The Upper Permian reef of north-east England developed along the western margin of the Zechstein basin. This bryozoan and shell-dominated reef contains a well-preserved fauna which the authors have studied extensively in the field and laboratory. This book contains a 16-page field guide for the identification of all the common fossils, using photographs, line drawings, and life mode reconstructions. In addition, four reef palaeocommunities are reconstructed. These provide a visual indication of changing faunal relationships during reef development and they are supported by relative abundance diagrams and a short description of the inferred ecology of each community. Sunderland Borough Council, in co-operation with the Nature Conservancy Council and the British Trust for Conservation Volunteers, have preserved the eight key localities which are described here. These have been chosen to illustrate the various reef facies types and they yield diagnostic faunas. Short notes on collecting and study techniques complete the text. This guide, to a unique reef complex, should be essential to all those interested in the Zechstein or in reef ecology, whether amateur or professional.

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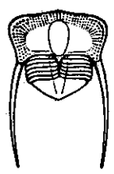

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ZECHSTEIN REEF FOSSILS AND THEIR PALAEOECOLOGY

By N. HOLLINGWORTH
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Return to Tim Pettigrew

PALAEONTOLOGICAL ASSOCIATION
FIELD GUIDES TO FOSSILS No. 3

Zechstein Reef Fossils and their Palaeoecology

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CONTENTS

INTRODUCTION

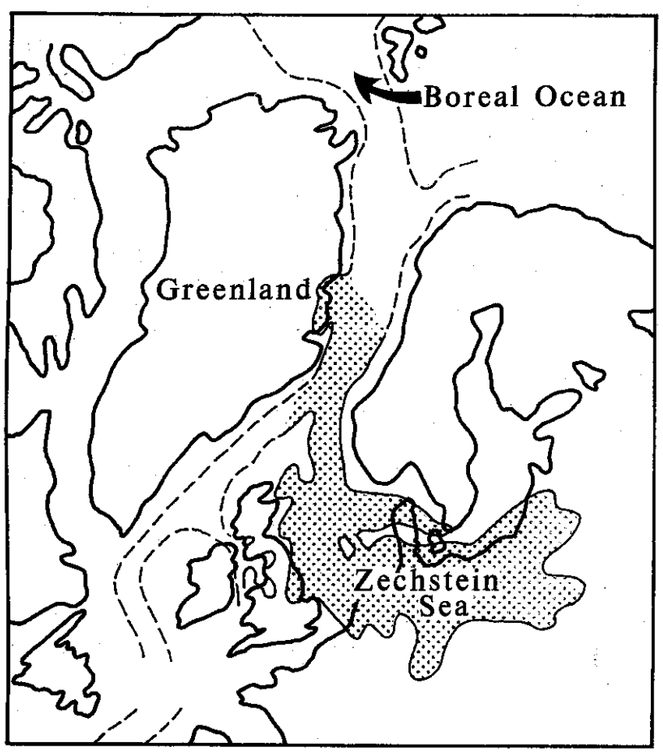
THE Upper Permian Zechstein Cycle 1 reef of the Sunderland area, north-east England has long been known to geologists as one of the classic collecting grounds for Upper Permian marine faunas. Humbledon and Tunstall Hills have yielded the most prolific fossils. Much of the shelly fauna was exhaustively collected and described during the last century. However, in common with many other ancient reefs, the Zechstein reef faunas are generally poorly-preserved due to pervasive dolomitization which has rendered most shelly fossils as friable moulds and casts which in most cases are difficult to identify, even to generic level.

Consequently, some of the classic monographs have been based on fossil material which is commonly indifferently preserved, despite the high quality of the descriptive texts. The discovery of previously unknown localities composed of undolomitized limestone, which have yielded a superbly-preserved shelly fauna, including gastropods with colour patterns preserved (see cover), has provided a great deal of new information on the palaeoecology and diagenesis of the reef.

This field guide covers localities where faunas are significantly better-preserved than any other comparable Zechstein faunas described in the literature. Furthermore, the reef localities and associated faunas have been chosen to evaluate the palaeoecology of one of the most spectacular fossil reef structures in Britain. To this extent, palaeocommunities identified at each locality have been graphically reconstructed. Each chosen site represents a particular stage in reef development from foundation to maturity. Other outcrops, found outside the Sunderland area, are not described in the guide. Most of these comprise the highest parts of the reef and are adequately described elsewhere in the literature. The sites covered in this guide have been preserved through the efforts of Sunderland Borough Council in co-operation with the Nature Conservancy Council and nearly all are scheduled as sites of special scientific interest (SSSI's). Hammering of permanent faces is not permitted, but weathered surfaces and scree slopes often yield good material. Visiting all of the localities described, should bring back to life the development of a unique reef.

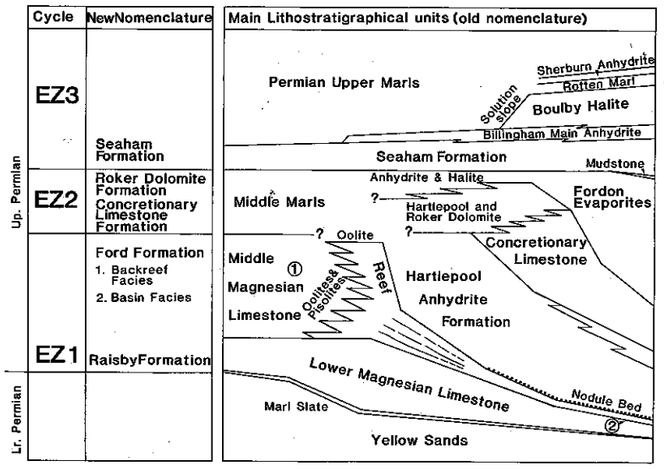
STRATIGRAPHY

The Upper Permian rocks in north-east England comprise a complex of carbonates and evaporites that were deposited along the western margin of the Zechstein Sea (text-fig. 1) during five evaporite cycles



TEXT-FIG. 1. Palaeogeographical reconstruction of north-west Europe during the Upper Permian. The Ford Formation reef formed along the western margin of the Zechstein basin in north-east England near the edge of a shallow carbonate platform. Modified from Taylor (1984).

(Smith 1981). Only rocks of the first two cycles are found within the immediate vicinity of Sunderland. Later cycles are present to the south of the area and are not described in this guide. Zechstein stratigraphy has recently been revised by Smith *et al.* (1986) and we use their new stratigraphic nomenclature. The traditional and new nomenclature are presented together in text-figure 2. Deposition of Upper Permian sediments (text-fig. 3) took place in two provinces separated by a palaeo-



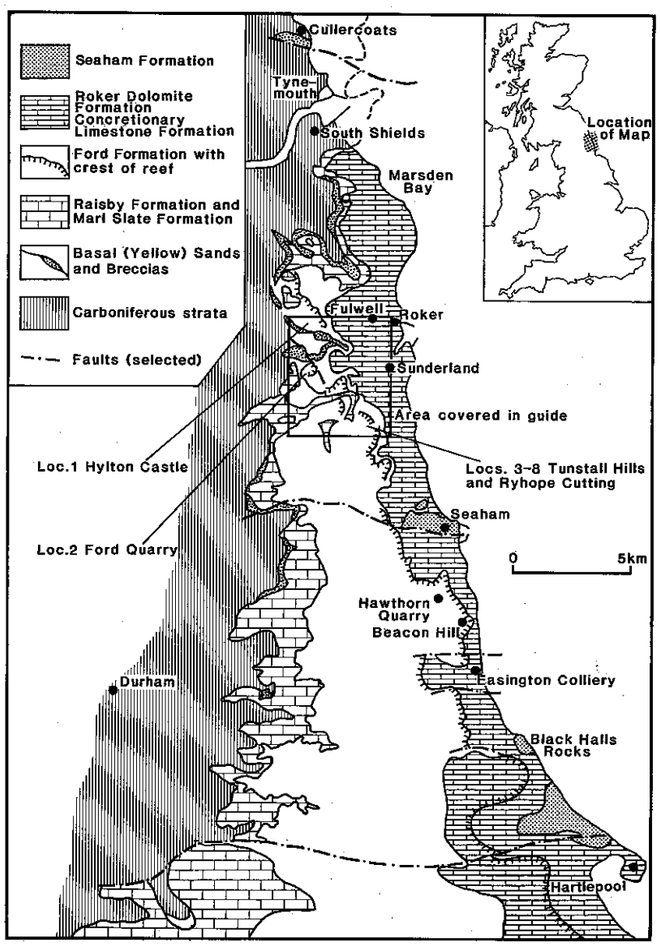
TEXT-FIG. 2. Main lithostratigraphical subdivisions of the Zechstein sequence in the Durham province. Only the first two cycles are exposed onshore in the Sunderland area. Cycles three to five are exposed in south Durham and beneath younger cover. Based on Smith *et al.* (1986).

Stratigraphy

high known as the Cleveland High. The Cleveland High separated the northern Durham province from the Yorkshire province to the south (Smith 1981). In the Durham province the marine Permian sequence includes a 100 m thick, north–south orientated, linear reef complex, within the Ford formation. From its most northerly outcrop at Down Hill (text-fig. 3), it can be traced southwards through the western suburbs of Sunderland into County Durham, where it is known to extend a short distance south-west of Hartlepool, a total distance of around 32 km (Trechmann 1932, Smith 1981). Tertiary uplift has given the reef a gentle southerly tilt and consequently most of the main exposures of the reef base and core occur in the Sunderland area. Further south successively higher stratigraphic levels are exposed within the reef where they have not been removed by erosion.

FOSSIL LOCALITIES

Text-figure 4 shows the main reef lithofacies types recognized by Smith (1958, 1981) and the relative stratigraphic positions and extent of the



TEXT-FIG. 3. Geographical distribution of localities referred to in the text and outcrop of Permian sediments in Tyne and Wear and County Durham. The reef forms surface outcrops between Downhill to the north of Sunderland and Hartlepool, a distance of 32 km. From Smith (1978), by permission of the Director, British Geological Survey.

TEXT-FIG. 4. Main reef lithofacies types based on Smith (1958, 1981), and relationship of localities 1 to 8 to the full reef profile. Vertical and horizontal scales are equal. Most of the reef outcrops in the Sunderland area are preserved as a series of isolated hills. To the south of Sunderland a fuller reef profile is preserved.

Locality 1. Lower Reef Core. Hylton Castle Road Cutting.
Locality 2. Various facies. Claxheugh Railway Cutting and Ford Quarry.
Locality 3. Reef Base. Rock Cottage, Tunstall Hills.
Locality 4. Reef Core. Maiden Paps South.
Locality 5. Reef Slope. Maiden Paps North.
Locality 6. Reef Talus. Ryhope Cutting.
Locality 7. Reef Core. Tunstall Hills East. Old Quarry.
Locality 8. Reef Crest. Tunstall Hills East. Old Trench.

localities referred to in the text in the context of the full reef profile. Each locality represents the most accessible exposure of each reef lithofacies type. These comprise: The lower reef core (Locality 1); backreef, reef core, incipient reef flat, reef crest and upper slope (locality 2); Reef base (locality 3); reef core (locality 4); upper reef slope (locality 5); reef talus (locality 6); reef core (locality 7); and the reef crest (locality 8). Text-figure 3 shows the geographical position of these localities with respect to the overall reef outcrop. Detailed site information is provided with reference to the appropriate ordinance survey 1:10000 (6 ins to 1 mile) maps which are illustrated in the faunal composition and ecology section (text-figs. 7, 11–13). The identification guide (pp. 13–32) gives illustrations, descriptions, and life mode reconstructions for 32 common fossils and indicates the localities at which they can be found. The section 'evolution of the reef complex' summarizes reef development citing the appropriate localities representing each stage. The faunal composition and ecology section gives a detailed account of each locality. Faunal densities are represented using percentage relative abundance bar diagrams. Each abundance histogram is number coded to a particular genus or species which is illustrated in the identification guide (pp. 13–32). For most localities the brachiopod *Dielasma* is used to infer population dynamics and is represented by a size-frequency distribution graph.

Locality 1. Text-figures 7, 8. Hylton castle SSSI. Road cutting. NZ 360589. Ford Formation, lower reef core. 50 m of lower reef core, exposed in road cutting, composed mostly of low interfering domes of cream- to buff-coloured bryozoan biolithite and algal laminite. Many of the domes are draped by algal laminites and separated by shelly pockets. Fossils weather loose, very abundant in scree. King (1850), Smith (1981). Sixteen species recognized, numbers: 1, 3, 4, 5, 6, 7, 9, 10, 11, 13, 15, 17, 19, 26, 27, 28.

Locality 2. Text-figures 9–11. Claxheugh Railway Cutting (disused) and Ford Quarry SSSI. NZ 3657. Ford Formation, backreef facies, reef core, incipient reef flat, reef crest and upper reef slope. Both quarry and railway cutting display the transition from west to east through backreef to reef crest, through bedded backreef dolomicrites into massive, friable, reef core dolomites. Fauna scattered, although there are some well-preserved specimens in isolated pockets. Collecting from loose material only. Trechmann (1945), Smith (1958, 1970, 1981). Fourteen species recognized, numbers: 1, 2, 5, 9, 10, 11, 13, 14, 15, 18, 21, 24, 25, 26.

Locality 3. Text-figures 12, 13, 15. Rock Cottage SSSI. Tunstall Hills. NZ 392543. Ford Formation, undolomitized basal reef coquina. This

is a permanent stepped exposure on a steep hill slope, 10 m² exposed, total height of 7 m. Shelly fauna is superbly-preserved and abundant in loose blocks (Tucker and Hollingworth 1986). Permission must be sought from the owners of Rock Cottage before access can be gained. Twenty-three species recognized, numbers: 1, 2, 3, 8, 9, 10, 11, 13, 14, 15, 16, 18, 19, 20, 22, 23, 26, 27, 28, 29, 30, 31, 32.

Locality 4. Text-figures 13, 16. Maiden Paps South, SSSI. Tunstall Hills, Trigonometric point. NZ 392544. Ford Formation, reef core. Small crag, 10 m high, composed of buff-brown crystalline, slightly dolomitic, massive algal-bryozoan biolithite. Well-preserved fauna in loose blocks. Fifteen species recognized, numbers: 1, 2, 9, 10, 11, 12, 13, 14, 18, 19, 26, 27, 28, 29, 31.

Locality 5. Text-figure 13. Maiden Paps North SSSI. Tunstall Hills. NZ 391548. Ford Formation, Upper reef slope. Small natural exposure near electricity sub-station, massive reef biolithites interspersed with sheet-like areas and pockets of cream to buff shelly talus. Thirteen species recognized, numbers: 1, 2, 9, 10, 14, 18, 19, 21, 26, 27, 28, 29, 31.

Locality 6. Text-figures 13, 17. Ryhope Railway Cutting SSSI. Tunstall Hills. NZ 397538. Ford Formation, reef talus. Cutting 70 m long. The western end of the outcrop consists of massive reef biolithite, eastern end of section composed of allochthonous blocks of algal-bryozoan biolithite, separated by sheets and pockets of rubbly shelly material. Diverse fauna in shelly pockets. Smith (1981). Twelve common species recognized, numbers: 1, 2, 3, 4, 6, 7, 10, 17, 26, 27, 28, 31.

Locality 7. Text-figures 13, 16. Tunstall Hills East, Old Quarry, SSSI. NZ 397539. Ford Formation, reef core. Extensive quarry face, 15 m high composed of buff-brown, massive algal-bryozoan biolithite. Fauna most abundant near eastern end of quarry; especially in loose blocks. Kirkby (1859), Trechmann (1914, 1945), Smith (1981). Sixteen species recognized, numbers: 1, 4, 5, 9, 10, 11, 13, 14, 18, 19, 21, 26, 27, 28, 29, 31.

Locality 8. Text-figure 13. Tunstall Hills East, Old trench. NZ 397542. Ford Formation, reef crest. 1 m of dark-brown, crystalline reef biolithite is exposed in a partially overgrown, shallow trench. Fauna is well-preserved and very abundant. Ten common species recognized, numbers: 1, 3, 4, 5, 9, 11, 21, 27, 28, 31.

ANALYTICAL TECHNIQUES

Relative Abundance

In this guide relative abundance is used as the basis for standardizing comparisons between various palaeocommunities within the Ford Formation reef. Relative abundance was calculated within each sample by dividing the number of individuals of each taxon by the total number of specimens recorded and is expressed as a percentage. These percentages are plotted as bar diagrams and give an instant visual indication of faunal composition for different samples collected from various reef facies (text-figs. 7, 13). A large bulk sample must be taken to produce a thorough quantitative profile. We consider our samples represent 98% of the most common species at each locality. The remaining 2% comprise rare fish and reptile remains which were not recorded in the bulk samples but have been found through general collecting. To evaluate the lateral distribution of faunal elements across the reef from west to east (backreef to reef crest), at Claxheugh railway cutting, sampling points were spaced at 1 m intervals and the number of individuals for each taxon were plotted on the transect as a bar chart (text-fig. 9). The width of the bar directly corresponds to the number of individuals recorded for each taxon.

As far as possible all of the fossils in the samples collected must be extracted and counted. The counting procedures required for each taxonomic group under consideration are different and produce variable degrees of accuracy. In our study brachiopods, gastropods, and nautiloids were counted as single individuals, crinoids were only counted as representing more than one individual when the number of ossicles probably exceeded those possessed by the organism. Echinoids are rare within the reef and the number of fragments ecountered did not exaggerate their relative abundance. Around 30% of the bivalves were found to be articulated in each sample. In these cases they were counted as individuals, where disarticulated shells were encountered the maximum number of either right or left valves was used.

Bryozoans posed a particular problem, as a single colony could be regarded as an individual unit. The majority of bryozoans found within the reef occur as smaller fragments, so 1 cm^2 of each fenestrate encountered was taken to represent one unit. The authors consider that the number of fragmented individuals does not give a biased overestimate of their abundance as they account for a large proportion of the overall reef fauna. Stick bryozoans (the trepostomes), were counted as 1 cm length of each colony representing one unit. It is recognized by the authors that the relative abundances calculated for each taxonomic group are by no means a measure of their original biological equivalence within a defined palaeocommunity, particularly with reference

to some localities where preservation is variable. Some of the palaeocommunities illustrated in this guide display variable degrees of faunal overlap, particularly as some generic elements, for example *Dielasma*, are found throughout the reef. Only where distinct spatial boundaries separate various faunal assemblages, has a palaeocommunity diagram been produced (text-figs. 8, 15–17).

The rates of reef growth and the longevity of the various taxa that comprised a palaeocommunity were probably highly variable through time and it is likely that the various samples analysed represent more than one life assemblage (biocoenosis). Comparison between palaeocommunities can still be justified as each sample represents a time-averaged accumulation and this is particularly valid in the evaluation of community evolution within the reef itself.

Frequency Distribution

The Ford Formation reef biota display a marked apparent upward decrease in size from reef base (Locality 3) to reef core (Locality 4). This was thought by Trechmann (1913, 1925) to represent faunal impoverishment due to growth in an environment where salinity gradually increased, leading first to 'stunting' and then final extinction of the entire reef biota. Smith (1981) pointed out that Trechmann's ideas were probably correct, although autogenic faunal succession (Walker and Alberstadt 1975), associated with approach to wave base, also may have been an important factor in influencing faunal distribution patterns. Analysis of population dynamics may help to evaluate whether salinity was a factor causing a decrease in faunal size or if environmental changes associated with reef growth were a cause of apparent stunting of the fauna. The brachiopod *Dielasma* is suitable as it is not facies restricted and is usually well-preserved occurring as calcite or dolomite casts. *Dielasma* is also found in monospecific masses and large, statistically-viable samples can be collected. It is also relatively easy to measure. Where sampling was possible for this guide, between ten and upwards of one hundred individuals were collected from each locality. The variation in sample size was partially due to outcrop size. The total length of the pedicle valve was used in all measurements.

The palaeoecological significance of size-frequency distributions has been described by many other workers, and it is not within the scope of this guide to discuss the details of their interpretation. The size-frequency distributions in this guide have only been used for comparative purposes. For those who wish to pursue the significance of size-frequency distributions and various case studies see Boucot (1953), Craig and Hallam (1963), Craig and Oertel (1966), McKerrow *et al.* (1969), Schmidt and Warme (1969), Richards and Bambach

(1975), and Fürsich & Kauffman (1984). Our interpretation of size-frequency distributions (e.g. text-figs. 7, 13) is described in detail for each locality under consideration in the faunal composition and ecology section (pp. 41–72).

Palaeocommunity Diagrams

One ultimate aim of palaeoecological studies is to reconstruct ancient communities. This is not straightforward because a great deal of information has been lost to the palaeontologist through predation, selective preservation, and post-mortem transportation. Palaeocommunity diagrams (text-figs. 8, 15–17) for each reef lithofacies type have been based upon quantitative sampling for faunal analysis at localities 1–8, field evidence from localities not described here, and lithological data. In modern marine benthonic communities as much as 80% of the biomass consists of soft-bodied organisms which, under normal processes of fossilization and diagenesis, are not preserved. Additionally, so much of the Permian reef in the Sunderland area has undergone dolomitization that even readily preservable hard parts such as shells etc. are sometimes poorly preserved and identification, even to generic level, is difficult. Consequently, the palaeocommunity diagrams for some localities are biased towards those species which were abundant and possessed hard parts. Therefore each community should be viewed as only a partial reconstruction, particularly since many of the reef lithologies have 'lost' their original fabrics and fauna through diagenesis.

PRESERVATION

Preservation of skeletal elements within the reef is highly variable, even within the same outcrop. This is due to the diagenetic history of the reef and the original mineralogy of the constituent organisms. As mentioned above, pervasive dolomitization has obliterated the primary reef fabric and fossils are generally poorly-preserved. There are notable exceptions, for example, the eastern end of Claxheugh railway cutting, Ford Quarry (locality 2) and the reef base at Tunstall Hills (locality 3), where fossil preservation is excellent.

The majority of Recent bivalves possess aragonitic shells (Tucker 1981) or, less commonly, a combination of calcite and aragonite, and as such are readily susceptible to alteration during diagenesis. A large proportion of the Ford Formation reef bivalves presumably also had aragonitic shells and, since the reef has been dolomitized, are commonly found as internal moulds. One notable exception is the reef bivalve *Pseudomonotis* which may have possessed a more stable calcitic shell (Newell and Boyd 1970) and is often found well-preserved even at

localities like 2 and 8 where fossil preservation is generally poor. Brachiopods are always found in a better state of preservation, even in dolomitized lithofacies, probably because they originally possessed more stable calcitic shells (Milliman 1974). Bryozoans may have had high Mg Calcite skeletons (Sandberg 1977) and display an enormous range in preservational states from internal moulds to external casts. At the reef talus locality (No. 6) bryozoans are often found as casts, which are coated by dolomite crystals giving a sugary appearance when viewed in strong sunlight. Echinoderms and crinoids are commonly replaced by single calcite or dolomite crystals, and often cleave upon extraction.

By comparison with Recent gastropods, the Permian reef forms also had aragonitic shells (Milliman 1974) and preservation is generally poor. Although dolomitization is often fabric destructive it may also be fabric replacive. Gastropods recovered locally from fine-grained reef crest dolomites at the eastern end of Ford Quarry, are often beautifully preserved, as dolospar casts, retaining original 'colour' patterns.

The reef base locality (No. 3) at Rock Cottage, Tunstall Hills is the only site where faunal preservation is generally excellent. All of the species known from the reef occur at this site although some are very rare (e.g. the fish *Janassa bituminosa*, text-fig. 14). Most of the coquinoid shelly fauna is preserved as calcite casts which, in thin section, preserve original shell microstructures in fine detail. Gastropods, particularly *Mourlonia* and *Naticopsis*, can be found retaining colour patterns (see cover and identification guide). Brachiopods, bryozoans, and bivalves are also well-preserved and are readily extractable in large numbers. The undolomitized reef base limestones at Tunstall Hills have also provided a great deal of new information on the diagenesis of the reef which is described by Tucker and Hollingworth (1986).

COLLECTING FROM THE REEF

All of the localities described in this guide are SSSI's and large scale fossil collecting is discouraged. However, good collections can be made from loose rubble, particularly from the reef base at Tunstall Hills and from the reef crest at Ford Quarry, where specimens can be picked up loose from weathered surfaces or scree slopes. A1 or $2\frac{1}{2}$ lb geological hammer plus a range of cold chisels should suffice for most field collecting. The majority of reef fossils are durable enough to survive transport during collection provided that they are well-wrapped in newspaper. Specimens from dolomitized reef lithofacies are often fragile and need to be placed in secure containers preferably with cotton wool or some other soft material.

CONSERVATION

Most of the fauna collected from the reef require little more than washing gently in warm water with a little detergent to remove soil, etc. Bryozoans are particularly fragile and will lose fine detail if they are cleaned too vigorously with a hard brush. Alternatively, specimens may be placed in an ultrasonic tank to remove soil from very delicate features, this method is particularly useful for spinose brachiopods. After washing, specimens must be thoroughly dried and stored in areas of low relative humidity. For specimens with adhering matrix, such as articulated brachiopods, gastropods, and bivalves a few well-placed light taps with a hammer and small cold chisel will usually release them completely from the rock. Disarticulated specimens can be prepared with a mounted needle or an engraving tool.

TAXONOMIC REVIEW OF THE REEF BIOTA

The taxonomy of the Permian reef flora and fauna was undertaken by workers such as William King, Richard Howse, James Kirkby, and Charles Taylor Trechmann. The first three authors had exhaustively collected and described nearly all of the Permian genera known today by the 1860s and it was not until 1945 that Trechmann described several new species from the Ford Formation.

However, despite a fairly extensive literature describing Zechstein stratigraphy, numerous taxonomic problems relating to the reef fauna remained until relatively recently. These taxonomic problems first arose when King (17 August 1848) and Howse (19 August 1848) published descriptive faunal catalogues almost simultaneously. King published his monograph in 1850 and added a supplement in 1856. Howse did not publish his supplement until 1857 and accused King of claiming priority over several of his species, which were described in Kings' catalogue published on 17 August 1848. This disagreement led to several nomenclatural problems, particularly with relation to the brachiopods.

Trechmann was well aware of the above problems and on several occasions advocated a complete revision of the Permian fauna (1913, 1921). The first detailed revision of the Permian reef biota was carried out by Logan (1962) who studied the bivalve and brachiopod fauna. Numerous early taxonomic problems were examined and several new genera were proposed. A monograph on the bivalves was produced (Logan 1967) but the brachiopods were never published.

The gastropod section of the King monograph (King 1850) was revised by Pattison (1977) who provided updated names. However, as with other genera in the same catalogue, the gastropods are poorly

preserved (having been collected from dolomitized lithologies) and it is likely that some of the illustrations are composite reconstructions. The recent discovery of an extensive well-preserved fauna from undolomitized reef-base limestones at Tunstall Hills has necessitated some revision of the gastropods for this guide.

Echinoderm faunas from the reef are confined to two genera a crinoid and an echinoid. The crinoid fauna has recently been revised by Donovan *et al.* (1986). The bryozoans were studied by Southwood (1985).

IDENTIFICATION GUIDE

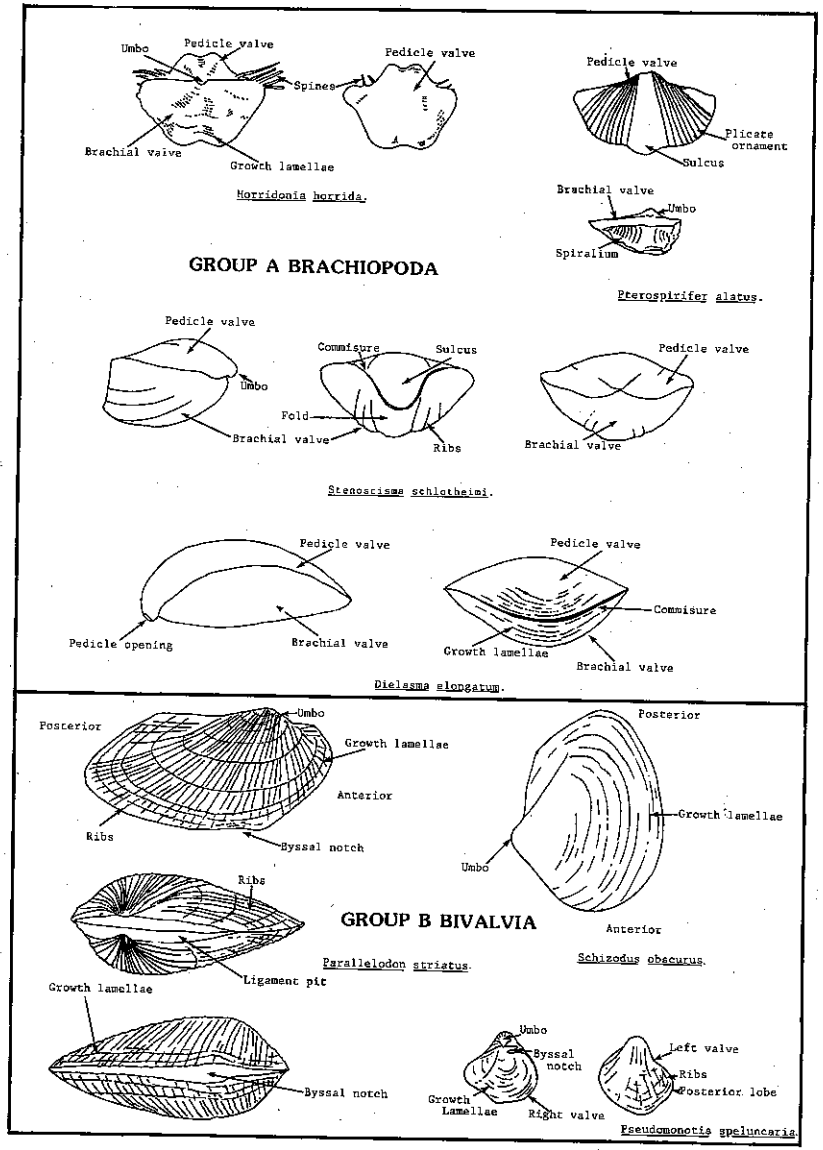
Most of the common shelly macrofossils from the reef, which are illustrated in the guide, are identified to specific level. A few forms are identified to generic level only. This is due to problems of species discrimination, e.g. for the bivalve *Bakevellia* which displays a wide degree of ecophenotypic variation. All of the genera and species illustrated can be found at the outcrops described in the guide but only the reef base at Tunstall Hills (locality 3) yields the entire range of reef fossils at one locality. Further details can be found in the various monographs mentioned in the taxonomic review.

Mode of Life Reconstructions

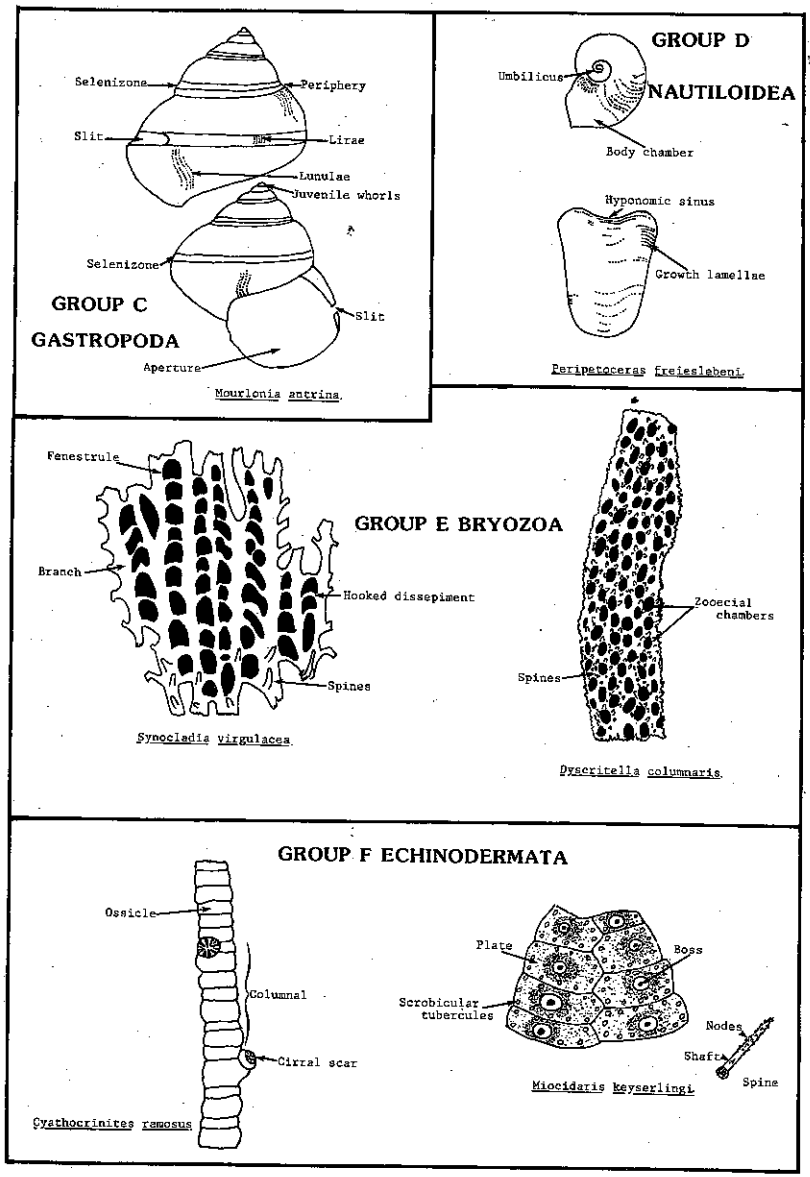
The adaptation of an organism to its physical environment is reflected in its morphology, physiology, and life history. Any palaeoecological information derived from fossil morphology is dependent upon a sound taxonomic base. There are several methods which can be used to interpret the functional morphology of a fossil organism and most studies have been based on two techniques. The first and most direct method is known as inference by homology. This is only applicable where identical fossil representatives of extant genera or species are known, and where the life habits, distribution, and relationship to the environment of the Recent representatives are well defined.

The interpretation of life habits in a large proportion of Palaeozoic fossils is somewhat speculative as one is dealing with extinct families, genera, or even higher categories which may be only distantly related to living forms. A large proportion of the EZ1 reef biotas are not represented by closely-related living genera so that postulated functional morphology and feeding habits are explained by analogy. Analogy involves the comparison of morphological features of fossil organisms with those of living organisms which may not be closely related to the fossil.

The life habits of the most abundant species found within the reef



TEXT-FIG. 5. Main morphological terms used in the description of the most-abundant reef genera.



are based upon sound taxonomic and morphological features established by earlier workers. Each reconstruction is based on comparative morphology, as some of the Permian shelly genera are represented by Recent forms which are assumed to have had similar modes of life to their Permian precursors. Much of the soft-part morphology is based upon speculative reconstructions.

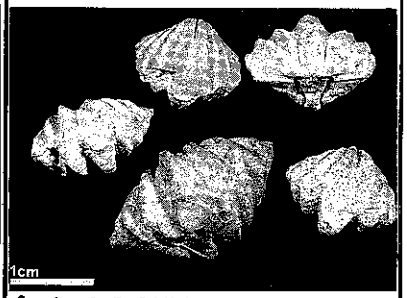
Use of the Guide

Text-figure 5 shows the main morphological features and terms used in the recognition and description of the most abundant reef genera. Each fossil species has been placed within one of six groups, group A: BRACHIOPODA, group B: BIVALVIA, group C: GASTROPODA, group D: NAUTILOIDEA, group E: BRYOZOA and group F: ECHINODERMATA. In the subsequent guide a photograph of the specimen is followed by a camera-lucida illustration showing one or more views. The main morphological features of each genus or species are then described. This is in turn supplemented by a reconstruction of mode of life, plus a short description of inferred feeding habit. Very rare taxa are only illustrated by camera-lucida drawings. The teeth and a complete reconstruction of the fish *Janassa bituminosa* are illustrated in text-figure 14 (p. 54). All of the species described in the identification guide, pages 17–32, are number coded to allow direct comparison with the relative-abundance histograms constructed for each locality (text-figs. 7, 13) and the palaeocommunity diagrams (text-figs. 8, 15–17).

GROUP A BRACHIOPODA

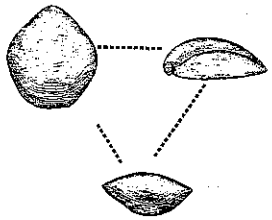
1. Superfamily: Terebratulacea
Family: Dielasmatidae
Subfamily: Dielasmatinae
Dielasma King
Dielasma elongatum (Schlotheim)

ALL LOCALITIES

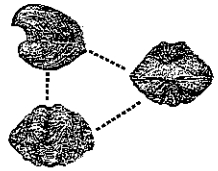


2. Superfamily: Spiriferinacea
Family: Spiriferinidae
Subfamily: Spiriferellinae
Spiriferellina King
Spiriferellina cristata (Schlotheim)

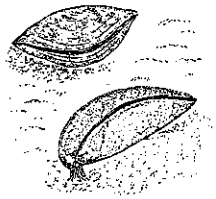
LOCALITIES. 2, 3, 4, 5, 6.



Shell is oval in outline, pedicle and brachial valves convex, pedicle valve with broad shallow sulcus and brachial valve with corresponding broad fold. Ornament of fine growth lamellae.



Shell is subquadrangular in outline. Coarsely plicate. Large interarea with open delthyrium. Non-alate. Prominent incurved umbo on pedicle valve. Plications rounded to angular. Strong angular fold and sulcus.



Epifaunal suspension feeder with thick fleshy functional pedicle. The pedicle may have divided into rootlets, penetrating the substrate to provide increased attachment. Often found as nests comprising a wide size range.

Epifaunal suspension feeder with functional pedicle. Commonly found as nests except on the upper reef slope.

3. Superfamily: Productacea
Family: Dictyoclostidae
Subfamily: Horridoniinae
Horridonia Chao
Horridonia horrida (J. Sowerby)

LOCALITIES. 1, 3, 6, 8.

Shell concavo-convex with pedicle valve strongly convex and thicker than brachial valve. Shell otherwise smooth apart from fine growth lamellae. Spines are scattered over the pedicle valve but are concentrated near the umbo and radiate in all directions from shell.

Semi-infaunal suspension feeder with non functional pedicle. The dense spine network probably provided stability in a soft substrate and may have acted as a trap to hold a mass of fine camouflaging sediment.

4. Superfamily: Stenoscismatacea
Family: Stenoscismatidae
Subfamily: Stenoscismatinae
Stenoscisma Conrad
Stenoscisma schlotheimi (Von Buch)

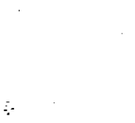
LOCALITIES. 1, 6, 7, 8.

Shell triangular to subquadrate in outline, pedicle valve strongly convex with broad shallow to deep sulcus. Brachial valve with corresponding fold. Ribs present on lateral flanks although there are some completely smooth forms.

Epifaunal suspension feeder with reduced pedicle, which may have acted as a tether only. On well preserved specimens marginal expansions occur at the shell edge, which probably increased stability on a soft substrate.

5. Superfamily: Strophalosiacea
Family: Strophalosiidae
Strophalosia King
Strophalosia sp. King

LOCALITIES. 1, 2, 7, 8.



Shell generally circular in outline and concavo-convex. Pedicle foramen closed. Brachial valve is moderately concave. Both valves are covered by a dense network of fine hair-like spines which radiate in all directions from the shell.

Semi-infaunal suspension feeder, mode of life similar to *Horridonia* but with denser network of spines.

6. Superfamily: Athyridacea
Family: Athyridae
Subfamily: Athyrinae
Cleiothyridina Buckman
Cleiothyridina pectinifera (J. de C. Sowerby)

LOCALITIES. 1, 6.

Shell equally biconvex, elliptical in outline. The pedicle valve has a prominent beak with open delthyrium. Shell ornamented with regular growth lamellae. On well preserved specimens concentric rows of fine hair-like spines occur on both valves. Commissure is straight.

Epifaunal suspension feeder with functional pedicle, commonly found as nests.

7. Superfamily: Spiriferacea
Family: Spiriferidae
Pterospirifer Dunbar
Pterospirifer alatus (Schlotheim)

LOCALITIES. 1, 6.

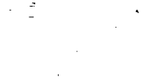
Shell rectangular in outline with maximum width along hinge line, lengthened to produce alate extremities. Pedicle valve with sulcus, brachial valve with fold. Both valves are ornamented by a variable number of rounded ribs, and fine growth lamellae.

Epifaunal suspension feeder with functional pedicle. Shell stability attained through extended hinge line to produce slender alae. The fold and sulcus may have served to separate inhalent and exhalent water currents. *Pterospirifer* is always found as single specimens, and may have been a solitary form.

8. Superfamily: Orthotetacea
Family: Schuchertellidae
Streptorhynchus King
Streptorhynchus pelargonatus (Schlotheim)

LOCALITY. 3.

Shell triangular in outline, pedicle and brachial valves convex. Pedicle valve twisted with high interarea. Hinge line short. Both valves ornamented by fine ribs and irregular growth lamellae.



Epifaunal suspension feeder. The twisted beak suggests some form of close attachment to hard substrates by a short pedicle. *Streptorhynchus* may have been a crevice dweller.

GROUP B BIVALVIA

9. Superfamily: Pteriacea
Family: Bakevelliidae
Bakevellia King
Bakevellia spp. (Schlotheim)

LOCALITIES. 1, 2, 3, 4, 5, 7, 8.

10. Superfamily: Arcacea
Family: Parallelodontidae
Parallelodon Meek and Worthen
Parallelodon striatus (Schlotheim)

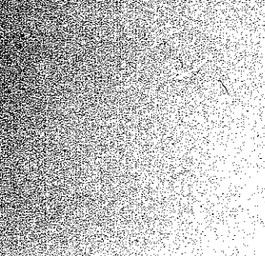
LOCALITIES. 1, 2, 3, 4, 5, 6, 7.

Shell mytiliform in outline, slightly inequivalve, posteriorly elongated. Right valve less convex than left valve. Beaks anteriorly placed. Cardinal area elongate with multivincular ligament pits. Ornament of fine commarginal growth lamellae. On some specimens growth lamellae sinuated near byssal notch.

Shell trapezoidal in outline, equivalve. Umbones prominent and sharply incurved near anterior end of shell. Posterior end rounded. Ornament consists of narrow beaded ribs. Ribs crossed by irregular growth lamellae which attenuate and become more sinuous near byssal notch, which is most prominent near mid-anterior part of shell.

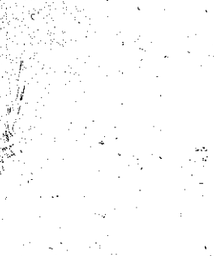
Epibyssate - endobyssate suspension feeder. Byssal attachment from antero-ventral part of shell. Foot reduced but functional, which would enable *Bakevellia* to secrete byssus. Possible crevice dweller.

Epibyssate suspension feeder. Many specimens exhibit a distinct byssal sinus suggesting strong byssal attachment from the ventral part of shell. *Parallelodon* was probably a nestler under boulders/pebbles or a crevice dweller.



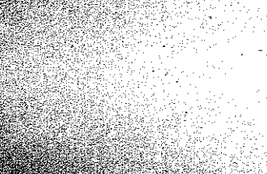
11. Superfamily: ?Pectinacea
Family: Pseudomonotidae
Pseudomonotis von Beyrich
Pseudomonotis speluncaria (Schlotheim)

LOCALITIES. 1, 2, 3, 4, 7, 8.



12. Superfamily: Carditacea
Family: Permophoridae
Stutchburia Etheridge jnr.
Stutchburia modioliformis (King)

LOCALITY. 4.



Shell is subtriangular in outline, inequivalve, left valve convex, with prominent rounded posterior lobe. Right valve flat to slightly convex, umbo small and possessing well defined byssal notch. Variable ornament on left valve consists of fluted growth lamellae and/or rounded radiating ribs.

Shell obliquely elongate, mytiliform. Both valves convex. Umbones anteriorly placed, beaks inward pointing. Hinge line short. Ornament consists of regular commarginal growth lamellae and faint radial ribs.

Epibyssate suspension feeder, clamped by thick byssus to substrate. Posterior lobe probably served to increase stability in a turbulent environment and prevent overturning.

Endobyssate suspension feeder. *Stutchburia* possessed a reduced but functional foot to secrete the byssus. Byssal attachment through antero-ventral part of shell.

13. Superfamily: Ambonychiacea
Family: Myalinidae
Liebea Waagen
Liebea squamosa (J. de. C. Sowerby)

LOCALITIES. 1, 2, 3, 4, 7.

14. Superfamily: Carditacea
Family: Permophoridae
Permophorus Chavan
Permophorus costatus (Brown)

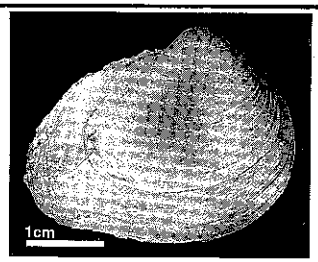
LOCALITIES. 2, 3, 4, 5, 7.

Shell mytiliform, similar to Recent mussels, but with low cardinal area for duplivinicular ligament. Prominent umbones at anterior end of shell. Hinge edentulous. Ornament consists of regular growth lamellae only. Lamellae display slight sinuation near mid-anterior part of shell.

Shell equivalve, rectangular in outline. Posteriorly elongate, umbones near anterior margin. Hinge line long with deep ligament pit. Surface ornament of irregular growth lamellae and a variable number of ribs which diverge posteriorly from the umbones. Byssal notch well developed in large individuals.

Epibyssate suspension feeder. Byssal attachment through anterior part of shell. Foot reduced but probably functional. Commonly forms monospecific clumps.

Endobyssate suspension feeder. Sinuation of growth lamellae at antero-ventral part of shell indicates point of byssal emergence. Foot reduced but probably capable of sluggish reburrowing if exhumed.

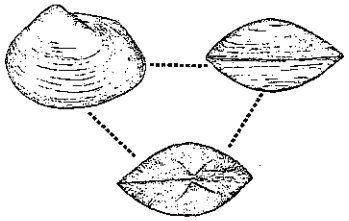


15. Superfamily: Trigoniacea
Family: Schizodidae
Schizodus de Verneuil and Murchison
Schizodus obscurus (J. Sowerby)

LOCALITIES. 1, 2, 3.

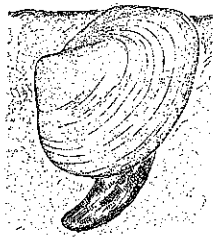
16. Superfamily: Edmondiacea
Family: Edmondiidae
Edmondia de Koninck
Edmondia elongata (Howse)

LOCALITY. 3.



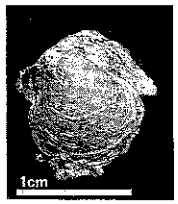
Shell thick, subtrigonal in outline, equivalve. Umbones prominent, inward pointing beaks, displaced slightly towards anterior. Anterior margin rounded, posterior margin subtruncate. Shell ornamented by fine commarginal growth lamellae.

Shell ovate, somewhat elongate and equivalve. Umbones not prominent, located near anterior margin of shell. Anterior and posterior margins evenly rounded. Surface ornament of regular commarginal growth lamellae only.



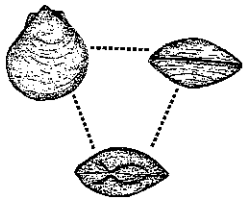
Shallow infaunal non-siphonate suspension feeder, with posterior margin parallel to substrate/water interface. Foot probably well developed to enable rapid burrowing.

Non-siphonate infaunal suspension feeder. Shallow burrower with active foot. Shell orientated in sediment with posterior margin parallel to substrate surface.



17. Superfamily: Aviculopectinacea
Family: Aviculopectinidae
Subfamily: Streblochondriinae
Streblochondria Newell
Streblochondria pusilla (Schlotheim)

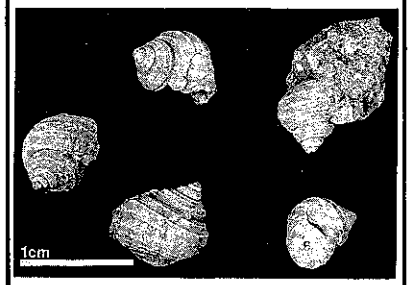
LOCALITIES. 1, 6.



Shell ovate, slightly inequivalve. Right and left valves convex. Anterior auricle slightly larger than posterior auricle. Umbonal beaks prominent and project beyond the hinge line. Shell ornament consists of fine concentric growth lamellae only.

Suspension feeder. Asymmetry of auricles and flatter right valve suggest epibyssate life habit with right valve resting on the substrate.

GROUP C GASTROPODA

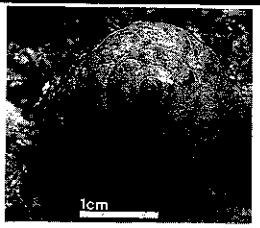


18. Superfamily: Platyceratacea
Family: Holopeidae
Yunnania Mansuy
Yunnania tunstallensis (Howse)

LOCALITIES. 2, 3, 4, 5, 7.

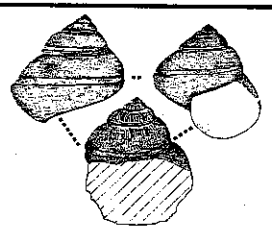
Shell turbiniform, with step-like profile near sutures. Upper slope of whorls near suture, flat to slightly angular and normal to coiling axis. Ornament of fine growth lines and faint revolving lirae.

? Algal grazer, does not display any of the features of platyceratids adapted to a coprophagous mode of life.

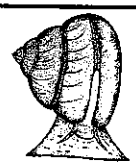


19. Superfamily: Pleurotomariacea
Family: Eotomariidae
Mourlonia de Koninck
Mourlonia antrina (Schlotheim)

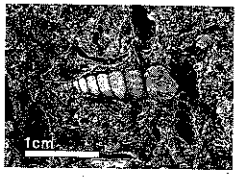
LOCALITIES. 1, 3, 4, 5, 7.



Shell turbiniform, though some specimens more trochiform. Whorl profile rounded, angular periphery, base rounded. First two whorls without selenizone. Selenizone flat to slightly concave. Slit open for about one third of largest whorl. Ornament of fine revolving lirae. Colour pattern sometimes preserved as a series of collabral bands.



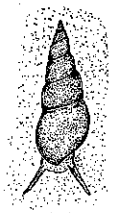
Algal grazer, probably confined to firm substrates. Shell carried at angle to foot, with columellar axis at around 60° to the visceral mass and shell twisted towards the rear. Faecal matter vented via the slit preventing clogging of gills and re-ingestion by snail.



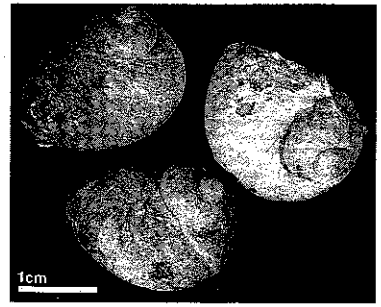
20. Superfamily: Subulitacea
Family: Meekospiridae
Meekospira Ulrich
Meekospira symmetrica (Howse)

LOCALITY. 3.

Shell sharply acuminate, numerous high whorls. Whorl profile between sutures slightly rounded. Ornamentation of faint growth lines.

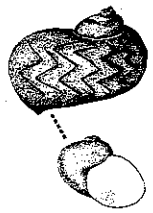


Algal grazer, ? detritus feeder. Recent high spired gastropods are mostly shell draggers. *Meekospira* was more than likely a shell dragger and consequently a slow moving, possibly burrowing form.

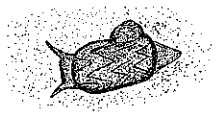


21. Superfamily: Neritacea
Family: Neritopsidae
Subfamily: Naticopsinae
Naticopsis M'Coy
Naticopsis minima (Brown)

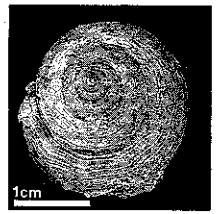
LOCALITIES. 2, 5, 7, 8.



Shell low spired, globular, 'naticiform'. Largest body whorl occupies largest proportion of shell. Whorl profile strongly rounded, slightly flattened near suture. Shell thickened near lip of aperture. Ornamentation consists of fine growth lines. Colour pattern sometimes preserved as a series of zig zag lines.

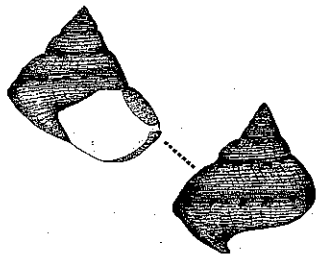


Algal grazer. Probably a slow moving form.

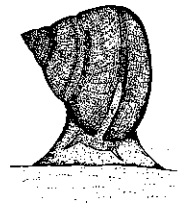


22. Superfamily: Pleurotomariacea
Family: Phymatopleuridae
Phymatopleura Girty
Phymatopleura verneuili (Geinitz)

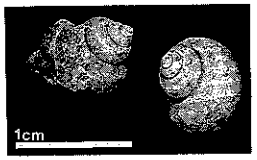
LOCALITY. 3.

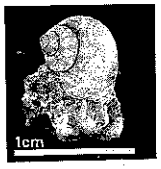


Shell strongly trochiform with step-like profile. Whorl profile angular with strong noded ornament below suture. Juvenile whorls devoid of ornament. Later whorls ornamented by complex reticulate network of sharp transverse and revolving lirae. Selenizone narrow, open for about one third of largest whorl.



Algal grazer. Shell probably held at angle to foot, with columellar axis at around 60° to the visceral mass and shell twisted towards the rear. *Phymatopleura* was probably confined to hard substrates. Faecal matter vented via the slit preventing clogging of gills and re-ingestion by snail. *Phymatopleura* was probably a slow moving form.



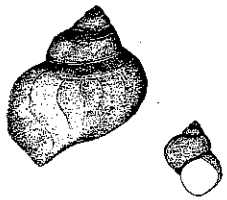


23. Superfamily: Loxonematacea
Family: Coelostylinidae
Coelostylina Kittl
Coelostylina permiana (Brown)

LOCALITY. 3.

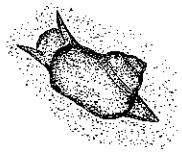
24. Superfamily: Anomphalacea
Family: Anomphalidae
Anomphalus Meek and Worthen
Anomphalus permianus (King)

LOCALITY. 2.



Shell turbiniform with step-like profile near sutures. Upper slope of whorl near suture flat to slightly angular and normal to coiling axis, bordered by sharp angulation. Outer portion of whorl rounded. Ornament of fine growth lines.

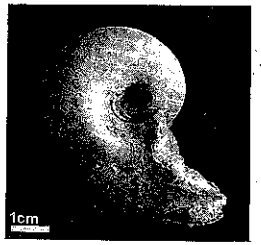
Shell small, robust, whorl profile rounded, gently arched between sutures, rounded at periphery. Base flat. Shell surface smooth, no ornament.



? Algal grazer. Probably a slow moving form. Abundant in cryptalgal laminites.

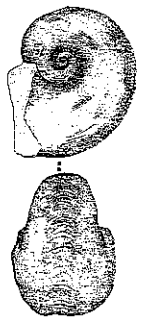
Algal grazer. Smooth shell may have been invested by the mantle.

GROUP D NAUTILOIDEA

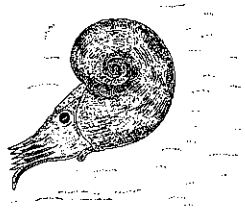


25. Superfamily: Clydonautilaceae
Family: Liroceratidae
Peripetoceras Hyatt
Peripetoceras freieslebeni (Geinitz)

LOCALITY. 2.

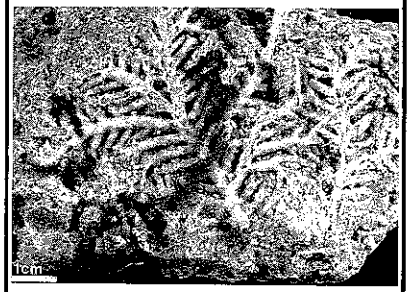


Shell strongly involute, globular with deep umbilicus. Whorl section depressed, venter rounded with median sulcus. V-shaped hyponomic sinus present on penultimate whorl.



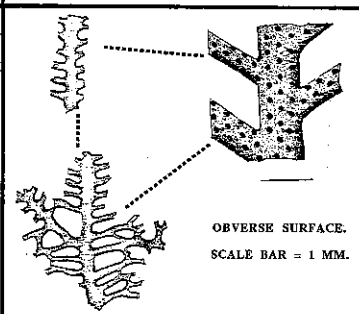
Nektonic, vagile carnivore/scavenger. Commonly found in monospecific masses particularly in reef crest lithofacies.

GROUP E BRYOZOA

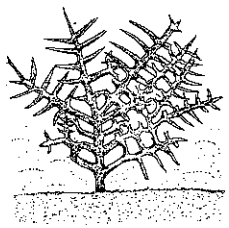


26. Family: Polyporidae
Subfamily: Acanthocladiinae
Acanthocladia King

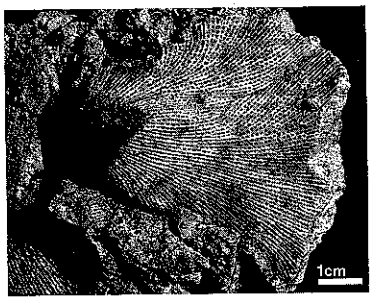
LOCALITIES. 1, 2, 3, 4, 5, 6, 7.



Colony erect, pinnate or bush-like with main branch which divides dichotomously to form subsidiary branches or pinnae. Where branches fuse, irregular fenestrules may form. Zooecial apertures on obverse surface only. Reverse surface smooth but may display fine striae.

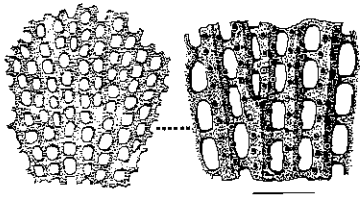


Suspension filter feeder. Colony probably formed from single erect branch attached to the substrate by spines near the colony origin. Bush-like colonies common.



27. Family: Fenestellidae
Fenestella Lonsdale
Fenestella retiformis (Schlotheim)

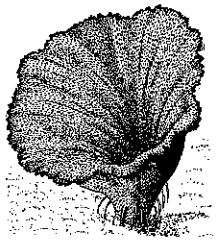
LOCALITIES. 1, 3, 4, 5, 6, 7, 8.



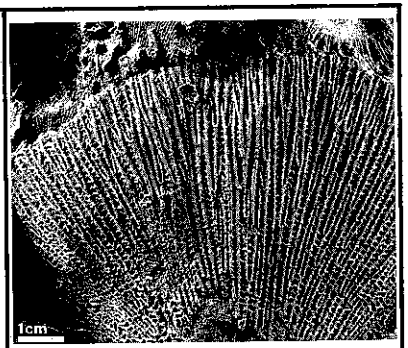
OBVERSE SURFACE.

SCALE BAR = 1 MM.

Colony erect, cone shaped, composed of thin dichotomously branching zoaria connected by short dissepiments. Fenestrules box-like. Zooecial apertures open on obverse surface only. Surface ornament confined to longitudinal striations only.

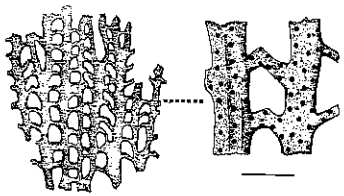


Suspension filter feeder. Holdfast weak. Colony was supported by numerous spines which occur abundantly on the reverse surface close to the colony origin. Colony size variable.



28. Family: Polyporidae
Subfamily: Acanthocladiinae
Synocladia King
Synocladia virgulacea (Sedgewick)

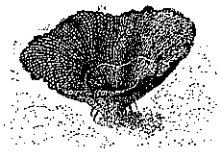
LOCALITIES. 1, 3, 4, 5, 6, 7, 8.



OBVERSE SURFACE.

SCALE BAR = 1 MM.

Colony erect, cone shaped, composed of relatively broad branches with some dichotomous branches. Fenestrules commonly irregular, bounded by hooked dissepiments. Subsidiary branches common near distal margins of colony. Zooecial chambers on obverse surface only.



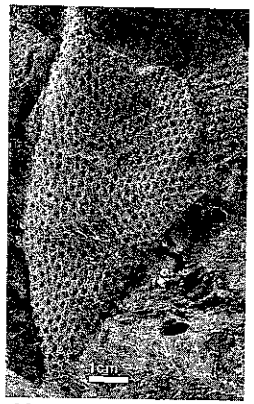
Suspension filter feeder. The colony origin is supported by a dense network of supportive spines. Colonies are commonly found complete as they have a 'stouter' framework than other fenestrates.

29. Family: Dyscritellidae
Dyscritella Girty
Dyscritella columnaris (Schlotheim)

LOCALITIES. 3, 4, 5, 7.

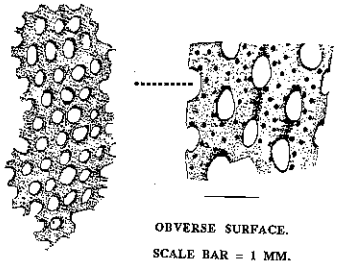
Colony erect to adnate (encrusting). Occurs as ramose, cylindrical branches, forming bush-like colonies, or flat encrusting sheets. Zooecial apertures open in all directions and surrounded by numerous short spines.

Suspension filter feeder. Forms both adnate and ramose colonies. Commonly found encrusting bivalves, especially *Pseudomonotis*.



30. Family: Polyporidae
Subfamily: Reteporidrinae
Kingopora Morozova
Kingopora ehrengerbi (Geinitz)

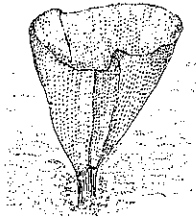
LOCALITY. 3.



OBVERSE SURFACE.

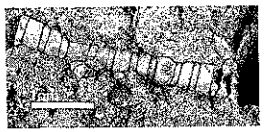
SCALE BAR = 1 MM.

Colony steeply erect, cone shaped. Fenestrules small, oval to circular in shape. Zooecial apertures found on the reverse surface. Near colony base, thick calcified holdfast developed. Small spines may be developed near the colony origin.



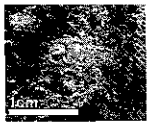
Suspension filter feeder. *Kingopora* is only found in the reef base and lower reef core. The fragile nature of the zoarium suggests that *Kingopora* could only tolerate low energy environments.

GROUP F ECHINODERMATA



31. Superfamily: Cyathocrinidae
Incertae familiae
Cyathocrinites Miller
Cyathocrinites ramosus (Schlotheim)

LOCALITIES. 3, 4, 5, 6, 7, 8.

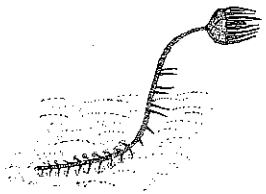


32. Family: Miocidaridae
Miocidaris Doderlein
Miocidaris keyserlingi (Geinitz)

LOCALITY. 3.

Cup broad and bowl shaped with radial arm facets, stem xenomorphic, dististele attached to substrate by cirriferous runner. The mesistele provided elevation of the crown above substrate level. Proxistele composed of numerous low columnals, probably flexible. Arms unknown apart from few dissociated brachials. Pinnules absent.

Test small, subspherical, radially symmetrical. Interambulacra wider than ambulacra, areoles well developed, surrounded by scrobicular tubercles. Primary tubercles perforate. Spines long and slender. Shaft ornamented by network of nodes or small projections.



Rheophilic suspension feeder. The flexible stem would have allowed the crown to change orientation in response to changes in current direction. *Cyathocrinites* may have formed crinoid meadows on the outer reef slope.

Vagile algal grazer, or opportunistic omnivore. Epifaunal, moving over hard substrates using spines, and tube feet, rasping algae etc. off substrates with lantern.

FEEDING STRATEGY OF THE REEF BIOTA

Most of the reef shelly biotas were epifaunal suspension-feeders and obtained their food near or above the substrate-water interface. This includes the brachiopods, bryozoans, crinoids, and some of the bivalves. The majority form the primary consumer level of the trophic pyramid. Deposit-feeding bivalves are absent and this implies that there was little organic detritus beneath the sediment-water interface in sediments behind the main reef. Browsing herbivores are almost exclusively represented by the gastropods. Higher feeding levels are represented by opportunistic scavengers, omnivorous, and carnivorous forms. This includes one echinoid genus, chitons, one nautiloid genus, fish, and a single tetrapod. The dominance of suspension feeders in the reef suggest that the water column above the substrate-water interface was rich in suspended food and organic detritus. Also the substrate was firm or lithified to allow attachment by epibyssate and pedunculate genera. The presence of quasi-infaunal forms, endobyssate, and rare infaunal genera suggests the localized presence of soft substrates within the main reef framework. The evidence of early-marine cements is consistent with the abundance of epifaunal genera as there would be widespread lithified substrates suitable for attachment by these forms. Finally, the water column was relatively clear with little suspended sediment. Laminites, presumably of algal origin, preserved throughout the reef, suggest that light effectively penetrated for several metres into the water column, and possibly well down the fore reef slope.

EVOLUTION OF THE REEF COMPLEX

Block reconstructions showing the evolution of the reef are illustrated in text-figure 6 which gives a summary of each stage, the stratigraphic location of the relevant palaeocommunity, and the locality where the particular stage of reef development can be directly observed. Further information is provided here including the location of outcrops displaying the latest stages of reef development that are found outside the area described in this guide. (Fuller ecological details for localities 1–8 are given in the faunal composition and ecology section, pp. 41–72.) The changes in faunal composition and diversity may be visualized, both vertically in time and laterally in space, using the reconstruction of selected palaeocommunities (text-figs. 8, 15–17). Differences in biotic composition within various reef sub-facies are attributed to the creation of reef microhabitats with variable environmental regimes, that were profoundly influenced by growth of the reef itself. Faunal changes in the reef may have been caused by autogenic or allogenic community succession described by Walker and Alberstadt (1975).

Stage 1; text-figs. 6, 15

The discovery of undolomitized reef-base limestones at Tunstall Hills (locality 3) has yielded a previously unknown, well-preserved shelly fauna, which has facilitated taxonomic descriptions and understanding of genera that were otherwise too poorly-preserved to be accurately identified. The reef is founded upon a coquina bank (Stage 1, locality 3), which contains an abundant and diverse fauna of brachiopods, bivalves, gastropods, and bryozoans (text-fig. 15) most of which are strictly stenohaline. The coquina contains a shelly fauna that occupied a variety of microhabitats. The fauna includes epifaunal, suspension-feeding bryozoans and quasi-infaunal, pedunculate, and ?cemented brachiopods. Epibyssate and endobyssate bivalves are common, as are vagile burrowing forms. Gastropods are diverse in the coquina but echinoderms are relatively rare. Higher feeding levels are represented

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TEXT-FIG. 6. Block reconstructions of the main stages in the evolution of the Ford Formation reef, based on Smith (1981) and Hollingworth and Tucker (1987).

Stage 4—Diversification

Reef dominated volumetrically by bryozoans. Distinct fore reef slope. Evolution of sub-communities within various reef sub-facies. Fauna diverse, but some genera, particularly spinose productids, abundant in reef talus and lower reef slope. Some differentiation in bryozoan distribution across reef. Reef talus palaeocommunity, text-fig. 17. Locality 6.

Stage 3—Growth

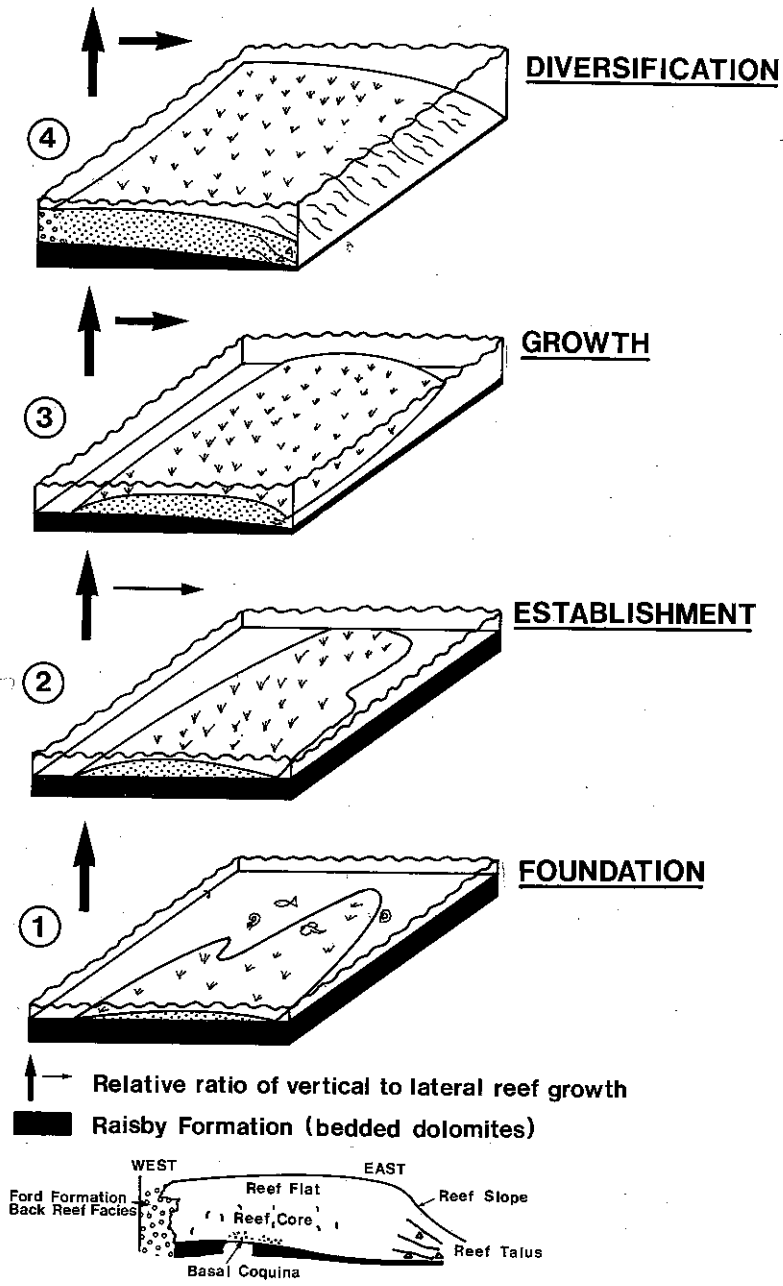
Continual basin subsidence matched by growth of reef vertically upwards and laterally basinwards. Initiation of talus wedge at edge of prograding reef. Evolution of niches within developing reef framework. Abundant marine cement precipitation. Lower reef core palaeocommunity, text-fig. 8. Locality 1.

Stage 2—Establishment

Rapid subsidence of basin and submergence of coquina bank. Establishment and growth of bryozoans upon lithified substrates. Fauna diverse and abundant with some niche differentiation. Bryozoans widely distributed. Abundant marine cement precipitation. Lower reef core palaeocommunity, text-fig. 8. Locality 1.

Stage 1—Foundation

Formation of coquina bank at edge of carbonate platform. Diverse and abundant cosmopolitan shelly biota. Water depths shallow in region of a few metres, with occasional and localized emergence of coquina. Abundant, voluminous, inorganic marine cement precipitation between bioclasts. Majority of shelly fauna cemented in life position. Reef base palaeocommunity, text-fig. 15. Locality 3.



by fish, for example, *Janassa bituminosa* (text-fig. 14). The reef base coquina accumulated where water depths were mostly in the order of 2 to 3 m, but with occasional and local emergence. Most shell transport was within the accumulating shell bank.

Stages 2 and 3; text-figs. 6–8

The precipitation of marine cements between bioclasts combined with the binding and baffling action of bryozoan frameworks finally led to the establishment and growth of the reef itself. These stages, 2 and 3, are represented by locality 3 reef base/reef core transition and locality 1, lower reef core (text-figs. 7, 8).

Sea level rise and/or basin subsidence led to submergence of the coquina bank (stages 2 and 3) and development of the lower reef core (text-figs. 7, 8; locality 1), which is dominated volumetrically by bryozoans. The lower reef core probably accumulated in fairly deep water (stages 3 and 4) with variable energy levels. There is a wide degree of

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TEXT-FIG. 6 continued.

Stage 8—Death

Rapid evaporative drawdown of Zechstein cycle 1 sea. Widespread catastrophic extinction of reef fauna. Subaerial exposure of reef flat, crest and slope. Deposition of anhydrite against steep outer reef slope. Early dolomitization of reef. Lithologies representing this stage are not present in the Sunderland area.

Stage 7—Maturity

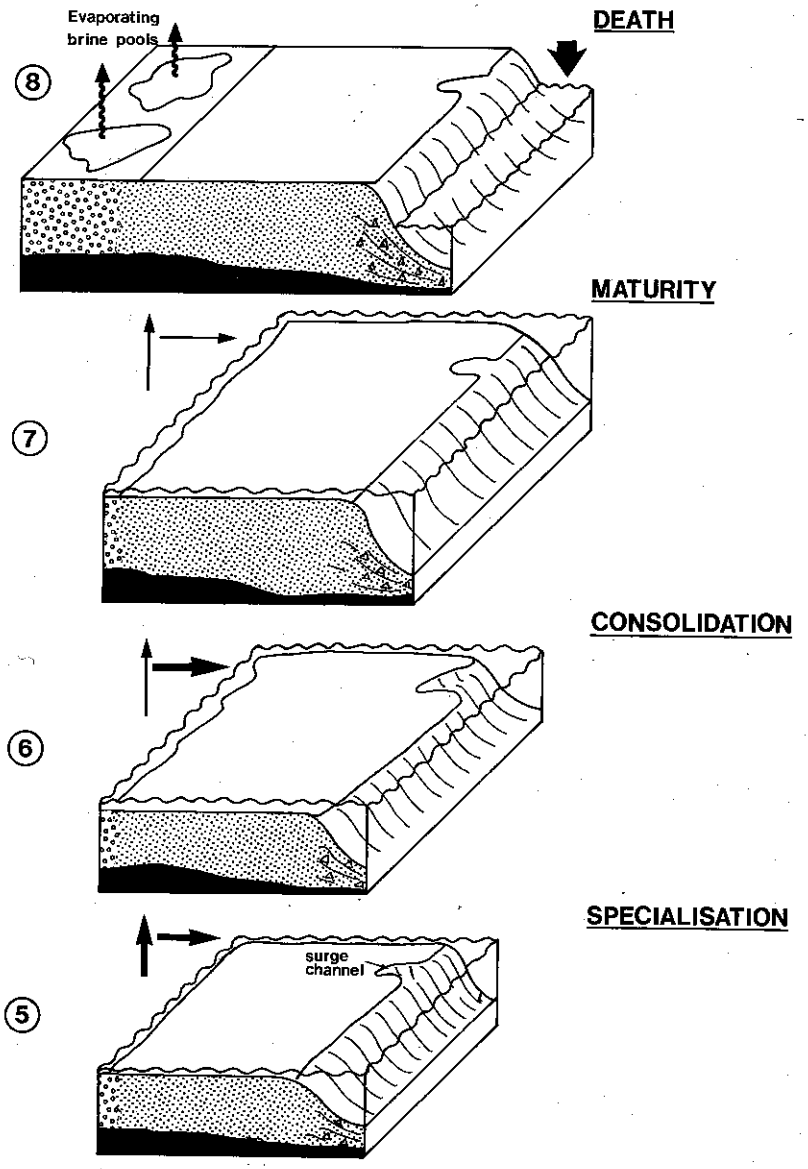
Maximum thickness (100 m) and width of reef (1 to 2 km). Highest diversity faunas found in reef crest and slope. Algal laminites abundant in reef flat. Extensive, contemporaneous inorganic cementation of reef flat laminites. Lithologies representing this stage are not present in the Sunderland area.

Stage 6—Consolidation

Extensive development of reef flat. Steep outer reef slope with large talus wedge. Rapid lateral growth basinwards, over talus contemporaneously eroded from reef crest. High-stress environment over reef flat. Faunal diversity maintained at reef crest and slope areas only. Complete restriction of large spinose productids to lower reef slope and talus areas. Marine cement precipitation abundant in reef flat and reef crest areas. Localities 5 and 8.

Stage 5—Specialization

Development of Reef flat. Upward growth limited to subsidence rate. Rapid basinwards migration over reef talus. Distinct sub-communities within reef sub-facies. Bryozoans specialized to various reef environments. Periodic subaerial exposure of reef flat in peritidal environment. Diverse fauna at reef crest. Development of surge channels. Backreef, Reef core, Reef crest; Locality 2. Reef core palaeocommunity, text-fig. 16. Localities 4 and 7.



faunal mixing (text-fig. 7), except for a few epibyssate bivalve genera occurring in association with bryozoan thickets. Crinoids are widely distributed in the lower reef core but become more abundant at higher levels only in the reef crest, slope, and talus areas. A similar distribution is observed for other reef taxa such as the large, quasi-infaunal productid *Horridonia* which is only found in the reef talus (text-fig. 17) when the reef reached sea level.

Stages 4 and 5; text-figs. 6, 16, 17

Distinct, specialized faunal communities (text-figs. 16, 17; localities 4, 6, 7) only evolved when the reef reached sea level (stages 4 to 5) and was migrating rapidly basinwards over its own talus. Upward growth was probably related to the rate of subsidence combined with possible sea-level fluctuations.

Faunal specialization (stage 5), was probably associated with the development of an extensive reef flat behind the prograding reef crest, a steep outer reef slope, and an extensive talus wedge (stages 5 to 6). Upper reef core lithofacies (locality 4), contain lower-diversity faunas although there may be larger numbers of individuals. The upper parts of the reef also contain *Dielasma* populations (text-fig. 13) that are composed mainly of juveniles which represent high mortality events.

Stages 6, 7, and 8

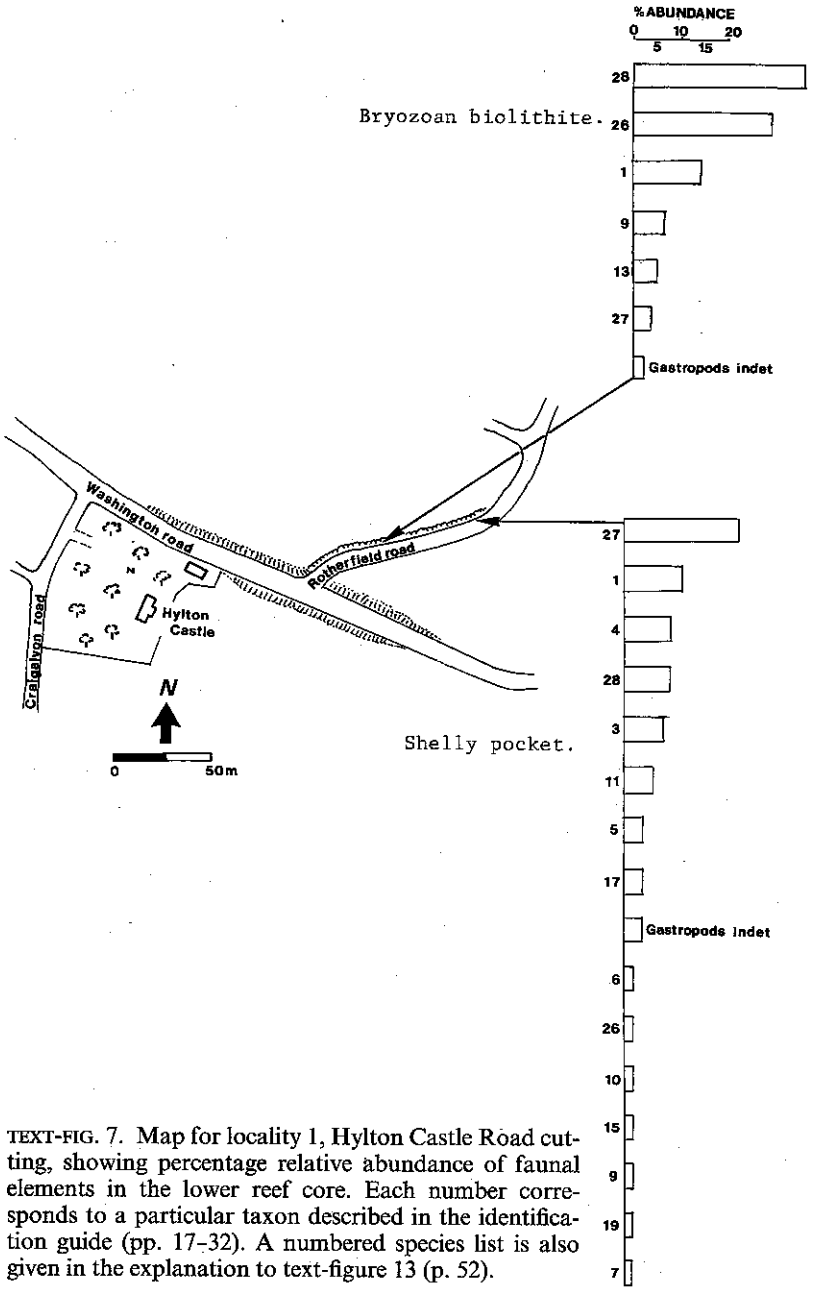
In the later stages of reef development (stage 6), highest faunal diversity and organic productivity became confined to a narrow zone bordering the reef crest and the fore reef slope (localities 5 and 8). High faunal diversity at the seaward margin of the reef was probably due to environmental conditions remaining at an optimum in these areas. The outer reef slope was probably over 90 m high when the reef was fully-developed and displays distinct faunal zonation down slope. This is apparent at Tunstall Hills but is best-developed where the full reef profile is preserved, particularly at Beacon Hill which is outside the Sunderland area (grid ref: NZ 442455). Fore reef slope zonation was probably related to hydrodynamic factors such as water depth and turbulence. The highest parts of the reef which represent stages 7 and 8 are missing from the Sunderland area as they have been removed by erosion. Where they are preserved, for example at Hawthorn Quarry (NZ 437463) and Castle Eden Dene (NZ 452405), the reef is mainly composed of algal laminites. Faunal diversity is very low, particularly in the reef flat with only two or three genera. The vertical decrease in diversity from the reef base to reef flat, observed by Trechmann (1913, 1945), was used in the past to suggest that the reef evolved in a progressively saline environment leading to stunting and final extinction of its fauna. However, time related reef crest and reef slope lithofacies contain high diversity faunas (maintained throughout reef development) and include several stenohaline taxa such as crinoids, nautiloids, and brachiopods. No evidence of 'stunting' or 'dwarfism' can be observed.

We consider it more likely that, as the reef grew, numerous microhabitats were created in the developing reef framework leading to faunal specialization. The approach of the reef to sea level and its basinwards progradation had a profound effect on the distribution of reef dwelling and building genera. Bryozoan species, such as *Kingopora*, are only found in the reef base and lower reef core, which probably accumulated in low energy environments. When the reef reached sea level *Kingopora* was confined to back reef, patch reef environments where energy conditions were also lower. Higher energy environments, in reef crest and upper slope localities within the main reef, are dominated by fenestrates with stout frameworks such as *Synocladia*. The above type of pattern is reflected in several other reef genera. For example, compare the reef base (text-fig. 15) and lower reef core palaeocommunities (text-fig. 8) where fragile spinose productids are present in the reef core but absent from the reef base, and delicate fenestrates are larger in the reef core and smaller in the reef base.

Earlier ideas of decreasing faunal diversity were in part due to a lack of comparison between time-equivalent reef core, reef flat, reef crest, and reef slope lithologies. If salinity was involved in causing reduced faunal diversity at higher levels in the reef its influence was probably more localized than widespread, and confined to the reef flat and upper reef core, e.g. Locality 4. However, increased environmental stress (e.g. storms affecting shallow water) may have been an equally (or more) important factor in reducing diversity in these communities.

The final demise of reef growth has been ascribed to a rapid increase in salinity to levels well above the tolerance limits of reef dwelling and building genera (Stage 8). This was possibly connected with evaporative drawdown of the Zechstein Sea terminating Zechstein Cycle 1 carbonate sedimentation and preceding evaporite deposition.

Shelly faunas in succeeding Cycle 2 and Cycle 3 carbonates never reached the same diversity as that seen in the Ford Formation reef. Bryozoans never formed major reef structures after the end Permian extinction event and later Triassic reefs were constructed mainly by sponges and hexacorals.



TEXT-FIG. 7. Map for locality 1, Hylton Castle Road cutting, showing percentage relative abundance of faunal elements in the lower reef core. Each number corresponds to a particular taxon described in the identification guide (pp. 17–32). A numbered species list is also given in the explanation to text-figure 13 (p. 52).

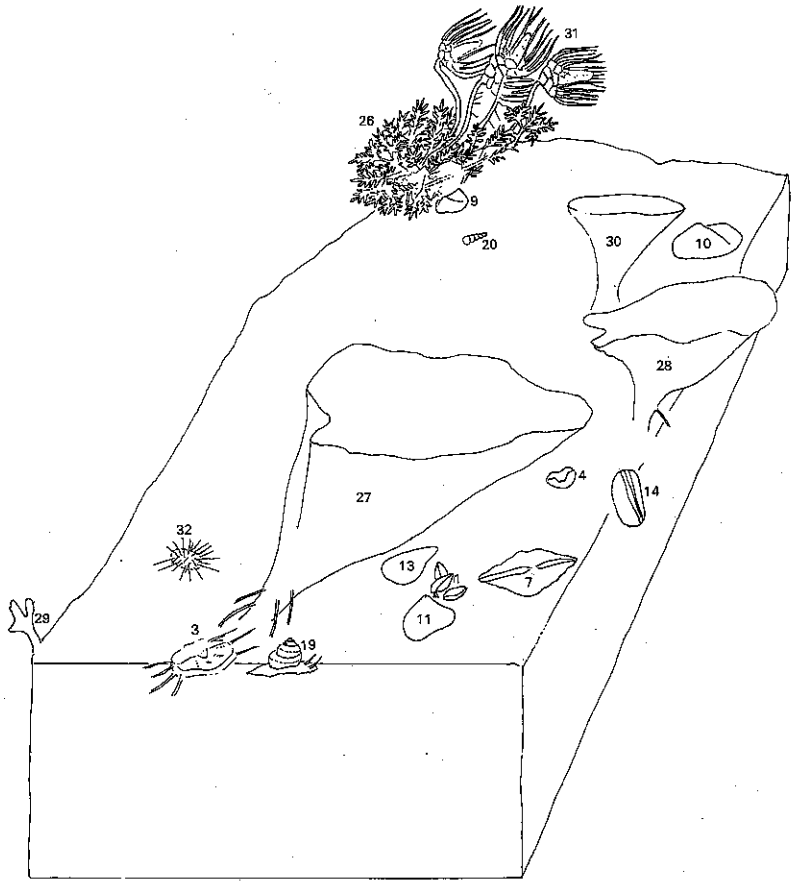
FAUNAL COMPOSITION AND ECOLOGY, LOCALITIES 1–8

Locality 1. Lower Reef Core; Hylton Castle Road Cutting; text-figs. 7, 8

Two samples were analysed, one from an area of laminated biolithite, and the other from a surrounding pocket of shelly dolomicrite. Faunal abundances are plotted as relative-abundance histograms (text-fig. 7). Compared to the reef base at Tunstall Hills (locality 3) the lower reef core at Hylton Castle contains a similar and equally diverse fauna, although there are some notable differences, particularly in the relative proportions of some taxa. There are no known occurrences of undolomitized lower reef core lithofacies at outcrop except for a small section in the excavated area at Rock Cottage, Tunstall Hills. Preservation is variable, but a large enough proportion of the original biocenosis is present to allow reconstruction of the lower reef core palaeocommunity (text-fig. 8). *Dielasma* specimens, though abundant, were too poorly preserved to allow the construction of a viable frequency histogram.

The composition and the relative proportions of the fauna within the bryozoan biolithite compared with that within shelly pockets are strikingly different (text-fig. 7). Seven genera were recorded in total and most of the biolithite is formed from an anastomosing network of fenestrate bryozoans and is dominated by *Synocladia* (37%), *Acanthocladia* (29%) and *Fenestella* (4%). All of the bryozoans are relatively complete and are in, or near, life position. *Synocladia* commonly has the colony holdfast preserved. Many of the bryozoan colonies are encrusted by laminated material. Within some of the bryozoan colonies, particularly *Acanthocladia*, an interstitial fauna, of small (juvenile), epibyssate bivalves of the genera *Liebea* and *Bakevellia*, also occurs. *Dielasma* forms 15% of the biolithite fauna. Nearly all of the *Dielasma* specimens were juveniles with only a few large individuals. No endobyssate or infaunal genera were recovered from the biolithite areas. The dense bryozoan colonies, particularly the bush-like forms such as *Acanthocladia*, would provide an ideal substrate and protective habitat for epibyssate bivalves and pedunculate brachiopods. It is possible that bivalve and brachiopod spat within the Ford Formation reef were attached to dead bryozoan colonies.

The shelly dolomicrite contains a much more diverse fauna with fifteen genera recorded in total. The bryozoan *Fenestella* accounts for just over 24% of the biota, commonly forming large, steeply-erect, cone-shaped colonies. Some specimens occur with the colony origin preserved. *Synocladia* and *Acanthocladia* are not as abundant as in the biolithite, forming 10 and 2% of the total biota respectively. *Synocladia* commonly occurs complete, but *Acanthocladia* is usually fragmented

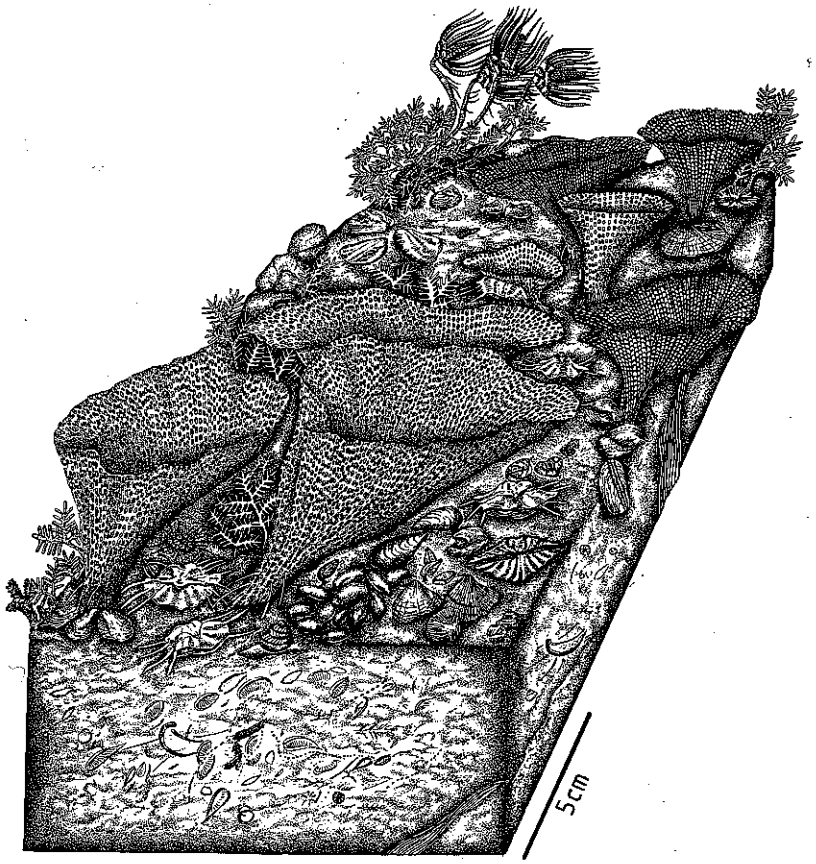


TEXT-FIG. 8. Reconstruction of the lower reef core palaeocommunity. Reproduced, with permission of the publishers, from Hollingworth and Tucker (1987) *In* Peryt, T. M. (ed.). Lecture Notes in Earth Sciences. 10, The Zechstein Facies in Europe. Springer-Verlag, Berlin.

Lower reef core faunas occur at locality 1. Species are numbered for easy reference to the identification guide (pp. 17–32) and for comparison with frequency distribution histograms (text-figs. 7, 13).

Key to species:

1. *Dielasma elongatum*
3. *Horridonia horrida*
4. *Stenoscisma schlotheimi*
7. *Pterospirifer alatus*
9. *Bakevellia* spp.
10. *Parallelodon striatus*
11. *Pseudomonotis speluncaria*
13. *Liebea squamosa*
14. *Permophorus costatus*
19. *Mourlonia antrina*
20. *Meekospira symmetrica*
26. *Acanthocladia* sp.
27. *Fenestella retiformis*
28. *Synocladia virgulacea*
29. *Dyscritella columnaris*
30. *Kingopora ehrengerbi*
31. *Cyathocrinites ramosus*
32. *Miocidaris keyserlingi*



and was probably derived from larger thicket-like colonies. *Kingopora* is notably absent from the fauna. Brachiopods are abundant in the dolomicrite and include the quasi-infaunal brachiopod *Horridonia* which forms about 8% of the fauna. The free-lying alate spiriferid *Pterospirifer* is also recorded. *Dielasma* displays a much wider size range than in the biolithite, with both large and small individuals together. *Stenoscisma* is relatively abundant at Hylton Castle accounting for just over 10% of the fauna. They occur mainly as isolated individuals, but usually in close proximity to each other. *Stenoscisma*, particularly larger forms, are interpreted to have employed a free-lying mode of life with the pedicle acting as a tether (see identification guide). The athyrid

Cleiothyridina accounts for 2% of the fauna, this brachiopod has a large pedicle opening and probably possessed a functional pedicle throughout ontogeny. Infaunal taxa are rare and consist mainly of the shallow burrowing, non-siphonate, trigoniid *Schizodus*. This indicates that some shelly pockets were unlithified.

Some bivalve species that do not occur within the biolithite, occur in the shelly dolomicrite, for example *Parallelodon* and *Pseudomonotis* both of which are epibyssate. *Pseudomonotis* displays a wide variety in shell shape and surface ornament, but this is a reflection of growth upon variable substrates and varies with different stages of ontogeny (Logan 1967).

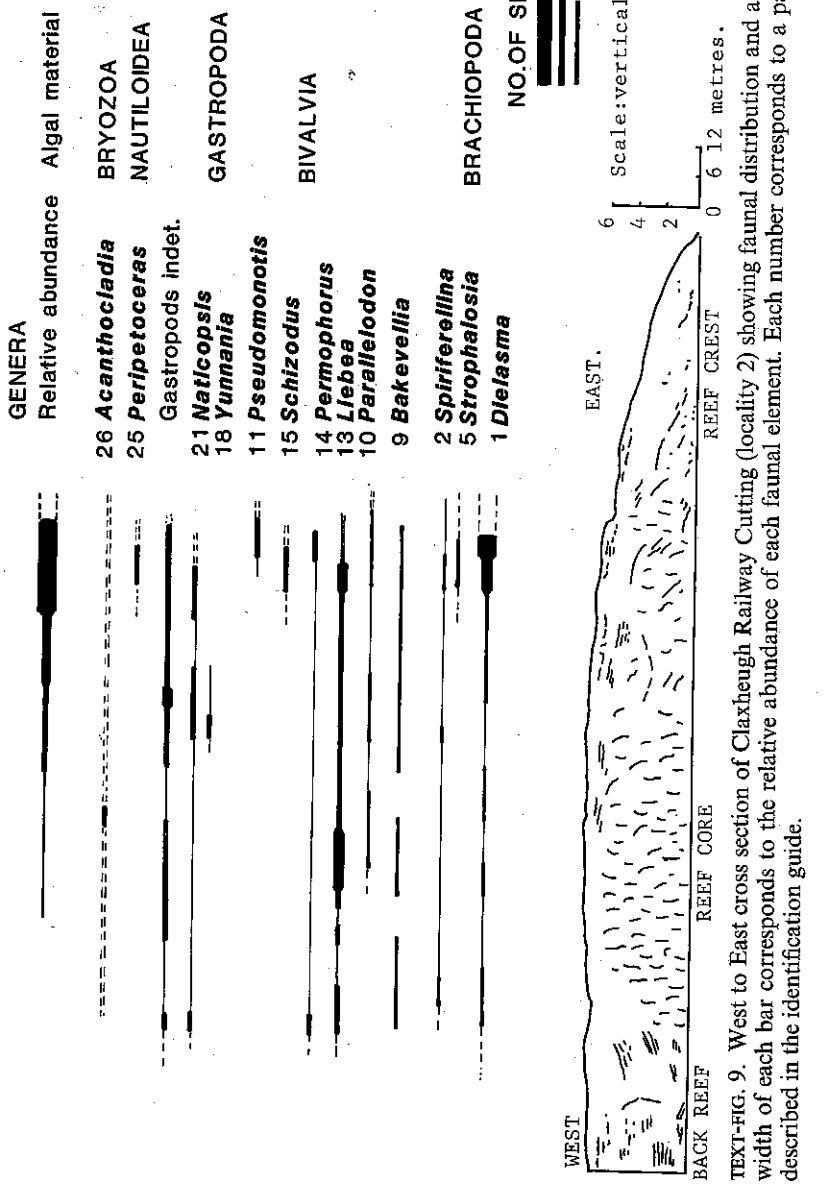
The pectinid *Streblochondria* is relatively abundant at Hylton Castle (text-fig. 7) and is also an epibyssate form. It is interesting to note that this bivalve is absent from higher reef core localities at Tunstall Hills (locality 3), and is found only in the reef talus during the latest stages of reef growth. A similar distribution pattern can be observed for the brachiopods *Cleiothyridina* and *Horridonia*.

Locality 2. Backreef, Reef Core, Reef Crest; Claxheugh Railway Cutting and Ford Quarry; text-figs. 9–11

No palaeocommunity reconstructions have been attempted at this locality as faunal preservation is generally very poor. The abundance of some taxa should be regarded as representing an approximate estimate only. Since the railway cutting is over 150 m long, random bulk samples were collected along the outcrop face, from west to east in Claxheugh railway cutting. The results are presented as a relative-abundance bar chart (text-fig. 9) which provides visual information on lateral faunal distribution across the reef. It is apparent that species diversity increases from west to east.

Backreef Facies. Bedded backreef dolomites in Claxheugh railway cutting have yielded a sparse fauna, consisting mainly of scattered, unidentifiable bivalve fragments. A localized patch of crinoid debris at the western end of Claxheugh railway cutting may represent an *in situ* backreef crinoid meadow as stem lengths exceed 10 cm in some places suggesting little or no transportation. Modern echinoderms break up rapidly after death and become widely scattered by current action and scavengers (Schafer 1972).

In Ford Quarry the backreef facies has yielded a diverse fauna described by Trechmann (1945) for which he gave a comprehensive list (Table 1) including one new brachiopod species. More abundant elements include quasi-infaunal brachiopods, such as *Strophalosia* sp., and endobyssate bivalves, such as *Permophorus costatus*. Epifaunal genera from these facies are rare. The dominance of infaunal, quasi-



TEXT-FIG. 9. West to East cross section of Claxheugh Railway Cutting (locality 2) showing faunal distribution and abundance. The width of each bar corresponds to the relative abundance of each faunal element. Each number corresponds to a particular taxon described in the identification guide.

TABLE 1. Ford Quarry, backreef facies fauna.

Dyscritella sp.	*? Aviculopinna prisca*†
Dielasma elongatum	*Bakevellia* sp.
*Neochonetes davidsoni**	*Pseudomonotis speluncaria*
Strophalosia sp.*	*Schizodus obscurus*†
Yunnania tunstallensis	*Janeia biarmica*†
Astartella vallisneriana†	

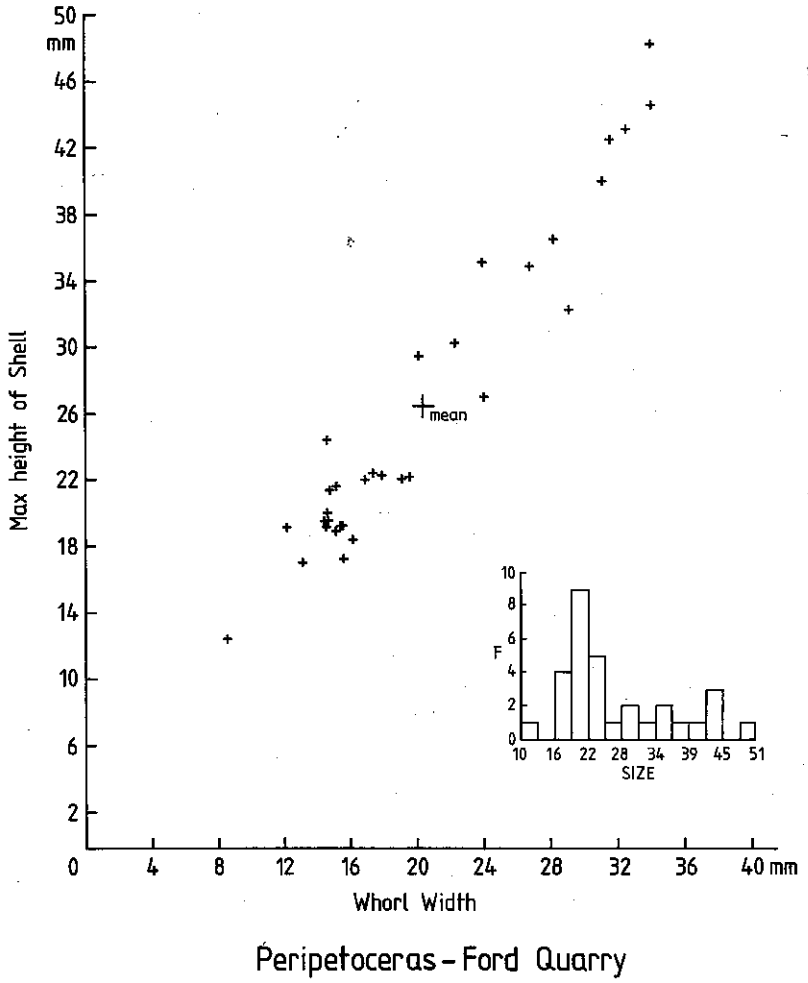
KEY
* Quasi-Infaunal brachiopods. † Infaunal bivalves.

infaunal, and endobyssate genera (Table 1) indicates an unlithified, soft substrate.

Reef Core. Reef core lithofacies at Claxheugh and Ford contain markedly different faunas in comparison to backreef environments and are dominated by epifaunal and epibyssate bivalves such as *Liebea* and *Bakevellia*. Pedunculate brachiopods, such as *Dielasma*, also occur, along with the gastropods *Mourlonia* and *Yunnania* which were probably algal grazers. The high percentage of epifaunal genera suggest the presence of hard, lithified substrates for attachment. It is also likely that bryozoan colonies, such as *Acanthocladia*, may have provided suitable attachment surfaces, but due to poor preservation the relationship of bryozoan colonies to epifaunal genera cannot be evaluated. Many reef core bryozoan colonies are encrusted by micritic algal laminae and this, combined with inorganic cement precipitation, in addition to providing suitable environments for attachment by epifaunal genera, also contributed a great deal to the reef framework itself.

Reef Crest. Infaunal shelly taxa are rare within the reef core but, in Ford Quarry, the infaunal bivalve *Schizodus* occurs. The presence of this bivalve indicates the occurrence of unlithified shelly or carbonate sand pockets between algal mats and bryozoan colonies. It is unlikely that *Schizodus* was transported from backreef to reef crest as valves of this species show no sign of abrasion and are often articulated. Experimental analysis on shell transport mechanisms indicate that bivalve valves separate soon after death (Chave 1964). Brachiopods tend to remain closed due to the valves being effectively locked together by a hinge and socket arrangement and to the absence of an elastic ligament.

The liroceratid nautiloid *Peripetoceras* occurs in the eastern face of Ford Quarry and at the eastern end of Claxheugh railway cutting in localized pockets where large numbers of individuals are concentrated (Pettigrew 1980). A complete size range from juveniles to mature conchs



TEXT-FIG. 10. Scatterplot and frequency distribution for *Peripetoceras freieslebeni* (Schlotheim). A complete size range, from small individuals to mature conchs, is present. All of the specimens were recovered from a fissure in reef crest lithofacies at the eastern end of Ford Quarry (locality 2).

is present (text-fig. 10). Specimens show little or no signs of abrasion or encrustation by epibionts. It is unlikely that the nautiloids were transported after death from the basin to be stranded on the reef by currents, as one would expect some abrasion and a predominance of

one size class to be present, for example, mature conchs. The wide range of individual sizes indicates a normal population and it is more likely that they lived on or near the reef. The orientation and position of the nautiloids imply that they accumulated in pockets or fissures between algal or bryozoan colonies. Modern nautiloids from the western Pacific are nocturnal in habit, only feeding during darkness when they migrate from deep to shallow waters on fore-reef slopes (Wells 1986). The fissures in Ford and Claxheugh are orientated parallel to the reef crest. These may have opened as blocks of reef-crest material slid down the steep, fore-reef slope (Smith 1981). Most of the fissures are filled by algal laminite, which commonly invests nautiloids and bioclastic debris. The debris is mainly composed of articulated brachiopods, for example *Dielasma*, and bivalves such as *Liebea* and *Schizodus*. It is possible that these fissures supported a cryptic fauna of infaunal bivalves, and may have provided possible shelter for *Peripetoceras* and other reef taxa.

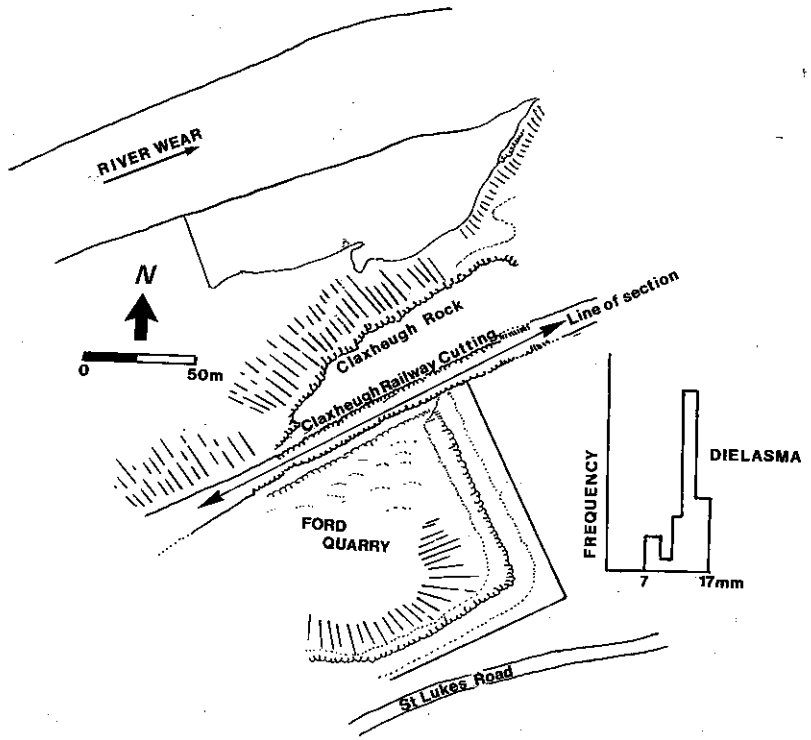
Gastropods are also abundant in reef-crest rocks particularly *Yunnania* and *Mourlonia* (many well-preserved as dolomicrite casts). This is correlated with an increase in the relative abundance of algal material (text-fig. 9) and *Yunnania* and *Mourlonia* were probably algal grazers.

Frequency Distribution For Dielasma. All of the specimens of *Dielasma* for statistical analysis were collected from the eastern end of Claxheugh railway cutting, and the eastern end of Ford Quarry where they are commonly found in an excellent state of preservation.

The collections from both localities produced a left-skewed distribution pattern (text-fig. 11). A small number of individuals occurred in the smaller size classes, with a nearly symmetrical peak in the larger size classes. This implies a population with a low infant mortality rate; however, this type of population is not common (Hallam 1967). According to Richards and Bambach (1975) this distribution pattern indicates a firm substrate and a lack of crowding, even in relatively dense colonies. The left-skewed distribution pattern may also reflect a failure to collect enough small individuals, or selective current removal of small individuals from the population (Cummins *et al.* 1986).

Locality 3. Reef Base; Rock Cottage, Tunstall Hills; text-figs. 12, 15

Outcrop Discovery and Excavation. Tunstall Hills forms a prominent NNW-SSE trending ridge about 2½ km to the south of Sunderland Town Centre (text-fig. 12). Two 'knolls' occur near the northwestern end of the hills and are known as the Maiden Paps. These hills form prominent topographic features in Sunderland Borough and a trig point has been placed upon the highest knoll at 112 m O.D. The steep southern flank of the hills has been accentuated by the presence of a



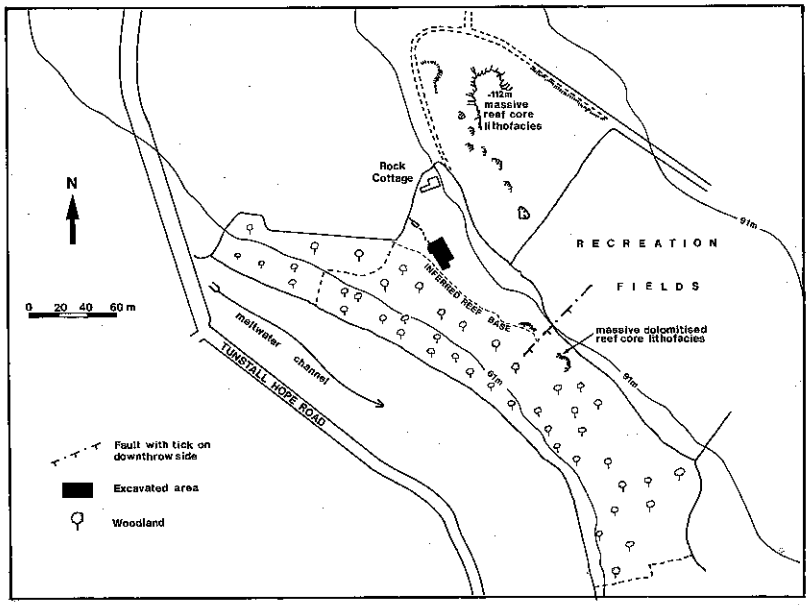
TEXT-FIG. 11. Map for locality 2 and frequency distribution for *Dielasma elongatum* (Schlotheim) collected from the eastern end of Claxheugh Railway Cutting.

former glacial meltwater channel which cuts through the Ford Formation reef and into the underlying Raisby Formation (text-fig. 12).

Old ordinance survey maps of the area reveal that the steep southern slope of the hills was free from vegetation and probably grazed by sheep until about 1900 when subsequent maps show scrub and woodland covering the site. Consequently, exposures within the wood are poor and confined to a few low crags. However, during 1983 preliminary fieldwork revealed the presence of a few slabs of undolomitized coquinoid limestones in some disused badger sets. The limestones contained an abundant and spectacularly-preserved shelly fauna unknown from other outcrops.

A small research excavation was funded by the Nature Conservancy Council in May 1985, to expose the full coquina succession and the

transition into the lower reef core (text-fig. 12). Several tons of material were removed during excavation work and a thorough quantitative profile of the entire reef base biota was undertaken. One new bivalve genus and two new fish genera were discovered, all of which were previously unknown from the Ford Formation reef.



TEXT-FIG. 12. Location of the reef base coquina at Rock Cottage, Tunstall Hills (locality 3) showing the excavated area. The extent of the coquina outcrop is shown along strike. See text-figure 13 for further data from locality 3.

The reef base locality at Rock Cottage represents the largest undolomitized area of reefal limestones at outcrop and the abundant and diverse shelly fauna is often superbly-preserved including colour-banded gastropods such as *Mourlonia* and *Naticopsis*. The role of early-marine cement precipitation and colour-pattern preservation is discussed in detail by Tucker and Hollingworth (1986). Brachiopods and bivalves are also well-preserved and are readily extractable in large numbers. Between April and July 1986, following local T.V. and newspaper coverage, Sunderland Borough Council, in conjunction with a Manpower Services Commission scheme, further extended the outcrop to include some lower reef core lithology. The locality has been

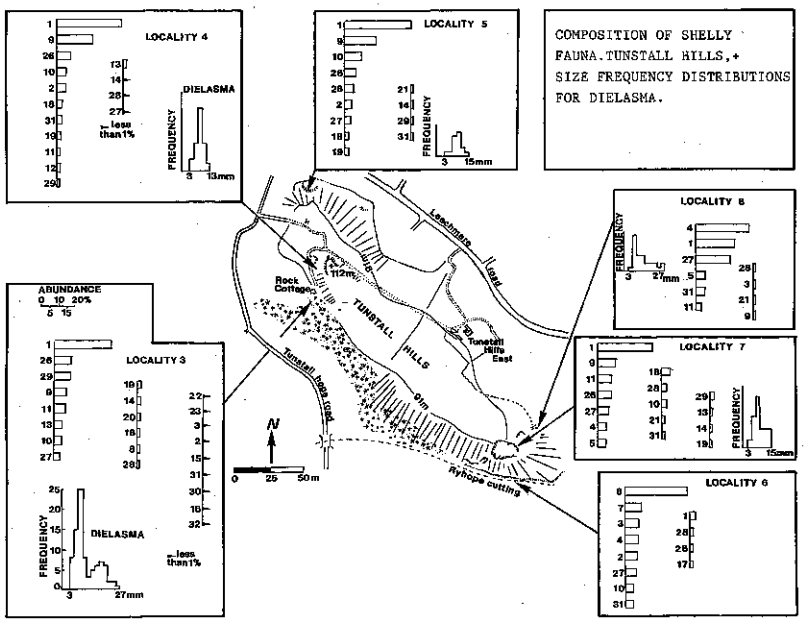
properly fenced and footpaths laid to allow ease of access by geological parties.

Reef Base. The relative-abundance histogram (text-fig. 13) differs from other reef localities, as it is dominated by the terebratulid *Dielasma*, which accounts for 37% of the reef base fauna. A large variation in shell size occurs and some of the largest specimens recorded from the reef have been recovered from this locality. All specimens, regardless of size, possess open pedicle foramens implying a functional pedicle throughout ontogeny. *Dielasma* was probably an epifaunal, low-level suspension filter feeder attached by its thick, fleshy pedicle to hard substrates. In a few cases *Dielasma* occurs at the reef base in small monospecific clumps with a complete range in size classes present. This is similar to Jurassic brachiopod nests reported by Hallam (1961) and Lower Cretaceous brachiopods described by Middlemiss (1962). Both are interpreted as life assemblages. *Dielasma* occurs locally in nests at higher stratigraphic levels within the reef.

Bryozoans are next most abundant and all of the species recorded within the reef complex occur at the base. The fenestrate *Acanthocladia* and trepostome *Dyscritella* both are commonly found as fragments of larger colonies. *Fenestella* is also found as fragments of larger colonies, but is comparatively rare accounting for just over 4% of the total. *Acanthocladia* originally formed delicate, bush-like colonies, similar to the ramose growth form of *Dyscritella*. Although ramose forms predominate, *Dyscritella* displays a wide degree of morphologic variation at the reef base and adnate growth forms can be collected encrusting the left (convex) valves of *Pseudomonotis*. The bryozoan *Kingopora* is unique to the reef base and is not known from higher levels within the entire reef complex. *Synocladia* is relatively uncommon and accounts for just over 12% of the fauna, in most instances it is complete, due to the stouter, more rigid zoarium. All of the bryozoans are epifaunal suspension feeders.

Bivalves form the third most abundant element of the reef base fauna accounting for nearly a quarter of the total. These comprise epibyssate genera, such as *Pseudomonotis*, *Liebea*, *Parallelodon*, and *Bakevellia* which may have been endobyssate (Logan 1967). Most bivalve genera display a wide range of sizes due to variable shell morphology. *Pseudomonotis* displays a wide degree of variation in shell shape, particularly with respect to the flat right valve. This is probably a reflection of attachment to a variety of substrates.

Gastropods form an important constituent of the reef base fauna and are commonly beautifully-preserved, in some cases retaining traces of original colour patterns (see identification guide). *Mourlonia* is the most abundant genus forming just over 2% of the gastropod fauna



TEXT-FIG. 13. Map for localities 3–8 in the Tunstall Hills area showing percentage relative abundance of faunal elements and frequency distribution for *Dielasma elongatum* (Schlotheim). Each number corresponds to a particular taxon described in the identification guide (pp. 17–32) and listed below.

Key to species:

1. *Dielasma elongatum*
2. *Spiriferellina cristata*
3. *Horridonia horrida*
4. *Stenoscisma schlotheimi*
5. *Strophalosia* sp.
6. *Cleiothyridina pectinifera*
7. *Pterospirifer alatus*
8. *Streptorhynchus pelargonatus*
9. *Bakevellia* spp.
10. *Parallelodon striatus*
11. *Pseudomonotis speluncaria*
12. *Stutchburia modioliformis*
13. *Liebea squamosa*
14. *Permophorus costatus*
15. *Schizodus obscurus*
16. *Edmondia elongata*
17. *Streblochondria pusilla*
18. *Yunnania tunstallensis*
19. *Mourlonia antrina*
20. *Meekospira symmetrica*
21. *Naticopsis minima*
22. *Phymatopleura verneuili*
23. *Coelostylina permiana*
24. *Anomphalus permianus*
25. *Peripetoceras freieslebeni*
26. *Acanthocladia* sp.
27. *Fenestella retiformis*
28. *Synocladia virgulacea*
29. *Dyscritella columnaris*
30. *Kingopora ehrengerbi*
31. *Cyathocrinites ramosus*
32. *Miocidaris keyserlingi*

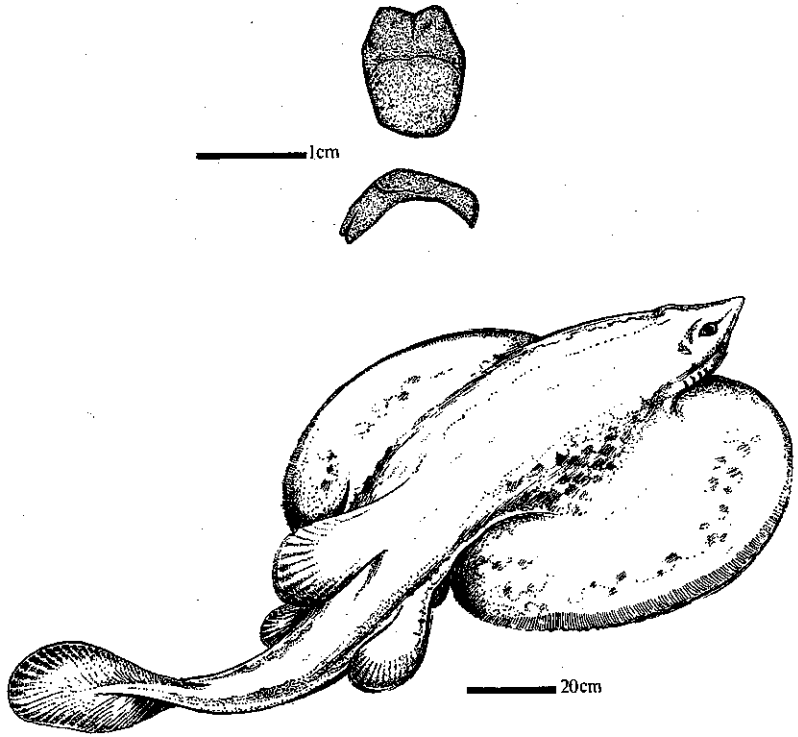
and was probably a browsing herbivore like Recent pleurotomarians (Linsley 1978). *Mourlonia* may also have been a detritus feeder. Other gastropods were probably algal grazers, e.g. *Meekospira*. Compared to other localities algae are generally quite well-preserved. The occurrence of small, soft limonitic patches within the coquina has been attributed to the former presence of algae.

Horridonia is comparatively rare in the lowermost part of the section, but increases in abundance upwards. Rarer genera of brachiopods, bivalves, and echinoids comprise less than 1% of the total (text-fig. 13). *Edmondia* is an extremely rare genus and occurs only at the reef base and in the lower reef core. *Schizodus* is somewhat more abundant and is commonly articulated with the posterior end pointing towards the substrate surface. *Edmondia* and *Schizodus* were probably shallow burrowing, non-siphonate, suspension filter feeders. Echinoderms are rare, comprising isolated pluricolumnals of *Cyathocrinites*. A single species of *Miocidaris* is the only echinoid known from the reef. Isolated spines and plates of *Miocidaris* are common at the reef base in the Tunstall Hills section, but are found only rarely at one other locality (Beacon Hill, p. 4). Specimens of the complete test, which had a maximum diameter of less than 1 cm, are much rarer. Most Recent cidaroids are browsing herbivores, rasping algae from hard substrates; they may also be detritus feeders and some are opportunistic carnivores (Smith 1984). *Miocidaris* may also have been an opportunistic carnivore and browsing herbivore.

One of the more interesting faunal elements recovered from the reef base are isolated fish teeth particularly from the elasmobranch ray *Janassa bituminosa* (text-fig. 14). The teeth of *Janassa* are slightly elongate, flattened peg-like and are an adaptation for shell crushing. Nearly complete specimens of *Janassa* from the German Kupferschiefer have been found with the remains of bryozoa and brachiopods within their visceral cavities (Schaumberg 1979). *Janassa* was probably a bottom-dwelling (nektobenthic) carnivore feeding on the abundant shelly fauna at the reef base.

Epifaunal bivalves dominate the reef-base fauna. Infaunal bivalves and quasi-infaunal brachiopods account for only a small percentage of the total. The paucity of endobyssate bivalves indicates that the substrate was not suitable for colonization by infaunal types. *Schizodus* and *Edmondia* are the only true, vagile infaunal bivalves and they were probably confined to unlithified, finer-grained skeletal sand pockets within the developing coquinoid framework. Evidence to support this is indicated by large numbers of *Schizodus* occurring within small areas of the coquina. Mostly the valves are articulated, and were probably cemented in life position.

The high faunal diversity within the coquina, and the excellent



TEXT-FIG. 14. The lower illustration shows a reconstruction of *Janassa bituminosa* (Schlotheim) based upon specimens from Schaumberg (1979). Isolated teeth, shown here in crown (upper illustration) and lateral (central illustration) views are found rarely amongst the reef fossils. *Janassa* was a predatory bottom-dwelling ray, feeding on the reef shelly fauna, crushing shells etc. with a platform-like battery of teeth.

preservation of much of the shelly fauna, probably represents a close approximation to the original composition of the biocoenosis. A reconstruction of the reef base palaeocommunity has therefore been made (text-fig. 15).

A large proportion of the reef base fauna is also strictly stenohaline, for example, echinoderms and brachiopods. The coquina bank probably accumulated in a clear-water, normal-marine environment where water depths were in the region of 2 to 3 m. Evidence of minor leaching and emergence (Tucker & Hollingworth 1986) indicates that locally the coquina bank grew above sea level. The haphazard orientation of much of the shelly fauna, but lack of abrasion, suggests that the coquina

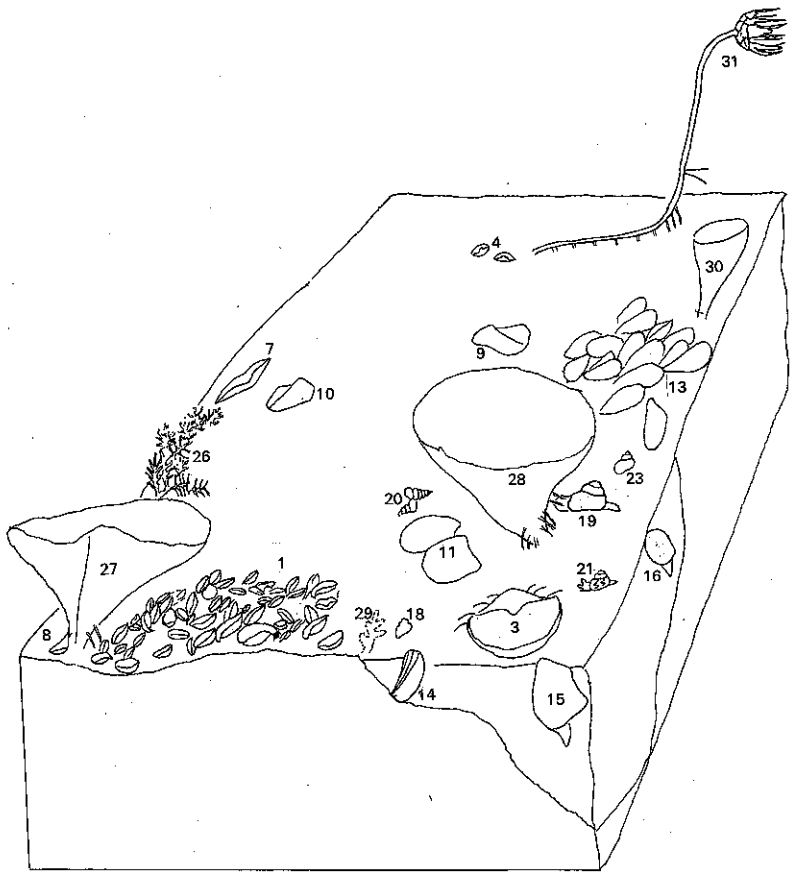
bank accumulated in a relatively low energy environment. Although there may have been periodic high-energy events such as storms, most shell transport was probably within the accumulating shell bank. The reef base displays full faunal mixing and contains a widely occurring shelly fauna. It is likely that there was an open connection between shelf and basin. The precipitation of marine cements between bioclasts was probably widespread. This provided an ideal substrate for the establishment of bryozoans and epifaunal bivalve genera, some of which were cemented in life position.

Frequency Distribution for Dielasma. The sample collected from the reef base (locality 3) produced a bimodal pattern with a large peak in the smaller size classes, a smaller number of individuals in the medium size classes, and a second peak in the large size classes (text-fig. 13). Bimodal distribution patterns can be caused by a variety of factors. Small immature specimens of *Dielasma* form the bulk of the sample. The juvenile peak probably represents a normal juvenile mortality rate, the steep decline in numbers in the medium size classes represents increased mortality during growth. The survivors which reached maturity, and form the larger size classes, produce the second peak. The steep drop after the largest size class represents death due to old age.

A high juvenile mortality rate for the reef base *Dielasma* populations could be due to several factors. Competition for ecospace from other individuals, or other genera, could be a contributory factor. Selective predation may also be another factor although there is no evidence of this. The trough between the small and large size classes may also be due to seasonal population recruitment (Craig and Oertel 1966). Population recruitment in Recent benthic, shelly faunas is mostly seasonal, even in tropical environments (Hallam 1967).

Rudwick (1962), in a study of Recent brachiopods, pointed out that successive peaks in frequency distributions may be the result of long-term recruitment patterns, i.e. a poor year for settlement follows a good one. Specimens of *Dielasma* collected from the reef base did not display any hiatuses, or crowded growth increments, which would indicate changing environmental conditions. 'Census' populations caused by catastrophic death and burial may also result in bimodal or multimodal distribution patterns similar to those observed by Hallam (1961) and Middlemiss (1962). These patterns may also represent successive broods.

Fürsich and Kauffman (1984) obtained bimodal distribution patterns for bivalve faunas from the Cretaceous of the USA. They concluded that bimodal patterns were obtained from areas where environmental conditions were most favourable. Unimodal patterns were produced

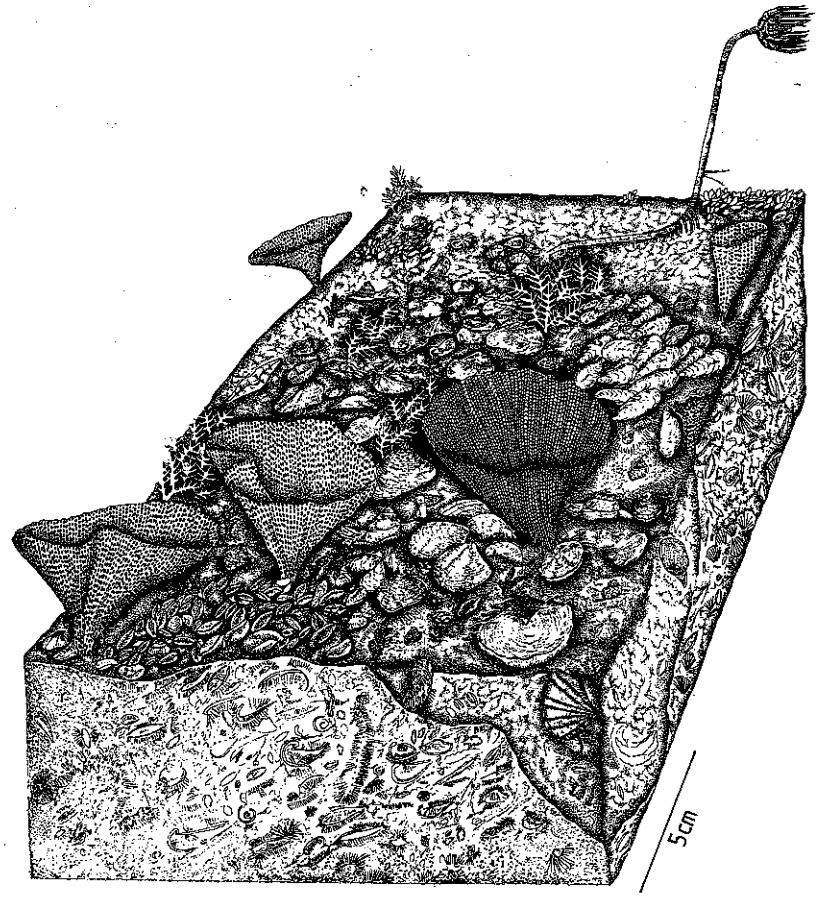


TEXT-FIG. 15. Reconstruction of the reef base palaeocommunity. Reproduced, with permission of the publishers, from Hollingworth and Tucker (1987) *In* Peryt, T. M. (ed.). Lecture Notes in Earth Sciences. 10, The Zechstein Facies in Europe. Springer-Verlag, Berlin.

Reef base faunas occur at locality 3. Species are numbered for easy reference to the identification guide (pp. 17–32) and for comparison with frequency distribution histograms (text-figs. 7, 13).

Key to species:

1. *Dielasma elongatum*
3. *Horridonia horrida*
4. *Stenoscisma schlotheimi*
7. *Pterospirifer alatus*



8. *Streptorhynchus pelargonatus*
9. *Bakevellia* spp.
10. *Parallelodon striatus*
11. *Pseudomonotis speluncaria*
13. *Liebea squamosa*
14. *Permophorus costatus*
15. *Schizodus obscurus*
16. *Edmondia elongata*
18. *Yunnania tunstallensis*
19. *Mourlonia antrina*
20. *Meekospira symmetrica*
21. *Naticopsis minima*
23. *Coelostylina permiana*
26. *Acanthocladia* sp.
27. *Fenestella retiformis*
28. *Synocladia virgulacea*
29. *Dyscritella columnaris*
30. *Kingopora ehrengerbi*
31. *Cyathocrinites ramosus*

for bivalves that lived in less favourable environments. In these cases, this was due to fluctuating salinities in an enclosed marine lagoon.

It is most likely that bimodality in *Dielasma* collected from the reef base reflects preservation of individuals from more than one population, and, as such, represents a recruitment pattern over an unknown length of time. The larger adult population may be attributable to increasingly favourable environmental conditions during accumulation of the coquina bank. This would result in more survivors reaching maturity. A possible environmental factor may be increased water depth giving larger areas suitable for colonization. Petrographic evidence from the section indicates that the coquina was subject to short-term periodic subaerial exposure (Tucker and Hollingworth 1986), and this would account for higher juvenile mortality rates.

To summarize, the reef base coquina contains an abundant and diverse fauna including numerous stenohaline genera. Salinites were almost certainly normal. There was an open connection between shelf and basin, with nutrient-rich waters permeating the coquina bank. The large numbers of *Dielasma*, and their large size, represents a time when environmental conditions were ideal for reef development.

Locality 4. Reef Core; Maiden Paps South; text-figs. 13, 16

Numerous juvenile specimens of *Dielasma* form nests and are the most abundant part of the biota present at this outcrop, accounting for over 38% of the fauna. Some nests are coated by finely-laminated ?algal structures. The relative proportions of the fauna in the core contrast sharply with the reef base containing large numbers of the epibyssate bivalve *Bakevellia* (21%) and fewer bryozoans (text-fig. 13). Other epibyssate genera (*Parallelodon* (5%), *Pseudomonotis* (1%) and *Liebea* (1.6%)) are relatively common. No infaunal bivalves occur. Other bivalves, such as *Permophorus* and *Stutchburia*, are interpreted to have adopted an endobyssate mode of life. Only two brachiopod genera were recorded from the reef core; the rhynchonellid *Stenoscisma* (3%), and the spiriferid *Spiriferellina* (5%). Large brachiopods are notably absent from the fauna, particularly the quasi-infaunal productid *Horridonia* and the alate spiriferid *Pterospirifer*.

Yunnania is the most abundant gastropod in the reef core forming just over 3% of the entire fauna. *Mourlonia* is also relatively common but gastropod species diversity is much reduced when compared to the reef base. Both *Mourlonia* and *Yunnania* have been interpreted as browsing herbivores and this implies that much of the laminated material that occurs within and between bryozoan colonies was algal in origin. It is worthwhile noting that there is a strong correlation between the numbers of gastropods and the abundance of algal material,

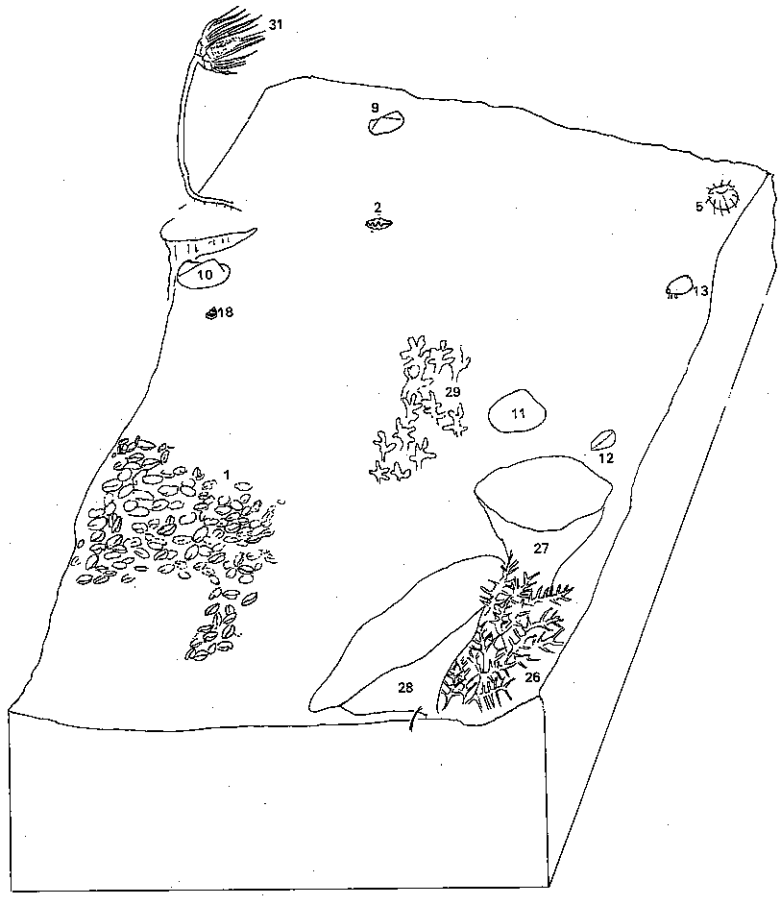
particularly in the upper parts of the reef. *Acanthocladia* and *Dyscritella* are some of the most characteristic reef core bryozoans. *Acanthocladia* forms 8% of the biota collected at locality 4 and occurs predominantly as small, ramose (10–20 cm), bun-shaped colonies, often invested in laminated material and sometimes containing an interstitial fauna of juvenile epibyssate bivalves.

Dyscritella accounts for just over 1% of the bryozoan fauna and occurs predominantly as small, compact, flat (adnate) colonies, the geometry of which implies growth in a shallow, current-agitated environment. *Fenestella* is rare and is commonly encountered as fragments of larger colonies, this is probably due to the lace-like, fragile nature of its zoarium. *Synocladia* colonies are usually more or less unbroken as they are stouter and more rigid than *Fenestella*.

The reef core at locality 4 contains a relatively low-diversity fauna (text-figs. 13, 16) and the population dynamics of *Dielasma* (text-fig. 13) indicate growth in a high stress environment. No infaunal bivalves are known, except for *Permophorus* and *Stutchburia*, which are interpreted as epibyssate suspension feeders. Epibyssate genera, such as *Parallelodon* and *Bakevellia*, occur in some numbers (text-fig. 16) implying the predominance of hard substrates.

The complete absence of large quasi-infaunal brachiopods, such as *Horridonia*, also indicates the lack of unlithified substrates, and a shallow water environment. The zoarial morphology of *Dyscritella* implies shallow water conditions as adnate colonies were probably better able to withstand higher current energies than ramose forms. Other bryozoans, particularly *Fenestella*, occur as small, flat, leaf-like zoaria (text-fig. 16) also indicating possible high energy (? seasonal), conditions.

Contemporaneous reef crest localities contain higher-diversity faunas except at locality 8 where a large proportion of the biota is too poorly-preserved to enable accurate generic identification. *Dielasma* displays a wider size range (text-fig. 13) than in the reef core and it is possible that the reef crest taxa inhabited a more favourable environmental regime where suspended organic detritus and other physio-environmental parameters were more ambient and organic productivity was at an optimum. *Dielasma* spat generated at the reef crest may have settled out behind the prograding reef, in an unfavourable, high-energy, shallow-water environment, leading to high mortality rates. Reduced taxon diversity in the reef core at locality 4 is probably a reflection of a combination of largely unmeasurable physio-environmental and ?physio-chemical parameters. It is likely that shelly biota in the reef core were profoundly affected by seasonal climatic events, particularly in a shallow-water, high-stress environment, leading to reduced diversity and possible subaerial exposure in a peritidal regime.

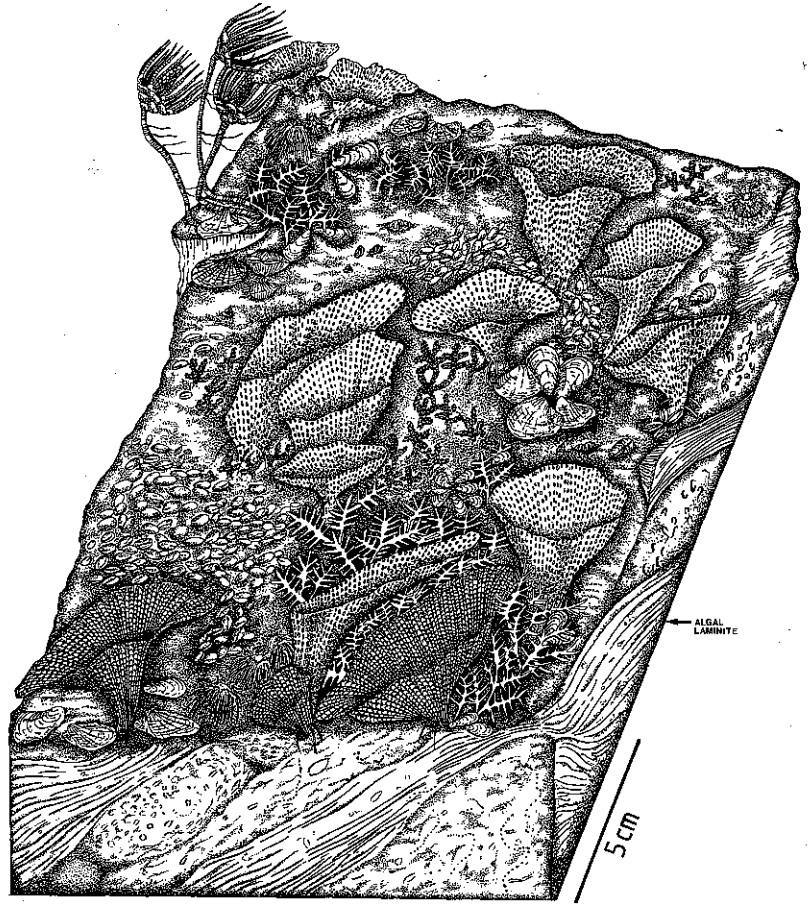


TEXT-FIG. 16. Reconstruction of the reef core palaeocommunity. Reproduced, with permission of the publishers, from Hollingworth and Tucker (1987) *In* Peryt, T. M. (ed.). Lecture Notes in Earth Sciences. 10, The Zechstein Facies in Europe. Springer-Verlag, Berlin.

Reef core faunas occur at localities 4 and 7. Species are numbered for easy reference to the identification guide (pp. 17–32) and for comparison with frequency distribution histograms (text-figs. 7, 13).

Key to species:

1. *Dielasma elongatum*
2. *Spiriferellina cristata*
5. *Strophalosia* sp.
9. *Bakevellia* spp.
10. *Parallelodon striatus*
11. *Pseudomonotis speluncaria*
12. *Stutchburia modioliformis*
13. *Liebea squamosa*
18. *Yunnania tunstallensis*
26. *Acanthocladia* sp.
27. *Fenestella retiformis*
28. *Synocladia virgulacea*
29. *Dyscritella columnaris*
31. *Cyathocrinites ramosus*



Frequency Distribution for Dielasma. Most of the *Dielasma* specimens collected at locality 4 are small and no large individuals were observed or collected at any of the other reef core outcrops studied here. The collection formed a bell-shaped distribution pattern (text-fig. 13, locality 4).

When compared to the frequency distribution patterns obtained from the reef base at Tunstall Hills, (text-fig. 13, locality 3), it is clear that there are no large individuals present in the reef core. The reef core at Maiden Paps South contains a large number of small individuals in the small to medium size classes with only a few moderately large individuals.

Boucot (1953) interpreted the bell-shaped distribution curve to represent a death or transported assemblage, with the smallest size classes removed from the assemblage by size-selective current winnowing. However, Craig and Hallam (1963) in the study of *Cardium edule* have indicated that the highest juvenile mortality is represented in the planktonic stages and this is not evident in adult populations. The resulting normal distribution curve is therefore representative of constantly increasing mortality throughout ontogeny.

Dielasma populations seen in the reef core at locality 4 are probably composed entirely of juveniles. It is more likely that the bell-shaped distribution pattern is indicative of a death assemblage, with a high juvenile mortality rate as there are no larger individuals present.

It may be possible that *Dielasma* reached maturity at a smaller size in the reef core and this, combined with a reduction in taxon diversity when compared to statigraphically lower levels, has been used as an example of faunal impoverishment due to increased salinity (Trechmann 1925, 1945). Boltovskoy and Wright (1976) have used Recent foraminifera as salinity indicators as they produce thinner tests, and reach maturity sooner, than those found in normal marine environments. *Dielasma* specimens of similar size recovered from the reef core do not possess thinner shells than their counterparts found in the reef base. Additionally, one would expect that if *Dielasma* reached maturity sooner in a high-stress, increasingly-saline environment, it would have a more variable morphology and closely-spaced (crowded ? irregular) growth increments (Segerstrale 1957).

Although the laminated outer shell of *Dielasma* tends to flake off during extraction a few specimens with well-preserved shells display widely-spaced growth increments with no evidence of attenuation, particularly near the commissure. It is most likely that *Dielasma* recovered from locality 4 are juvenile individuals that have suffered a catastrophic high-mortality event, with none surviving to reach maturity. Normal distribution patterns for Recent bivalve death assemblages studied in Texas Bays (Cummins *et al.* 1986) are rare, and this has been attributed to size-selective taphonomic processes affecting bivalve shelly faunas in unstable, shallow-water, shifting-sand environments.

There is very little evidence of size sorting in the reef core and the majority of shelly faunas are complete with a low degree of fragmentation. Most specimens of *Dielasma* collected were articulated and displayed no evidence of abrasion resulting from transportation.

It is likely that the *Dielasma* 'nests' observed in the reef core are autochthonous, preserved in or near life position, and possibly cemented in place by aragonite (now calcitized). Nests of juvenile *Dielasma* occur in other reef core and reef flat localities, which are probably contemporaneous. Some nests are completely invested by algal laminite, are preserved in near life position, and contain individuals which comprise two or three small size classes, producing a unimodal distribution pattern.

Maiden Paps South is stratigraphically the highest locality within the reef core at which *Dielasma* can be collected. Specimens recovered from stratigraphically equivalent, time-related, reef crest and slope lithofacies yield *Dielasma* displaying a wider range in size and with both juveniles and adults present (text-fig. 13). Taxon diversity is generally higher in reef crest and slope areas, except at locality 8 where preservation is poor, but the wider size range expressed by *Dielasma* implies more favourable environmental conditions.

There are several reasons which would account for *Dielasma* death assemblages in the reef core at locality 4. Increased salinity causing stunting is unlikely as, apart from growth increments and gross shell morphology discussed earlier, the presence of strictly stenohaline genera such as crinoids and brachiopods (text-fig. 16) indicates that salinities were near normal. Additionally, there are few examples in the geological record portraying stunting as a result of increased salinities (Hallam 1961).

There is more evidence connecting stunting and reduced diversity in brackish environments (Fürsich and Kauffman 1984), and Segerstrale (1957) has illustrated the changes in biotic composition and faunal size across a salinity gradient from 'normal' marine to freshwater in the Baltic. As the environment becomes less saline, marine bivalves and gastropods show a decrease in diversity and a corresponding decrease in shell size and thickness (dwarfism). It is possible that high mortality in reef core *Dielasma* specimens may have been caused by reduced salinity due to sudden freshwater influx in a monsoonal climatic regime leading to catastrophic mortality. Goodbody (1961) and Paul (1942) have illustrated high mortality in Recent reef flat biotas caused by freshwater run-off combined with low tides in tropical monsoonal latitudes.

Palaeolatitude information indicates that the Zechstein Sea occupied an area roughly 10° N. of the equator (Taylor 1984), just inside the 'trade winds' belt, with wind directions dominantly from the east to north-east. The western margin of the Zechstein Sea may have been subject to a seasonal monsoonal regime. The Ford Formation reef core shelly faunas probably inhabited a shallow-water, high-stress environment in the reef core or reef flat. The different palaeocommunities inhabiting the Ford Formation reef were probably strongly influenced by seasonal events. Subaerial exposure of the reef core may have had a profound effect on *Dielasma* populations. However, other environmental parameters, such as localized increased salinity towards the

lagoonal margin of the reef leading to higher mortality rates, cannot be completely discounted.

Locality 5. Reef slope; Tunstall Hills North; text-fig. 13

Most of the fossils at this locality occur as internal or external moulds and casts and are often difficult to extract complete. Identification of individuals to generic level is possible in most cases. Shelly patches within the dolomite contain abundant specimens of *Dielasma* which account for just over 40% of the total fauna recorded (text-fig. 13). The only other brachiopod encountered is *Spiriferellina* comprising 4% of the total. *Horridonia*, *Pterospirifer* and *Stenoscisma* are not present at this outcrop. *Synocladia* (5%) and *Acanthocladia* (6%) are the most abundant bryozoans. *Acanthocladia* commonly occurs as broken fragments but the majority of *Synocladia* colonies were encountered complete and were preserved close to life position. *Fenestella* zoaria are preserved as fragments and were probably derived from larger individuals. The trepostome *Dyscritella* is relatively rare, forming small, ramose zoaria. Bivalves, such as *Bakevellia* (18%) and *Parallelodon* (9%), are generally disarticulated, although single specimens of *Permophorus* can be found with both valves united. No bivalves with an inferred infaunal mode of life are found at this locality. Gastropods are sufficiently well-preserved to facilitate identification to generic level. These comprise *Yunnania* (2%), *Mourlonia* (2%) and *Naticopsis* (1%). The outcrop contains numerous scattered ossicles of the crinoid *Cyathocrinites* which account for just over 1% of the total fauna recorded.

The complete absence of infaunal and quasi-infaunal taxa indicate that substrates were probably lithified and unsuitable for colonization by these forms. Furthermore, the reef slope was probably too steep to allow the establishment of an infaunal biota. All of the brachiopods recorded at this locality probably possessed functional pedicles throughout ontogeny. *Spiriferellina* has an open delthyrium, whereas *Dielasma* was clearly attached by a strong pedicle judging from the size of the pedicle opening. The absence of brachiopods without functional pedicles suggests that the steep, upper reef slope was only suitable for epifauna which could attach themselves effectively to a hard substrate. The bivalves *Bakevellia* and *Parallelodon* were probably attached by a network of strong byssal threads. It is interesting to note that other reef slope localities (e.g. Beacon Hill p. 4) contain a fauna of juvenile brachiopods, particularly *Stenoscisma*, on the upper reef slope. This is probably due to these brachiopods possessing a functional pedicle during the early stages of ontogeny. In adult forms the pedicle opening is restricted. The pedicle was probably retained to serve as a tether, but could not support an adult form on a near-vertical substrate.

Acanthocladia and, to a lesser extent, *Fenestella* were probably derived from higher reef core localities. *Synocladia*, though not the most abundant bryozoan, forms large, flat colonies which are complete. It is likely that they are preserved close to life position. Several specimens were observed with their obverse surfaces facing outwards towards the basin.

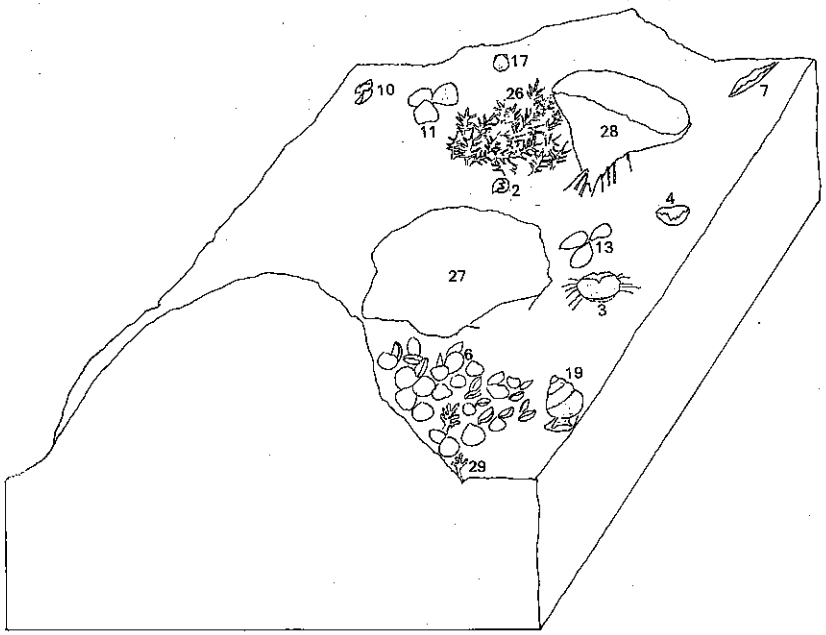
Kerkmann (1969) considered *Synocladia* to be the dominant bryozoan in EZ1 reef slope lithofacies in German reefs, an environment which he indicated as having higher-energy conditions than other reef facies. It is probable that the upper reef slope at Tunstall Hills was also subject to higher-energy conditions. *Synocladia* zoaria are more robust than other bryozoan taxa and could probably tolerate higher-energy conditions to the exclusion of other species.

Frequency Distribution for Dielasma. Complete specimens of *Dielasma* are difficult to extract due to preservation as hollow, calcite casts. The frequency histogram (text-fig. 13, locality 5) displays a slightly left-skewed distribution pattern with a large, nearly symmetrical peak in the larger size classes, but with few very large individuals and a small number of individuals in the smallest size classes. This indicates a low juvenile mortality rate (Richards and Bambach 1975), but may be a reflection of the small sample size due to poor preservation. Cummins *et al.* (1986) indicated that negatively-skewed distribution patterns demonstrated the effectiveness of size-selective taphonomy. On a steep outer reef slope this may be due to the selective removal of smaller forms by current action.

Locality 6. Reef Talus; Ryhope Cutting; text-figs. 13, 17

The fauna within the derived blocks is allochthonous at this locality but surrounding shelly areas contain a diverse and abundant autochthonous fauna. The sample analysed was collected from a large area of shelly dolomicrite near the western end of the section.

The athyrid *Cleiothyridina* is the most abundant brachiopod in the talus accounting for 38% of the total (text-fig. 13). Some specimens, with the interior of the shell empty or partially filled by sediment, contain well-preserved spiralia. *Dielasma* is rare but specimens observed were often large, although small individuals also occur. Large, spinose quasi-infaunal productids, such as *Horridonia*, are abundant, forming 8% of the total. Although many specimens are orientated at all angles, they clearly have not suffered much post-mortem transportation as they commonly have intact spines and are articulated. They are probably preserved close to life position. The free-lying spiriferid *Pterospirifer* is also common and is found with alate margins up to 6 cm in length. Epifaunal pedunculate brachiopods, such as *Stenoscisma* and *Spiriferellina*, are fairly common (text-fig. 13). Large specimens of *Stenoscisma*



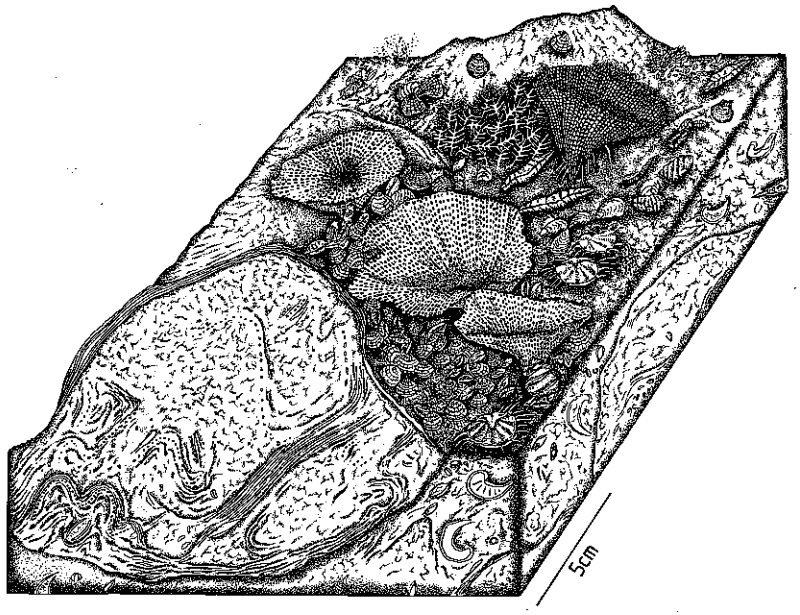
TEXT-FIG. 17. Reconstruction of the reef talus palaeocommunity. Reproduced, with permission of the publishers, from Hollingworth and Tucker (1987) *In* Peryt, T. M. (ed.). Lecture Notes in Earth Sciences. 10, The Zechstein Facies in Europe. Springer-Verlag, Berlin.

Reef talus faunas occur at locality 6. Species are numbered for easy reference to the identification guide (pp. 17–32) and for comparison with frequency distribution histograms (text-figs. 7, 13).

Key to species:

2. *Spiriferellina cristata*
3. *Horridonia horrida*
4. *Stenoscisma schlotheimi*
6. *Cleiothyridina pectinifera*
7. *Pterospirifer alatus*
10. *Parallelodon striatus*
11. *Pseudomonotis speluncaria*
13. *Liebea squamosa*
17. *Streblochondria pusilla*
19. *Mourlonia antrina*
26. *Acanthocladia* sp.
27. *Fenestella retiformis*
28. *Synocladia virgulacea*
29. *Dyscritella columnaris*

were probably attached with a reduced, but functional, pedicle. Epibyssate bivalves are rare, disarticulated and fragmentary, and possibly derived from higher slope localities. No infaunal taxa are known. The only other bivalve recorded is *Streblochondria*, which is inferred to be a byssate form and accounts for just over 2% of the fauna. Bryozoans



make up a large proportion of the biota volumetrically but are commonly fragmentary, particularly *Acanthocladia* (2%) and *Synocladia* (2%), and may have been derived from higher slope localities. *Fenestella* accounts for 7% of the total, forming large, steeply-erect, cone-shaped zoaria. Crinoids are fragmentary with columnal lengths rarely exceeding 2 to 3 cm. It is probable that the crinoids were derived from higher reef-slope areas.

Although crinoids are widely distributed throughout the lower reef core, they only become abundant in reef crest and slope areas during later stages of reef growth. The large numbers of quasi-infaunal and free-lying brachiopods such as *Horridonia* indicate that the rubbly pocket analysed was unlithified, although the derived blocks indicate early lithification of the reef itself. *Horridonia* becomes progressively rarer up the reef slope, which indicates that suitable unlithified substrates were less widespread at higher levels. Steep dips in the outer reef slope are also an important factor in that free-lying brachiopods, particularly *Pterospirifer*, would be easily dislodged by current activity. The zoarial morphology of *Fenestella* mirrors the morphology of specimens documented from the lower reef core at Hylton Castle, forming large, cone-shaped colonies.

It is apparent that the reef talus shelly fauna is relatively distinct

from other reef communities and a reef talus palaeocommunity has been reconstructed (text-fig. 17). The reef talus palaeocommunity is clearly depth-related as the outcrop at Ryhope represents a talus wedge which accumulated at the front of the steep fore-reef slope where water depths were greatest. Brachiopods such as *Horridonia* with large, delicate spines, and the presence of delicate fenestrates, indicate relatively quiet deep-water conditions, probably well below storm wave base. Owing to poor preservation and relative rarity, a viable number of well-preserved *Dielasma* specimens could not be collected for statistical treatment. However, a large size range is apparent with both small and large individuals present in the talus.

Locality 7. Reef Core; Tunstall Hills East, Old Quarry; text-fig. 13

The composition of the fauna is very similar to that of the reef core at Maiden Paps South (text-fig. 13, locality 4) and is dominated numerically by *Dielasma* (34%) (*Dielasma* 38% at locality 4). *Bakevellia* is also abundant (10%) along with *Pseudomonotis* which accounts for just over 8% of the entire biota. *Pseudomonotis* is more abundant in the reef core at the eastern end of Tunstall Hills than at locality 4, as are bryozoans. *Fenestella* forms just over 7% of the fauna and *Synocladia* which is rare at locality 4 forms less than 1% of the fauna in the reef core at the eastern end of Tunstall Hills. Other fenestrates, such as *Acanthocladia*, are relatively common and form just over 8% of the total biota. *Dyscritella* comprises 2% of the fauna at the eastern end of the old quarry, some specimens encrust the convex left valves of *Pseudomonotis*. As with locality 4, adnate colonies tend to predominate over ramose forms. *Kingopora ehrengerbi* is notably absent.

Infaunal bivalves are absent apart from the endobyssate form *Permorphorus* which accounts for just over 1% of the fauna. *Parallelodon* forms 3% of the total. Two other brachiopod genera, apart from *Dielasma*, were collected from the quarry. These are the pedunculate rhynchonellid *Stenoscisma* (5%) and the quasi-infaunal productid *Strophalosia*. Larger, quasi-infaunal productids, such as *Horridonia*, and free-lying forms, such as *Pterospirifer*, are absent. The proximity of this outcrop to the reef crest is indicated by the presence of numerous scattered columnals of the crinoid *Cyathocrinites*, which are noticeably more abundant near the extreme eastern end of the quarry. Algal laminae encrust many of the bioclasts and have been attributed to a genus similar to *Archaeolithoporella* (Smith 1981). They are generally poorly-preserved and no quantitative estimates could be made. The presence of algae may be correlated with a slight increase in the abundance of gastropods which are interpreted as browsing herbivores, particularly *Yunnania* which forms 5% of the fauna.

Delicate features are preserved on bryozoan zoaria and *Strophalosia* is often in life position with its hair-like spines intact and completely covering the shell. Bivalves, such as *Pseudomonotis*, are usually preserved with both valves articulated. *Bakevellia* tends to occur as isolated valves, but *Parallelodon* is usually complete. *Permorphorus* is often found complete or as articulated gaping valves. The complete absence of infaunal genera indicates the predominance of hard substrates and the abundance of synsedimentary cements testifies to a rigid reef core framework ideally suited to epifaunal genera.

Compared to the reef base (locality 3) and the lower reef core (locality 1) stratigraphically higher locations in the reef such as Maiden Paps South (locality 4) and the old quarry, (locality 7), contain faunas which display a reduction in diversity, although individual genera, for example epibyssate bivalves, are relatively more abundant. Contemporaneous reef crest (locality 8), slope, and talus areas (locality 6) contain slightly higher diversity faunas with fewer individuals and a wider range of *Dielasma* size classes. Field relationships and faunal evidence suggests that soon after stages 1 to 4 (foundation to diversification text-fig. 6) reef growth probably matched or slightly exceeded subsidence rates (or sea level rise) and that reef core lithofacies developed in a relatively shallow, high-energy environment. This is reflected in the zoarial morphology of fenestrate and trepostome bryozoans which indicates relatively shallow water.

The reef core is relatively homogeneous at outcrop, consisting of bryozoan frameworks which acted as loci for the precipitation of marine cements and encrustation by various algae. This accounts for the absence of infaunal bivalve taxa as any unlithified pockets between bryozoan or algal colonies were probably widely scattered and too small to support a viable population. The only quasi-infaunal productid found in the reef core is *Strophalosia*. Epibyssate suspension feeding bivalves, such as *Parallelodon*, and brachiopods, such as *Stenoscisma*, show a marked increase in abundance when compared to lower stratigraphic levels.

There is little evidence of faunal mixing within the reef core at Tunstall Hills. This may be a reflection of outcrop size. Although the two localities, (Maiden Paps South, locality 4 and old quarry, locality 7) are separated with no intervening outcrops, (text-fig. 13), faunal composition is broadly similar, yielding large numbers of epibyssate bivalves, pedunculate brachiopods, no infaunal taxa and a restricted suite of bryozoans. When the reef core palaeocommunity (text-fig. 16) is compared to the reef base palaeocommunity (text-fig. 15) it is clear that there is some degree of faunal specialization in the reef core. This may be correlated with the diversification and domination stages in vertical (time-related) reefal successions described by Walker and Alberstadt

(1975). Higher reef core and reef flat lithofacies exposed to the south of Sunderland contain statistically distinct faunas with a few dominant genera and large numbers of individuals. It is apparent that the reef core at Tunstall Hills, although containing a somewhat specialized fauna, is not dominated by one or two component genera. Consequently, reef core faunas and associated lithofacies represent both the diversification and specialization phases described in text-figure 6 as contemporaneous reef slope and talus localities also contain specialized faunas occupying several trophic levels.

Frequency Distribution for Dielasma. *Dielasma* is often well-preserved within the bindstones and most specimens are articulated and show no signs of abrasion. In contrast to specimens collected from the stratigraphically equivalent reef core locality at Maiden Paps South (locality 4), the frequency histogram (text-fig. 13, locality 7) shows a positive (or right-)-skewed distribution pattern.

A large number of individuals make up the smaller size classes and only a few individuals form the larger size classes. A few specimens, with well-preserved outer shells, displayed widely-spaced growth increments with no crowding near the commissure. Boucot (1953) interpreted such a pattern as indicating a high juvenile mortality rate, possibly due to rapid burial of juveniles, or ecospace competition with other epifaunal genera. The skewness may also indicate that *Dielasma* was a widely-adapted genus with a high reproductive capacity and rapid growth and maturation in a variety of reefal niches. Positive skewness may also imply a temporal pattern of larval settlement (Cummins *et al.* 1986).

Locality 8. Reef Crest; Tunstall Hills East, Old Trench; text-fig. 13

Possibly due to preservational bias, bivalves tend to be generally poorly-preserved at this locality and the outcrop is dominated by brachiopods, particularly *Stenoscisma* and *Dielasma* which form 32% and 24% of the fauna respectively (text-fig. 13). No infaunal taxa are known although quasi-infaunal brachiopods, such as *Strophalosia* (6%) and *Horridonia* (2%), are relatively abundant. Fenestrate bryozoans particularly *Fenestella* are common, forming just over 21% of the total. *Synocladia* is rare, accounting for 1% of the bryozoans present. The trepostome *Dyscritella* is absent. *Pseudomonotis* accounts for only 3.2% of the total biota present, whilst the only other bivalve recorded is *Bakevellia*. Gastropods are rare and poorly-preserved and *Naticopsis* is the only gastropod identified at this locality. The crinoid *Cyathocrinites* accounts for 4% of the total fauna, but is relatively more abundant than at other localities and indicates a reef crest type lithology.

Quasi-infaunal brachiopods, which are commonly in life position with intact spines, suggest the presence of ?extensive uncemented

pockets within the main reef crest framework. Epibyssate bivalves, such as *Bakevellia* and *Pseudomonotis*, and the pedunculate brachiopod *Dielasma*, are dominant numerically, from which it can be inferred that hard substrates were also present. Evidence from radial fibrous calcite in nearby reef core lithofacies, interpreted as replaced synsedimentary marine cements (Tucker and Hollingworth 1986), indicates that marine cements were possibly abundant precipitates in reef crest lithofacies.

Fenestella is commonly found as steeply-erect, cone-shaped colonies, preserving very delicate morphological features such as supporting spines and holdfasts. The bryozoans at the old trench locality are probably preserved in life position. Occasional specimens provided a substrate for further bryozoan encrustation, as some bindstone masses are composed of several sub-colonies.

It is not clear whether the trench locality at Tunstall Hills is typical of reef crest lithofacies because of the limited extent of the outcrop. Other (text-fig. 13) localities, albeit at higher stratigraphic levels, contain different suites of taxa particularly at Beacon Hill (p. 4). The old trench locality may be atypical but this is difficult to assess as there are no other comparable (time-related) exposures.

It is apparent, however, that the reef crest facies at Tunstall Hills accumulated under several metres of water as delicate fenestrate bryozoans and fragile spinose productids could not tolerate a high-energy environment. Evidence from other reef crest localities, particularly Ford Quarry (locality 2), indicates that the prograding reef crest was clearly subaqueous (Smith 1981) during development of the reef core stages 4 and 5 (text-fig. 6).

Frequency Distribution for Dielasma. Considerably fewer individuals were recovered from the reef crest than at other localities, this is due partly to outcrop size. Despite a complete range in size classes present (text-fig. 13, locality 8) the majority of individuals are from the smaller size classes, with a few individuals in the medium to large size classes. The histogram shows a positively-skewed pattern.

The presence of large individuals implies that at least some survived to reach maturity and it is possible that, if the outcrop was more extensive, a bimodal pattern would emerge if more individuals were added to the sample. Several factors could account for *Dielasma* reaching a larger size in the reef crest. The reef crest probably represents an area where organic productivity was at its highest and suspended organic material was most abundant. Faunal and field evidence indicates that the reef crest at Tunstall Hills prograded basinwards and was submerged under several metres of water, but probably above wave base. This would provide an ideal environment for suspension feeding, pedunculate brachiopods, particularly *Dielasma*, where suspended

organic detritus would be most concentrated by current action. In contrast, reef core lithofacies which are probably contemporaneous in age contain assemblages of *Dielasma* which indicate high juvenile (possibly catastrophic?) mortality rates with few, if any, individuals reaching maturity. The reasons for this are discussed on pages 61 to 64.

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