v. 10, p. 182-507.
- BORG, F. 1933. A revision of the Recent Heteroporidae (Bryozoa). Zool. Bidr. Uppsala, v. 14, p. 253-394.
- BOUCOT, A.J. 1953. Life and death assemblages among fossils. Am. J. Sci., v. 251, p. 25-40.
- BRETNALL, R.W. 1926. Palaeontological contributions to the geology of Western Australia, Series VII, no. XIII, descriptions of some Western Australian fossil Polyzoa. W.A. geol. Surv. Bull., 88.
- BRILLOUIN, L. 1962. Science and information theory (2nd ed.) 347 pp.

Academic Press, New York.

- BRONDOS, M.D. AND KAESLER, R.L. 1976. Diversity of assemblages of Late Paleozoic Ostracoda. pp. 213-234. In SCOTT, R.W. and WEST, R.R. (Eds), Structure and classification of paleocommunities, 291 pp. Dowden, Hutchinson and Ross, Stroudsburg.
- BRONN, H.G. 1825. System der Urweltlichen Pflanzenthier durch Diagnose, Analyse und Abbildung der Geschlechter erläutert 48 pp. Mohr, Heidelberg.
- BROOD, K. 1970. On two species of Saffordotaxis (Bryozoa) from the Silurian of Gotland, Sweden. Stockholm Contrib. Geol., v. 21, p. 57-68.
- BROOD, K. 1972. Cyclostomatous Bryozoa from the Upper Cretaceous and Danian in Scandinavia. Stockholm Contrib. Geol. v. 26, 464 pp.
- BROOD, K. 1973. Palaeozoic Cyclostomata (a preliminary report). pp. 247-256. In LARWOOD, G.P. (Ed.) Living and fossil Bryozoa. 634 pp. Academic Press, London.
- BULLIVANT, J.S. 1968. The method of feeding of lophophorates (Bryozoa, Phoronida, Brachiopoda). N.Z. Jl. mar. Freshwat. Res., v. 2, p. 135-146.
- BURCKLE, L.H. 1960. Some Mississippian fenestrate Bryozoa from Central Utah. J. Paleont., v. 34, p. 1077-1098.
- 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, v. 1. T. & W. Boone (London).
- CHRONIC, B.J. 1949. Upper Paleozoic of Peru, p. II. Invertebrate Paleontology. In NEWELL, N.D., CHRONIC, B.J. and ROBERTS, T.G.

Upper Paleozoic of Peru.

- CONDRA, G.E. 1902. New Bryozoa from the Coal Measures of Nebraska. Am. Geol., v. 30, p. 337-358.
- CONDRA, G.E. and ELIAS, M.K. 1944. Study and revision of Archimedes (Hall). Spec. Pap. geol. Soc. Am., v. 53, 243 pp.
- COOK, P.L. 1977. Colony-wide water currents in living Bryozoa. Cah. Biol. Mar., v. 18, p. 31-47.
- COOK, P.L. and CHIMONIDES, P.J. 1980. Further observations on water current patterns in living Bryozoa. Cah. Biol. Mar., v. 21, p. 393-402.
- COWEN, R. and RIDER, J. 1972. Functional analysis of fenestellid Bryozoan colonies. Lethaia, v. 5, p. 145-164.
- CRISP, D.J. and SOUTHWARD, A.J. 1961. Different types of cirral activity in barnacles. Phil. Trans. Roy. Soc. Ser. B., 243, p. 271-308.
- CROCKFORD, J. 1941a. Permian Bryozoa of Eastern Australia. J. Proc. R. Soc. N.S.W., v. 74, p. 397-418.
- CROCKFORD, J. 1941b. Permian Bryozoa from Eastern Australia. Part II. New species from the Upper Marine Series of New South Wales. J. Proc. R. Soc. N.S.W., v. 74, p. 502-519.
- CROCKFORD, J. 1943. Permian Bryozoa of Eastern Australia. Part III. Batostomellidae and Fenestrellinidae from Queensland, New South Wales and Tasmania. J. Proc. R. Soc. N.S.W., v. 76, p. 258-267.
- CROCKFORD, J. 1944a. Bryozoa from the Permian of Western Australia. Part I. Cyclostomata and Cryptostomata from the North-west Basin and Kimberley district. Proc. Linn. Soc. N.S.W., v. 69, pt. 3-4, p. 139-175.

- CROCKFORD, J. 1944b. Bryozoa from the Wandagee and Nooncanbah series (Permian) of Western Australia. Jl. R. Soc. West. Aust., v. 28, p. 165-185.
- CROCKFORD, J. 1944c. A revision of some previously described species of Bryozoa from the Upper Palaeozoic of Western Australia. Jl. R. Soc. West. Aust., v. 28, p. 187-199.
- CROCKFORD, J. 1945a. Stenoporids from the Permian of New South Wales and Tasmania. Proc. Linn. Soc. N.S.W., v. 70, p. 9-24.
- CROCKFORD, J. 1945b. A Bryozoan fauna from the Lake's Creek Quarry, Rockhampton, Queensland. Proc. Linn. Soc. N.S.W., v. 70, p. 125-134.
- CROCKFORD, J. 1951. The development of Bryozoan faunas in the Upper Palaeozoic of Australia. Proc. Linn. Soc. N.S.W., v. 76, p. 105-122.
- CROCKFORD, J. 1957. Permian Bryozoa from the Fitzroy Basin, Western Australia. Aust. Bur. Miner. Resour. Geol. Geophys. Bull., 34, 136 pp.
- CUFFEY, R.J. 1967. Bryozoan Tabulipora carbonaria in the Wreford Megacyclothem (Lower Permian) of Kansas. Kans. Univ. Pal. Contribs. Paper 1, p. 1-96.
- CUFFEY, R.J. 1971. Bryozoans in the Modern reefs of Northern Eleuthera Island (Bahamas). VIII Int. Sed. Congress, Prog. with Abstr.; (Heidelberg), p. 19.
- CUFFEY, R.J. 1972. The roles of Bryozoans in modern coral reefs. Geol. Rdsch. 61, 2, p. 542-550.
- CUFFEY, R.J. 1973. An improved classification, based upon numerical taxonomic analyses, for the higher taxa of Entoprocta and

- Ectoproct Bryozoans. pp. 549-564. In LARWOOD, G.P. (Ed.) Living and fossil Bryozoa 634pp. Academic Press, London.
- CUFFEY, R.J. 1974a. Bryozoan involvement in reefs and bioherms through geologic time. A.A.P.G. and S.E.P.M. Annual Meetings Abstracts, v. 1, p. 22.
- CUFFEY, R.J. 1974b. Delineation of Bryozoan constructional roles in reefs from comparison of fossil bioherms and living reefs. Proc. 2nd Int. Coral reef Symposium, 1, p. 357-364.
- CUFFEY, R.J. 1977. Bryozoan contributions to reefs and bioherms through geologic time. Studies in Geology no. 4, A.A.P.G., p. 181-194.
- CUFFEY, R.J. 1985. Expanded reef-rock textural classification and the geologic history of Bryozoan reefs. Geology, v. 13, p. 307-310.
- CUFFEY, R.J. and FOERSTER, B. 1975. Autecology of the Bryozoan Crisia eburnea in the modern reefs of Bermuda. In S. POUYET (Ed.) "Bryozoa 1974". Docum. Lab. Géol. Fac. Sci. Lyon, hors-série 3, (Fasc. 2), p. 357-368.
- CUFFEY, R.J. and MCKINNEY, F.K. 1982. Reteporid cheilostome Bryozoans from the modern reefs of Enewetak atoll, and their implications for Palaeozoic fenestrate Bryozoan paleoecology. Pacif. Geol. 16, p. 7-13.
- CUMINGS, E.R. 1904. Development of some Paleozoic Bryozoa. Am. J. Sci. v. 17, no. 97, p. 49-78.
- CUMINGS, E.R. 1905. Development of Fenestella. Am. J. Sci. v. 20, no. 117, p. 169-180.
- DAVIS, J.C. 1973. Statistics and data analysis in Geology 550 pp. Wiley (New York).

- de KONINCK, L.G. 1863. Descriptions of some fossils from India, discovered by Dr. A. Fleming, of Edinburgh. Q. Jl. geol. Socl. Lond., v. 19, p. 1-19.
- de KONINCK, L.G. 1877. Descriptions of Palaeozoic fossils of New South Wales. Mem. geol. Surv. N.S.W. Palaeontology 6.
- DODD, J.R. AND STANTON, R.J. 1981. Paleoecology, concepts and applications. 559 pp. Wiley (New York).
- d'ORBIGNY, A. 1849. Description de quelques genres nouveaux de Mollusques Bryozoaires. Rev. Mag. Zool., ser. 2, v. 1, p. 499-504.
- d'ORBIGNY, A. 1850. Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés. 394 pp. Victor Masson, Paris.
- DREYER, E. 1961. Die Bryozoen des Mitteldeutschen Zechsteins. Freiberger ForschHft, CIII, p. 7-27.
- DUMÉRIL, A.M.C. 1806. Zoologie analytique, ou methode naturelle de classification des animaux, rendue plus facile à l'aide de tableaux synoptiques. 344 pp. Paris.
- DUNAEVA, N.N. AND MOROZOVA, I.P. 1967. Osobennosti razvituja i sistematicheskoye polozheniye nekotorykh pozdnepaleozoyskikh Trepostomat. Paleont. Zh. no. 4, p. 86-94. (Evolutionary features and systematic position of some late Palaeozoic Trepostomata).
- DUNAEVA, N.N. and MOROZOVA, I.P. 1975. Revision of the Suborder Fenestelloidea. In S. POUYET (Ed.) "Bryozoa 1974" Docum. Lab. Géol. Fac. Sci. Lyon hors-série 3, (fasc. 1), p. 225-233.
- DUNCAN, P.M. 1873. On the Genus Palaeocoryne, Duncan and Jenkins, and

- its affinities. Q. Jl. geol. Soc. Lond., v. 29, p. 412-417.
- DYRYNDA, P.E.J. 1981. A preliminary study of patterns of polypide generation-degeneration in marine cheilostome Bryozoa, pp. 73-81. In LARWOOD, G.P. and NIELSEN, C. (Eds). Recent and fossil Bryozoa. 334 pp. Olsen and Olsen (Fredensborg).
- DZIK, J. 1981. Evolutionary relationships of the early Palaeozoic 'cyclostomatous' Bryozoa. Palaeontology, v. 24, p. 827-861.
- EGGLESTON, D. 1972. Factors influencing the distribution of sublittoral ectoprocts off the South of the Isle of Man (Irish Sea). J. nat. Hist., v. 6, p. 247-260.
- EHRENBERG, C.G. 1837. Die fossilen Infusorien und die lebendige Dammerde, vorgetragen in der Akademie der Wissenschaften zu Berlin 1836 und 1837. Berlin, Druck der Königl. Akademie der Wissenschaften. 27 pp.
- ELIAS, M.K. 1937. Stratigraphic significance of some Late Paleozoic fenestrate Bryozoans. J. Paleont. v. 2, p. 306-334.
- ELIAS, M.K. 1957. Late Mississippian fauna from the Redoak hollow formation of Southern Oklahoma, part 1. J. Paleont., v. 31, p. 370-427.
- ELIAS, M.K. and CONDRA, G.E. 1957. Fenestella from the Permian of West Texas. Mem. geol. Soc. Am., 70, 158 pp.
- ENGEL, B.A. 1975. A new ? Bryozoan from the Carboniferous of Eastern Australia. Palaeontology, v. 18, p. 571-605.
- ETHERIDGE, R. JUN. 1873. In explanation of sheet 23, Lanarkshire, Central Districts, Appendix III. Mem. Geol. Surv. Scotland, p. 101.
- ETHERIDGE, R. JUN. 1877. Notes on Carboniferous Polyzoa. Ann. Mag.

- Nat. Hist., v. 20, p. 30-37.
- FRITZ, M.A. 1932. Permian Bryozoa from Vancouver Island. Trans. R. Soc. Can., v. IV, p. 93-106.
- FÜRSICH, F.T. 1979. Genesis, Environments and Ecology of Jurassic hardgrounds. Neues Jb. Geol. Paläont. Abh. 158, p. 1-63.
- GAUTIER, T.G. 1970. Interpretive morphology and taxonomy of Bryozoan genus Tabulipora. Kans. Univ. Pal. Contribs., 48, p. 1-21.
- GAUTIER, T.G. 1972. Growth, form, and functional morphology of Permian acanthocladid Bryozoa from the Glass Mountains, West Texas. Unpubl. Ph.D. Thesis, University of Kansas.
- GAUTIER, T.G. 1973. Growth in Bryozoans of the Order Fenestrata. pp. 271-274. In LARWOOD, G.P. (Ed.) Living and fossil Bryozoa 634 pp. Academic Press, London.
- GEINITZ, H.B. 1846. Grundriss der Versteinerungskunde. Arnoldische Buchhandlung, Dresden und Leipzig.
- GEINITZ, H.B. 1848. Die Versteinerungen des deutschen Zechsteingebirges. 26 pp. In GEINITZ, H.B. and GUTBIER, A. Die Versteinerungen des Zechsteingebirges und Rothliegenden oder des permischen Systemes in Sachsen. Arnoldische Buchhandlung, Dresden und Leipzig.
- GEINITZ, H.B. 1861. Dyas oder die Zechsteinformation und das Rothliegende. Leipzig.
- GILCHRIST, B.M. 1960. Growth and form of the brine shrimp Artemia salina (L.) Proc. zool. Soc. Lond., v. 134, p. 221-235.
- GIRTY, G.H. 1908. The Guadalupian fauna. Prof. Pap. U.S. geol. Surv., 158, 651 pp.
- GIRTY, G.H. 1910. New genera and species of Carboniferous fossils

- from the Fayetteville Shale of Arkansas. Ann. N.Y. Acad. Sci., v. 20, no. 3, pt. II, p. 189-238.
- GOLDFUSS, A. 1826-1833. *Petrefacta Germaniae*. 252 pp. Arnz and Co. (Düsseldorf).
- GORJUNOVA, R.V. 1975. The Permian Bryozoa of Pamir. Trudy paleont. Inst., v. 148, 127 pp. [in Russian].
- HALL, J. 1885. On the mode of growth and relations of the Fenestellidae. Rep. St. Geol. N.Y., p. 35-46.
- HARMELIN, J-G. 1973. Morphological variations and ecology of the Recent cyclostome Bryozoan "Idmonea atlantica" from the Mediterranean. pp. 95-106. In LARWOOD, G.P. (Ed.). Living and fossil Bryozoa, 634 pp. Academic Press, London.
- HARMELIN, J-G. 1975. Relations entre la forme zoariale et l'habitat chez les Bryozoaires cyclostomes. Conséquences taxonomiques. pp. 369-384. In S. POUYET (Ed.) "Bryozoa 1974". Docum. Lab. géol. Fac. Sci. Lyon, hors-série 3, (fasc. 2).
- HARWOOD, G.M., SMITH, D.B., PATTISON, J. and PETTIGREW, T. 1982. Field Excursion Guide EZ82. 53 pp.
- HENNIG, W. 1966. Phylogenetic Systematics 263 pp. Univ. of Illinois Press, (Urbana, Illinois).
- HOWSE, R. 1848. A Catalogue of the Fossils of the Permian System of the Counties of Northumberland and Durham, drawn up at the request of the Tyneside Naturalists' Field Club. Trans. Tyneside Nat. Fld. Cl., v. 1, p. 219-264.
- JACKSON, J.B.C. 1979. Morphological strategies of sessile animals, pp. 499-555. In LARWOOD, G.P. and ROSEN, B.R. (Eds). Systematics Association Special Volume no. 11 "Biology and Systematics of

- Colonial Organisms", 589pp. Academic Press, London and New York.
- JACKSON, J.B.C. and WINSTON, J.E. 1982. Ecology of cryptic coral reef communities. 1. Distribution and abundance of major groups of encrusting organisms. J. exp. mar. Biol. Ecol., v. 57, p. 135-147.
- JAMES, N.P. 1983. Reef Environment, pp. 346-462. In SCHOLLE, P.A., BEBOUT, G.D. and MOORE, C.H. Carbonate depositional environments. A.A.P.G. Mem. 33, 708 pp.
- JAMES, U.P. 1878. Descriptions of newly discovered species of fossils from the Lower Silurian formation, Cincinnati group. The Palaeontologist, no. 1, p. 1-8.
- JEBRAM, D. 1973. Preliminary observations on the influences of food and other factors on the growth of Bryozoa. With the description of a new apparatus for cultivation of sessile plankton feeders. Kieler Meeresforsch., 29, p. 50-57.
- JEBRAM, D. 1975. Effects of different foods on Conopeum seurati (Canu) (Bryozoa Cheilostomata) and Bowerbankia gracilis Leidy (Bryozoa Ctenostomata). pp. 97-108. In S. POUYET (Ed.). "Bryozoa 1974". Docum. Lab. Géol. Fac. Sci. Lyon. hors-série 3, (fasc. 1).
- JEBRAM, D. 1979. Interrelations of nutrition, food uptake, and growth in Bryozoans. pp. 121-140. In LARWOOD, G.P. and ABBOTT, M.B. (Eds). Advances in Bryozoology. 639 pp. Academic Press, London and New York.
- JOHNSTON, G. 1847. A History of the British Zoophytes, 2nd ed, v. 1, 488 pp. v. 2, 74 pls. John Van Voorst, London.

- KERKMANN, K. 1967. Zur Kenntnis der Riffbildungen in der Werraserie des thüringischen Zechsteins. Frieberger ForschHft., C213, p. 123-143.
- KERKMANN, K. 1969. Riffe und Algenbänke im Zechstein von Thüringen. Freiberger ForschHft., C252, p. 1-85.
- KING, W. 1848. A catalogue of the organic remains of the Permian rocks of Northumberland and Durham. pp. 5-16. Published by the author, Newcastle-upon-Tyne.
- KING, W. 1849. On some Families and Genera of Corals. Ann. Mag. Nat. Hist., 2nd Series, v. 3, p. 388-390.
- KING, W. 1850. The Permian fossils of England. 258 pp. Palaeontogr. Soc. (Monogr.).
- KIRKBY, J.W. 1857. On some Permian fossils from Durham. Q. Jl. geol. Soc. Lond., v. 13, p. 213-218.
- KIRKBY, J.W. 1859. On the Permian Chitonidae. Trans. Tyneside Nat. Fld. Cl., v. 3, p. 238-262.
- KIRKBY, J.W. 1860. On Permian Entomostraca from the Shell-limestone of Durham. Trans. Tyneside Nat. Fld. Cl., v. 4, p. 122-170.
- KORN, H. 1930. Die Cryptostomen Bryozoen des Deutschen Perms. Leopoldina, v. 6, p. 342-377.
- LEE, G.W. 1912. The British Carboniferous Trepostomata. Mem. geol. Surv. Gr. Br. Palaeont., v. 1, p. 135-195.
- LEVERSEE, G.J. 1972. Field and laboratory studies on the effect of water currents on morphology and feeding in the sea whip. Leptogorgia. Am. Zool., v. 12, p. 719.
- LIEBE, K.T. 1881. Erläuterung zur geologischen Specialkarte von Preussen. Blatt. Neustadt gradabtheilung, 71, no. 15.

- LIKHAREV, B. 1926. Quelques Bryozoaires du Permien supérieur du gouvernement de Vologda. Bull. Comm. géol. Leningrad, v. 43, p. 1011-1036. [In Russian, with French Abstract].
- LOGAN, A. 1962. A revision of the Palaeontology of the Permian limestones of County Durham. Unpubl. Ph.D. Thesis, Univ. of Durham.
- LONSDALE, W. 1839. In MURCHISON, R.I., The Silurian System, pt. 2, John Murray, London.
- LONSDALE, W. 1844. Description of six species of corals from the Palaeozoic formation of Van Diemen's Land. In DARWIN, C. Geological observations on the volcanic islands visited during the voyage of H.M.S. Beagle, together with some brief notes on the geology of Australia and the Cape of Good Hope. Appendix to Pt. 1, p. 178-185.
- MALECKI, J. 1977. Permian Bryozoans from Southern Spitsbergen and Bjornoya (Svalbard). Stud. Geol. Pol., vol. 51, p. 75-88.
- MALZAHN, E. 1968. Über neue Funde von Janassa bituminosa (Schloth.) im niederrheinischen Zechstein. Geol. Jb., 85, p. 67-96.
- MARGALEF, R. 1968. Perspectives in Ecological Theory. 111 pp. Univ. Chicago Press, Chicago, London.
- MAYR, E. 1968. Theory of Biological Classification. Nature, v. 220, no. 5167, p. 545-548.
- MCCOY, F. 1844. A synopsis of the characters of the Carboniferous Limestone fossils of Ireland. 207 pp. Dublin.
- MCKINNEY, F.K. 1977. Functional interpretation of lyre-shaped Bryozoa. Paleobiology, v. 3, p. 90-97.
- MCKINNEY, F.K. 1978. Astogeny of the lyre-shaped Carboniferous

- fenestrate Bryozoan Lyroporella. J. Paleont., v. 52, p. 83-90.
- MCKINNEY, F.K. 1980a. Erect spiral growth in some living and fossil Bryozoans. J. Paleont., v. 54, p. 597-613.
- MCKINNEY, F.K. 1980b. The Devonian fenestrate Bryozoan Utropora Pořta. J. Paleont., v. 54, p. 241-252.
- MCKINNEY, F.K. 1981. Intercolony fusion suggests polyembryony in Paleozoic fenestrate Bryozoans. Paleobiology, v. 7, p. 247-251.
- MCKINNEY, F.K. 1983. Asexual colony multiplication by fragmentation: an important mode of genet longevity in the Carboniferous Bryozoan Archimedes. Paleobiology, v. 9, p. 35-43.
- MCKINNEY, F.K. and BOARDMAN, R.S. 1985. Zooidal Biometry of Stenolaemates. In NIELSEN, C. and LARWOOD, G.P. (Eds) Bryozoa: Ordovician to Recent (In Press).
- MCKINNEY, F.K. and RAUP, D.M. 1982. A turn in the right direction: simulation of erect spiral growth in the bryozoans Archimedes and Bugula. Paleobiology, v. 8, p. 101-112.
- MCNAIR, A.H. 1937. Cryptostomatous Bryozoa from the Middle Devonian Traverse Group of Michigan. Mich. Univ. Mus. Paleontol. Contrib., v. 5, p. 103-170.
- MICHELL, S.J. 1970. Fluid and Particle Mechanics. 342 pp. Pergamon Press, Oxford.
- MILLER, T.G. 1961. Type specimens of the genus Fenestella from the Lower Carboniferous of Great Britain. Palaeontology, v. 4, p. 221-242.
- MILLER, T.G. 1962. North American species of Fenestella from the Carboniferous of Great Britain. J. Paleont., v. 36, p. 120-125.

- MILNE-EDWARDS, H. 1838. Mémoire sur les Crisies, les Hornères et plusieurs autres Polypes vivants ou fossiles dont l'organisation est analogue à celle des Tubulopores. Annls. Sci. nat. 2nd serie, 9, p. 193-238.
- MONTY, C. 1982. Microbial accretions and cavity dwelling stromatolites in reefs and mounds. Eleventh Int. Congress on Sed. McMaster, p. 28.
- MOORE, R.C. 1929. A bryozoan faunule from the Upper Graham formation, Pennsylvanian, of North Central Texas. J. Paleont., v. 3, p. 1-27 and p. 121-156.
- MOROZOVA, I.P. 1960. Osnovy paleontologii. Mshanki, brakhiopody. p. 71. Moscow, Izd-vo, Akad. Nauk SSSR. (Fundamentals of Palaeontology. Bryozoa and Brachiopods) [In Russian].
- MOROZOVA, I.P. 1961. The Devonian Bryozoa of the Minusinsk and Kuznets basins. Trudy paleont. Inst., v. 86, 172 pp. [In Russian].
- MOROZOVA, I.P. 1962. On the systematics and phylogeny of Fenestelloidea. Paleont. Zh., t.4, p. 104-115. [In Russian].
- MOROZOVA, I.P. 1965. Bryozoa. pp. 183-197. In REZHENTZEV, V.E. and SARIECHEVA, T.G. (Eds). Development and change in marine organisms from the border of the Palaeozoic and Mesozoic. Trudy paleont. Inst., v. 106, 431 pp. [In Russian].
- MOROZOVA, I.P. 1970. Mshanki pozdnej Permi. Turdy paleont. Inst., v. 122, 347 pp. (Bryozoa of the Late Permian deposits). [In Russian].

- MOROZOVA, I.P. 1973. New and little-known structures of Fenestelloidea. pp. 327-333. In LARWOOD, G.P. (Ed.) Living and fossil Bryozoa, 634 pp. Academic Press, London and New York.
- MOROZOVA, I.P. 1974. Revision of the bryozoan genus Fenestella Paleont. Zh. 1974 no. 2, p. 54-67.
- NEKHOROSHEV, V.P. 1926. Lower Carboniferous Bryozoa from the Kuznetsk basin. Bull. Comm. géol. Leningrad, v. 43, p. 1237-1290. [In Russian].
- NEKHOROSHEV, V.P. 1932. A microscopic method for investigation of Paleozoic bryozoans of the family Fenestellidae. Vses. Geologorazv. Ob'yedin. Izv., v. 51, no. 17, p. 279-303. [In Russian].
- NICHOLSON, H.A. and LYDEKKER, R. 1889. A manual of palaeontology for the use of students with a general introduction on the principles of palaeontology. 885 pp. Blackwood, Edinburgh and London.
- NIELSEN, C. 1970. On metamorphosis and ancestrula formation in cyclostomatous bryozoans. Ophelia, 7, p. 217-256.
- ODUM, E.P. 1971. Fundamentals of Ecology. 574 pp. W.B. Saunders Co., Philadelphia.
- OLALOYE, F. 1974. Some Penniretepora (Bryozoa) from the Viséan of County Fermanagh with a revision of the generic name. Proc. R. Ir. Acad., 74, Sect. B., no. 28, p. 471-506.
- PALMER, T.J. and FÜRSICH, F.T. 1974. The ecology of a Middle Jurassic hardground and crevice fauna. Palaeontology, v. 17, p. 507-524.
- PATTISON, J. 1977. Catalogue of the type, figured and cited specimens in the King collection of Permian fossils. Bull. geol. Surv. Gt. Br., no. 62, p. 33-44.

- PHILLIPS, J. 1836. Illustrations of the geology of Yorkshire. Part 1, the Yorkshire coast. 254 pp. John Murray, London.
- PHILLIPS, J. 1841. Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon and West Somerset. 231 pp. Longmans, Brown, Green and Longmans, London.
- POHOWSKY, R.A. 1973. A Jurassic cheilostome from England. pp. 447-461. In LARWOOD, G.P. (Ed.) Living and fossil Bryozoa, 634 pp. Academic Press, London and New York.
- POPEKO, L.I. and GORELOVA, N.G. 1975. On the possibility of Fenestella genus objective grouping, pp. 235-245. In S. POUYET (Ed.) "Bryozoa 1974". Docum. Lab. Géol. Fac. Sci. Lyon, hors-série 3 (fasc. 1).
- REED, F.R.C. 1927. Palaeozoic and Mesozoic fossils from Yun-nan. Mem. geol. Surv. India Palaeont. indica, v. 10, no. 1, p. 1-291.
- REYMENT, R.A. 1971. Introduction to Quantitative Paleoecology, 226 pp. Elsevier, Amsterdam, London, New York.
- ROMANTCHUK, T.V. 1966. Novye permskie mshanki Khabarovskogo kraja. Paleont. Zh., 2, p. 42-48. (New Permian bryozoans from Khabarovsk Krai). [In Russian].
- ROMANTCHUK, T.V. 1967. New bryozoans of the Order Trepostomata of the Upper Permian of the Khabarovsk territory. Paleont. Zh., 2, p. 69-73. [In Russian].
- ROMANTCHUK, T.V. 1981. New Permian Trepostomata and rhabdomesids from Khabarovsk Krai, Russian SFSR. Paleont. Zh. 4, p. 53-64. [In Russian].
- ROMANTCHUK, T.V. and KISELEVA, A.V. 1968. Novye pozdne-permskie mshanki Dal'nego Vostoka. Paleont. Zh., 4, p. 55-60. (New Late

- Permian bryozoans of the Far East). [In Russian].
- ROSS, J.R.P. 1979. Permian Ectoprocts in Space and Time. pp. 259-276. In GRAY, J. and BOUCOT, A.J. (eds). Historical biogeography, plate tectonics, and the changing environment. Oregon State University Press, Corvallis.
- RUDWICK, M.J.S. 1970. Living and Fossil Brachiopods. 199 pp. Hutchinson University Library, London.
- RYLAND, J.S. 1970. Bryozoans. 175 pp. Hutchinson University Library, London.
- RYLAND, J.S. 1976. Physiology and ecology of marine bryozoans. Adv. mar. Biol., v. 14, p. 285-443.
- SAKAGAMI, S. 1961. Japanese Permian Bryozoa. Palaeont. Soc. Japan Spec. Paper 7, 59 pp.
- SAKAGAMI, S. 1968a. Permian bryozoa from Khao Phrik, near Rat Buri, Thailand. Geology and Palaeontology of S.E. Asia, v. 4, p. 45-66.
- SAKAGAMI, S. 1968b. Permian bryozoa from Khao Chong Krachok, Peninsular Thailand. Geology and Palaeontology of S.E. Asia, v. 4, p. 67-81.
- SAKAGAMI, S. 1968c. Permian bryozoa from Khao Ta Mong Rai, Peninsular Thailand. Geology and Palaeontology of S.E. Asia, v. 5, p. 47-67.
- SAKAGAMI, S. 1970a. Addition to the Permian bryozoa from Ko Muk, Peninsular Thailand. Geology and Palaeontology of S.E. Asia, v. 8, p. 43-68.
- SAKAGAMI, S. 1972. The Triassic bryozoa from Kusaka, Sakaura Basin, Shikoka, Japan. Trans. Proc. palaeont. Soc. Japan, 85, p. 275-

- SAKAGAMI, S. 1973a. Some Permian bryozoa from Pahang, Malaya. Geology and Palaeontology of S.E. Asia, v. 12, p. 63-73.
- SAKAGAMI, S. 1973b. Permian bryozoa from Khao Raen, near Rat Buri, Thailand. Geology and Palaeontology of S.E. Asia, v. 12, p. 75-89.
- SAKAGAMI, S. 1975. Permian Bryozoa from Khao Hin Kling, near Phetchabun, North-Central Thailand. Geology and Palaeontology of S.E. Asia, v. 16, p. 33-43.
- SAKAGAMI, S. 1976a. Palaeobiogeography of the Permian bryozoa on the basis of the Thai-Malayan district. Geology and Palaeontology of S.E. Asia, v. 17, p. 155-172.
- SAKAGAMI, S. 1976b. On the Permian bryozoa from the Northern part of Sainbeyli, Central Turkey. Trans. Proc. palaeont. Soc. Japan, 103, p. 398-405.
- SAKAGAMI, S. and SAKAI, A. 1979. Triassic Bryozoans from the Hidaka Group in Hokkaido, Japan. Trans. Proc. palaeont. Soc. Japan, 114, p. 77-86.
- SAKAGAMI, S. and SUGIMURA, A. 1981. Permian bryozoan biostratigraphy of the Akiyoshi Limestone group, Japan. Proc. Japan Acad., v. 57, Ser. B, no. 4, p. 119-122.
- SCHAUMBERG, G. 1979. Neue Nachweise von Bryozoen und Brachiopoden als Nahrung des permischen Holocephalen. Janassa bituminosa (SCHLOTHEIM). Philippia, VI/1, p. 3-11.
- SCHLOTHEIM, E. von. 1813. Beiträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. Taschenbuch für die gesammte Mineralogie mit Hinsicht und die neuesten Entdeckungen.

- Joh. Christ. Hermannschen Buchhandlung, Frankfurt am Main.
- SCHLOTHEIM, E. von. 1816-1817. Beyträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. p. 13-36.
- SCHLOTHEIM, E. von. 1820. Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung einer Sammlung versteinerter und fossiler Überreste des Thier - und Pflanzenreichs der Vorwelt erläutert. 437 pp. Gotha, in der Becker'schen Buchhandlung.
- SCHNEIDER, D. 1959. Der Aufbau der Bugula - Tierstöcke und seine Beeinflussung durch Aussenfaktoren. Biol. Zbl., 78, p. 250-283.
- SCHOPF, T.J.M. 1969. Paleoeecology of Ectoprocts (Bryozoans). J. Paleont., v. 43, p. 234-244.
- SCHOPF, T.J.M. 1976. Environmental versus genetic causes of morphologic variability in bryozoan colonies from the deep sea. Paleobiology, v. 2, p. 156-165.
- SCHOPF, T.J.M. and DUTTON, A.R. 1976. Parallel clines in morphologic and genetic differentiation in a coastal zone marine invertebrate: the bryozoan Schizoporella errata. Paleobiology, v. 2, p. 255-264.
- SCHOPF, T.J.M., 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, v. 6, p. 466-476.
- SCOFFIN, T.P. 1972. Cavities in the reefs of the Wenlock Limestone (Mid-Silurian) of Shropshire, England. Geol. Rdsch., 61, p. 565-578.

- SEDGWICK, Rev. A. 1829. On the geological relations and internal structure of the Magnesian Limestone and the lower portions of the New Red Sandstone Series in their range through Nottinghamshire, Derbyshire, Yorkshire and Durham to the Southern extremity of Northumberland. Trans. geol. Soc. Lond. 2d Series, v. 3, p. 3-10
- SHINN, E.A. 1969. Submarine lithification of Holocene carbonate sediments in the Persian Gulf. Sedimentology, v. 12, p. 109-144.
- SHISHOVA, N.A. 1960. Novye permskie Mshanki Zapadnago Zabajkalja. Paleont. Zh., 1, p. 73-83. [In Russian].
- SHISHOVA, N.A. 1968. Novyj otryad Paleozojskikh Mshanok. Paleont. Zh., 1, p. 129-132. (A new order of Palaeozoic bryozoa). (In Russian, translation in Paleontol. J., v. 2, no. 1, p. 117-121).
- SHRUBSOLE, G.W. 1881. Further notes on the Carboniferous Fenestellidae. Q. Jl. geol. Soc. Lond., v. 37, p. 178-189.
- SHRUBSOLE, G.W. 1882. Thamniscus; Permian, Carboniferous and Silurian. Q. Jl. geol. Soc. Lond., v. 38, p. 341-346.
- SHULGA-NESTERENKO, M.I. 1936. Fenestella and Archimedes from the Middle Pechora region of the North Ural. Akad. Nauk SSSR Poliarnaia Komissia Trudy, v. 28, p. 233-285. [In Russian].
- SHULGA-NESTERENKO, M.I. 1941. Lower Permian bryozoa of the Urals. Trudy paleont. Inst., v. 5, p. 1-226. [In Russian].
- SHULGA-NESTERENKO, M.I. 1949. Funktsionalnoe, filogeneticheskoe i stratigraficheskoe zhachenie mikrostruktury skeletnykh tkanej mshanok. Trudy paleont. Inst., v. 23, 67 pp. (Functional, phylogenetic and stratigraphic significance of the microstructure of bryozoan skeletal material) [In Russian].

- SHULGA-NESTERENKO, M.I. 1951. Carboniferous fenestellids of the Russian platform. Trudy paleont. Inst., v. 32, p. 1-161. [In Russian].
- SHULGA-NESTERENKO, M.I. 1952. New Lower Permian bryozoa from the area of the Urals. Trudy paleont. Inst., v. 37, 84 pp. [In Russian].
- SILÉN, L. 1944. The main features of the development of the ovum, embryo and oocidium in the oöciferous bryozoa Gymnolaemata. Ark. Zool. 35, 17, p. 1-34.
- SILÉN, L. and HARMELIN, J-G. 1974. Observations on living Diastoporidae (Bryozoa Cyclostomata), with special regard to polymorphism. Acta. Zool. v. 55, p. 81-96.
- SIMONSEN, A.H. and CUFFEY, R.J. 1980. Fenestrate, pinnate and ctenostome bryozoans and associated barnacle borings in the Wreford Megacyclothem (Lower Permian) of Kansas, Oklahoma and Nebraska. Kans. Univ. Pal. Contribs. Paper 101, p. 1-38.
- SIMPSON, G.B. 1895. A handbook of the genera of the North American Paleozoic Bryozoa. Rep. St. Geol. N.Y. p. 407-608.
- SIMPSON, G.G. 1961. Principles of Animal Taxonomy. 247 pp. Columbia University Press, New York.
- SMITH, D.B. 1958. Observations on the Magnesian Limestone reefs of Northeastern Durham. Bull. geol. Surv. Gt. Br., 15, p. 71-84.
- SMITH, D.B. 1970a. Permian and Trias. In HICKLING and GRACE (Eds). Geology of Durham County. Trans. nat. Hist. Soc. Northumberland, v. 48, pp. 66-91.
- SMITH, D.B. 1978. Sheet 21, Sunderland. Geological Survey of Great Britain (England and Wales). Ordnance Survey, Southampton.
- SMITH, D.B. 1981. The Magnesian limestone reef complex of North East

- England. SEPM spec. publ. no. 30, p. 161-186.
- SOKAL, R.R. and SNEATH, P.H.A. 1963. Principles of Numerical Taxonomy. 359 pp. W.H. Freeman and Co., San Francisco and London.
- SOULE, J.D. and SOULE, D.F. 1974. The bryozoan-coral interface on coral and coral reefs. pp. 335-340. In A.M. CAMERON et al. (Eds). Proceedings of the 2nd International Congress on Coral Reefs.
- STEBBING, A.R.D. 1973. Observations on colony overgrowth and spatial competition, pp. 173-183. In LARWOOD, G.P. (Ed.) Living and Fossil Bryozoa 634 pp. Academic Press, London and New York.
- STRATHMANN, R. 1973. Function of lateral cilia in suspension feeding of lophophorates (Brachiopoda, Phoronida, Ectoprocta). Mar. Biol., v. 23, p. 129-136.
- STRATTON, J.F. 1975. Ovicells in Fenestella from the Speed Member, North Vernon Limestone (Eifelian, Middle Devonian) in Southern Indiana, U.S.A. pp. 169-177. In S. POUYET (Ed.) "Bryozoa 1974" Docum. Lab. Géol. Fac. Sci. Lyon hors-série 3, (fasc. 1).
- STRATTON, J.F. 1981. Apparent ovicells and associated structures in the fenestrate bryozoan Polypora shumardii Prout. J. Paleont., v. 55, p. 880-884.
- STRATTON, J.F. and HOROWITZ, A.S. 1975. Studies of the flow of water through models of Polypora, p. 425-438. In S. POUYET (Ed.) "Bryozoa 1974". Docum. Lab. Géol. Fac. Sci. Lyon hors-série 3, (fasc. 2).
- STUCKENBERG, A.A. 1895. Korallen und Bryozoen der Steinkohlenablagerungen des Ural und des Timan. Mém. Com. géol.

- St. Pétersbourg, v. 10, no. 3, p. 1-244.
- TAVENER-SMITH, R. 1966a. Ovicells in fenestrate cryptostomes of Visean age. J. Paleont. v. 40, p. 190-198.
- TAVENER-SMITH, R. 1966b. The micrometric formula and the classification of fenestrate cryptostomes. Palaeontology, v. 9, p. 413-425.
- TAVENER-SMITH, R. 1969a. Skeletal structure and growth in the Fenestellidae. Palaeontology, v. 12, p. 281-309.
- TAVENER-SMITH, R. 1969b. Wall structure and acanthopores in the bryozoan Leioclema asperum. Lethaia, v. 2, p. 89-97.
- TAVENER-SMITH, R. 1971. Polypora stenostoma: A Carboniferous bryozoan with cheilostomatous features. Palaeontology, v. 14, p. 178-187.
- TAVENER-SMITH, R. 1973a. Fenestrate bryozoa from the Viséan of County Fermanagh, Ireland. Bull. Br. Mus. nat. Hist. (Geol.), 23, p. 389-493.
- TAVENER-SMITH, R. 1973b. Some aspects of skeletal organization in bryozoa. pp. 349-359. In LARWOOD, G.P. (Ed.) Living and Fossil Bryozoa 634 pp. Academic Press, London and New York.
- TAVENER-SMITH, R. 1975. The phylogenetic affinities of fenestelloid bryozoans. Palaeontology, v. 18, p. 1-17.
- TAVENER-SMITH, R. and WILLIAMS, A. 1972. The secretion and structure of the skeleton of living and fossil bryozoa. Phil. Trans. R. Soc. series B., v. 264, p. 97-159.
- TAYLOR, J.C.M. 1984. Late Permian-Zechstein. pp. 61-83. In GLENNIE, K.W. (Ed.). Introduction to the Petroleum Geology of the North Sea. 236 pp. Blackwell Scientific Publications, Oxford.

- TAYLOR, P.D. 1977. The Palaeobiology and Systematics of some Jurassic Bryozoa. Unpubl. Ph.D. Thesis, University of Durham.
- TAYLOR, P.D. 1979. The inference of extrazoooidal feeding currents in fossil bryozoan colonies. Lethaia, v. 12, p. 47-56.
- TAYLOR, P.D. 1980. Stomatopora voigtiana (King 1850): A cyclostome bryozoan from the Permian of County Durham. Proc. Yorks. geol. Soc., v. 42, p. 621-626.
- TAYLOR, P.D. 1985. Carboniferous and Permian species of the cyclostome bryozoan Corynotrypa Bassler, 1911 and their clonal propagation. Bull. Br. Mus. nat. Hist. (Geol.), 38, p. 359-372.
- TERMIER, H. and TERMIER, G. 1971. Bryozoaires du Paléozoïque supérieur de l'Afghanistan, Docum. Lab. Géol. Fac. Sci. Lyon, no. 47, p. 1-52.
- TRECHMANN, C.T. 1913. On a mass of anhydrite in the magnesian limestone of Hartlepool and on the Permian of South-East Durham. Q. Jl. geol. Soc. Lond., v. 69, p. 184-218.
- TRECHMANN, C.T. 1925. The Permian formation in Durham. Proc. Geol. Ass., v. 36, p. 135-145.
- TRECHMANN, C.T. 1942. Borings in the Permian and Coal Measures around Hartlepool. Proc. Yorks. geol. Soc., v. 24, p. 313-327.
- TRECHMANN, C.T. 1944. On some new Permian fossils from the Magnesian limestone near Sunderland. Q. Jl. geol. Soc. Lond., v. 100, p. 333-354.
- TRIZNA, V.B. 1939. Materials on the stratigraphie and oil occurrence in the South Urals. Trans. Geol. Oil Inst. ser. A, fasc. 115.
- TRIZNA, V.B. 1948. Permian bryozoa from the Sulva river. Trudy vses. nauchno-issled. geol. Inst., v. 31, p. 137-188. [In Russian].

- TRIZNA, V.B. 1950. K kharakteristike rifovykh i sloistykh fatsij tsentral'noj chasti Ufimskogo plato. Trudy vses. nauchno-issled. geol. Inst. no. 179, p. 331-453. (Characteristics of the reef and stratified facies of the central part of the Ufimian Plateau). [In Russian].
- TRIZNA, V.B. 1961. The Early and Middle Carboniferous bryozoans from some regions of the Western slope of the urals. Trudy vses. nauchno-issled. geol. Inst., 179, p. 27-160. [In Russian].
- TUCKER, M.E. and HOLLINGWORTH, N.T.J. In press. The Upper Permian Reef (EZ1) of North East England: Diagenesis in a Marine to evaporitic setting. In SCHROEDER, J. and PURSER, B. (eds.), Reef Diagenesis. Springer Verlag (Berlin).
- ULRICH, E.O. 1890. Palaeozoic Bryozoa. Ill. geol. Surv. no. 8, p. 283-688.
- UTGAARD, J. 1973. Mode of colony growth, autozooids and polymorphism in the bryozoan order Cystoporata. pp. 317-360. In BOARDMAN, R.S., CHEETHAM, A.H. and OLIVER, W.A. (Eds) Animal Colonies. 603 pp. Dowden, Hutchinson and Ross, Stroudsburg.
- UTGAARD, J. and PERRY, T.G. 1960. Fenestrate bryozoans from the Glen Dean Limestone (Middle Chester) of Southern Indiana. Indiana dept. Cons. geol. Surv. Bull., no. 19, 32 pp.
- VALENTINE, J.W. 1971. Resource supply and species diversity patterns. Lethaia, v. 4, p. 51-61.
- VINE, G.R. 1879. On Palaeocoryne and the development of Fenestella Hardwickes Science Gossip, v. 15, p. 225-229 and 247-249.

- VINE, G.R. 1883. Fourth report of the committee, consisting of Dr. H.C. Sorby and Mr. G.R. Vine appointed for the purpose of reporting on fossil Polyzoa. Rep. Br. Ass. Advmt. Sci., 53, p. 161-209.
- VISKOVA, L.A. 1981. Brood chambers in Recent and fossil marine bryozoans. Paleont. Zh., no 4, p. 35-52.
- WAAGEN, W.H. and PICHL, J. 1885. Salt Range Fossils. Mem. geol. Surv. India Palaeont. indica, ser. 13, v. 1, p. 771-834.
- WAAGEN, W.H. and WENTZEL, J. 1886. Salt Range Fossils. Mem. geol. Surv. India Palaeont. indica, ser. 13, v. 1, p. 835-924.
- WALKER, K.R. and ALBERSTADT, L.P. 1975. Ecological succession as an aspect of structure in fossil communities. Paleobiology, v. 1, p. 238-257.
- WINSTON, J.E. 1978. Polypide morphology and feeding behaviour in marine Ectoprocts. Bull. mar. Sci., 28, p. 1-31.
- WINSTON, J.E. 1979. Current related morphology and behaviour in some Pacific coast bryozoans. pp. 247-267. In LARWOOD, G.P. and ABBOTT, M.B. (Eds) Advances in Bryozoology. 639 pp. Academic Press, London and New York.
- YANG, K.C. and LOO, L.H. 1962. Palaeozoic Bryozoa of Qilianshan. In Geology of Qilianshan, 4(5), Sci. Publ. House, Beijing, China. [In Chinese].
- YOUNG, J. 1877. Notes on a new method of fixing fronds of Carboniferous Polyzoa on a layer of Asphalt, to show the celluliferous face. Proc. nat. Hist. Soc. Glasgow, 3, p. 207-210.

- YOUNG, J. and YOUNG, J. 1874. On Palaeocoryne and other polyzoal appendages. Q. Jl. geol. Soc. Lond., v. 30, p. 684-689.
- ZITTEL, K.A. 1880. Handbuch der Paleontologie 765 pp. R. Oldenbourg, München and Leipzig. (Bryozoa, p. 573-641).

