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PALAEONTOLOGICAL AND SEDIMENTOLOGICAL STUDIES ON THE UPPER SILURIAN LUDLOW - DOWNTON SERIES TRANSITION IN THE WELSH BORDERLANDS AND SOME PHANEROZOIC BONE-BEDS

By

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volume 1 of 2 volumes

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SUMMARY

Upper Silurian faunas and sediments in sections of Upper Leintwardinian (Ludlovian) to Middle Downtonian (Ledbury Formation) age in Wales and the Welsh Borderland are examined and recorded. These studies have been concentrated in the Ludlow-Much Wenlock region,Salop. However,material from the Brookend Borehole,Tites Point,Usk,Woolhope,May Hill,Builth Wells,Kerry, and the Long Mountain has also been examined.

The faunal study shows a change in the Ludlovian shelf sea from a high diversity, low dominance fauna of articulate brachiopods,molluscs, and bryozoans in the Upper Leintwardinian through to a lower diversity, higher dominance fauna in the Upper Whitcliffian.

Both trace fossils and shelly fossils were examined and the numeric distribution of the latter was recorded in about 30 sections.

One new species of articulate brachiopod, Lingula corftonensis and one new genus and species of trace fossil, Thelodontites corftonensis is described. Size,orientation and distribution data is presented for a number of Whitcliffian and Downtonian mollusc,crinoid,brachiopod,ostracod,algal, polychaete and trace fossil species.

X.R.F.,X.R.D., S.E.M., and grain size studies have been made on some of the sediments. In the Ludlow region, the Ludlow - Downton transition represents a change from a low energy subtidal environment into an intertidal environment. An embedded Markov chain analysis is used to demonstrate that shell sheets in Whitcliffian sediments formed as the result of random depositional processes (e.g. storms).In the Ludlovian Basin, turbidites,megavarves and rhythmites were observed. In the Ludlow - Much Wenlock region the Ludlow - Downton series transition is considered to have coincided with a major change in the geochemical nature of the sea.

The Ludlow Bone - Bed and Temeside Bone - Bed are placed in both an environmental perspective and a geological perspective. Bone - Beds of Devonian,Carboniferous,Triassic, and Pliocene age from Britain,Ireland, and Germany have been examined in the Latter context. A scale of bone weathering has been applied to vertebrate material in bone - beds. Population size distributions of the Pleistocene Waltonian
l.c/ Red Crag Mollusc Glycimeris glycimeris in sediments immediately overlying the Suffolk Bone-Bed are also discussed.

Quartz euhedra in both the Ludlow and Rhaetic Bone - Beds have been examined. X.R.F.,X.R.D.,and microprobe analyses of phosphatic nodules in the Ludlow Bohe - Bed are presented. The genesis of these nodules is discussed.

Shell transport of Recent intertidal molluscs and ostracods at Sales Point,Bradwell,Essex is discussed.

The work described in this thesis has been done by myself with collaboration on joint papers as follows:-

Paper 8

Atkins - Collection of material + text

Antia - Identification of most of the fauna + text

Paper 11

Lockley - Finding Ordovician <u>Schizocrania</u>,diagram + text

Antia - Finding Silurian <u>Schizocrania</u> + text

Paper 13

Whitaker - Basic model of silica diagenesis (p.121,123,125) Photographs Fig.2 a - n, p - z;Fig.3 a,b,e,f,j - l; Fig.5 a,b;Fig.6, b,h,l. Constructive critisim of early drafts + comments on points omitted in quartz section and where text should be expanded

Antia - Collection of material, basic text, figure captions, references,proof reading,Photographs Fig. 1 a - x; Fig. 2,o;Fig.3, c - i; Fig.5 c - l; Fig.6, a, c - g Diagram Fig. 4, Making up of plates

Paper 15

Sykes - Collection of bone-bed,sample disaggregation, introduction, + conclusions + stratigraphy + methods + comments on revisions

Antia - Scanning electron microscope section & analysis, + S.E.M. text + Conclusions, + introduction + manuscript revision + Plate + text Figure

Paper 16

Al- Sheikhly & Antia wrote text & tried out methods jointly

Paper 17

Atkins & Antia contribution was jointly written

LIST OF CONTENTS

CONTENTS OF THE THESIS POCKET

LIST OF PAPERS

Paper 1

FAUNAS FROM THE UPPER SILURIAN,UPPER LUDLOVIAN, WHITCLIFFE BEDS IN THE LUDLOW - MUCH WENLOCK DISTRICT,SALOP,ENGLAND.

(Submitted to the *Geol.J.*)(in press)

Paper 2

SHELL LAMINAE AND SHELL ORIENTATION IN THE UPPER SILURIAN, WHITCLIFFE BEDS,(U.K.). - accepted for publication 1980/1981

(Submitted to *Palaeogeography,Palaeoclimatology,Palaeoecology*)

Paper 3

THE TYPE SECTION OF THE UPPER SILURIAN LUDLOW BONE-BED AND THE LUDLOW - DOWNTON SERIES BOUNDARY AT LUDLOW, SALOP, ENGLAND.

(Submitted to the Mercian Geol.) published 1980, vol. 7 pt 4 p. 289 - 320

Paper 4

COMMENTS ON THE ENVIRONMENTS AND FAUNAS ACROSS THE LUDLOVIAN - DOWNTONIAN BOUNDARY (UPPER SILURIAN) AT SIEFTON, SALOP.

(Accepted for publication in the Geol. J.) published (1979) vol. 14 pt. 2, pp 127 - 134

Paper 5

THE LUDLOW - DOWNTON SERIES TRANSITION (UPPER SILURIAN) AT CORFTON, ASTON MUNSLOW, SHIPTON, BROCKTON, NETHERTON, AND LYE.

(Submitted to the Geol. J.) (in press)

Paper 6

AUTHIGENIC GYPSUM IN MARINE SEDIMENTS - A COMMENT.

(Published in *Marine Geol.* (1979) vol.31,pp.M1 - M4)

Paper 7

THE TEMESIDE BONE-BED:AN ANALYSIS OF ITS OCCURRENCE AND ENVIRONMENTAL SIGNIFICANCE IN THE LATE SILURIAN - EARLY DEVONIAN MARINE REGRESSION IN WALES AND THE WELSH BORDERLAND.

(Submitted to the *Mercian Geol.*) To be published 1980 vol 8 pt.1

Paper 8

PRIDOLIAN MARINE FOSSILS FROM THE SUPPOSEDLY UPPER LEINTWARDINIAN (LUDLOVIAN) CENNEN BEDS OF THE CENNEN VALLEY.

(Written with D.R.Atkins, submitted to the *Geol.Mag.*)

Paper 9

COMMENTS ON *SPIRORBIS LEWISII* (POLYCHAETA:SERPULIDAE).

(Submitted to the *Geol.J.*)

Paper 10

POSSIBLE DISPERSAL MECHANISMS ACCOUNTING FOR ANOMALOUS OCCURENCES OF THE LOWER PALAEOZOIC BRACHIOPOD *SCHIZOCRANIA*.

(Written with M.G.Lockley, and submitted to *Palaeontology*)
published 1980, vol 23, pt 3, pp. 707 - 713

Paper 11

THELODONTITES CORFTONENSIS GEN.ET SP. NOV.: A NEW TRACE FOSSIL SPECIES FROM THE BRITISH SILURIAN LUDLOW BONE-BED.

(Submitted to the J.Paleont.) To be published 1981

Paper 12

BONE-BEDS:A REVIEW OF THEIR CLASSIFICATION,OCCURRENCE,GENESIS, DIAGENESIS,GEOCHEMISTRY,PALAEOECOLOGY,WEATHERING,AND MICROBIOTAS.

(Published in the Mercian Geol. (1979) vol. 7,pp. 93 - 174)

Paper 13

A SCANNING ELECTRON MICROSCOPE STUDY OF THE GENESIS OF THE UPPER SILURIAN LUDLOW BONE BED.

(Written with J.H.McD.Whitaker, published in W.B.WHALLEY (ed.) *Scanning electron microscopy in the study of sediments*, GeoAbstracts,Norwich, (1979) pp. 119 - 136)

Paper 14

PHOSPHATE PEBBLES: A KEY TO THE RECOGNITION OF A SUBMARINE DISCONTINUITY AT THE LUDLOVIAN - DOWNTONIAN BOUNDARY (UPPER SILURIAN) IN THE WELSH BORDERLANDS.

(Submitted to the Trans.Roy.Soc.Edin.)

Paper 15

THE SURFACE TEXTURES OF QUARTZ GRAINS FROM A RHAETIAN BONE-BED, BLUE ANCHOR BAY, SOMERSET.

(Written with J.H.Sykes, Accepted for publication in the *Mercian Geol.*) published vol 7, pp.205 - 210 (1979)

Paper 16

PREPARATION TECHNIQUES FOR THE S.E.M. EXAMINATION OF PALAEONTOLOGICAL AND SEDIMENTOLOGICAL MATERIAL.

(Written with S.S.J.Al - Sheikhly, as a departmental handout, Accepted for publication in *Outcrop*, Journal of the Glasgow University Students Geological Society) published 1980, vol 7 pp54 - 59

Paper 17

DISCUSSION CONTRIBUTIONS TO A PAPER READ BY Dr.J.K.LEGGETT AT THE BLACK SHALES MEETING OF THE GEOLOGICAL SOCIETY OF LONDON, 2nd May 1979.

(Both of the contributions have been submitted to the *Jl.Geol.Soc.Lond.*) published 1980, vol 137 pt 2 pp154 -156.

LIST OF TABLES

Paper 1

Paper 2

Paper 3

Paper 4

Paper 5

Paper 6

Paper 7

Paper 9

Paper 11

Paper 12

Paper 14

Paper 15

LIST OF TEXT - FIGURES

Paper 1

Paper 2

Paper 3

Paper 4

Paper 5

Paper 7

Paper 9

Paper 10

Paper 11

Paper 12

Paper 13

Paper 14

Paper 15

LIST OF PLATES

Paper 1

Paper 5

Paper 7

Paper 11

Paper 12

Paper 14

Paper 15

LIST OF APPENDIX CONTENTS

LIST OF ABBREVIATIONS

Most of the abbreviations used in this thesis are in common usage. For example ca. (Circa.) meaning about. However, other abbreviations are in common geological use, e.g.

X.R.D. - X-Ray Diffraction
X.R.F. - X-Ray Refraction
S.E.M. Scanning Electron Microscopy

or are explained in the text where they first appear, as in the instance of formuli.
As a general rule the abbreviations U.L.B., L.W.B., U.W.B., L.B.B., T.B.B., may (unless otherwise stated in the text) be taken to mean the Upper Leintwardine Beds, Lower Whitcliffe Beds, Upper Whitcliffe Beds, Ludlow Bone-Bed, Temeside Bone-Bed, respectively.
The generic names of species are commonly reduced to their first initial after their first mention in the text or a table within a given chapter.

INTRODUCTION

PRESENTATION AND FORMAT

Published and unpublished papers:The papers submitted within this volume and listed on pages i - vii & xvii include 18 items of which 4 are published, 3 are in press and 11 are submitted to divers journals. At the editors request the paper written with M.G.Lockley and submitted to Palaeontology (Paper 10) is currently being revised following referee's critisim for inclusion in Palaeontology as a short note.

General aims and arrangement of the papers: It was originally my intention to investigate the palaeoecology of the transition from the top marine Ludlovian into the non - marine Downtonian throughout the Welshborderlands by making detailed numeric faunal collections from a variety of sections (July - August,1976). However,it soon became apparent shortly after this project had been started that (1) much of the faunal work I had intended to do had already been done (cf. Calef,1972;Watkins,1975), (2) the controls on the biostratigraphy of this time interval were poor making accurate correlations between neighbouring sections difficult if not impossible (cf.Holland et al,1963;Lawson & Whitaker,1968; Turner,1973;Siveter,1974;1978;Aldridge,1975), and (3) the sedimentology of the top Ludlovian and basal Downtonian was poorly understood (cf. Hobson,1960;Allen & Tarlo,1963;Bailey & Rees,1973;Allen,1974a). Consequently the aims of this project were changed in order to plug some of the major gaps in the published data relating to the Ludlovian - Downtonian transition. The subsequent study was concentrated on two major themes. The first examined the faunal and environmental changes across the Ludlovian - Downtonian transition, the second examined bone - beds throughout the geological column in an attempt to interpret the many bone - beds present in the basal Downtonian of the Ludlow district.

Theme 1 - Palaeontological and sedimentological studies: Papers 1 - 11 are included in this theme. They grew out of an original project which attempted to define the numerical communities (sensu Calef & Hancock,1974;Duff,1975) of the top Ludlovian and Basal Downtonian. However, in the light of recent studies which have shown that a considerable amount of shell transport occurs in both intertidal and subtidal environments this is clearly impossible (e.g. Boscence,1972,1979a,b;Farrow,1974;Lingwood, 1976;Antia,1977;Alexandrowicz,1978;Farrow *et al*,1978 and others) The earlier numeric palaeoecological studies of the top Ludlovian showed a continuum of faunal change (Calef,1972) which may relate to depth (Calef & Hancock,1974;.Hancock *et al*, 1974) or differing palaeoenvironments (Watkins,1975).

In this study faunal distributions in a number of Whitcliffian sections were examined (Paper 1) and some analyses of the shell layers within them were made (Paper 2). The first study confirmed the change in faunal composition from the Upper Leintwardine Beds to the Lower Whitcliffe Beds which had been demonstrated elsewhere (Holland *et al*,1963;Lawson & Whitaker,1968), and described the faunas and sediments of the two new sections described by White & Lawson (1978 - sections B & C) through this boundary. Changes in faunal diversity and density through the Whitcliffian were examined and appear to confirm the earlier observations of Calef (1972) and Watkins (1975). Size distributions of four ostracod species are discussed and a new Whitcliffian lingulid brachiopod described (Paper 1).

The sedimentological study in Paper 2 provided confirmation of Watkins'(1975) hypothesis that the shell sheets in the Whitcliffian were storm - generated, and it attributed some of the various shell orientations in the sediments to the disturbance effect of bioturbating organisms.

The group of papers 3 - 6 concentrate on faunal and sedimentological variations at the Ludlow - Downton boundary. Their aim is to reexamine the boundary in the type area. The faunal results confirmed the observations of Elles & Slater (1906), Robertson (1927),Shaw (1969) and White & Coppack (1978), and suggest that the stratotype section at Ludford (Ludlow) could be maintaied as the Holostratotype section of the Ludlow - Downton boundary (cf. Paper 3). Accessory sections through the boundary (Papers 4 - 6) show similar faunal and sedimentological changes at the boundary. Both intertidal and subtidal Downtonian environments have been identified (Papers 4 - 7) and their respective faunas discussed (Papers 5 & 7).

Some of the more interesting individual species have been examined from both Whitcliffian and Downtonian sediments. These include Spirorbis,Schizocrania, trace fossils and ostracods. (Papers 1,3,5,9,10,11).

A section containing an anomalous Leintwardinian fauna (Squirrell & White,1978) was examined and reassigned to the Downtonian (Paper 8).

The faunas and sediments of the Temeside and Ledbury Formations were examined. However, the observations (Paper 7) made in this context, while supporting previous faunal work, appear to conflict with both the stratigraphical and sedimentological interpretations of Allen (1974a,b) in detail.

The environmental setting and palaeogeography of the Whitcliffian and Downtonian is also discussed (Paper 7,17), in order to place all the sections and faunas examined in their environmental context.

Although this model is by no means completely satisfactory it explains the available data better than its predecessors (Hobson,1960; Holland & Lawson,1963;Bailey,1968;Bailey & Rees,1973; Watkins &

Berry,1977;Antia,1979 (Paper 12)) and discusses faunal changes with changing environments on a dichotomous basis (Paper 7). Theme 2 - Bone - Beds: At the Ludlow - Downton boundary a number of bone - beds are present (Elles & Slater,1906). Such deposits are difficult to explain (see Allen,1974a) and appear to coincide with a faunal and sedimentological changes in some areas (e.g.Ludlow - cf.Elles & Slater,1906) and form part of a continuous sediment sequence in others (e.g. Tites Point - see Cave & White,1972). Consequently in order to be able to explain these deposits they were subjected to a fairly detailed study. The initial preliminary study (Paper 13) of the Ludlow Bone -Bed observed some euhedral quartz grains,These were sent to Dr Whitaker, who had found similar grains in the Brent Sandstone Formation, for his expert opinion, and the results included in a joint paper (Paper 13). Subsequent studies on euhedral quartz grains in the Rhaetic Bone - Bed made in conjunction with Mr J.H.Sykes (Paper 15) showed a number of possible sources for quartz euhedra in bone -beds. These observations have in part been confirmed by recent studies on quartz transport (Wilson,1979;Mulgrew,Personal communication,1979). The S.E.M. techniques used in these studies are outlined in paper 16.

These studies left the basic problem of bone-bed genesis unsolved. Consequently, the whole subject was briefly reexamined (Paper 12). This study resulted in the development of a new bone - bed classification replacing the inadequate classifications of Reif (1971) and Sykes (1977) and a total reexamination of the concept of bone - bed genesis. During the course of this study it became apparent that the published sediment and faunal changes across the Muschelkalk Grenzbonebed (see Reif,1969,1974 and others), were similar to the changes across the Ludlow - Downton boundary. In order to check the validity of these observations a number of Muschelkalk Grenzbonebed localities were visited (Paper 12). The resulting data was used (Paper 12) to critically reexamine the concept of bone-bed prefossilisation, which had been expounded by Reif (1969,1971).Following publication of a paper by Behrensmayer (1978) on bone weathering it became apparent (Paper 12) that bone weathering could reveal important information relating to the genesis of bone-beds. This general examination of bone-beds (Paper 12) left a number of major problems unresolved.

The first major problem was the significance of phosphate pebbles in bone - beds. This has been discussed with respect to the Ludlow Bone-Bed in paper 14. A similar study by C.J.Duffin (Ms, submitted to the Mercian Geol.) on the Rhaetic Bone-Bed showed conclusively that the phosphate nodules are mostly coprolitic material. This observation is not true of the phosphate nodules in the Ludlow Bone - Bed, even though some phosphatic coprolites are present (Paper 13). In some other bone - beds, e.g. the Suffolk Bone - Bed, it appears that the nodules have been reworked from older deposits (Reid,1890:Paper,12).

The second major problem involved the genetic significance of bone - beds . This problem has been dealt with respect to the British Silurian bone - beds by the present author, and similar more detailed or equally detailed studies have been conducted by Dr. J.Marshall (Ph.D.thesis 1978, Bristol University), on the British Carboniferous Bone - Beds,Mr.M.Mayall (Ph.D. thesis to be submitted late 1979, early 1980,Reading University) on the Rhaetic Bone - Bed, and Prof. J.Conkin (Louisville University) on the Devonian Bone - Beds of the Northern U.S.A.. These and other more ancient studies suggest that there may be number of environmental situations in which bone - beds occur. These may be summarised as follows:-

1. Subtidal environments containing fluctuating currents (e.g. Whitcliffian Bone - Beds (Paper 14) and Diester - Haass & Schrader,1979).
2. Subtidal and intertidal environments containing fluctuations in salinity and oxygen content of the water column. e.g. Some Downtonian Bone-Beds, Rhaetic Bone-Beds, and the recent Mellum Bone - Bed (cf. Antia, 1979; Sch$_a$fer,1972).
3. Intertidal or subtidal concentration of the deposit from the reworking of vertebrate poor sediments. e.g. The Suffolk Bone - Bed, The German Rhaetic Bone - Bed (Antia,1979; Aepler,1974).
4. Reworking of a fish mass mortality

Any combination of these four processess could result in the formation of a bone - bed. However,Bone - Beds appear to characterise unstable environmental conditions and commonly occur for this reason at the junction of two widely differing chemical, or physical environments, both in transgressive and regressive sequences. As yet, insufficient information is available to explain why bone - beds are not a commoner sediment type in the Geological record.

Problems left unresolved: All the problems tackled in this thesis could have been tackled in greater depth. However, the major problems left incompletely resolved in this study may be listed as follows:-

1. The biostratigraphy of the Whitcliffian and Downtonian. (This problem requires detailed faunal and floral transects through the stage and series both in the type area and elsewhere. Such studies would involve experts on ostracods,chitinozoa, acritarchs, spores, megainvertebrate faunas, conodonts,fish, and other microfossil groups, and take many years if not

decades to complete).

2. The sedimentology and palaeogeography of the Whitcliffian and Downtonian.

   (This problem requires excellent stratigraphic controls (which are currently lacking) in order to be resolved. However, at the present time detailed studies could be made on the diagenesis, mineralogy, and genesis of many of the sediment types present. Particular emphasis needs to placed on the sedimentology of the May Hill,Tites Point,Woolhope region, the Ludlovian basin and its margins, sediment source and the evolution of palaeocurrent directions, and the effect of rising positive areas in the region over this time period).

3. The biostratinomy of the Whitcliffian and Downtonian.

   (This problem needs to be resolved prior to any detailed palaeoecological studies. Detailed studies could be made of shell breakage, wear, and transport in sediments of differing environments and the amount of faunal intermixing,and depletion of faunas by dissolution,biogenic decay and currents, assessed).

4. The environmental significance and taxonomy of Downtonian and Whitcliffian trace fossils.

   (This study has shown that in the Ludlovian basin trace fossils form good indicators of fluctuating chemical environments. However, the taxonomy of these species is unknown. Similarly trace fossils are abundant throughout this time period, and many of the forms present appear to have had restricted environmental distributions, and to have played a major part in both the bioerosion of sediments and sediment reworking. It is envisaged that any future trace fossil studies would view them in both an environmental and taxonomic context).

5. The palaeoecology of the Whitcliffian and Downtonian faunas and their functional morphology.

(This problem has been attempted by Calef(1972) and Watkins(1975). However, before any trophic or community models for this period are outlined which can be believed, a number of problems have to be tackled. These include a complete revision of the taxonomy of all macro and micro faunas and floras present in these sediments, and an analysis of their functional morphology. These studies should precede any investigations of the environmental distribution of individual or groups of (communities)of species. Following, detailed sedimentological and biostratinomic studies it should then be possible to present an idea of faunal distributions and food webs in a variety of palaeoenvironments).

Each of these topics could still form the basis of one or more Ph.D. projects, and are listed in the order in which they should (in the authors opinion) be tackled.

Use of this work by others:At the time of writing the published work in this thesis is being included in the ongoing studies of a number of vertebrate palaeontologists, and Muschelkalk and bone - bed sedimentologists, including T.Ainger,C.J.Duffin,J.H.Sykes,J.Conkin,& M.Mayall, and in the diagenetic studies of a number of oil companies (Papers 6,12, 13).

Location of specimens: On the advice of Dr.J.D.Lawson specimens showing good or exceptional preservation of faunas were kept and deposited in a variety of museums, the remainder were discarded. Ostracod,bone-bed samples and some shell deppsits have been deposited with Ludlow Museum. Faunas from Mortimer Forest have been deposited with the

the Institute of Geological Sciences London. Other faunas have been deposited with the National Museum of Wales. Good Crinoids ostracods and conodonts are with C.Franzen,D.Siveter,R.Aldridge respectively. Some pachythecids have been deposited with D.Edwards.

Acknowledgements:This project has involved assistance from many people most of whom have been acknowledged in the text. However,I would particuarly like to thank (1) Mr.J.Norton and his museum staff at Ludlow for enthusiastically looking after my specimens while I was on field work, for numerous discussions, loans of equiptment, advice on which localities to visit and assistance with transporting my specimens from the field to Ludlow Museum for temporary storage. (2) the numerous publicans and farmers who graciously gave me permission to demolish their car parks and rocky crags on their property, and even removed herds of bullocks from their fields to allow me to work undisturbed. (3) C.Farrow,M.Murray, and D.Skinner for showing me how to use the microprobe,Scanning electron microscope and X - Ray diffractometer. Both J.D.Lawson and D.R. Atkins kindly transported my specimens to Glasgow from Ludlow.

The diagrams in papers 4,12 & 13 were drafted by Mrs M.Leeper.Mr.D.Mclean assisted with photography.

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REFERENCES

AEPLER,R. 1974. Der Rhätsandstein von Tübingen - ein Kondensiertes Delta.N.Jb.Geol.Palaont.Abh. vol.142,pp.113 - 162.

ALDRIDGE,R.J. 1975. The stratigraphic distribution of conodonts in the British Silurian. Jl.geol.Soc.Lond.,vol.131,pp.607-618.

ALEXANDROWICZ,S.H. 1978. A quantitative study on the origin of Dreissena polymorpha shell accumulations, in Szczecin Bay,Baltic Se Bull.Acad.Pol.Sci.,vol.25,pp.75 - 82.

ALLEN,J.R.L. 1974a. Sedimentology of the Old Red Sandstone (Siluro-Devonian) in the Clee Hills Area,Shropshire,England.Sediment. Geol.,vol.12,pp.75 - 167.

ALLEN,J.R.L. 1974b. Studies in fluviatile sedimentation:implications of pedogenic carbonate units,Lower Old Red Sandstone,Anglo-Welsh outcrop.Geol.J.,vol.9,pp.181 - 208.

ALLEN,J.R.L. & TARLO,L.B. 1963. The Downtonian and Dittonian facies of the Welsh Borderland.Geol.Mag.,vol.100,pp.129 - 155.

ANTIA,D.D.J. 1977. A comparison of diversity and trophic nuclei of live and dead molluscan faunas from the Essex Chenier Plain, England.Paleobiology,vol.3,pp.404 - 414.

ANTIA,D.D.J. 1979. Bone-Beds: a review of their classification, occurence,genesis,diagenesis,geochemistry,palaeoecology, weathering, and microbiotas. Mercian Geol.,vol.7,pp.93 - 174.

BAILEY,R.J. 1969. Ludlovian sedimentation in South Central Wales. In Wood,A.(ed.) Pre-Cambrian and Lower Palaeozoic rocks of Wales and the Welsh Borderland Cardiff. pp.283 - 301.

BAILEY,R.J. & REES,A.I. 1973. A magnetic fabricstudy of the late Whitcliffian (U.Silurian) siltstones from the Welsh Borderland. Geol.J.,vol.8,pp.179 - 188.

BEHRENSMAYER,A.K. 1978. Taphonomic and ecological information from bone-weathering.Paleobiology,vol.4,pp.150 - 162.

BOSCENCE,D.W.J. 1976. Ecological and sedimentological studies on some carbonate sediment producing organisims.Co.Galway,Ireland. Ph.D. thesis,Reading University.

BOSCENCE,D.W.J. 1979a. Trophic analysis of communities and death assemblages.Lethaia,vol.12,p.120.

BOSCENCE,D.W.J. 1979b. Live and dead faunas from coralline algal gravels,Co.Galway.Palaeontology. vol.22,pp.449 - 478.

CALEF,C.E. 1972.Palaeontological and stratigraphical studies in the Ludlow in Wales and the Welsh Borderlands.Ph.D.thesis.Oxford Univers

CALEF,C.E. & HANCOCK,N.J. 1974. Wenlock and Ludlow marine communities in Wales and the Welsh Borderland.Palaeontology,vol.17,pp.779-810.

CAVE,R. & WHITE,D.E. 1972. The exposures of Ludlow rocks and associated beds at Tites Point and near Newnham,Gloucestershire. Geol.J., vol.7,pp.239 - 254.

DUFF,K.L. 1975. Palaeoecology of a bituminous shale - the Lower Oxford Clay of Central England.Palaeontology,vol.18,pp.443 - 482.

ELLES,G.L. & SLATER,I.L. 1906. The highest Silurian rocks of the Ludlow District.Jl.geol.Soc.Lond.,vol.62,pp.195 - 220.

FARROW,G.E. 1974. On the ecology and sedimentation of *Cardium* shell sands and transgressive shell banks on Traigh Mhor,Island of Barra,Outer Hebrides. Trans.R.Soc.Edinb.,vol.69,pp.203 - 227.

FARROW,G.E.,CUCCI,M., & SCOFFIN,T.P. 1978. Calcareous sediments on th nearshore continental shelf of Western Scotland.Proc.R.Soc.Edin. vol.76b,55 - 76.

HANCOCK,N.J.,HURST,J.M., & FURSICH,F.T. 1974. The depths inhabited by Silurian Brachiopod communities. Jl.geol.Soc.Lond., vol.130, pp.151 - 156.

HOBSON,J.S.C. 1960. The sedimentary petrology of the Downton Castle Sandstone Formation in Wales and the Welsh Borderland. Ph.D.thesis. Birmingham University.

HOLLAND,C.H.,LAWSON,J.D.,WALMSLEY,V.G. 1963. The Silurian rocks of the Ludlow District,Shropshire.Bull.Brit.Mus.(Nat.Hist.). vol.8, pp. 93 - 172.

LAWSON,J.D. & WHITAKER,J.H.McD. 1968. Correlation of the Leintwardine Beds.Geol.J. vol.6,pp.329 - 332.

LINGWOOD,P.F. 1976. The biostratinomy of some recent molluscan communities in Liverpool Bay.Ph.D.thesis,Liverpool University.

REID,C. 1898. The Pliocene deposits of Britain. Mem.Geol.Surv.H.M.S.O. 326 p.

REIF,W.-E. 1969. Bonebeds an der Muschelkalk - Keuper - Grenze in Ostwurttemberg.Dip.Arbeit.Tubingen. University. 123p.

REIF,W.-E. 1971. Zur genese der Muschelkalk-Keuper-Grenzbonebeds. N.Jb.Geol.Palaont.Abh.,vol.139,pp.369 - 404.

REIF,W.-E. 1974. Profile des Muschelkalk - Keuper - Grenzbereichs im Jagsttal (Trias,Baden - Wurttemburg).Oberrhein Geol.Abh. vol.23,pp.43 - 54.

ROBERTSON,T. 1927. The highest Silurian rocks of the Wenlock district.Mem.Geol.Surv.Prog.for. 1926. pp. 80 - 97.

SHAFER,W. 1972. Ecology and palaeoecology of marine environments. Oliver & Boyd. Edingburgh. 567p.

SHAW,R.W.L. 1969. Beyrichiacean ostracodes from the Downtonian of Shropshire.Geol.För.Stock.Förh.,vol.91,pp.52 - 72.

SIVETER,D.J. 1974. The superfamily Beyrichiacea (Ostracoda) from the Silurian and Devonian Systems of Britain. Ph.D. thesis.Leicester University.

SIVETER,D.J. 1978. The Silurian.Geol.J. Spec.Issue.No.8,pp. 57 - 100.

SQUIRRELL,H.C. & WHITE,D.E. 1978. Stratigraphy of the Silurian and Old Red Sandstone of the Cennen Valley and adjacent areas,South-East Dyfed,Wales.Rept.Inst.Geol.Sci.No.76/6

SYKES,J.H. 1977.British Rhaetic Bone-Beds.Mercian Geol.,vol.6,pp. 197 - 240.

TURNER,S. 1973. Siluro-Devonian thelodonts from the Welsh Borderland.Jl.Geol.Soc.Lond.,vol.129,pp.537 - 584.

WATKINS,R. 1975. Benthic community organisation in the Ludlow Series of the Welsh Borderland. Ph.D. thesis,Oxford University.

WATKINS,R. & BERRY?W.B.N. 1977. Ecology of a late Silurian fauna of Graptolites and associated organisms.Lethaia,vol.10,pp.267 - 286.

WHITE,D.E. & COPPACK,B.C. 1978. A new section showing the junction between the Ludlow and Downton Series in the Much Wenlock area, Shropshire. Bull.Geol.Surv.G.B.No. 62,pp.25 - 32.

WHITE,D.E. & LAWSON,J.D. 1978. The stratigraphy of new sections in th Ludlow series of the type area, Ludlow,Salop,England.Inst.Geol.Sci. Rep., 78/30.

WILSON,P. 1979. Surface features of quartz sand grains from the Brassington Formation.Mercian Geol.,vol.7,pp. 19 - 30.

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Faunas from the Upper Silurian, Upper Ludlovian, Whitcliffe Beds in the Ludlow - Much Wenlock District, Salop., England.

by

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ABSTRACT

Faunal lists for 17 sections in the Whitcliffe Beds are given. Changes in faunal diversity and dominance are discussed. Length-height plots for *Scaldianella* cf. *simplex*, *Hebellum* cf. *tetragonum*, *Cytherellina siliqua* and *Neobeyrichia lauensis* are presented. A new brachiopod *Lingula corftonensis* sp. nov. is described. Drill holes, annelid and bryozoan borings were observed.

INTRODUCTION

The Upper Silurian, top Ludlovian, Whitcliffe Beds of the Ludlow - Much Wenlock district contain a fauna (cf. Elles & Slater, 1906; Holland et al., 1963; Shergold & Shirley, 1968), which has been assigned to the Salopina or Protochonetes brachiopod community or association (e.g. Calef, 1972; Calef & Hancock, 1974; Boucot, 1975; Lawson, 1975; Watkins, 1978, 1979). However, at the present time no detailed quantitative studies of Whitcliffian faunas exist, and consequently, any community studies on these sediments should be treated with caution. Especially since recent biostratinomic studies have shown that at a given locality the composition of the in situ live calcareous invertebrate fauna is often very different to the composition of the associated dead shell fauna (e.g. Lingwood, 1976; Antia, 1977; Boscence, 1979a,b).

Some recent studies (e.g. Holland et al., 1963; Lawson, 1975) suggested that the faunal composition of the Whitcliffe Beds may vary throughout its thickness, decreasing in diversity towards its top (Calef & Hancock, 1974). The purpose of this study is to try and determine if such changes do occur in the Whitcliffe Beds.

One new species of brachiopod Lingula corftonensis was recorded in this study.

17 localities were visited during the course of this study (Fig. 1). The faunas and sediments from 12 of these sections are described in Tables 1 and 2. The remainder are described in the text.

Lower Whitcliffian sections

Two sections in the Lower Whitcliffe Beds were examined

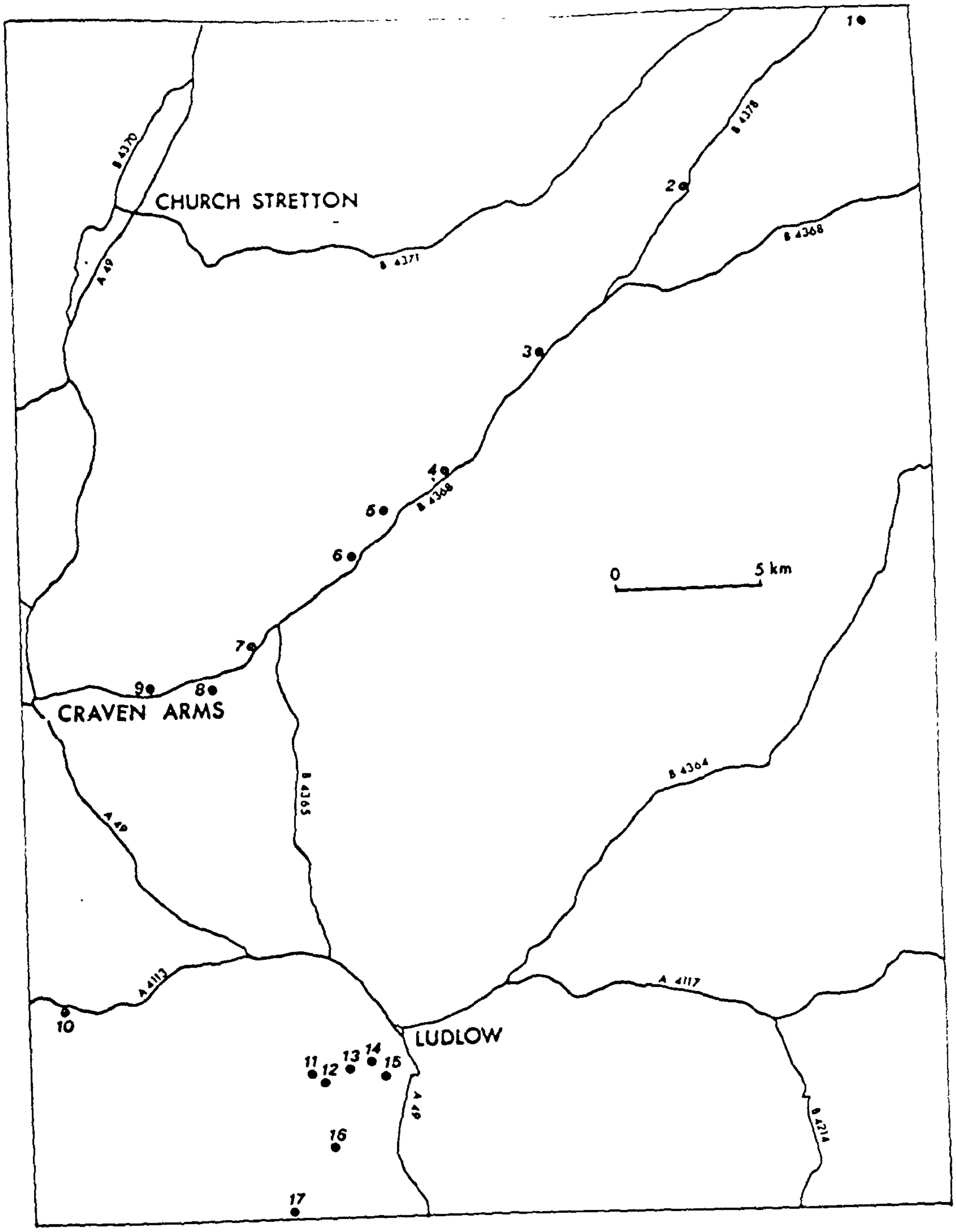


Fig. 1. Sketch map of the Church Stretton - Ludlow District indicating positions of localities documented in this study relative to the principal roads. 1. Cullaughton; 2. Brockton; 3. Broadstone; 4. Munslow; 5. Aston Munslow; 6. Diddlebury;. 7. Culmington; 8. Shawbank; 9. Greenway Cross; 10. Hill pike; 11. Quarry on Ludlow - Deepwood Road; 12. Mortimer Forest; 13. Whitcliffe Common (Locality 7, Table 1); 14. Whitcliffe Common (Locality 6, Table 1); 15. Whitcliffe Common; 16. Overton Quarry; 17. Deer Park Road Section.

Table 1. Summary of sediments in 12 sections in the
[illegible]

Locality	Description
1. Hill pike (GR.SO 437 759)	Contorted and slumped siltstones, containing both lenticular and parallel laminated silts and clays.
2. Shawbank (GR. SO 471 829)	Ripple laminated siltstones.
3. Culmington (GR.SO 481 837)	Ripple laminated and bioturbated siltstones.
4. Diddlebury (GR.SO 504 857)	Bioturbated and rippled poorly fossiliferous siltstones containing some thin shell laminae.
5. Greenway Cross (GR.SO 458 828)	Bioturbated siltstones containing thin shell laminae.
6. Whitcliffe Common (GR.SO 507 745)	Ripple laminated and bioturbated siltstones containing some shell lenses.
7. Whitcliffe Common (GR.SO 505 744)	Slumped, contorted bedded and bioturbated siltstones containing shell debris.
8. Mortimer Forest (GR.SO 498 744)	Bioturbated siltstones containing scattered shell debris.
9. Callaughton (GR.SO 619 976)	Ripple, lenticular, and wavey bedded siltstones and mudstones containing local scour channels and shell sheets.
10. Brockton (GR.SO 578 938)	Lenticular bedded and wavey bedded, bioturbated siltstones.
11. Munslow (GR.SO 524 875)	Rippled siltstones containing thin (3 - 8 mm thick) clay bands.
12. Aston Munslow (GR.SO 511 867)	Slumped, parallel and ripple laminated calcareous siltstones.

Table 2. Faunas from the Upper Whitcliffe Beds in the Ludlow - Much Wenlock District.
1 = Hillpike; 2 = Shawbank; 3 = Culmington; 4 = Diddlebury; 5 = Greenway Cross
6 = Whitcliffe Common (G.R. SO 507 745); 7 = Whitcliffe Common (G.R. SO 505 744);
8 = Mortimer Forest; 9 = Callaughton; 10 = Brockton; 11 = Munslow;
12 = Aston Munslow.

	1	2	3	4	5	6	7	8	9	10	11	12
BRACHIOPODS												
Craniops implicatus	2.63	-		-	-	-	-	-	5.39	3.79	-	3.30
Howellella elegans	-	-	0.11	-	-	-	-	-	-	-	-	-
Lingula lata	-	-	0.44	-	-	-	-	-	0.08	-	-	-
Microsphaeridiorhynchus nucula	7.41	14.14	27.00	15.83	4.93	13.71	28.76	24.62	26.70	22.35	29.44	33.05
Orbiculoidea rugata	0.01	0.19	1.11	1.90	1.50	1.12	0.68	-	0.06	-	-	1.37
Protochonetes ludloviensis	72.78	67.38	46.77	59.92	59.12	20.68	49.31	25.37	18.83	29.79	51.50	36.91
Salopina lunata	17.34	6.67	15.00	14.12	20.16	57.20	14.38	16.41	33.12	38.69	12.18	17.07
BIVALVES												
Fuchsella amygdalina	0.22	8.64	3.66	1.52	4.50	2.39	6.84	28.35	7.34	1.70	0.25	3.03
Goniophora cymbaeformis	0.37	0.19	-	-	-	0.03	-	-	0.36	1.03	-	1.37
Nuculites ovata	-	0.58	-	-	-	-	-	2.98	-	-	-	-
Pterinea tenuistriata	-	-	-	-	-	0.03	-	-	0.49	-	-	-
Pteronitella retroflexa	-	1.37	3.55	-	-	-	-	-	-	0.03	-	-
GASTROPODS												
Loxonema obsoletum	-	-	-	1.14	0.82	1.26	-	-	0.24	0.48	-	1.10
Naticopsis cf. *trevorpatriciorum*	-	-	-	-	0.13	-	-	-	-	-	-	-
CEPHALOPODS												
Kionoceras angulatum	-	-	-	0.19	0.13	0.23	-	-	0.04	-	-	-
Leurocycloceras sp.	-	-	-	-	-	0.23	-	-	-	0.03	-	-
Michelinoceras sp.	-	-	-	1.14	0.54	-	-	0.74	0.84	0.36	3.69	0.27
OTHER MOLLUSCS												
Bucanopsis expansus	-	-	-	0.38	-	-	-	-	-	-	-	0.27
Hyolithes forbesi	-	-	-	0.19	0.13	0.03	-	-	0.01	-	0.08	-
BRYOZOAN COLONIES												
Ceramopora sp.	-	-	-	2.29	0.96	-	-	-	0.13	-	-	-
Leioclema sp.	-	-	-	0.19	1.37	-	-	1.49	0.89	1.03	-	-
Rhopalonaria sp.	-	-	-	-	0.13	-	-	-	-	-	-	-
OSTRACODS												
Calcaribeyrichia torosa	-	0.19	-	-	0.13	0.03	-	-	0.07	-	-	0.27
Cytherellina siliqua	0.05	0.39	0.66	-	3.01	1.12	-	-	0.27	0.66	-	-
Kuresaaria circulata	-	-	-	-	0.13	0.19	-	-	0.13	-	-	-
OTHER FOSSILS												
Cornulites sp.	-	-	-	-	0.13	-	-	-	0.03	-	-	-
Crinoid ossicles	-	-	-	-	0.07	-	-	-	9.71	-	-	-
Ozarkodina sp.	-	-	-	-	-	0.03	-	-	-	-	-	-
'Serpulites' longissimus	-	0.19	1.66	1.14	-	-	-	-	-	-	2.83	-
Tentaculites tenuis	-	-	-	-	0.27	-	-	-	-	-	-	-
Sample size	5879	509	900	524	729	3012	146	134	8674	3292	1165	363

in this study (Fig. 1; 2). They were the Overton Quarry and adjacent track sections, which have been briefly described by Holland *et al*. (1963), Lawson (1973, 1976, 1977) and White & Lawson (1978), and the Deer Park Road section which has been briefly described by Lawson (1976, 1977) and White & Lawson (1978). Both sections are in Mortimer Forest and within four miles of Ludlow. The earlier studies on these Whitcliffian sections have (1) recorded the thicknesses of sediment present, (2) the position of the boundary between the Upper Leintwardine Beds and the Lower Whitcliffe Beds. They describe the former as flaggy olive-grey, calcareous siltstones containing *Neobeyrichia lauensis*, *Aegiria grayi*, *Shaleria ornatella*, *Calymene puellaris*, *Encrinurus stubblefieldi* and *Cytherellina siliqua*. The Lower Whitcliffe Beds are described as thickly flaggy calcareous greenish grey siltstones containing a less diverse fauna, which includes *Microsphaeridiorhynchus nucula*, *Protochonetes ludloviensis*, *Dayia navicula*, *Orbiculoidea rugata*, *Fuchsella amygdalina* and '*Serpulites*' *longissimus*.

1. Overton Quarry (G.R. SO 497 725)

The quarry and adjacent track sections 200 m east of Sunnydingle cottage along the Mary Knoll valley were examined. The relative position of each section is illustrated by White & Lawson (1978). The sediment log for this section is given in Fig. 2. The distribution of faunas in the section is given in Table 3. The Upper Leintwardine Beds exposed in the track below Overton Quarry consists of highly bioturbated siltstones in which most of their internal lamination has been destroyed by bioturbation. Although the shells tend to be randomly dispersed throughout the sediment, some shell layers are present. Indi-

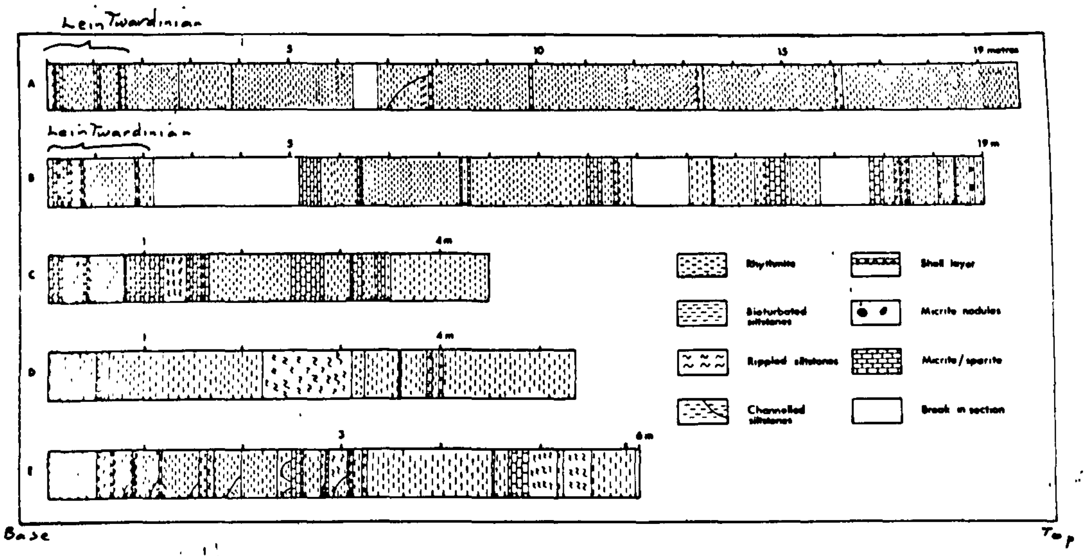


Fig. 2. Sediment logs for five sections examined from the Whitcliffian and Leintwardinian of the Ludlow District:-

A. Deer Park Road section;

B. Overton Quarry section and both overlying and underlying track sections;

C. Broadstone Farm section;

D. Quarry on Deepwood - Ludlow Road;

E. Quarry on Whitcliffe Common. Many of the sediment layers above 3.3 m in this section are slumped.

Table 3. Faunal list for Overton Quarry and adjacent track sections (n = 6161)
1 = Upper Leintwardine Beds, basal 2.04 m of section in Fig. 2; 2/5 Overton Quarry Lower Whitcliffe Beds. Positions relative to quarry base are as follows:-
2 = 0 - 2.28 m; 3 = 2.28 - 3.65 m; 4 = 3.65 - 6.30 m; 5 = 6.30 - 9.64 m; 6 = the 2.26 m of sediment in the track section above Overton Quarry in the Lower Whitcliffe Beds.

	1	2	3	4	5	6
BRACHIOPODS						
Aegiria grayi (Davidson)	2.21	0.54	0.78	-	-	-
Atrypa reticularis (Linnaeus)	1.15	-	0.58	-	-	-
Craniops implicatus (J. de C. Sowerby)	0.23	-	0.05	-	-	-
Dayia navicula (J. de C. Sowerby)	1.78	2.05	-	0.28	-	6.30
Howellella elegans (Muir Wood)	0.51	-	-	-	-	-
Leptaena depressa (J. de C. Sowerby)	0.42	-	-	-	-	-
Lingula lata J. de C. Sowerby	-	-	5.60	-	-	-
Lingula lewisi J. de C. Sowerby	1.66	-	-	-	-	-
Microsphaeridiorhynchus nucula (J. de C. Sowerby)	24.03	9.52	17.11	3.90	22.03	13.18
Orbiculoidea rugata (J. de C. Sowerby)	0.10	1.22	0.60	-	-	-
Protochonetes ludloviensis Muir Wood	9.79	33.42	38.08	91.56	58.82	73.61
Salopina lunata (J. de C. Sowerby)	39.56	13.22	4.73	3.80	12.52	4.66
Shagamella ludloviensis Boucot & Harper	0.22	-	-	-	-	-
Shaleria ornatella (Davidson)	0.93	-	-	-	-	-
Sphaerirhynchia wilsoni (J. Sowerby)	0.11	-	-	-	-	-
BIVALVES						
Cardiola interrupta (Sowerby)	-	-	9.18	0.80	-	-
Fuchsella amygdalina (J. de C. Sowerby)	1.92	5.12	5.86	-	3.03	0.80
Goniophora cymbaeformis (J. de C. Sowerby)	-	4.11	-	-	-	0.06
Nuculites antiquaas (J. de C. Sowerby)	-	1.10	-	-	-	-
Nuculites ovata (J. de C. Sowerby)	-	-	-	-	-	0.03
'*Pterinea*' *tenuistriata* (McCoy)	-	3.08	-	0.12	-	0.06
Pteronitella retroflexa (Wahlenberg)	0.03	1.80	-	-	-	0.03
GASTROPODS						
Cyclonema corallii (Sowerby)	-	-	0.40	-	-	-
Loxonema obsoletum (J. de C. Sowerby)	-	4.70	0.41	-	1.25	0.00
Naticopsis cf. *trevorpatriciorum* Peel	-	2.22	-	-	-	-
CEPHALOPODS						
Kionoceras angulatum (Wahlenberg)	-	-	2.11	-	-	-
'*Orthoceras*' sp.	0.28	4.45	3.93	-	0.13	0.17
Paraphragmites ibex (J. de C. Sowerby)	0.03	-	-	0.16	-	-
OTHER MOLLUSCS						
Bucanopsis expansus (J. de C. Sowerby)	-	1.82	0.05	-	0.13	-
Hyolithes forbesi (Sharpe)	0.07	-	-	-	-	-
BRYOZOAN COLONIES						
Ceramopora sp.	1.43	7.57	0.05	-	0.13	0.04
Leioclema sp.	4.38	0.1	6.81	-	0.13	0.18
OSTRACODS						
Calcaribeyrichia tegula Siveter	-	-	-	-	0.06	0.68
Cavellina sp.	0.10	-	-	-	-	-
Cytherellina siliqua Jones	1.02	-	0.30	-	-	-
Hebellum cf. *tetragonum* (Krause)	1.84	1.38	0.63	0.24	-	-
Kuresaaria circulata (Neckaja)	2.09	-	-	-	-	0.02
Neobeyrichia lauensis (Kiesow)	0.97	-	-	-	-	-
Scaldianella cf. *simplex* (Krause)	3.08	-	0.40	-	-	0.11
ANNELIDS						
Arabellites sp.	0.07	0.54	-	-	-	-
'*Serpulites*' *longissimus* J. de C. Sowerby	1.20	4.41	0.45	-	0.47	0.70
TRILOBITES						
Calymene sp.	0.14	-	-	-	-	-
Encrinurus sp.	0.83	-	-	-	-	-
OTHER FOSSILS						
Crinoid columnals	-	-	0.05	-	-	-
Cornulites sp.	0.28	-	-	-	-	-
Ischnacanthus kingi Woodward	0.03	-	-	-	-	-
'*Onchus*' sp.	-	-	-	-	-	0.03
Ozarkodina sp.	0.10	-	-	-	-	-

Table 4. Faunal list for the Deer Park Road Section (n = 18,047)
1 = Upper Leintwardine Beds (1.28 m) 2/7 = Lower Whitcliffe Beds. Sample Positions in section with respect to the Leintwardinian/Whitcliffian Boundary are:-
2 = 0 - 3.10 m; 3 = 3.10 - 5.96 m; 4 = 5.96 - 9.14 m; 5 = 9.14 - 11.61 m; 6 = 11.61 - 14.59 m; 7 = 14.59 - 17.15 m.

	1	2	3	4	5	6	7
BRACHIOPODS							
Aegiria grayi (Davidson)	0.67	-	-	-	-	-	-
Craniops implicatus (J. de C. Sowerby)	9.51	0.34	0.28	0.78	0.01	0.03	0.07
Dayia navicula (J. de C. Sowerby)	0.3	15.54	10.03	0.04	0.03	0.11	-
Isorthis sp.	0.08	-	-	0.17	0.47	0.11	4.67
Howellella sp.	0.27	0.34	0.07	-	-	-	-
Lingula lewisi J. de C. Sowerby	0.10	-	-	-	0.31	0.08	0.03
Lingula lata J. de C. Sowerby	0.02	-	-	-	0.04	0.24	-
Microsphaeridiorhynchus nucula (J. de C. Sowerby)	24.55	6.70	3.64	4.70	15.14	18.42	23.88
Orbiculoidea rugata (J. de C. Sowerby)	0.01	-	0.12	-	1.08	0.29	-
Protochonetes ludloviensis Muir Wood	1.22	23.52	54.48	75.16	69.12	43.22	43.92
Salopina lunata (J. de C. Sowerby)	16.31	14.20	7.62	16.81	8.47	13.43	6.82
Shagamella ludloviensis Boucot & Harper	0.14	-	-	-	0.01	-	-
Shaleria ornatella (Davidson)	0.10	-	-	-	-	-	-
BIVALVES							
Cardiola interrupta (Sowerby)	-	0.46	0.39	-	0.06	-	-
Fuchsella amygdalina (J. de C. Sowerby)	0.88	10.60	5.21	0.7	0.52	11.81	13.44
Goniophora cymbaeformis (J. de C. Sowerby)	-	0.18	-	-	0.04	0.10	-
Grammysia sp.	-	-	0.28	-	-	-	-
Modiolopsis sp.	-	0.3	-	0.11	-	-	-
Nuculites antiquas (J. de C. Sowerby)	-	1.24	0.46	-	-	0.11	-
Nuculites ovata (J. de C. Sowerby)	0.88	0.54	0.00	-	-	0.03	0.07
Pterinea lineata (J. de C. Sowerby)	-	-	0.06	-	-	-	-
Pterinea tenuistriata (McCoy)	-	-	0.95	-	-	-	-
Pteronitella retroflexa (Wahlenberg)	0.01	-	0.07	-	-	-	-
Solenomya sp.	-	-	0.07	-	-	-	-
GASTROPODS							
Cyclonema corallii (J. de C. Sowerby)	0.04	0.44	0.51	0.22	0.31	0.11	-
'Liospira sp.	0.04	-	-	-	-	0.03	-
Loxonema gregarium (J. de C. Sowerby)	-	-	-	-	-	0.05	-
Loxonema obsoletum (J. de C. Sowerby)	-	0.88	0.28	0.17	-	0.23	0.03
Murchisonia sp.	-	0.10	0.07	-	-	-	-
Naticopsis cf. trevorpatriciorum Peel	-	-	-	-	-	0.03	-
CEPHALOPODS							
Kionoceras angulatum (Wahlenberg)	0.28	-	0.60	-	-	0.06	0.50
Michelinoceras bullatum (J. de C. Sowerby)	0.08	2.16	4.30	0.17	1.22	0.78	0.89
'Orthoceras' sp.	0.58	4.10	0.26	0.01	0.11	0.16	1.34
Paraphragmites ibex (J. de C. Sowerby)	-	-	0.76	-	0.11	-	1.32
OTHER MOLLUSCS							
Bucanopsis expansus (J. de C. Sowerby)	-	-	0.14	-	-	-	-
Hyolithes forbesi (Sharpe)	-	1.00	0.70	-	0.14	1.14	0.02
TRILOBITES							
Calymene sp.	1.98	-	-	-	-	-	-
Encrinuris sp.	0.42	-	0.05	-	-	-	-
BRYOZOAN COLONIES							
Ceramopora sp.	0.05	0.38	2.33	0.45	0.25	0.53	0.28
Leioclema sp.	1.35	3.60	4.30	0.81	0.50	2.84	0.07
Rhopalonaria sp.	-	-	-	0.01	-	-	-
OSTRACODS							
Amygdalina sp.	-	-	-	-	0.01	-	-
'Beyrichia' sp.	0.88	3.40	-	1.02	0.15	-	1.00
Calcaribeyrichia tegula Siveter	-	-	-	-	0.01	-	-
Cavellina cf. primaria Saro	0.08	0.10	0.00	-	-	-	-
Cytherellina siliqua Jones	2.44	-	0.60	0.35	0.21	-	0.13
Hebellum cf. tetragonum (Krause)	9.60	2.08	1.08	0.87	0.06	0.03	0.17
Hebellum cf. triviale Gailite	0.10	-	-	-	-	-	-
Neobeyrichia lauensis (Kiesow)	10.58	-	-	-	-	-	-
Neobeyrichia scissa Martinsson	0.08	-	-	-	-	-	-
Nyhamnella sp.	0.10	-	-	-	0.01	-	-
Scaldiana simplex (Krause)	15.17	7.34	1.08	0.79	0.23	0.08	0.07
ANNELIDS							
Keilorites sp.	-	-	0.06	-	-	-	-
Spirobis lewisii J. de C. Sowerby	-	0.10	0.14	-	0.13	-	-
'Serpulites' longissimus J. de C. Sowerby	0.58	0.82	0.58	0.01	0.04	2.58	2.34
OTHER FOSSILS							
Ozarkodina sp.	0.02	-	-	0.02	-	-	-
Solitary coral	-	-	-	-	-	1.43	-
Ischnacanthus kingi Woodward	-	-	-	-	0.05	-	-
Cornulites sp.	-	-	-	-	0.13	-	-

vidual layers may be enriched in S. ornatella, S. lunata, and/or M. nucula.

Bedding, when present, consists of parallel laminated alternating dark and light silt layers (between 8 and 15 alternations per 1 cm vertical thickness of sediment) which resemble modern rhythmites (cf. Reineck & Singh, 1973). Two carbonate concretion or nodule bands were noted in this section. Their relative position in the section, size and sphericity measurements are given in Fig. 3. Similar concretions have been described in detail by Cherns (1977) and may have formed within a few centimetres of the sediment water interface, prior to excavation and their concentration on the sediment surface. Some of the concretions on the lower layer have been encrusted by the bryozoan Ceramopora sp.

One nodule appeared to have formed within an orthocone phragmocone. It contained three specimens of the tentaculite Nowakia sp. (identified by Dr. C. J. Burton) posteriorly attached to its inner surface with their apertures facing downwards. The infaunal and semi-infaunal bivalves Fuchsella amygdalina and Goniophora cymbaeformis were observed to occur as closed articulated paired valves with vertically orientated hinge lines in apparent life orientation (cf. Cherns, 1977).

Bryozoans (Ceramopora sp.) were observed encrusting on 'Serpulites' longissimus, Atrypa recticularis, cephalopod and bivalve shells.

The Lower Whitcliffe Beds were seen in Overton Quarry and the overlying track section. They contain a higher overall density of shells than the underlying Upper Leintwardine Beds (Fig. 4). Most of their internal lamination has been destroyed by bioturbation locally and thin parallel laminated siltstones

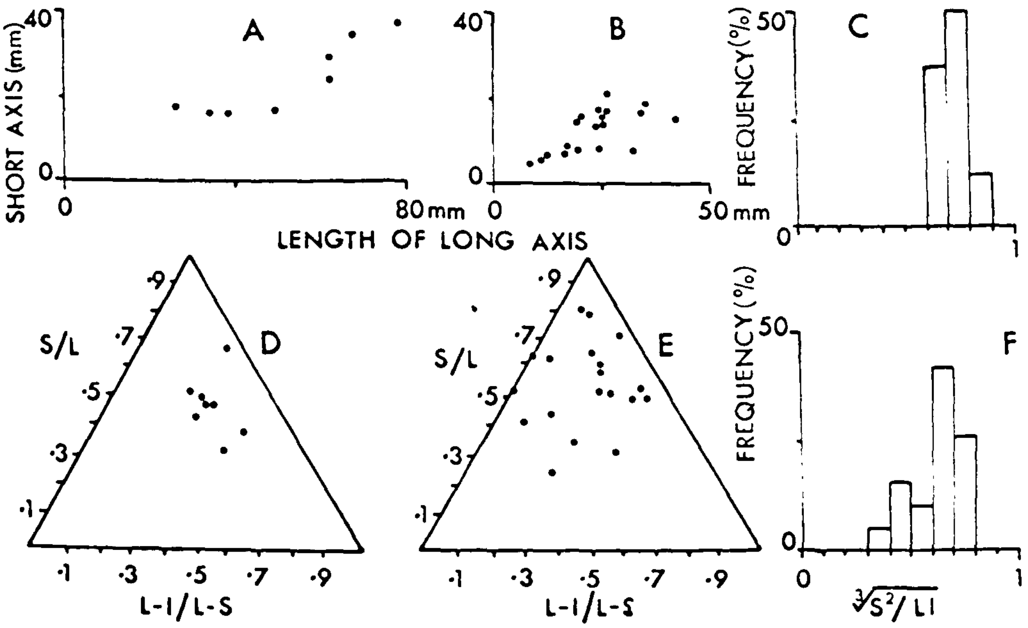


Fig. 3. Carbonate nodules from the Upper Leintwardine Beds in the track section immediately below Overton Quarry:-

A. Length of longest axis/length of shortest axis plots for (A) nodules from 165 cm above the base of the section in Fig. 2B and (B) from the base of the section in Fig. 2B. Sphericity form graphs for the two layers are given in D and E respectively. The effective settling sphericity frequency histograms

for these nodules are given in Fig. 3C, F, respectively.

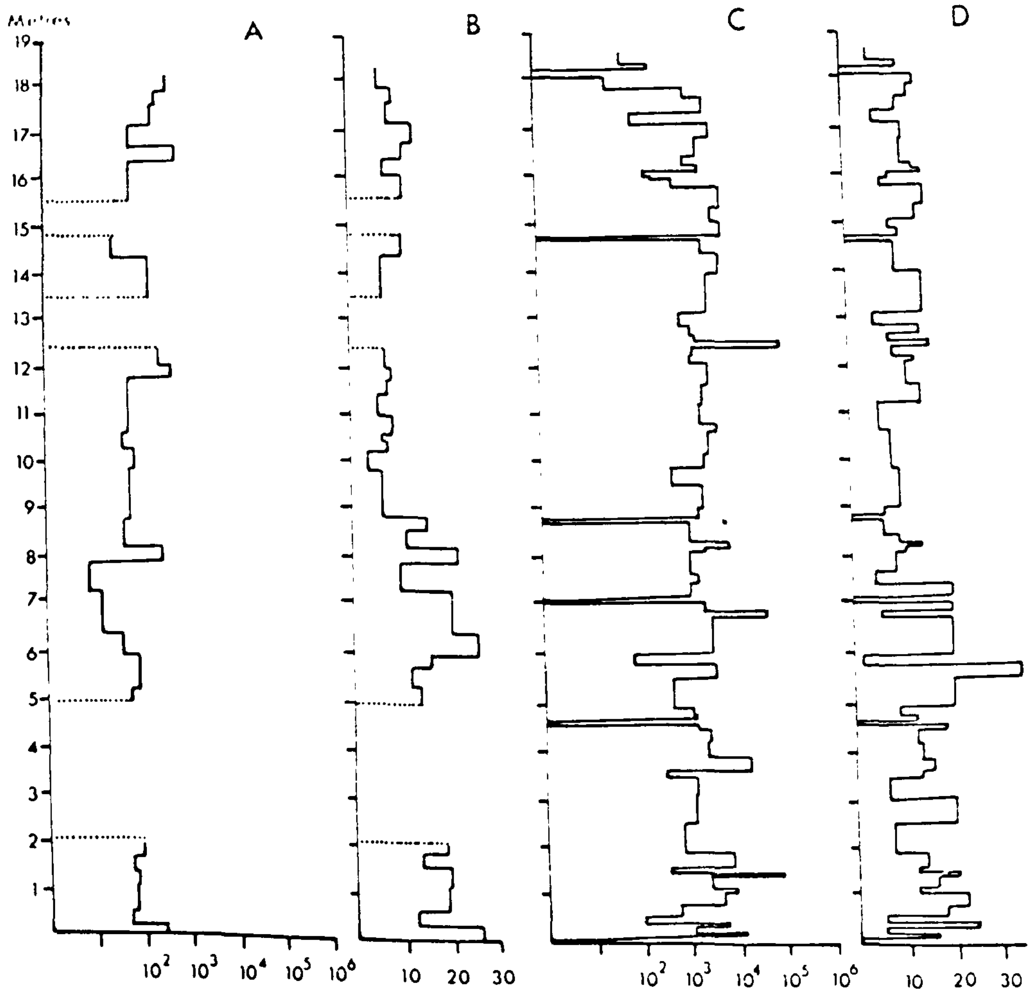


Fig. 4. Fossil density and diversity profiles of the Deer Park lane section and Overton Quarry sections. Diversity expressed as No. of species per thousand individuals. Calculated assuming a log normal faunal distribution (cf. Sanders, 1968; Duff, 1975). Density of Overton Quarry sections expressed as No. of fossils per 2 kg rock. Density of Deer Park lane section expressed as No. of fossils per m^2 bedding plane surface area.

A. Density profile Overton Quarry (mid portion) and the Upper Leintwardinian track section (lower portion) and the overlying Lower Whitcliffe Beds track section (uppermost portion).

B. Diversity profile of the Overton Quarry sections.

C. Density profile of the Deer Park Road section.

D. Diversity profile of the Deer Park Road section.

Sediment profiles of the two sections are given in Fig. 2.

and ripple laminated siltstones are present. The latter occur most commonly in the upper part of the section (wave length 10 - 25 cm; amplitude 5 - 15 mm).

F. amygdalina occurs *in situ* and the species *S. lunata*, *M. nucula*, *D. navicula* and *P. tenuistriata* occur as articulated valves. Many of the shells present have been encrusted by bryozoans. Both orthocone and bivalve fragments contain rare *Clionoides* sp. and *Rhopalonaria* borings.

Discrete shell sheets (up to 5 mm thick) and shell lenses (up to 10 cm thick) composed of abraded disarticulated shells and shell fragments are also present.

2. *Deer Park Road section* (G. R. SO 497717)

This section (Fig. 1 & 2) may be divided into two lithological subdivisions at a point, which appear to correspond to the Whitcliffian - Leintwardinian boundary as determined by the faunas (Table 4). The criteria used here to recognise the Whitcliffian - Leintwardinian boundary have been outlined by Holland *et al*. (1963) and Lawson & Whitaker (1968).

The Leintwardinian sediments consist of parallel laminated siltstones, which closely resemble rhythmites, and bioturbated siltstones in which all lamination has been destroyed. They contain a low diversity fauna, which increases in diversity in rare shell layers (Fig. 4). This increase in diversity may relate to (1) an input of exotic species into the environment during the storm which generated the shell sheet (cf. Watkins & Berry, 1977) and (2) the colonisation of the shell sheet by an epifauna adapted for life on a hard substrate.

The overlying Whitcliffian sediments are more bioturbated than the Leintwardinian sediments, they contain minor irregular erosion surfaces and scour channels up to 80 cm in depth. The sediments contain some rippled coarse siltstone sheets and shell sheets. However, increased biogenic activity in these sediments may have resulted in a complete mixing of some of these layers with the over and underlying silts to produce a fairly high overall shell density and faunal diversity throughout the Lower Whitcliffe Beds (Fig. 4). *F. amygdalina* and *L. lata* were observed *in situ*. Articulated shells of *M. nucula*, *P. ludloviensis*, *D. navicula*, *S. lunata*, *S. simplex*, *H. tetragonum* and *C. siliqua* were also observed.

Upper Whitcliffe Beds

Three sections in the Upper Whitcliffe Beds were examined in detail. They include (1) the stratotype section for the junction of the Lower Whitcliffe Beds and the Upper Whitcliffe Beds, (2) a section in the upper Whitcliffian of Ludlow and (3) the upper Whitcliffian section at Broadstone Farm.

Twelve other sections in the Upper Whitcliffe Beds were briefly examined and the faunal lists compiled for each are presented in Table 2. Details of their sediments and location are presented in Table 1. These tables show that *C. torosa* is the dominant Whitcliffian beyrichiacean ostracod and that the fauna of the Upper Whitcliffe Beds is dominated by articulate brachiopods. Most of the shells in these samples occurred as disarticulated valves and fragmentary remains.

Whitcliffe Common: Holostratotype section of the Lower-Upper Whitcliffe Beds Boundary (G.R. SO 509 742)

The faunal distributions and the stratigraphic significance of this quarry on Whitcliffe Common have already been described

Table 5. Faunal distributions across the Upper Whitcliffe Beds - Lower Whitcliffe Beds Boundary in the stratotype section. (n = 3210)

	UPPER WHITCLIFFE BEDS										LOWER WHITCLIFFE BEDS							
Position of sampled unit	3.3	2.9	2.5	2.1	1.8	1.3	0.9	0.5	0.2	0.0	0.2	0.5	0.9	1.3	1.7	2.0	2.4	2.9 m
BRACHIOPODS																		
Craniops implicatus		-	-	0.3	-	-	-	-	0.9	-	-	0.4	-	-	-	-	-	-
Lingula corftonensis		-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	1.6
Lingula lata		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.1
Microsphaeridiorhynchus nucula		0.8	2.1	7.8	10.4	2.3	6.9	27.5	17.2	77.1	48.4	21.3	20.6	-	50.0	21.6	61.4	-
Orbiculoidea rugata		-	-	-	-	-	4.6	-	1.8	-	3.2	0.2	-	-	-	5.0	7.8	-
Protochonetes ludloviensis		-	1.0	1.0	6.2	1.8	39.5	12.0	59.0	5.0	38.4	62.0	31.0	93.7	-	20.0	0.7	2.2
Salopina lunata		96.4	95.6	88.5	82.6	95.7	46.5	55.1	14.5	8.4	9.2	6.6	-	-	-	20.0	21.9	23.0
OSTRACODS																		
Calcaribeyrichia torosa		-	-	-	-	-	-	-	-	-	-	0.1	-	-	-	-	-	-
Cytherellina siliqua		-	-	-	-	-	2.3	-	0.9	-	0.3	-	-	-	-	-	-	-
Kuresaaria circulata		-	-	-	-	-	-	-	-	-	-	0.1	-	-	-	-	-	-
BIVALVES																		
Fuchsella amygdalina		-	-	-	0.3	-	-	-	-	-	-	0.8	-	-	31.2	31.6	0.7	2.2
Conicphora cymbaeformis		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.8
Pterinea cf. *tenuistriata*		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.7	-
Solenomya sp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.4	-
OTHER MOLLUSCS																		
Hyolithes forbesi		-	-	-	0.3	-	-	-	2.7	-	-	0.1	-	-	6.2	-	-	4.4
Loxonema conicum		-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BRYOZOANS																		
Ceramopora sp.		-	-	0.6	-	-	-	-	0.9	-	0.1	-	-	-	-	-	-	-
Leioclema sp.		-	-	-	-	-	-	-	-	-	0.1	-	-	-	-	-	5.6	-
CEPHALOPODS																		
Michelinoceras bullatum		-	-	-	-	-	-	-	-	-	-	0.1	-	-	6.2	-	-	0.5
Paraphragmites ibex		-	-	-	-	-	-	-	-	-	0.1	0.1	-	-	-	-	-	-
Leurocycloceras sp.		1.7	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
OTHER FOSSILS																		
Crinoid columnals		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5
Keilorites sp.		-	-	-	-	-	-	3.4	-	-	-	3.1	48.2	-	-	-	-	39.8
Pterygotus sp.		-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	1.6	-	-
Serpulites longissimus		0.9	-	-	-	-	-	1.7	1.8	-	0.1	5.6	-	6.3	-	-	-	1.1
Thelodus parvidens		-	-	-	-	-	-	-	-	-	-	0.8	-	-	-	-	-	-
Arabellites sp.		-	-	-	-	-	-	-	-	-	-	0.8	-	-	6.2	-	-	-

(Holland et al., 1963). A faunal list for the section is given in Table 5. Its sediments [illegible] section. (Fig. 2) have been divided into two lithostratigraphic formations - the Upper Whitcliffe Beds and the Lower Whitcliffe Beds (Holland et al., 1963).

1. The Lower Whitcliffe Beds consist of a cyclic sequence of sedimentation. The basal unit of each cycle consists of a calcareous bioturbated siltstone (10 - 45 cm thick) containing thin layers rich in shell debris. The internal structure of these silts has been largely destroyed by bioturbation. However, locally, unbioturbated areas or poorly bioturbated patches are present. These indicate that the sediment originally consisted of a mixture of parallel and ripple laminated silts and dark muds similar to those present (p. 29-31) in Deepwood quarry in the Upper Whitcliffe Beds (G.R. SO 492 742). These siltstone units frequently contain vertically orientated orthocone fragments (indicating deposition in less than 10 m of water (Raup, 1973)) and an in situ fauna of F. amygdalina. The latter are present in small dispersed clumps of similar size and density to those recorded (p. 31) in the Deepwood quarry.

The uppermost surface of this unit is frequently rippled (wave length 25 - 35 cm) with ripple troughs cutting into previously deposited sediment, indicating that the rippling resulted from an erosive rather than a depositional process. This eroded surface also contains some scour channels (up to 1.5 m wide and 15 cm deep). These channels are commonly infilled by shell debris at their base, which is overlain by ripple and cross laminated silts. Along any one erosion surface the channels are spaced at intervals of 1 to 10 m. Frequently the sediments in the channels are bioturbated suggesting that their formation and sediment infilling predated the formation of the erosion surface.

Immediately overlying the channelled erosion surface are parallel laminated calcareous silts (up to 15 cm thick) containing well rounded platy clay pebbles (up to 3 cm in diameter and 4 mm thick) and a fauna rich in Keilorites fragments, rare trace fossils and rare shells.

This cycle where shelf silts and clay deposition is followed by (1) the development of a scoured erosion surface and (2) the deposition of laminated silts is repeated four times in the section

2. The Upper Whitcliffe Beds consist of rippled and parallel laminated alternating clay-silt laminae, containing shell gravel mega-ripples (wave length 0.5 - 3 m; amplitude 5 - 17 cm), scour channels (up to 1 m in width, 10 - 19 cm deep) infilled with shell debris and/or coarse silt, shell patches and convolute slump bedding similar in structure to head slumps produced in a slump head region (cf. Lewis, 1971; Woodcock, 1976).

Just below the junction of the Lower and Upper Whitcliffe Beds is a layer rich in air heave structures.

The fauna of the Upper Whitcliffe Beds and Lower Whitcliffe Beds in this section are similar. The main difference is that S. lunata is the dominant brachiopod in the Upper Whitcliffe Beds, while in the Lower Whitcliffe Beds, three articulate brachiopod species (S. lunata, M. nucula and P. ludloviensis) occur commonly.

Ludlow - Deepwood Road: Upper Whitcliffe Beds

A quarry just off the Ludlow to Deepwood Road (G. R.

Table 6. Faunal list for the Quarry in the Upper Whitcliffe Beds on the Ludlow - Deepwood Road (n = 1608)

Height above base of section (cm)
0 62 159 225 326 389 537

BRACHIOPODS						
Lingula corftonensis	-	3.50	-	-	-	-
Lingula lata	-	1.75	-	0.23	-	-
Lingula lewisi	-	-	-	-	0.24	-
Microsphaeridiorhynchus nucula	27.90	19.29	22.96	11.26	18.59	7.15
Orbiculoidea rugata	-	1.75	1.48	1.17	1.20	1.02
Protochonetes ludloviensis	6.97	28.07	10.37	24.88	14.25	31.69
Salopina lunata	5.81	8.77	16.29	39.43	17.39	21.47
BIVALVES						
Fuchsella amygdalina	27.90	21.05	35.55	0.46	4.58	3.88
Goniophora cymbaeformis	1.16	-	-	-	0.24	0.20
Modiolopsis sp.	-	-	0.74	-	-	0.40
'*Pterinea*' *tenuistriata*	-	-	-	-	0.24	-
GASTROPODS						
Loxonema obsoletum	-	1.75	-	3.28	0.24	0.61
Murchisonia sp.	3.48	7.01	0.74	0.93	-	-
Naticopsis cf. *trevorpatriciorum*	-	-	-	0.46	0.96	-
CEPHALOPODS						
Kionoceras angulatum	-	-	1.48	-	-	-
Michelinoceras bullatum	-	-	2.96	0.23	0.96	0.20
'*Orthoceras*' spp.	2.32	-	1.48	1.87	0.24	1.22
Paraphragmites ibex	-	-	1.48	-	-	0.20
OTHER MOLLUSCS						
Bucanopsis expansus	-	1.75	-	0.23	-	-
Hyolithes forbesi	-	-	-	0.70	0.72	0.46
BRYOZOANS						
Ceramopora sp.	-	-	-	-	0.48	-
Leioclema sp.	1.16	-	17.77	1.87	7.00	7.97
Rhopalonaria sp.	-	-	-	-	0.24	0.20
ANNELIDS						
Arabellites sp.	-	-	-	-	0.24	-
'*Serpulites*' *longissimus*	4.65	3.50	-	4.92	10.14	10.02
Spirorbis sp.	-	-	-	0.23	-	3.27
OSTRACODS						
Amygdalella sp.	1.16	-	-	0.93	-	-
Calcaribeyrichia torosa	1.16	-	-	-	0.72	0.40
Cytherellina siliqua	4.65	1.75	0.74	2.11	9.42	4.08
Hebellum cf. *tetragonum*	4.65	-	-	1.17	7.00	3.47
Kuresaaria circulata	2.32	-	-	4.22	1.44	1.84
Londinia sp.	1.16	-	-	-	-	-
Nyhamnella sp.	2.32	-	-	0.70	-	-
Thilipsura sp.	1.16	-	-	0.23	3.38	0.20
OTHER FOSSILS						
Crinoid columnals	-	-	-	0.23	-	-
Echinoid spine	-	-	-	0.23	-	-
Ozarkodina sp.	-	-	0.74	-	0.24	-
Sample size	86	57	135	426	414	489

SO 492 742) contains some 5.5 m of calcareous sediment (Fig. 2) which have been assigned to the Upper Whitcliffe Beds (Holland et al., 1963). The sediment consists of parallel laminated silts, scattered layers of shell debris, rippled coarse silt layers with erosive bases (wavelength 20 - 30 cm; silt layer thickness 5 - 10 cm), rippled shell gravel sheets, scour channels (up to 60 cm wide; 15 - 20 cm deep), infilled with cross bedded silts and/or shell gravel, discontinuous patches (up to 1 m in diameter) of dark parallel laminated clays, and lenticular bedded silts and clays.

The scour channels are infilled asymmetrically by coarse silt and/or shell gravel containing steeply inclined layers. Such channels are thought (McKee, 1957) to be produced by diagonally passing currents in intertidal or shallow subtidal marine environments (McKee, 1957; Reineck & Singh, 1973). The thin shell layers and some of the silt layers in the section may have originated as storm deposits (cf. Watkins & Berry, 1977; Hurst & Watkins, 1978).

The sediment log for this section is given in Fig. 2 and a Table of faunal distributions in Table 6. All the species recorded are typical Whitcliffian forms (cf. Holland et al., 1963). Some in situ specimens of F. amygdalina are present in small patches covering some 0.5 - 1 m^2 and containing between 10 and 65 individuals.

Broadstone

The roadside section in the Upper Whitcliffe Beds at Broadstone Farm (G.R. SO 543 897) near Shipton was examined. The fauna present is documented in Table ~~7~~ and contains typical Whitcliffian species (cf. Holland et al., 1963).

Table 7. Fauna from the road section in the Upper Whitcliffe Beds opposite Broadstone Farm (n = 2621)

	Distance above base of section (cm)														
	0	14	35	42	62	82	89	123	152	186	260	294	322	347	386
BRACHIOPODS															
Craniops implicatus		-	-	-	-	-	-	-	-	-	-	-	-	0.97	-
Lingula lata		-	-	-	-	-	-	-	-	-	-	0.76	-	-	-
Microsphaeridiorhynchus nucula		3.72	11.40	10.07	4.68	18.36	49.27	2.14	8.33	37.68	25.42	26.15	51.15	30.73	51.83
Orbiculoidea rugata		-	-	-	-	-	0.36	-	-	-	1.12	-	0.51	1.46	-
Protochonetes ludloviensis		95.21	71.92	83.20	95.31	72.95	39.85	88.57	51.66	56.52	29.94	33.84	43.73	56.09	42.64
Salopina lunata		-	2.63	0.74	-	-	-	-	-	1.44	-	6.15	-	0.48	1.10
Schizocrania striata (J. de C. Sowerby)		-	-	-	-	-	1.08	7.14	-	-	-	-	0.25	-	-
BRYOZOAN COLONIES															
Ceramopora sp.		-	-	-	-	1.02	-	-	-	-	0.56	-	1.53	0.48	-
Leioclema sp.		-	-	-	-	0.51	1.81	-	-	-	5.64	6.15	-	-	-
Rhopalonaria sp.		-	-	-	-	-	-	-	-	-	10.16	-	-	-	-
BIVALVES															
Fuchsella amygdalina		-	-	-	-	-	0.36	-	1.66	-	9.03	10.00	0.51	1.46	-
Goniophora cymbaeformis		-	-	-	-	1.53	3.98	-	-	-	1.12	-	-	-	-
Modiolopsis sp.		-	-	-	-	-	-	-	-	-	0.56	-	-	-	-
Nuculites ovata		0.53	-	-	-	-	0.36	-	-	-	0.56	3.84	-	-	-
'Pterinea' tenuistriata		-	-	-	-	-	-	-	-	-	0.56	-	-	-	-
Solenamya sp.		-	-	-	-	-	-	-	-	-	-	1.53	-	-	-
CEPHALOPODS															
Leurocycloceras sp.		-	0.87	-	-	-	-	-	-	-	-	-	-	-	-
Orthoceras sp.		-	-	-	-	-	0.36	1.42	-	-	1.69	6.15	-	0.48	1.10
Paraphragmites ibex		-	-	-	-	-	-	-	-	-	2.25	-	-	-	-
OTHER MOLLUSCS															
Bucanopsis expansus		-	-	-	-	-	-	-	-	-	2.25	-	-	-	-
Hyolithes forbesi		-	-	-	-	0.51	-	-	1.66	-	0.56	0.76	0.25	-	-
ANNELIDS															
Keilorites sp.		-	-	-	-	0.51	-	-	35.00	-	0.56	-	-	-	-
'Serpulites' longissimus		-	12.28	5.97	-	4.08	2.53	0.71	1.66	4.34	7.34	4.61	-	1.95	0.36
OSTRACODS															
Calcaribeyrichia torosa		-	-	-	-	-	-	-	-	-	-	-	-	0.48	-
Kuresaaria circulata		-	-	-	-	-	-	-	-	-	-	-	-	5.85	2.20
Nyhamnella sp.		-	-	-	-	-	-	-	-	-	-	-	-	-	0.36
OTHER FOSSILS															
Crinoid columnals		0.53	-	-	-	-	-	-	-	-	-	-	-	-	-
Ozarkodina sp.		-	-	-	-	-	-	-	-	-	-	-	0.25	0.92	-
Sample size		188	114	268	64	196	276	140	60	138	177	130	391	205	272

The sediments in the section consist of rhythmite like, parallel laminated flaggy siltstones containing between 5 and 12 alternating dark and light laminae in a 1 cm vertical section. Local bioturbated layers contain in situ specimens of Fuchsella amygdalina. Some shell layers infilling scour hollows, or forming shell pavements are scattered through the section.

DISCUSSION

The faunal lists (Tables 2 - 7) show that the uppermost Upper Leintwardine Beds (Upper Ludlovian) contain a diverse fauna of ostracods and brachiopods, which is replaced by a lower diversity (Fig. 4) higher dominance Lower Whitcliffe Beds fauna (Table 8). This fauna is then replaced by an even lower diversity (Table 2) higher dominance fauna in the Upper Whitcliffe Beds (Table 8).

Although such changes could reflect real ecological variations with changing environment, they could equally well reflect changes in post mortem sorting and transport. Since a high dominance value could be expected in a highly transported well sorted shell deposit (e.g. Antia, 1977).

The dominance index used here may be defined (McNaughton, 1967) as follows

Assemblage dominance index = $100 \times (y_1 - y_2)/y$

where y_1 = abundance of most abundant species

y_2 = abundance of second most abundant species

y = total abundances for all species.

The changes in assemblage dominance noted in Table 8 also correspond to changes in the lithological nature of the sediments. For example the Upper Leintwardine Beds at the Deer Park Road section consist of rhythmites (indicating quiescent conditions) and thin shell laminae which were probably introduced by storms. The resultant fauna is dominated by small species (Table 4) and contains a low dominance value (Table 8). However, the more bioturbated Leintwardinian sediments by Overton Quarry containing a similar fauna (Table 3), possess a higher dominance value (Table 8). This higher value could have resulted from the preferential destruction of the smaller shells (e.g. ostracods) in the sediment by the bioturbating organisms.

The change from the Upper Leintwardine Beds to the Lower Whitcliffe Beds is marked initially by a drop in species dominance followed by a rapid increase. This change also corresponds to (1) a lithological change from rhythmite type sedimentation to the deposition of rippled siltstones containing scour channels, storm generated shell sheets and abundant bioturbation, which probably represent a higher energy and perhaps more oxic environment; and (2) a faunal change in which benthic molluscs become more abundant and increase in diversity.

The higher energy conditions and bioturbation would have resulted in the removal and preferential destruction of the smaller and more delicate shells and the preferential preservation of the more robust species, resulting in an increase of assemblage dominance which may relate to biogenic and sedimentological processes rather than the original ecological community.

This point is further demonstrated in the Upper Whitcliffe Beds, which represent a still higher energy environment (Antia, 1979c) where faunal diversity is low and faunal dominance high (Table 8; Fig. 5). However, when the assemblage dominance index is low (e.g. Upper Whitcliffe Beds quarry on Ludlow Deepwood Road - Table 6), then ostracods and other smaller elements of the fauna appear to be commoner.

Table 8. Dominance index values for a number of sections in the Upper Leintwardine Beds (U.L.B.), Lower Whitcliffe Beds (L.W.B.) and Upper Whitcliffe Beds (U.W.B.). The dominance index used is defined as the relative abundance of the two commonest species in the sample. Note that dominance appears to increase from the U.L.B. into the U.W.B..

The Table and sample numbers refer to tables in the text.

Table and sample No.		U.L.B.	L.W.B.	U.W.B.
Table 3	1	63.59	-	-
	2	-	42.94	-
	3	-	55.19	-
	4	-	95.46	-
	5	-	80.85	-
	6	-	86.79	-
Table 4	1	40.86	-	-
	2	-	39.06	-
	3	-	62.10	-
	4	-	91.97	-
	5	-	84.26	-
	6	-	71.64	-
	7	-	67.80	-
Table 2	1	-	-	91.12
	2	-	-	81.52
	3	-	-	73.77
	4	-	-	75.75
	5	-	-	79.28
	6	-	-	77.88
	7	-	-	78.07
	8	-	-	53.72
	9	-	-	59.82
	10	-	-	68.48
	11	-	-	80.94
	12	-	-	69.96

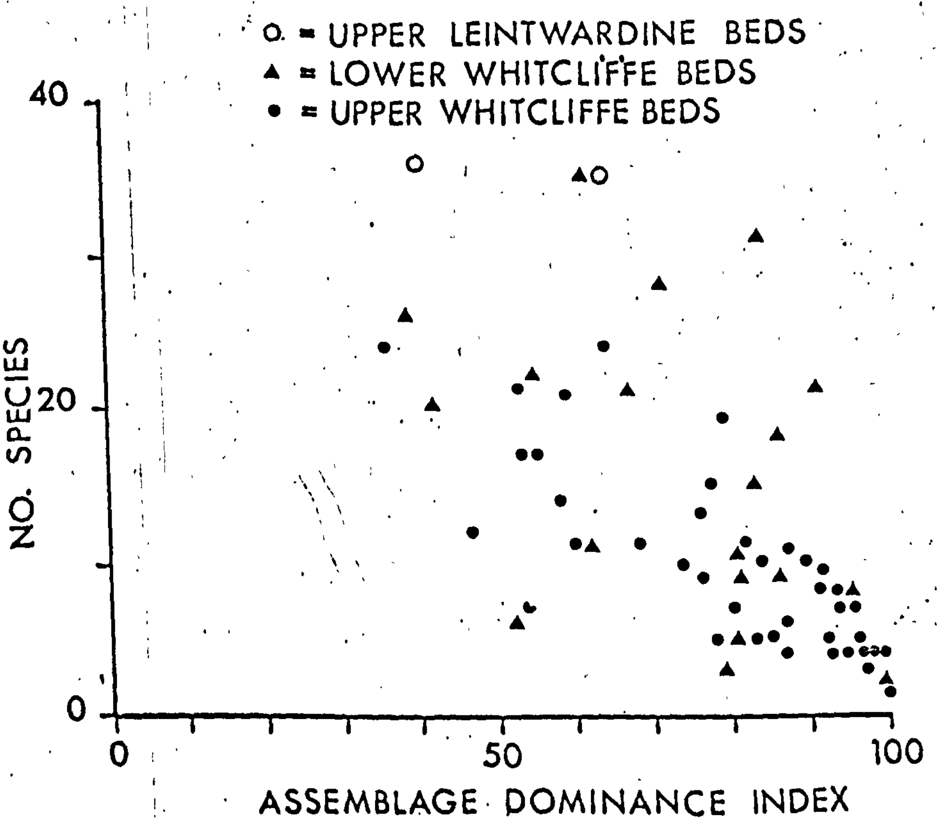


Fig. 5. Relationship between dominance and species diversity in the Upper Leintwardine Beds and Whitcliffe Beds.

An examination of the relationship between dominance and species diversity for these sediments (Fig. 5) shows a slight tendency for dominance to be 'low' when diversity is 'high', but this relationship is not tight. Similarly the most abundant and second most abundant species vary from sample to sample (see Tables 2 - 7). However, the percentage of occurrence of each species as the dominant or second most abundant species in an assemblage is indicated in Table 9. It is interesting to note that a positive relationship exists between the dominance index and the diversity of the dominant species. This relationship probably reflects the increase in environment instability and sedimentological sorting between the Upper Leintwardine Beds and the Upper Whitcliffe Beds.

PALAEONTOLOGICAL NOTES

1. *Lingula corftonensis* sp. nov.

Systematic description

Family	Lingulidae Menke, 1828
Genus	*Lingula* Bruguiere, 1797
Species	*Lingula corftonensis* sp. nov (Plate 1a,b)
Synonym	*Lingula* sp. nov. Antia & Whitaker, 1979 *Lingula* sp. nov. Antia, 1979a

Holotype: Brachial valve from the Upper Whitcliffe Beds at Ludlow (G.R. SO 491 742). I.G.S. collection number GSM104241A (Plate 1a).

Holotype measurements: Length = 7.5 mm; Width = 5 mm; Shell thickness = 0.1 - 0.2 mm; Median septum = 7 mm.

Paratype: Pedicle valve from the Upper Whitcliffe Beds at Ludlow (G.R. SO 491 742). IGS collection No GSM104241B

Derivation of name: Named after the village of Corfton, Salop.

Table 9. Dominant species in the Upper Leintwardine Beds (U.L.B.), Lower Whitcliffe Beds (L.W.B.) and Upper Whitcliffe Beds (U.W.B.). Where y_1 = most abundant species, y_2 = second most abundant species.

Dominant Species	Percent frequency of occurrence					
	U.L.B.		L.W.B.		U.W.B.	
	y_1	y_2	y_1	y_2	y_1	y_2
BRACHIOPODS						
D. navicula	-	-	-	10.5	-	-
M. nucula	50	50	10.5	52.6	10.5	63.1
P. ludloviensis	-	-	68.2	15.5	55.2	18.4
S. lunata	50	50	-	21.0	28.9	7.8
S. striata	-	-	-	-	-	2.6
BIVALVE						
F. amygdalina	-	-	10.5	-	5.2	2.6
ANNELIDS						
Keilorites sp.	-	-	10.5	-	-	2.6
S. longissimus	-	-	-	-	-	2.6

PLATE CAPTION

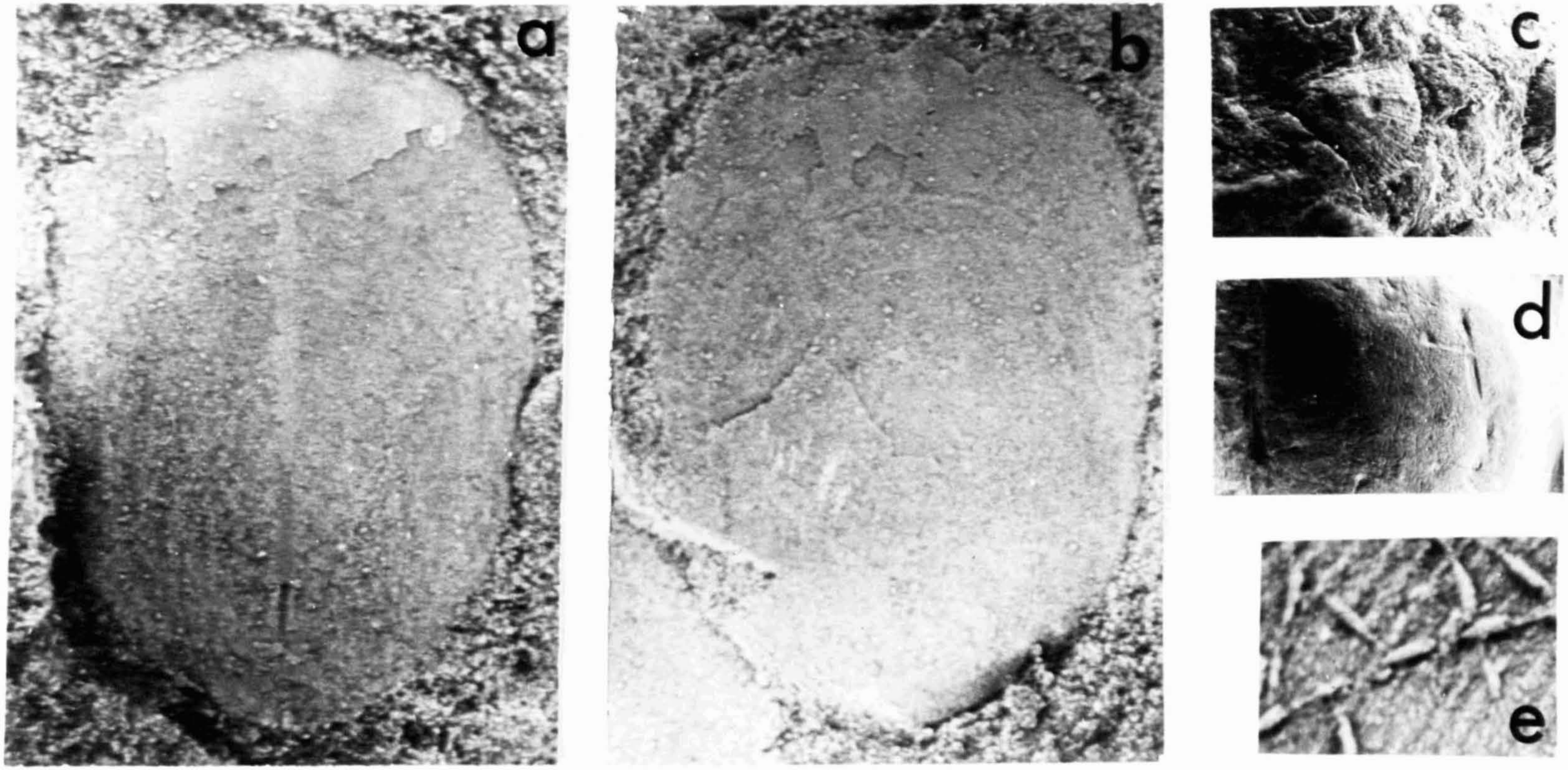
Plate 1 (a) Holotype of _Lingula corftonensis_ Antia. Brachial valve. GSM 104241A.

(b) Paratype of _Lingula corftonensis_ Antia. Pedicle valve. GSM 104241B.

(c) Drill hole on _Salopina lunata_ (X 1).

(d) Annelid boring on _Pteronitella retroflexa_ (X 1).

(e) _Rhopalonaria_ borings on _Protochonetes ludloviensis_ (X 10).


a
b
c
d
e

Description: Subquadrate to subovoid, slightly biconvex, thin shelled lingulid brachiopod; about 60% as wide as long; sides almost parallel with a slightly curved anterior margin and a blunt beak (130 - 140° apical angle); ornament consists of very faint (often absent) concentric growth lines (1 - 2 mm apart). Brachial valve is characterised by a strongly developed median septum extending anteriorly for about 90 - 95% of the valve's length.

Remarks: The species occurs throughout the Upper Whitcliffe Beds in the Ludlow to Much Wenlock region of the Welsh Borderlands. It appears to be most abundant in the Ludlow to Aston Munslow region within 1 m of the Ludlow Bone-Bed and locally forms up to 25% of the shelly fauna.

2. Scaldianella simplex (Krause)

This species has recently been redescribed and illustrated by Sarv (1977). Its muscle scar is centrally placed and illustrated for the first time in Fig. 6.

A length/height plot (Fig. 6) for the carapace shows a clear separation into a number of discrete clusters which are interpreted here as representing individual moult stages. As with other species of the genus there are no distinctive dimorphic features in the adult moults (Adamezak, 1966).

Density and distribution - The species occurs most commonly in upper Leintwardinian and Lower Whitcliffian shell deposits (as carapaces and valves) and as isolated valves in the surrounding silts. In the silts it rarely occurs in densities of greater than 200 valves per m^2 bedding plane surface area, while in the shell beds it occurs in densities of up to 38,000 carapaces and valves per m^2.

This data allows a number of possible inferences to be

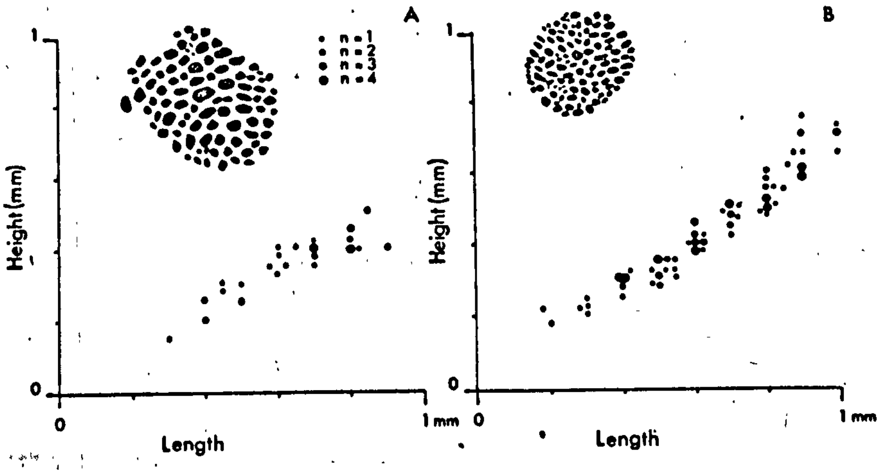


Fig. 6. Muscle scars and length/height plots of (a) Hebellum cf. tetragonum and (b) Scaldienella cf. simplex. Note that 9 discrete clusters (moults) are present on the length/height plot of S. cf. simplex.

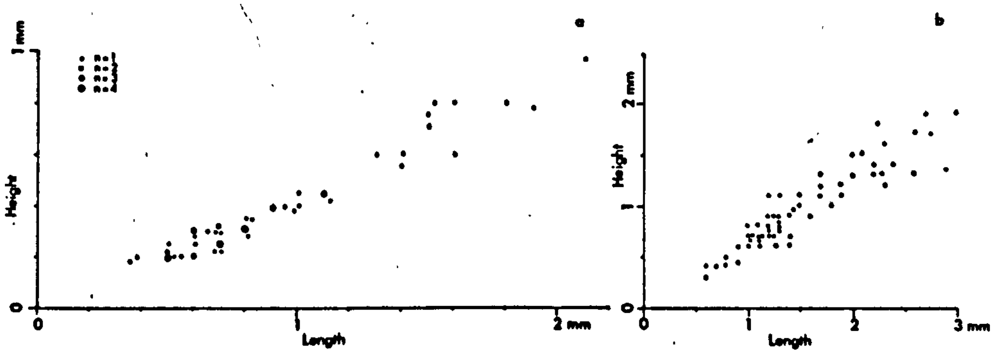


Fig. 7. Length/height plots of (a) Cytherellina siliqua and (b) Neobeyrichia lauensis.

made with respect to the life habits of this species. If it was a benthic form then it probably preferred to live in either (1) the pores presented by a shelly substrate (i.e. was an interstitial species), or (2) on a hard substrate such as those afforded by regions rich in patchily distributed shell debris.

Alternatively, the ostracods may represent a transported assemblage which was concentrated in the shelly layers.

In conclusion it can be suggested that *S. simplex* may have been an interstitial species feeding on detritus, which inhabited shelly substrates. However, proof of this is lacking and other interpretations may be equally plausable.

3. *Neobeyrichia lauensis*, *Cytherellina siliqua* and *Hebellum tetragonum*

These three species of ostracod are common in uppermost Leintwardinian sediments. They have been described and figured elsewhere (Straw, 1934; Martinsson, 1962; Copeland, 1964; Shaw, 1971; Siveter, 1974, 1978; Sarv, 1977). The muscle scar of *Hebellum tetragonum* is placed centrally within the shell and illustrated in Fig. 6. These species have the length/height relationships illustrated in Fig. 6 & 7 and unlike *S. simplex* do not show a distinct division into moult stages. *N. lauensis* occurs most commonly in ostracod shell sheets in association with *Neobeyrichia scissa*, other beyrichids and smooth ostracods (e.g. *H. tetragonum*, *C. siliqua*).

It is possible that the sediments in which these ostracods are found supported an algal growth and the species *N. lauensis* and *C. siliqua* may have been phytic forms. *H. tetragonum* like *S. simplex* occurs in higher densities in the shelly horizons of the lower Whitcliffian and upper Leintwardinian. It might, like

S. simplex, have been an interstitial detrivore.

4. Borings on brachiopod and molluscan shells

Three types of shell boring were recorded from Whitcliffian sediments. They included drill holes, annelid borings and bryozoan borings. The latter two types of boring are commonly infilled with limonite.

1. Drill holes (Plate 1e)

Four articulate brachiopods containing drill holes were observed in a collection of about 50,000 Whitcliffian shells. All four specimens came from the Upper Whitcliffe Beds at Siefton (British National Grid Reference SO 475 833). They consist of two bored pedicle valves of *P. ludloviensis* Muir Wood, a bored brachial valve of *M. nucula* and a bored pedicle valve of *S. lunata* (J.de C. Sowerby). Their drill hole diameters vary from 1.5 to 2 mm.

Similar drill holes have been recorded on a variety of Ordovician and Silurian brachiopods by Fenton & Fenton (1930, 1931), Bucher (1938), Fischer (1962), Cameron (1967), Carriker & Yochelson (1968), Rohr (1976) and others. These drill holes are probably a result of biological predation (cf. Dudley & Vermeij, 1978) and could have been made by predatory gastropods (cf. Fenton & Fenton, 1931; Bucher, 1938; Cameron, 1967; Taylor, 1970) or cephalopods (Pilson & Taylor, 1961). Since no active carnivorous gastropods are known to occur in the British Whitcliffian (cf. Peel, 1978), it is probable that the observed drill holes were produced by a rare soft bodied invertebrate or cephalopod.

2. Annelid borings (Plate 1f)

About 30 examples of shells bored by annelids were recorded in the Whitcliffian. All the borings were on bivalves and cephalopods belonging to the species P. retroflexa and Michelinoceras sp. Borings of similar morphology have been illustrated by Mclearn (1924, pl.4, fig.13) on the Ludlovian brachiopod Schizophorella arisaigensis Mclearn, by Antia (1979a) on the Ludlovian bivalve P. retroflexa, and by Fenton & Fenton (1932, 1935, pl.37, fig.9,12, pl.40, fig.13), Stainbrook (1938, pl.30, fig.4) and Jux (1964) on the Devonian brachiopods Atrypa iowensis Fenton & Fenton and Atrypa waterlooensis Webster.

All these borings can be assigned to the genus Clionoides Fenton & Fenton (1932, p.47) and [illegible] the species Clionoides thomasi Fenton & Fenton. They were originally thought to have been made by sponges (Fenton & Fenton, 1932). However, more recent studies suggest that they were made by boring polychaete worms (Jux, 1964).

3. Bryozoan borings (Plate 1g)

Bryozoan borings occur commonly on molluscan shells and more rarely on brachiopod shells. They have been assigned to the genus Rhopalonaria in the past (Straw, 1932)

CONCLUSIONS

This study has identified about 55,000 Whitcliffian and uppermost Leintwardinian fossils belonging to 69 species from 17 sections in the Ludlow - Much Wenlock region and observed drill holes, bryozoan and annelid borings on both brachiopod and molluscan shells. Measurements of length and height were made of four ostracod species S. simplex, H. tetragonum, C.

siliqua and *N. lauensis*, and the moult stages of *S. simplex* identified. Faunal diversity and density were also recorded in the Lower Whitcliffian sections of Deer Park Road and Overton Quarry. A sediment change from rhythmites to rippled and bioturbated shelly silts was also noted.

The faunas tended to be dominated by articulate brachiopods, notably *D. navicula*, *P. ludloviensis*, *M. nucula*, and *S. ornatella*, and the bivalve *F. amygdalina*.

Although many authors (e.g. Calef, 1972; Watkins, 1979) have described communities from the Whitcliffe Beds, the absence of *in situ* representatives of most species (e.g. the articulate brachiopods), and the common occurrences of transported and fragmented shell debris, makes it unlikely that any meaningful conclusions can be drawn in the near future about these Whitcliffian organisms and the communities in which they lived, without a very detailed study of Whitcliffian palaeoenvironments and the functional morphology and palaeogeographic distribution of individual species and their fragmentary remains.

ACKNOWLEDGEMENTS

I wish to thank Dr. J. D. Lawson for suggesting I embark on this project and for critically reading the manuscript; Dr. M. Keen for his critical comments on the ostracod sections of this paper; Mr. J. Norton for discussion and for temporarily storing my specimens in Ludlow Museum. This work was supported by a N.E.R.C. Grant. Detailed faunal lists of the Deer Park Road and Overton Quarry sections have been deposited in Glasgow University (Antia, 1979; Ph.D. thesis). Many of the specimens

discussed in this study have been deposited with the Institute of Geological Sciences Museum and the National Museum of Wales.

REFERENCES

ANTIA, D. D. J. 1977 A comparison of diversity and trophic nuclei of live and dead molluscan faunas from the Essex Chenier Plain, England. Paleobiology, 3, 404-414.

ANTIA, D. D. J. 1979a Comments on the environments and faunas across the Ludlow - Downton boundary (Upper Silurian) at Siefton, Salop. Geol. J.

ANTIA, D. D. J. 1979b Authigenic gypsum in marine sediments - a comment. Marine Geol., 31, M1-M4.

ANTIA, D. D. J. 1979c Bone-beds: A review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering, and microbiotas. Mercian Geol., 7, 93-174.

BOSENCE, D. W. J. 1979a Live and dead faunas from coralline algal gravels, Co. Galway. Palaeontology, 22, 449-478.

BOSENCE, D. W. J. 1979b Trophic analysis of communities and death assemblages. Lethaia, 12, 120.

BOUCOT, A. J. 1975. Evolution and extinction rate controls. Elsevier, 427 pp.

BUCHER, W. H. 1938 A shell-boring gastropod in a Dalmanella bed of upper Cincinnatian age. Am. J. Sci., 36, 1-7.

CALEF, C. E. 1972 Palaeoecological and stratigraphical studies of the Ludlow in Wales and the Welsh Borderlands. Ph.D. thesis, Oxford University, Oxford.

CALEF, C. E. & HANCOCK, N. J. 1974 Wenlock and Ludlow marine communities in Wales and the Welsh Borderlands. Palaeontology, 17, 779-810.

CAMERON, B. 1967 Oldest carniverous gastropod found in Trentonian (Middle Ordovician) brachiopods. *J. Paleont.*, **41**, 147-150.

CARRIKER, M. R. & ROCHELSON, E. L. 1968 Recent gastropod boreholes and Ordovician cylindrical borings. *U.S. Geol. Surv. Prof. Paper*, *593-B*, B1-B23.

CHERNS, L. 1977 *The palaeoecology of the Lower Leintwardine of Wales and the Welsh Borderlands*. Ph.D. thesis, Glasgow University.

COPELAND, M. J. 1964 Stratigraphic distribution of Upper Silurian Ostracoda, Stonehouse Formation, Nova Scotia. *Bull. Geol. Surv. Canad.*, **117**, 1-13.

DUDLEY, E. C. & VERMEIJ, G. J. 1978 Predation in time and space: drilling in the gastropod *Turritella*. *Paleobiology*, **4**, 436-441.

FENTON, C. L. & FENTON, M. A. 1931 Some snail borings of Paleozoic age. *Am. Mid. Nat.*, **12**, 522-528.

FENTON, C. L. & FENTON, M. A. 1932 Boring sponges in the Devonian of Iowa. *Am. Mid. Nat.*, **13**, 42-54.

FENTON, C. L. & FENTON, M. A. 1935 Atrypae described by Clement L. Webster and related forms (Devonian, Iowa). *J. Paleont.*, **9**, 369-384.

HOLLAND, C. H., LAWSON, J. D. & WALMSLEY, V. G. 1963 The Silurian rocks of the Ludlow District, Shropshire. *Bull. Brit. Mus.* (Nat. Hist.), **8**, 93-172.

JUX, U. 1964 Kommensalen oberdevonischer Atrypen aus Bergisch Gladbuch (Rheinisches Schiefergebirge). *N. J. Geol. u. Paleont. Mon.*, 676-681.

LAWSON, J. D. 1973 New exposures on forestry roads near Ludlow. *Geol. J.*, **8**, 279-284.

LAWSON, J. D. 1975 Ludlow benthonic assemblages. Palaeontology, 18, 509-525.

LAWSON, J. D. 1976 Ludlow Res. Group Bull. No. 23

LAWSON, J. D. 1977 Nature conservancy excavations in Mortimer Forest, Ludlow. Ludlow Res. Group Bull. No. 24, 21-22.

LAWSON, J. D. & WHITAKER, J. H. McD. 1968 Correlation of the Leintwardine Beds. Geol. J., 6, 329-332.

LEWIS, K. B. 1971 Slumping on a continental slope included at 1°-4°. Sedimentology, 16, 97-110.

LINGWOOD, P. E. 1976 **The biostratinomy of some recent molluscan communities in Liverpool Bay. Ph.D. thesis, Liverpool University.**

McKee, E. D. 1957 Flume experiments on the production of stratification and cross stratification. J. Sed. Pet., 27, 129-134.

McLEARN, F. H. 1924 Palaeontology of the Silurian rocks of Arisaig, Nova Scotia. Mem. Geol. Surv. Canada, 137, 1-180.

McNAUGHTON, S. J. 1968 Structure and function in Californian grasslands. Ecology, 49, 962-972.

PEEL, J. S. 1978 Faunal succession and mode of life of Silurian gastropods in the Arisaig group, Nova Scotia. Palaeontology, 21, 285-306.

PILSON, M. E. Q. & TAYLOR, J. D. 1961 Hole drilling by Octopus. Science, 134, 1366-1368.

REINECK, H.-E. & SINGH, I. B. 1973 Depositional sedimentary environments. Springer Verlag, New York, 439pp.

ROHR, D. M. 1976 Silurian predator borings in the Brachiopod Dicaelosia from the Canadian Artic. J. Paleont., 50, 1175-1179.

SARV, L. 1977 Early Cavellinids in the Siluhian of the East Baltic p.259-283. In Kaljo, D. (ed.). Facies and Fauna of the Baltic Silurian. Acad. Sci. Estonian S.S.R. Inst. Geol. Tallin.

SHAW, R. W. L. 1971 Ostracoda from the Under barrow, Kirkby Moor, and Scout Hill Flags (Silurian) near Kendal, Westmorland. Palaeontology, 14, 595-611.

SIVETER, D. J. 1974 The Superfamily Beyrichiacea (Ostracoda) from the Silurian and Devonian Systems of Britain. Ph.D. thesis, Leicester University, Leicester.

SIVETER, D. J. 1978 The Silurian. In Bate, R. and Robinson, E. (eds). A stratigraphical index of British Ostracoda. Geol. J. Spec. Issue No. 8, 57-100.

STAINBROOK, M. A. 1938 Atrypa and Stropheodonta from the Cedar Valley Beds of Iowa. J. Paleont., 12, 229-256.

STRAW, S. H. 1932 The fauna of the Palaeozoic rocks of the Little Missenden Borings. Sum. Pr. Geol. Surv. G.B., 112-142.

TAYLOR, J. D. 1970 Feeding habits of predatory gastropods in a Tertiary (Eocene) molluscan assemblage from the Paris Basin. Palaeontology, 13, 254-260.

WATKINS, R. 1978 Bivalve ecology in a Silurian shelf environment. Lethaia, 11, 4-56.

WATKINS, R. 1979 Benthic community organization in the Ludlow series of the Welsh Borderland. Bull. Brit. Mus. (Nat. Hist.) Geol., 31, 175-280.

WHITE, D. E. & LAWSON, J. D. 1978 The stratigraphy of new sections in the Ludlow Series of the type area, Ludlow, Salop., England. Inst. Geol. Sci. Rep., 78/30.

ADDITIONAL REFERENCES

DUFF,K.L. 1975.Palaeoecology of a bituminous shale - the Lower Oxford Clay of Central England.Palaeontology,vol.18,pp. 443 - 482.

HURST,J.M. & WATKINS,R. 1978. Evolutionary patterns in a Silurian Orthide Brachiopod. Geol. et Palaont. , vol.12, pp. 73 - 102.

RAUP,D.M. 1973. Depth inferences from vertically imbedded Cephalopods.Lethaia,vol.6,pp. 212 - 226.

SANDERS,H.L. 1968. Marine benthic diversity: a comparative study. Am.Mid. Nat.,vol. 102,pp.243 - 282.

WATKINS,R. & BERRY,W.B.N. 1977. Ecology of a late Silurian fauna of graptolites and associated organisms.Lethaia,vol.10, pp. 267 - 287.

WOODCOCK,N.H. 1973. The structure of the slump sheets in the Ludlow Series East of Central Wales. Ph.D.thesis.London University.

Shell Laminae and Shell Orientation in the Upper Silurian, Whitcliffe Beds

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ABSTRACT

An embedded Markhavian chain analysis was used to demonstrate that Whitcliffian shell sheets formed as a result of non-cyclic random depositional processes such as storms. Shell particle orientation was also examined and a relationship between bryozoan encrustation and shell orientation on bioturbated substrates was observed.

Paper : For Palaeogeography, Palaeoclimatology, Palaeoecology

INTRODUCTION

Within the Upper Ludlovian series sediments of the Welsh Borderlands shell laminae occur commonly (e.g. Cherns, 1977, 1979; Watkins & Berry, 1977) and are generally considered to represent storm deposits. (Watkins & Berry, 1977; Hurst & Watkins, 1978.) In the Whitcliffe Beds these deposits vary greatly in both their particle densities and thicknesses. Most are less than 5 mm thick, but may on occasion reach thicknesses in excess of 150 mm. The thinner shell sheets (<5 mm) either occur as discontinuous layers often traceable laterally within a section for 2 to 10 m, containing shells and shell fragments varying in density from 2,000 to 100,000 shell particles per square metre of bedding plane surface area, (e.g. G.R. SO 49867/27) or as a shelly ripple trough infill (e.g. SO 513742).

The thicker shell sheets either form parts of shell megaripples (wavelength 0-5 to 10 m, amplitude 4 to 15 cm) or infill small scour channels suggesting that they may all represent shell lag concentrations by current, wave and storm activities. Examples of each type of the thicker shell concentrates, are present in the sections at G.R. SO 510742, & 492744. Although most of the thin shell sheets overlie laminated or bioturbated silts some are associated with sand sheets, vertebrate remains and small semiphosphatised pebbles. Both the thin and thick shelly laminae locally truncate or scour into the bedding of the underlying sediment. If they result from storm activity as suggested (Watkins & Berry, 1977; Hurst & Watkins, 1978) then they should form as a result of non cyclic random depositional processes (Jones & Dixon, 1976).

MARKOVIAN ANALYSIS

One method of determining whether or not a sediment results from a non cyclic random depositional process is the Markov Chain analysis (cf. Anderson & Goodman, 1957; Krumbein & Dacy, 1969; Selley, 1969; Dacy & Krumbein, 1970; Dovston, 1971; Hattori, 1973; Mial, 1973; Jones & Dixon, 1976 etc). Two types of Markovian analysis exist. The first samples the lithology at a fixed sample interval, while the second samples each succeeding sediment type. This latter method, which is known as a first order or embedded Markov chain analysis, was used to determine whether or not the shell layers result from non cyclic random depositional processes. It determines in simple steps the relationship between a given layer and the next layer succeeding it. The starting point for such an analysis is the transition count matrix. This is a two dimensional array which tabulates the frequency of all the possible vertical lithological transitions in a given stratigraphic succession. The lower bed of each transition couplet in the matrix (f_{ij}) is given by the row number (i) of the matrix and the upper bed by the column number (j).

In the Whitcliffe Beds, 4 metres of sediment (vertical section) from each of the Upper Whitcliffe Beds (G.R. SO 492744), 'middle' Whitcliffe Beds (G.R. SO 510742) and Lower Whitcliffe Beds (G.R. SO 71274886) were examined and a transition count matrix compiled for the 1110 sediment layer transitions observed (Table 1). From the transition count matrix, two probability matrices can be derived (Mial, 1973). The first determines the probability (r_{ij}) of a given state i being succeeded by a given state j and may be represented as follows:

(1) $r_{ij} = s_j/(t - s_i)$ where t = total number of beds

s_i = row sum

s_j = column sum

The second gives the actual probability of the given transition occurring in each section.

(2) $p_{ij} = f_{ij}/s_i$

In order to determine whether or not a given transition occurs at a greater than random frequency it is helpful to construct a difference matrix (Mial, 1973).

(3) $d_{ij} = p_{ij} - r_{ij}$

The positive values of a difference matrix indicate transitions with a greater than random frequency of occurrence.

The transition count matrix, independent trials probability matrix, transition probability matrix and difference matrix for the Whitcliffe Beds are given in Tables 1,2,3, 4, 5. The nature of the cyclic processes present may be derived by following the positive values of the d matrix (Fig. 1). Transitions not indicated on this diagram (Fig. 1) may be attributed to the occurrence of non cyclic random changes in the nature of the depositional mechanisms of the sea floor. For example, the change from coarse silts to thin shell laminae was recorded 35 times and the change from fine silts to shell laminae was recorded 20 times. Both these transitions resulted from random depositional processes.

Thus thin shell laminae overlying silt layers may result from random events such as storms. However the Markovian analysis indicates that some shell laminae are found on the top or base of rippled sands, as the result of cyclic depositional processes.

PARTICLE ORIENTATIONS IN THE SHELL LAMINAE OF THE WHITCLIFFE BEDS

Studies on the orientation of concavo-convex particles (e.g. bivalve shells and shell fragments) have tended to concentrate on the sedimentological rather than the biological aspects of shell orientation with only a few exceptions (e.g. Clifton, 1971). These sedimentological studies have been mainly concerned with identifying the velocities in flumes required to initiate movement of shells of different size shape and orientation (e.g. Menard & Boucot, 1951; Johnson, 1957; Brenchley & Newall, 1970) and have shown that motion of an object takes place when the stress imparted to its surface by the passage of waters flowing past it is greater than the inertial forces keeping it in place.

Consequently this threshold velocity will vary (even if the current velocity remains constant) with respect to the morphology and orientation of different shells and the substrate on which they rest (Brenchley & Newall, 1970) and result in certain sizes and shapes (e.g. Worsley & Broadhurst, 1975) of shells being preferentially removed from an assemblage, because they have a lower threshold velocity than other shells in the same assemblage (see also Wilson, 1967; Brenchley & Newall, 1970; Trewin, 1973; Grinell, 1974; Alexandrowicz, 1978, etc.). Others have suggested (Clifton & Bloggs, 1970; Clifton, 1971) that smaller shells are more easily transported because they are more frequently overturned to an unstable concave up position by biogenic activity and ripple

Table 1. Transition count matrix for the Whitcliffe Beds

Lithofacies		1	2	3	4	5	6	7	8	9	10
Laminated silt	1	0	10	447	35	1	10	0	2	3	1
Rippled quartz silt sheets	2	5	0	6	6	0	0	0	1	0	0
Grey clay/silt	3	457	6	0	20	0	5	1	2	1	0
Thin shell laminae (<5 mm)	4	40	3	18	0	0	0	0	1	0	0
Pebbly shell laminae	5	0	0	1	0	0	0	0	0	0	0
Thick shell sheets (>5 mm)	6	11	1	1	0	0	0	0	1	0	0
Vertebrate rich shell laminae (<5 mm)	7	0	0	1	0	0	0	0	0	0	0
Rippled carbonate silt sheets	8	2	3	1	2	0	0	0	0	0	0
Bonebeds	9	3	0	0	1	0	0	0	0	0	0
Bentonitic clay	10	0	0	1	0	0	0	0	0	0	0

Table 2. Independent trials probability matrix

	1	2	3	4	5	6	7	8	9	10
1	0.00	0.03	0.79	0.10	0.00	0.02	0.00	0.01	0.00	0.00
2	0.47	0.00	0.43	0.05	0.00	0.01	0.00	0.00	0.00	0.00
3	0.83	0.03	0.00	0.10	0.00	0.02	0.00	0.01	0.00	0.00
4	0.49	0.02	0.45	0.00	0.00	0.01	0.00	0.00	0.00	0.00
5	0.46	0.02	0.42	0.05	0.00	0.01	0.00	0.00	0.00	0.00
6	0.47	0.02	0.43	0.05	0.00	0.00	0.00	0.00	0.00	0.00
7	0.46	0.02	0.42	0.05	0.00	0.01	0.00	0.00	0.00	0.00
8	0.47	0.02	0.43	0.05	0.00	0.01	0.00	0.00	0.00	0.00
9	0.46	0.02	0.43	0.05	0.00	0.01	0.00	0.00	0.00	0.00
10	0.46	0.02	0.42	0.05	0.00	0.01	0.00	0.00	0.00	0.00

$= r_{ij}$

Table 3. Transition probability matrix

$$\begin{array}{c|cccccccccc|}
 & 1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 & 9 & 10 \\
1 & 0.00 & 0.01 & 0.87 & 0.06 & 0.00 & 0.01 & 0.00 & 0.00 & 0.00 & 0.00 \\
2 & 0.27 & 0.00 & 0.33 & 0.33 & 0.00 & 0.00 & 0.00 & 0.05 & 0.00 & 0.00 \\
3 & 0.92 & 0.01 & 0.00 & 0.04 & 0.00 & 0.01 & 0.00 & 0.00 & 0.00 & 0.00 \\
4 & 0.64 & 0.04 & 0.29 & 0.00 & 0.00 & 0.00 & 0.00 & 0.01 & 0.00 & 0.00 \\
5 & 0.00 & 0.00 & 1.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
6 & 0.78 & 0.07 & 0.07 & 0.00 & 0.00 & 0.00 & 0.00 & 0.07 & 0.00 & 0.00 \\
7 & 0.00 & 0.00 & 1.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
8 & 0.25 & 0.37 & 0.12 & 0.25 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
9 & 0.75 & 0.00 & 0.00 & 0.25 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 \\
10 & 0.00 & 0.00 & 1.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00 & 0.00
\end{array} = p_{ij}$$

Table 4. Difference matrix

$$\begin{array}{c|cccccccccc|}
 & 1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 & 9 & 10 \\
1 & 0.00 & {}^{-}0.02 & 0.08 & {}^{-}0.04 & 0.00 & {}^{-}0.01 & 0.00 & {}^{-}0.01 & 0.00 & 0.00 \\
2 & {}^{-}0.20 & 0.00 & {}^{-}0.10 & 0.28 & 0.00 & {}^{-}0.01 & 0.00 & 0.05 & 0.00 & 0.00 \\
3 & 0.09 & {}^{-}0.02 & 0.00 & {}^{-}0.06 & 0.00 & {}^{-}0.01 & 0.00 & {}^{-}0.01 & 0.00 & 0.00 \\
4 & 0.15 & 0.02 & {}^{-}0.16 & 0.00 & 0.00 & {}^{-}0.01 & 0.00 & 0.00 & 0.00 & 0.00 \\
5 & {}^{-}0.46 & {}^{-}0.02 & 0.58 & {}^{-}0.05 & 0.00 & {}^{-}0.01 & 0.00 & 0.00 & 0.00 & 0.00 \\
6 & 0.31 & 0.05 & {}^{-}0.36 & {}^{-}0.05 & 0.00 & 0.00 & 0.00 & 0.07 & 0.00 & 0.00 \\
7 & {}^{-}0.46 & {}^{-}0.02 & 0.58 & {}^{-}0.05 & 0.00 & {}^{-}0.01 & 0.00 & 0.00 & 0.00 & 0.00 \\
8 & {}^{-}0.22 & 0.35 & {}^{-}0.31 & 0.20 & 0.00 & {}^{-}0.01 & 0.00 & 0.00 & 0.00 & 0.00 \\
9 & 0.29 & {}^{-}0.02 & {}^{-}0.43 & 0.20 & 0.00 & {}^{-}0.01 & 0.00 & 0.00 & 0.00 & 0.00 \\
10 & {}^{-}0.46 & {}^{-}0.02 & 0.58 & {}^{-}0.05 & 0.00 & {}^{-}0.01 & 0.00 & 0.00 & 0.00 & 0.00
\end{array} = d_{ij}$$

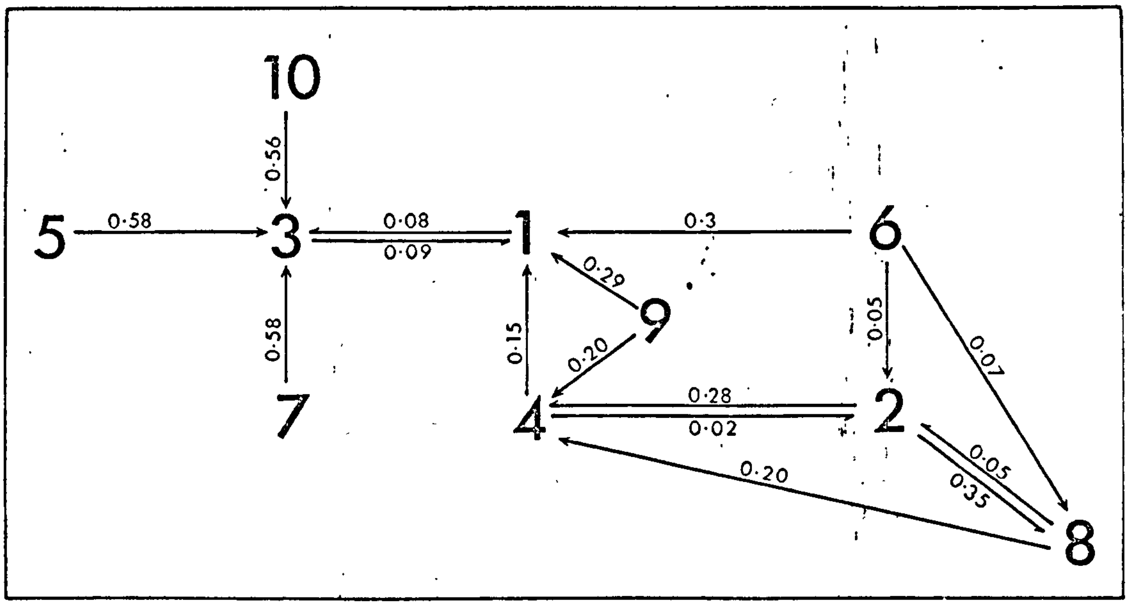

Figure 1. Cyclic processes in the Whitcliffe Beds. Large numbers indicate the sediment type (see Table 1). The small figures represent the greater than random probability of each transition occurring as derived from the d matrix, Table 4.

migration. A concave up particle orientation is generally regarded as unstable because the shape encourages uplift and is not as streamlined as a concave down oriented particle.

Flume studies suggest that concave up oriented shells are among the first to be transported while concave down oriented particles usually develops scour hollows around their margins, into which they progressively sink and are buried (Menard & Boucot, 1951; Johnson, 1957, Brenchley & Newall, 1970, Futterer, 1978). Particles which are transported tend to move either by (1) sliding (Brenchley & Newall, 1970, Futterer, 1978) or (2) by rolling (Menard & Boucot, 1951) or (3) by floating concave up held above the substrate surface by tension (Lingwood, 1976; West, 1978, pers. com.; Futterer, 1978). This surface tension may result from wave induced oscillatory currents causing enough instability to partially suspend a particle and allow it to be transported at velocities lower than those which would normally be expected to transport it.

Morphology appears to have had little effect on shell orientation. However, the more compact a concavo-convex particle is the more likely it is to be transported, because the threshold velocity will decrease with decreasing size and/or increasing sphericity (cf. Menard & Boucot, 1951; Behrens & Watson, 1969).

Thus current and wave activity appears to orientate concavo-convex particles to a hydrodynamically stable concave down orientation and may preferentially orient the length of the elongate valves parallel to or normal to the direction of current flow (Brenchley & Newall, 1970, Antia & Wood, 1977, etc.).

In shell beds (more than 2 or 3 shell layers thick), e.g. the Essex Cheniers, four types of shell orientation are present (1) spirally imbricate structures (Greensmith & Tucker, 1968), (2) a close packing arrangement of shells oriented both concave up and concave down, (3) imbricate stacked shells, dominantly oriented concave down, and (4) shell layers all oriented concave down. These orientations are produced by both wave and current activity, and can be modified by biogenic activity both on and within the sediment.

In general, shells and shell fragments scattered on a substrate in a current and/or wave influenced environment tend to be oriented concave down. However, particles migrating across small ripples can be oriented concave up, but in such cases the degree of concave up orientation decreases with increasing particle size (Clifton & Bloggs, 1970).

In quiet water environments with slack current and wave activity shell particles are commonly observed concave up (Emery, 1968). These orientations can result from biogenic predatory feeding activities (Pye, pers. com., 1978) or from the movements of scavenging and predatory organisms in and on the substrate reorientating shells from an original concave down to a concave up orientation (Clifton, 1971). Such surface reorientated shells are characterised by a positive relationship between particle size and a concave up orientation, while particles reorientated in the substrate should show a random orientation (Clifton, 1971).

In the upper Silurian of the Welsh Borderlands bedding planes containing concave up orientated, vertical or obliquely orientated shells have been recorded (Whitaker, 1961; Jones, 1969) in low energy environments normally containing little current activity (Jones, 1969; Cherns, 1977). These orientations could result from either current activity, predatory feeding activity or biogenic movement, and all three processes could produce shell deposits which could be attributed to non cyclic random changes in the depositional processes (cf. Reineck & Singh, 1973).

In this study the orientations of shells, and their size distributions in five sections containing Whitcliffian strata were examined. The valve orientations of concavo-convex fossils were noted, as were the relative orientations of features on the shells. These orientations are presented in Fig. 2, and show a progressive increase in the proportion of concave up particles related to a similar increase in substrate bioturbation. The size orientation graphs (Fig. 3a, b) show that the degree of convex up orientation increases with increasing shell size in the current influenced rippled substrates (Fig. 3a) mirroring a similar trend for particle orientations in modern current influenced environments (Clifton, 1971). This pattern contrasts sharply with the orientation of particles in the markedly bioturbated sediment where a reverse situation exists (i.e. the degree of concave up orientation increases with increasing particle size (Fig. 3b)), producing an orientation pattern similar to

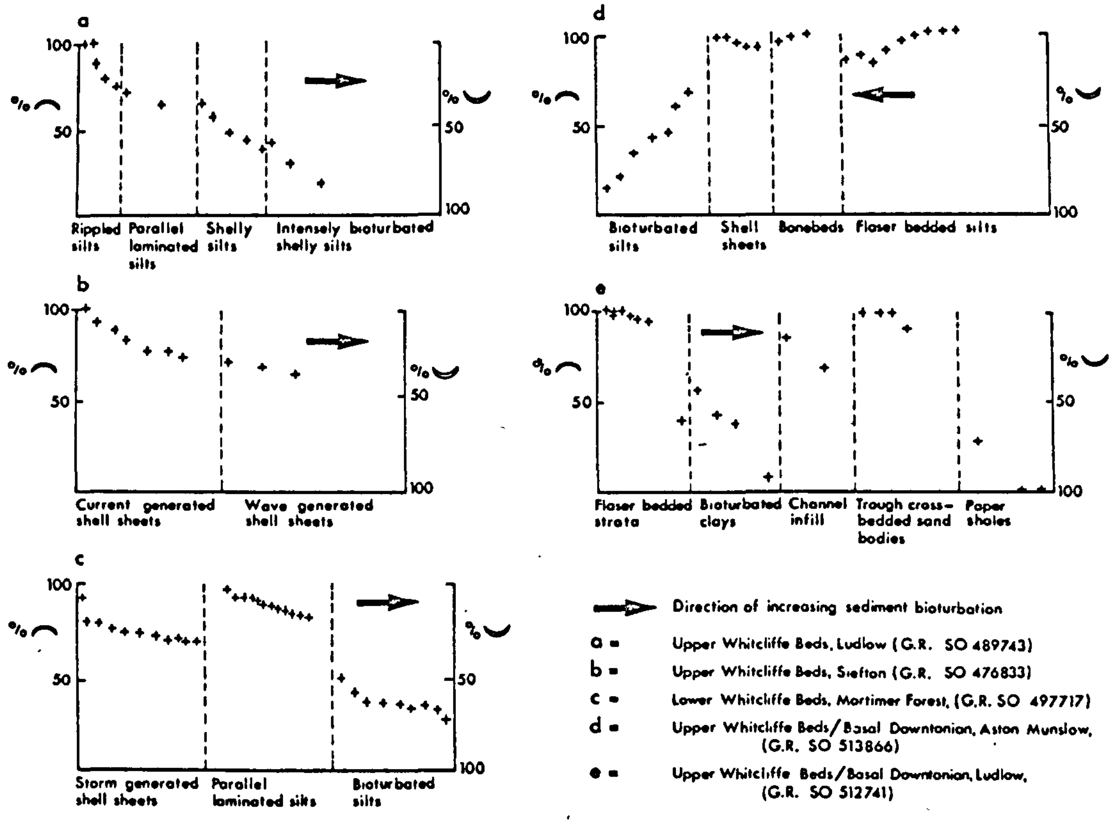

Figure 2. Valve orientations of shells in five sections through the Upper Whitcliffe Beds.

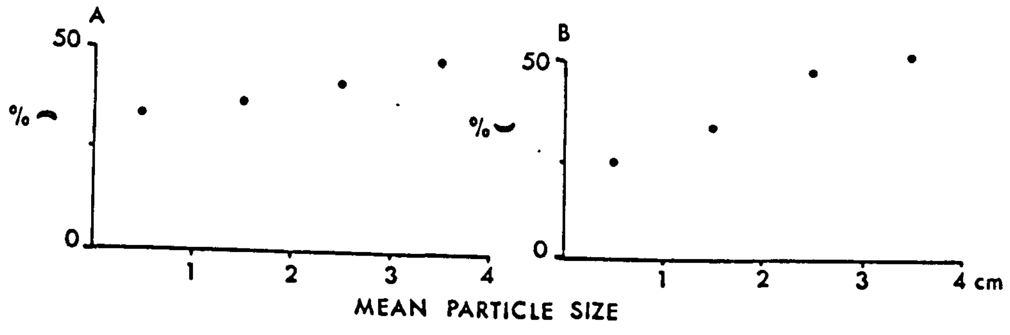

Figure 3. a) Size orientation graph showing that the degree of convex up orientation increases with increasing shell size on a rippled substrate. b) Size orientation graph showing the reverse situation on a bioturbated sediment substrate.

that produced by predator scavenger activity at the present time (Clifton, 1971).

Since the particles observed in the shell laminae were transported shell fragments scattered on a substrate surface, their degree of reorientation may be a function of the degree of contemporary scavenger-predator activity within and on the substrate. If the rate of shell reorientation due to this activity is known, then the time interval between the deposition of successive sediment layers can be calculated. If the epifauna is also studied estimates of benthic productivity and studies of epifaunal encrustation can be made.

Clifton (1971) observed that 42% of his concave down orientated particles were reorientated to a concave up orientation by the bioturbation activities of scavengers over a period of 40 days. This represents a simplistic rate of 1% a day! However, since the proportion of concave down particles will decrease with time even though bioturbation rates in the substrate may remain constant, it follows that the length of time it takes to reorientate 1% of the initial particle population should increase with time. For example, given a reorientation rate of 1% per day, it follows that after 10 days 9.5% of the particles would have been reorientated and after 100 days 61% would have been reorientated. This rate of decrease in the apparent rate of reorientation is expressed graphically in Fig. 4 and may be described on a daily basis in the form

$R_t = k *(R_{t-1}-(R_{t-1}/100))$ where R = Proportion of shells orientated concave down

k = is a rate of reorientation constant which may be termed a bioturbation rate.

Although it is impossible to determine the actual particle reorientation rates of the Whitcliffe sediments, it is interesting to note that there is an apparent relationship between the density of shell encrustation by bryozoa and shell orientation on bioturbated substrates (Fig. 5). Such a relationship may be time related and could be exploited in palaeoecological and sedimentological studies as an aid to the recognition of very minor omission surfaces and their relative exposure times.

The thicker shell sheets commonly show a slight inclined orientation of

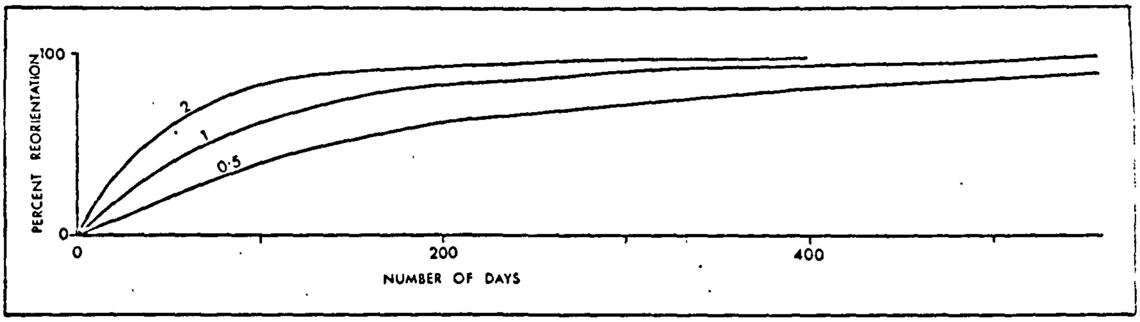

Figure 4. Graph showing percent of shells reoriented for a number of different bioturbation rates.

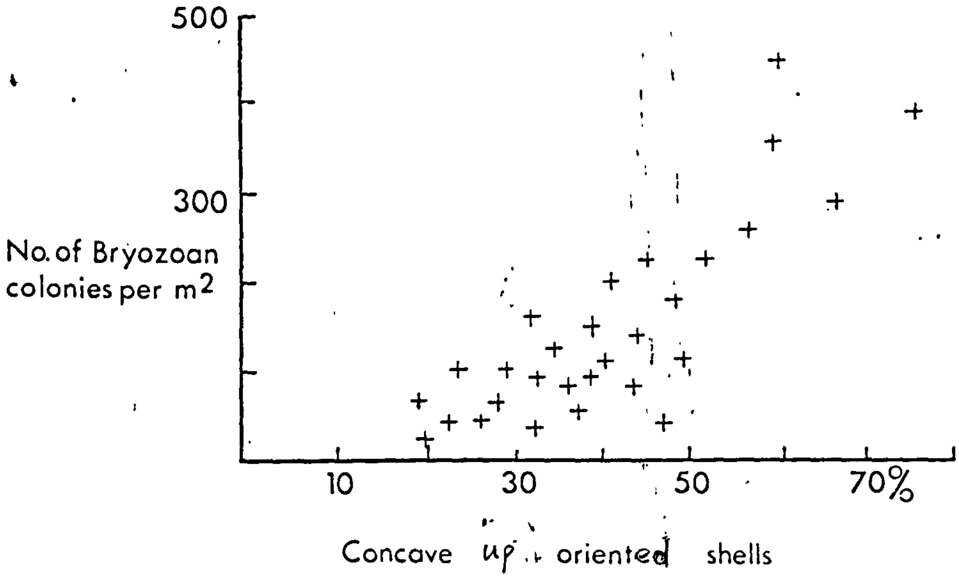

Figure 5. Graph showing an apparent relationship between shell orientation and bryozoan encrustation.

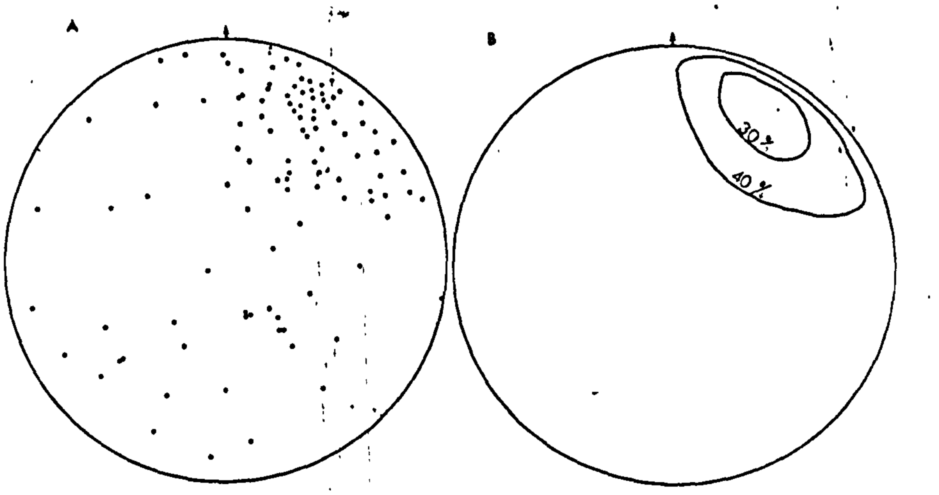

Figure 6. Equal area projection of poles to the commisure plane on the brachiopod. *Protochonetes ludloviensis* Muir Wood from a rippled shell sheet about 5 cm thick in the road cutting opposite Broadstone Farm (G.R. SO 543898).

their convex up oriented shells, as is indicated in Fig. 6.

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REFERENCES

ALEXANDROWICZ, S.W. 1978. A quantitative study of the origin of Dreissena polymorpha shell accummulations in Szczecin Bay, Baltic Sea. Bull. Acad. Pol. Sci., 25, 75-82.

ANDERSON, T.W. & GOODMAN, L.A. 1957. Statistical inference about Markov Chains. Ann. math. Statist. 28, 89-110.

ANTIA, D.D.J. & WOOD, B.A. 1977. Some aspects of the palaeoecology of the E_1b zone of the Edale Shales (Namurian) in the Edale Valley, Derbyshire. Mercian Geol. 6, 179-196.

BEHRENS, E.W. & WATSON, R.L. 1969. Differential sorting of Pelecypod valves in the swash zone. J. Sediment. Petrol. 39, 159-165.

BRENCHLEY, P.J. & NEWALL, G. 1970. Flume experiments on the orientation and transport of models and shell valves. Palaeogeogr. Palaeoclimatol. Palaeoecol. 7, 185-220.

CHERNS, L. 1977. The palaeoecology of the Lower Leintwardinian (Upper Silurian) of the Welsh Borderlands and Wales. Ph.D. thesis, Glasgow University.

CHERNS, L. 1979. The environmental significance of Lingula in the Ludlow Series of the Welsh Borderland and Wales. Lethaia 12, 35-46.

CLIFTON, H.E. 1971. Orientation of empty pelecypod shells and shell fragments in quiet water. J. Sed. Pet. 41, 671-682.

CLIFTON, H.E. & BLOGGS, S.J. 1970. Concave-up pelecypod (Psephidia) shells in shallow marine sand, Elk River Beds, Southwestern Oregon. J. Sediment. Petrol. 40, 888-897.

DACY, M.F. & KRUMBEIN, W.C. 1970. Markovian models in stratigraphic analysis. J. int. Ass. mathl. geol. 2, 175-191.

DOVETON, J.H. 1971. An application of Markov Chain analysis to the Ayrshire Coal Measures Succession. Scott. J. geol. 7, 11-27.

EMERY, K.D. 1968. Positions of empty pelecypod valves on the continental shelf. J. Sed. P et. 38, 1264-1269.

FUTTERER, E. 1978. Hydrodynamic behaviour of biogenic particles. N. Geol. Jahr. Abl. 157, 37-42.

GREENSMITH, J.H. & TUCKER, E.V. 1968. Imbricate structure in Essex off-shore shell banks. Nature 220, 1115-1116.

GRINELL, R.S. Jr. 1974. Vertical orientation of shells on some Florida oyster reefs. J. Sediment. Petrol. 44, 116-122.

HATTORI, I. 1973. Mathematical analysis to discriminate two types of sandstone-shale alternations. Sediment. 20, 331-345.

HURST, J.M. & WATKINS, R. 1978. Evolutionary patterns in a Silurian Orthide Brachiopod. Geol. et Palaeont. 12, 73-102.

JOHNSON, R.G. 1957. Experiments on the burial of shells. J. Geol. 65, 527-535.

JONES, M.D. 1969. The palaeogeography and palaeoecology of the Leintwardine Beds of Leintwardine, Herefordshire. M.Sc. thesis, Leicester University.

JONES, B. & DIXON, O.A. 1976. Storm deposits in the Read Bay Formation (Upper Silurian), Somerset Islands, Artic Canada (an application of Markov chain analysis). J. Sed. Pet. 46, 393-401.

KRUMBEIN, W.C. & DACY, M.F. 1969. Markov Chains and embedded chains in geology. J. int. Ass. mathl. geol. 1, 79-96.

LINGWOOD, P.F. 1976. The biostratinomy of some recent molluscan communities in Liverpool Bay. Ph.D. thesis, Liverpool University.

MENARD, H.W. & BOUCOT, A.J. 1951. Experiments on the movements of shells by water. Am. J. Sci. 249, 131-151.

MIAL, A.D. 1973. Markov chain analysis applied to an ancient alluvial plain succession. Sediment. 20, 347-366.

REINECK, H.E. & SINGH, I.B. 1973. Depositional sedimentary environments. Springer Verlay, New York.

SELLEY, R.C. 1969. Studies of sequence in sediments using a simple mathematical device. Q. Jl. geol. Soc. Lond. 125, 557-581.

TREWIN, N.H. 1973. Sorting of bivalve populations in a beach environment. Geol. J. 8, 307-316.

WATKINS, R. & BERRY, W.B.N. 1977. Ecology of a late Silurian fauna of graptolites and associated organisms. Lethaia. 10, 267-287.

WHITAKER, J.H. McD. 1962. The geology of the area around Leintwardine.

Q. Jl. geol. Soc. Lond. 118, 319-351.

WILSON, J.B. 1967. Palaeoecological studies on shell-beds and associated sediments in the Solway Firth. Scott. J. Geol. 3, 329-371.

WORSLEY, D. & BROADHURST, F.M. 1975. An environmental study of Silurian atrypid communities from southern Norway. Lethaia. 8, 271-286.

3

The type section of the Upper Silurian Ludlow Bone-Bed and the Ludlow - Downton Series Boundary at Ludlow, Salop, England.

by

David D. J. Antia

Summary

The fauna, sediment, facies, mineral, grain size and quartz grain sphericity distributions through the holostratotype section of the Upper Silurian Ludlow - Downton Series Boundary at Ludlow are examined. It is suggested that the Ludlow Bone-Bed rests conformably on the top Ludlovian sediments in the section. The section is considered to represent a transition from a subtidal micrite environment through into first intertidal sand and mudflats (containing a poorly developed mudmound topography) and then intertidal beach or backbeach environments.

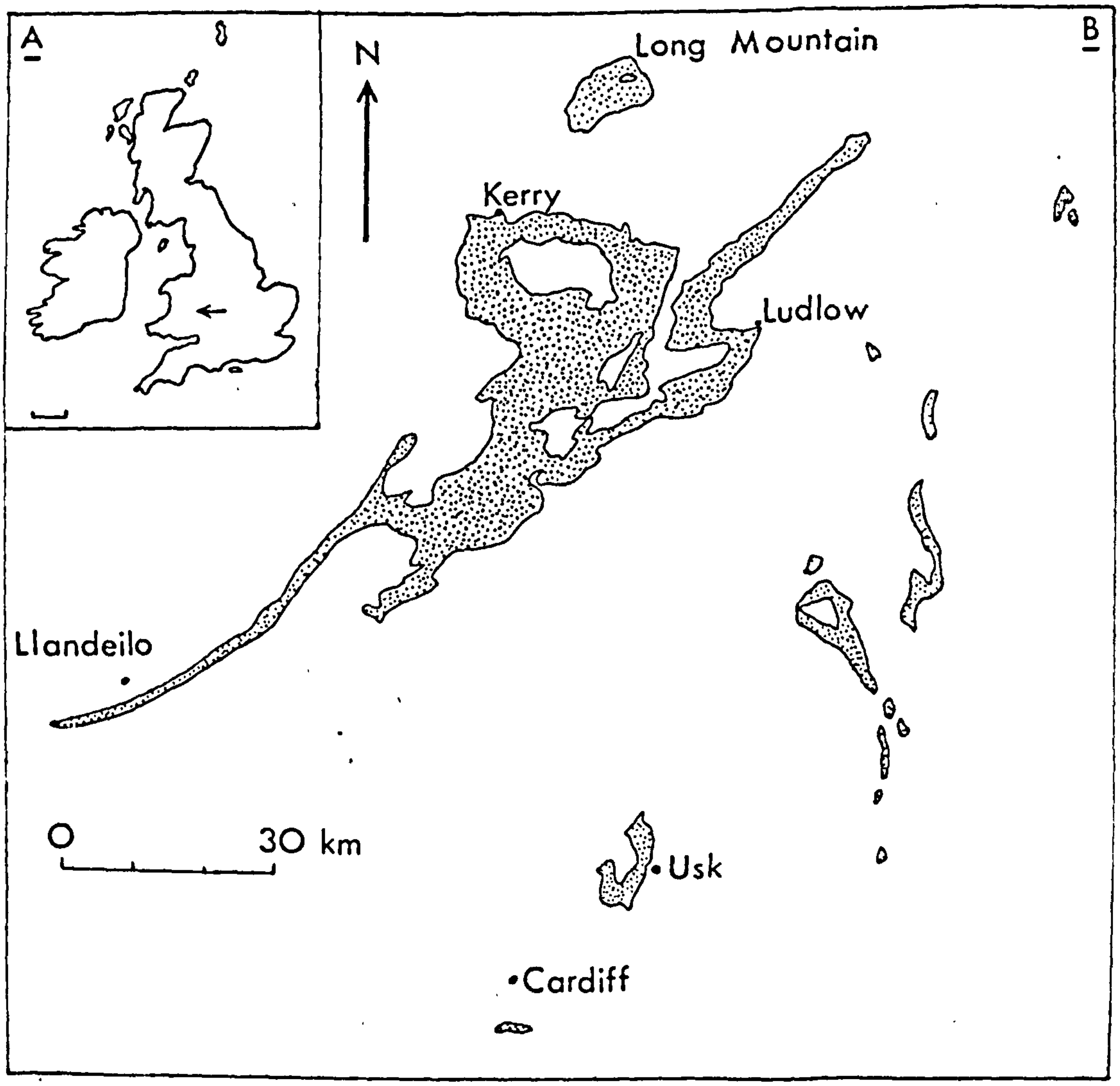
Introduction

The Ludlow Bone-Bed is an unusual Upper Silurian deposit which marks the junction between the marine Ludlovian and 'non-marine' Downtonian sediments in the Ludlow region (Text-Fig. 1).

Most early Silurian-Devonian researchers who recorded the Ludlow Bone-Bed appear to have been concerned primarily with the regional mapping, local lithostratigraphy and the recording of fossils present in the Bone-Bed (e.g. Hinde, 1862; Walmsley, 1959).

Many early workers (e.g. Murchison, 1839; Phillips, 1848) believed that the Bone-Bed formed in a shallow shelf sea near the shore. This view was modified slightly by Stamp (1920) who suggested that the Ludlow Bone-Bed formed subtidally in a shallow sea and marked the commencement of an isostatic rise in sea level (op. cit. p.70). He later (Stamp, 1923) modified his ideas after observing that the lithology of the Bone-Bed varied laterally from a vertebrate coquina near Ludlow, to a sandy, phosphatic conglomerate at May Hill. This revised model suggested that the Ludlow Bone-Bed represented a major unconformity (Stamp, 1923; p.282 & 387), and formed as a shallow water deposit in a brackish lake. The fish found in the bone-bed were considered to have fed on lingulids (Stamp, 1923, p.387).

Clearly Stamp's (1923, p.282) revised model was greatly influenced by contemporary ideas concerning the origin and nature of Bone-Beds. He reluctantly (Stamp, 1920) endorsed the suggestion that bone-beds heralded the beginning rather than the end of geological periods, series or stages. The latter view-point had been accepted by the Germans in dealing with the



Text-Fig. 1: Location map showing the outcrop of Ludlovian sediments in the Welsh Borderlands.

Muschelkalk Grenzbonebed, which marks the junction of the Muschelkalk and Lettenkeuper (see Reif, 1969 for a historical review), while the former view was widely held in Britain, especially with regard to the formation and significance of the Rhaetic Bone-Bed. This was because the Rhaetic Bone-Bed was considered to represent the start of the Rhaetic (cf. Short, 1904) and contained sediments and faunas which differed markedly from those in the underlying Keuper Marls (cf. Jukes-Browne, 1892; Richardson, 1901, 1911; Short, 1904). A parallel can be found here between the published accounts of the Ludlovian-Downtonian transition, the Keuper-Rhaetic transition, and the Muschelkalk-Lettenkeuper transition. All three transitions contained a very marked sediment - faunal assemblage change denoted by a bone-bed.

The Ludlow-Downton transition was known (cf. Elles & Slater, 1906) to be represented by the Ludlow Bone-Bed which separated a sequence of grey calcareous flags (Ludlovian) from a sequence of olive green silts and yellow sands (Downtonian). The faunas present in the two sediment types were also very different and distinctive (cf. ~~Davidson & Maw, 1881;~~ Elles & Slater, 1906). Likewise, the Keuper-Rhaetic transition was thought to be marked by the Rhaetic Bone-Bed which was considered to represent the change from green unfossiliferous marls to dark grey and black clays and sandstones containing a shelly fauna and abundant vertebrate remains (see Sykes, 1977, for a review of the pre 1920's research on this transition). The Muschelkalk Grenzbonebed was also known (Wagner, 1913) to mark a similar faunal change, and a sediment change from white shelly Muschelkalk limestones to black shales (Lettenkeuper). The faunas above and below the bone-bed are markedly different (Wagner, 1913; Antia, 1979a).

Thus Stamp's (1920) suggestion that the Ludlow Bone-Bed should mark the base of the Downtonian was following the precedent set by British Rhaetic stratigraphers. His suggestion that the Bone-Bed marked a major unconformity was also well founded with respect to the current genetic theories of bone-bed formation. At that time (1920 - 1923) a number of theories regarding the origin and nature of bone-beds had been proposed.

They were commonly considered to cover vast areas, as had been demonstrated in the Middle Devonian Columbus Limestone of Ohio (Orton, 1878), the British Rhaetic Bone-Bed (Richardson, 1901; Wickes, 1904), the British Suffolk Bone-Bed (Reid, 1890) and the West German Muschelkalk Grenzbonebed (Wagner, 1913). As Stamp (1923) had just demonstrated that the Ludlow Bone-Bed also covered a large geographic area, he could reasonably assume that since it marked a change in faunas and sediments like the other Bone-Beds, that it formed under similar conditions. ~~Even~~

Although it had been suggested that bone-beds resulted either from an increased abundance of vertebrates in the sea (Orton, 1878) or when marine animals entered hypersaline lakes (Jukes-Browne, 1892) or from the aftermath of a severe storm (Short, 1904), or from concentration due to a reduced rate of sediment deposition (Newberry, 1889), by 1920, the popular theory accepted by all the major researchers on each bone-bed was the suggestion that bone-beds were subtidal condensation deposits, frequently containing erosive unconformable bases. This theory had been proposed by Newberry (1889) for the Ohio Bone-Beds, Richardson (1901) for the Rhaetic Bone-Bed, Wagner (1913) for the Muschelkalk Grenzbonebed and Reid (1890) for the Suffolk Bone-Bed. Consequently, the proposal by Stamp (1923) that the Ludlow Bone-Bed was deposited as a subtidal condensation deposit was accepted without controversy by the geological establishment.

This suggestion that bone-beds formed as condensation deposits was expounded by the major authorities on strata containing bone-beds for the next decade (e.g. Kendall & Wroot, 1924; Arkell, 1933), and may have accounted for the apparent reluctance of Ludlovian and Downtonian researchers to comment on the genesis of the Ludlow Bone-Bed over the next three, to four decades (e.g. Earp, 1938, 1940; Lawson, 1955; Walmsley, 1959). After the mid-1950's some authors did comment on the genesis of the Ludlow Bone-Bed, but only to reiterate or expand Stamp's (1923) model.

By 1965, two modifications to Stamp's model had been proposed. The first expanded his model and suggested that the Bone-Bed represented a shallow marine condensation deposit formed in brackish waters, in which the fine grained detritus had been winnowed away by wave and current action to leave fish remains in the residual fraction (cf. McFarlane, 1927; Romer, 1955; Dennison, 1956; Squirrell, 1958; Hobson, 1960; Tucker, 1960; Whitaker, 1962). In accepting and outlining this model these authors had accepted and included some of the major advances in the concept of bone-bed formation which had been outlined by Wells (1944) and Donovan (1955). However, controversy still raged with respect to a freshwater or a marine origin for the fish (cf. Romer, 1955; Dennison, 1956).

The second modification of Stamp's (1923) model accepted his suggestion that the Ludlow Bone-Bed represented a major unconformity and considered the Bone-Bed to have marked a period of regional shoaling and retreat of the sea in the Welsh Borderlands, preceding a marine regression, which deposited the bone-bed as a transgressive strand line deposit above an eroded land surface of earlier shelf deposits (Allen, 1962; Allen & Tarlo, 1963).

This latter model basically endorsed the general model of bone-bed formation outlined by Wells (1944).

Following a critical re-examination of the sediments across the Ludlovian-Downtonian transition, Allen (1974) concluded that although the Bone-Bed formed as a transgressive strand plain lag concentrate, it could have represented a time either (1) when fine terrigenous clastics were witheld from the region or (2) when extensive erosion of the vertebrate poor Ludlovian beds occurred. This new model was unacceptable to Antia & Whitaker (1979) who accepted the notion outlined by Calef & Hancock (1974) and McKerrow (1979) that the Ludlovian-Downtonian transition represented a continuous marine regression. They could find no sedimentological or faunal evidence to support the contention that the Ludlow Bone-Bed represented a major or even a minor disconformity, but agreed with Allen (1962, 1974) in suggesting that the Ludlow Bone-Bed is a lag concentrate deposited on a strand plain. However, they accounted for the concentration of vertebrate remains and the presence of abraded and perfect quartz euhedra, by suggesting that the vertebrate material was derived from the offshore erosion of vertebrate poor clays and silts, followed by the concentration and onshore migration of this vertebrate debris. This model is significantly different from previous genetic models for the Ludlow Bone-Bed because it (1) assumed that the Bone-Bed formed as part of a continuous sequence of sedimentation during a period of marine regression (i.e. did not represent an unconformity and is diachronous) and (2) suggested that the vertebrate material present had been excavated from contemporaneous offshore sediments after they had been diagenetically altered (i.e. prefossilised). This model echoed to an extent the new models of bone-bed formation outlined by

Reif (1969, 1971, 1974, 1976), Aepler & Reif (1971), Aepler (1974), Frey et al., (1974) and Duffin & Gadzicki (1977), which suggested that most of the vertebrate material present in bone-beds had been reworked from slightly older sediments after it had been diagenetically altered (prefossilised).

Following an examination of the sediments and faunas in and across the Muschelkalk Grenzbonebed, Antia (1979a) suggested that most of the criteria (Reif, 1969, 1971; Maisey, 1978) used to recognise prefossilised bone-beds were misleading, and that many supposedly prefossilised bone-beds (e.g. the Muschelkalk Grenzbonebed, the British Rhaetic and Upper Silurian Bone-Beds) might not be prefossilised deposits. Antia's (1979a) refutation of the prefossilisation of these bone-beds hinged on four observations.

(1) The apparent similarity of vertebrate and quartz grain size distributions noted by Reif (1969, 1971, 1976) and Aepler (1974) resulted from diagenetic post-sedimentation overgrowths on the quartz grains, rather than a syndepositional sorting of material of similar density as suggested by Reif (1969, 1971, 1976).

(2) The geochemistry of the phosphatic clasts in the Bone-Beds (vertebrate, invertebrate and phosphorite) was dependent on the porosity of the sediment and the geochemistry and mineralogy of the bone-beds matrix.

(3) Many of the vertebrate grains contained 'fresh' microborings while phosphatic invertebrate, or phosphorite debris with an identical chemical composition at the present time did not, thus suggesting that there were nutritional differences between the vertebrate and non-vertebrate grains at the time of deposition (Antia & Whitaker, 1979).

(4). Many of the vertebrate grains contain fragile syndepositional weathering features which would have been removed by abrasion if the material had been prefossilised, or would have rendered the grains to a fragility which would not have withstood transport.

Following the recognition of syndepositional weathering features on vertebrate grains in the Ludlow Bone-Bed, Antia (1979a) suggested that they may have been buried in the Bone-Bed within 10 years of the death of the fishes from which they were derived. Since mass mortalities of fish occur in some recent seas every 7 - 14 years (Antia, 1979a), it is possible that the Ludlow Bone-Bed formed as a result of an offshore mortality of fish followed by an onshore migration of fish debris into the intertidal zone.

At Birmingham, a phosphatic quartz-rich fish debris layer which has been correlated with the Ludlow Bone-Bed (King & Lewis, 1912) probably formed subtidally as a result of local changes in the chemistry of the sea water (Antia, 1979b), though this has still to be proven.

Since 1920, three major environmental models for the genesis of the Ludlow Bone-Bed have been proposed. They are:-

(1) Formation as a lag concentrate in a shallow lake or sea (Stamp, 1920, 1923; Tucker, 1960).

(2) Formation as an intertidal lag concentrate deposited as a transgressive sea swept over Ludlovian sediments following a rapid marine regression (Allen, 1962, 1974; Allen & Tarlo, 1963).

(3) Formation as an intertidal lag concentrate deposited during a marine regression (Antia & Whitaker, 1979; Antia, 1979a).

In this study the faunal and sediment changes across the Ludlow Bone-Bed are documented in its stratotype section at

Ludlow, Salop, in order to help place the Bone-Bed in its environmental context.

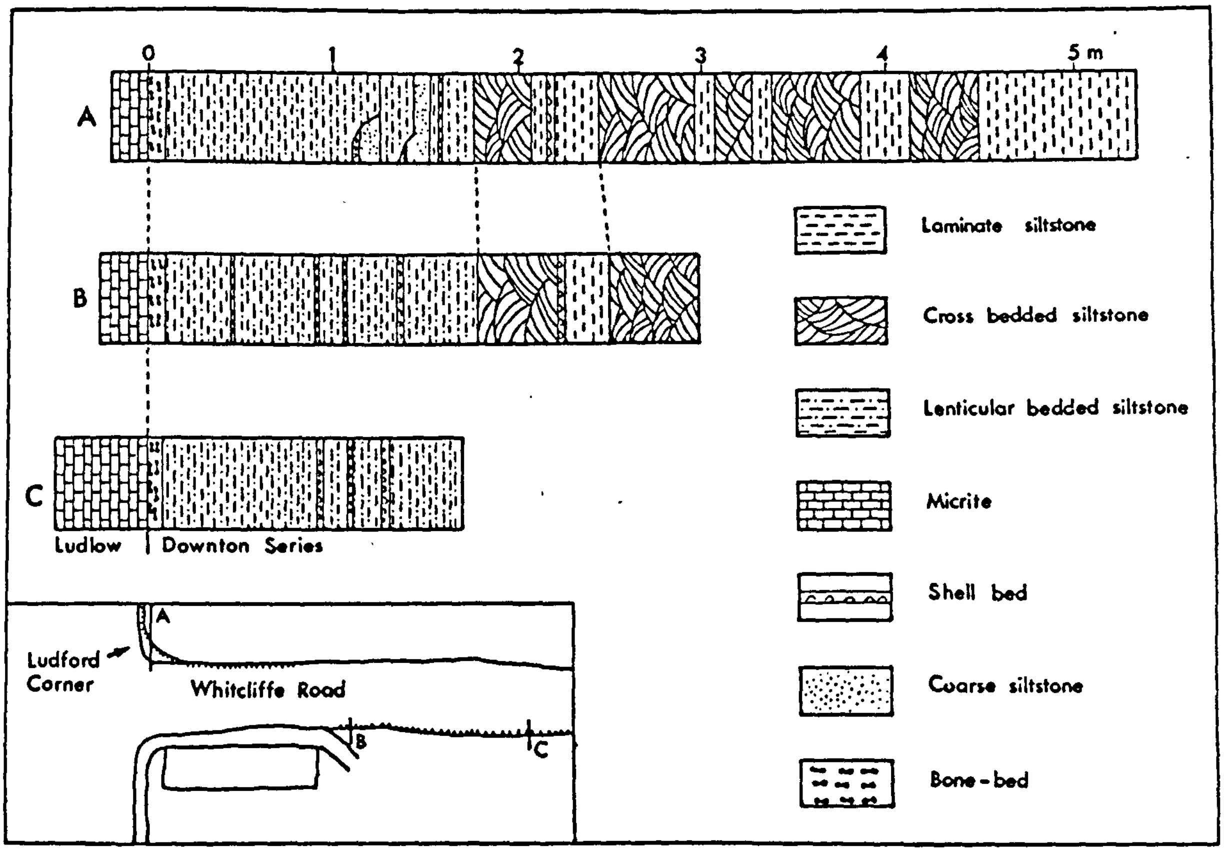
Stratotype section of the Ludlow Bone-Bed

The type section of the Ludlow Bone-Bed at the junction of Whitcliffe Road and the Ludlow to Leominster Road at Ludford, Ludlow (G.R. SO 5123 7413) is currently the stratotype section of the Ludlow - Downton Series Boundary (White, 1950; Holland et al., 1963) and the Whitcliffe Beds - Downton Castle Formation Boundary (Holland et al., 1963).

Two major controversies have been connected with this section. The first dealt with the genesis of the Ludlow Bone-Bed and remains unresolved. The second concerns the positioning of the Silurian-Devonian Boundary. Many authors (e.g. Stamp, 1923; White, 1950) have advocated that the stratotype section for this boundary should be the Ludford Section, with the actual boundary being taken as the base of the Ludlow Bone-Bed (e.g. Stamp, 1920; 1923; White, 1950). This boundary controversy has been settled and the section is now wholly Silurian (cf. Martinsson, 1977).

Faunal lists for the section are given in Tables 1 - 3. They confirm earlier suggestions (Elles & Slater, 1906) that the Ludlovian - Downtonian Boundary is represented by a marked faunal change.

The sediments present in the section (Text-Fig. 2) have been examined and described by Elles & Slater (1906), Allen (1974), Antia & Whitaker (1979), Antia (1979a). They record a Whitcliffian facies of grey limestones overlain by a thin bone-bed and a Downtonian sequence of siltstones, sandstones and bone-beds. The bone-bed horizon has attracted the most scientific attention and was described in detail by Antia & Whitaker (1979). The other



Text-Fig. 2: Sediments recorded at three points on the Ludford corner - Whitcliffe Road Section. The micrite corresponds to Facies A, the Bone-bed to Facies B, the lenticular bedded siltstones to Facies C, and the laminate and cross bedded siltstone to Facies D.

Table 1. Faunas present above the Ludlow - Downton Boundary at the Junction of the Leominster - Ludlow Road and Whitcliffe Road (Transect A, Text-Fig. 2).

	Height above boundary (cm)				
	0 – 55	55 – 122	122 – 157	157 – 246	246 – 493
BRACHIOPODS					
Lingula cornea (J. de C. Sowerby)	-	-	-	-	0.26
Lingula minima (J. de C. Sowerby)	47.97	13.97	5.72	66.24	7.59
BIVALVES					
Grammysia sp.	-	-	0.03	-	-
Leodispis barrowsi Reed	-	-	-	-	0.26
Modiolopsis complanata (J. de C. Sowerby)	2.70	5.18	1.75	5.71	-
Sdenamya sp.	-	0.14	-	-	-
GASTROPODS					
Loxonema gregarium (J. de C. Sowerby)	9.48	0.14	0.03	-	-
'Platyschisma' williamsi (J. de C. Sowerby)	0.67	0.14	-	-	-
Turbocheilus helicites (J. de C. Sowerby)	-	13.68	0.42	0.57	-
OSTRACODS					
Cytherellina siliqua Jones	7.43	1.44	2.81	5.79	12.56
Lerpiditia cf. *marginata*	0.67	-	-	-	-
Londinia kiesowi (Krause)	8.78	1.58	1.12	1.71	13.87
Frostiella groenvalliana Martinsson	13.51	18.44	48.84	16.00	18.84
Hebellum cf. *tetragonum* (Krause)	-	0.14	4.92	0.57	-
Nynamella sp.	0.67	0.57	4.72	0.57	2.35
Primitia cf. *mundula*	-	0.28	0.26	-	-
FISH					
Cythaspis sp.	2.02	-	-	-	-
Logania ludlowiensis Gross	4.05	41.06	25.59	-	0.26
Gomphonchus tenuistriata Ag.	-	0.14	0.03	-	-
Thelodus parvidens Ag.	5.40	0.28	3.50	-	-
OTHER FOSSILS					
Calcareous tubes (<3mm length)	-	1.58	0.06	2.85	-
Ceratiocaris sp.	0.67	-	-	-	-
Pterygotus sp.	2.70	0.14	0.06	-	0.26
Plant debris	+	+	+	+	+
Pachytheca sphaerica Hooker	3.37	-	0.39	-	40.57
Sample Size	148	694	3024	175	382

Table 2. Faunas across the Ludlow - Downton Boundary at Ludlow (Transect B, Text-Fig. 2).

	Height above the boundary (cm)						
	-18	0	23	67	114	154	254
BRACHIOPODS							
Lingula sp. nov.	2.00	-	-	-	-	-	
Lingula lata (J. de C. Sowerby)	7.63	-	-	-	-	-	
Lingula minima	-	20.67	14.11	6.00	11.70	12.92	
Howellella elegans	4.01	-	-	-	-	-	
Microsphaeridiorhynchus nucula (J. de C. Sowerby)	23.29	1.11	-	-	-	-	
Orbiculoidea rugata (J. de C. Sowerby)	0.80	-	-	-	-	-	
Protochonetes ludloviensis Muir Wood	10.84	2.79	-	-	-	-	
Salopina lunata (J. de C. Sowerby)	40.16	10.61	-	-	-	-	
BIVALVES							
Fuchsella amygdalina (J. de C. Sowerby)	1.20	-	-	-	-	-	
Goniophora cymbaeformis (J. de C. Sowerby)	2.00	-	-	-	-	-	
? Leodispis barrowsi	-	-	-	-	-	0.38	
Modiolopsis sp.	0.80	-	-	-	-	-	
Modiolopsis complanata	-	7.26	65.88	14.00	14.88	27.86	
Pteronitella retroflexa (Wahlenberg)	0.40	-	-	-	-	-	
GASTROPODS							
Loxonema gregarium	-	0.55	-	-	-	-	
Loxonema obsoletum (J. de C. Sowerby)	0.80	-	-	-	-	-	
Turbocheilus helicites	-	7.26	2.94	9.00	-	0.38	
OSTRACODS							
Calcaribeyrichia torosa Jones	0.80	-	-	-	-	-	
Cytherellina siliqua	0.80	16.20	4.70	16.00	6.38	11.45	
Frostiella groenvalliana	-	21.22	-	51.50	58.51	40.07	
Londinia kiesowi	-	11.73	8.23	3.00	3.19	3.81	
Nodibeyrichia verrucosa Shaw	1.60	0.55	-	-	-	-	
Nynamella sp.	-	-	-	-	-	0.76	
OTHER FOSSILS							
Calcareous tubes	-	-	-	-	-	1.90	
Cornulites sp.	0.40	-	-	-	-	-	
Hyolithes forbesi (Sharpe)	0.80	-	-	-	-	-	
Pachytheca sp.	-	-	4.11	0.50	5.31	0.38	
Thelodus sp.	-	C	+	+	+	+	
Gomphonchus tenuistriata	0.40	-	-	-	-	-	
Sample Size	249	179	170	200	94	262	

Table 3. Faunas across the Ludlow - Downton Boundary on Whitcliffe Road, Ludford.
(Transect C, Text-Fig. 2) - vertebrate faunas have been excluded from this layer.

	Height above boundary (cm)										
	-35	-25	-15	0	10	20	41	67	89	119	147
BRACHIOPODS											
Craniops implicatus (J. de C. Sowerby)	3.92	16.59	0.88	0.46	1.20	-	-	-	-		-
Howellella elegans	0.41	0.42	5.30	0.34	-	-	-	-	-		-
Lingula sp. nov.	0.20	1.70	3.53	0.81	-	-	-	-	-		-
Lingula lata	0.61	8.08	7.96	1.27	-	-	-	-	-		-
Lingula minima	-	-	-	9.53	29.51	16.49	52.68	31.57	4.87		-
Microsphaeridiorhynchus nucula	8.67	3.40	7.07	12.32	-	-	-	-	-		-
Orbiculoidea rugata	-	0.42	0.88	-	0.60	-	-	-	-		-
Protochonetes ludloviensis	46.28	5.95	16.81	5.69	1.20	-	-	-	-		-
Salopina lunata	36.98	60.42	57.52	38.37	2.40	-	-	-	-		-
BIVALVES											
Fuchsella amygdalina	-	-	0.88	-	-	-	-	-	-		-
Goniophora cymbaeformis	0.61	0.85	-	0.23	-	-	-	-	-		-
Modiolopsis complanata	-	-	-	-	-	4.89	-	5.26	17.07		55.20
Nuculites ovata (J. de C. Sowerby)	-	0.42	-	0.23	-	-	-	-	0.48		-
Pterinea tenuistriata	-	0.42	-	0.46	-	-	-	-	-		-
Pteronitella retroflexa	0.61	-	-	0.23	-	-	-	-	-		-
Solenamya sp.	-	-	-	-	-	0.51	-	-	-		0.45
GASTROPODS											
Cymbularia carinata (J. de C. Sowerby)	-	-	-	-	-	0.25	-	-	-		-
Loxonema conicum (J. de C. Sowerby)	-	-	-	0.11	-	-	-	-	-		-
Loxonema gregarium	-	-	-	0.46	1.20	6.95	2.15	5.26	1.95		-
Loxonema obsoletum	-	-	0.88	0.58	-	0.25	-	-	-		-
Turbocheilus helicites	-	-	-	3.60	0.60	5.41	-	-	7.31		2.71
OTHER MOLLUSCS											
Bucanopsis expansus (J. de C. Sowerby)	-	0.42	-	0.34	-	-	-	-	-		-
Leurocycloceras sp.	-	0.42	-	-	-	-	-	-	-		-
OSTRACODS											
Calcaribeyrichia torosa	0.61	-	-	-	-	-	-	-	-		-
Cytherellina siliqua	-	-	-	0.11	-	-	2.15	-	8.78		3.16
Frostiella groenvalliana	-	-	-	9.53	14.45	23.96	15.05	38.59	14.14		33.48
Hebellum cf. tetragonum	-	-	-	0.93	-	0.77	4.30	-	0.48		-
Kuresaaria circulata	-	-	-	0.58	0.48	2.06	-	-	-		0.44
Londinia kiesowi	-	-	-	10.46	22.89	18.04	23.65	10.52	42.43		2.71
Lophoctonella sp.	-	-	-	0.23	-	-	-	-	-		-
Nynamella sp.	-	-	-	2.20	0.60	0.51	-	-	-		0.44
Nodibeyrichia verrucosa	0.61	-	-	0.46	-	-	-	-	-		-
BRYOZOAN COLONIES											
Leioclema sp.	-	-	-	0.23	-	-	-	-	-		-
Rhopalonaria sp.	-	0.42	-	0.11	-	-	-	-	-		-
OTHER FOSSILS											
Calcareous tubes	-	-	-	-	-	-	-	7.01	1.46		0.44
Cornulites sp.	-	-	-	0.34	-	-	-	-	-		-
Eurypterid fragments	-	-	-	6.81	15.66	18.04	-	1.75	0.97		0.90
Ozarkodina sp.	-	-	-	-	0.60	-	-	-	-		-
Pachytheca sp.	-	-	-	-	3.61	1.80	-	-	-		-
'Serpulites' sp.	-	-	-	-	0.60	-	-	-	-		-
Plant debris	-	-	-	+	+	+	+	+	+		+
Sample Size	484	235	113	860	166	388	93	57	205		221

facies have attracted less interest (e.g. Allen & Tarlo, 1963; Holland et al., 1963; Allen, 1974a). In this study the environmental interpretations of each facies as outlined by Allen (1974), Antia & Whitaker (1979), Antia (1979) are assumed to be basically correct. Consequently, this study will concentrate on the distribution of faunas, sediments and facies in the section and their interpretation.

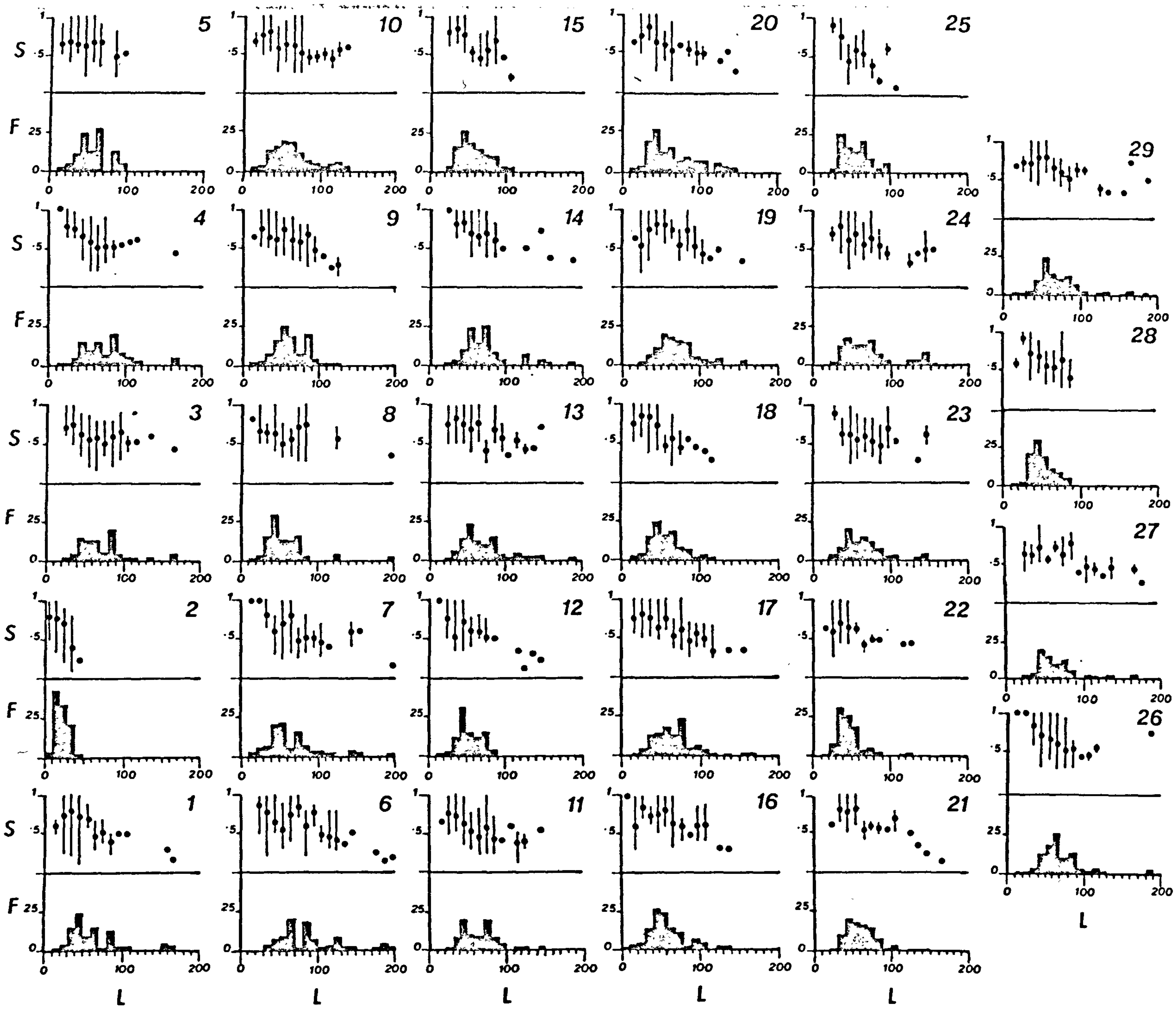
Four sedimentary facies have been recognised at Ludford (Allen, 1974) and are described in the ensuing text. Their distribution through the section is indicated in Text-Fig. 2.

Facies A - Upper Whitcliffe Beds

This facies consists of an interbedded sequence of shelly calcareous siltstones and dark mudstones. The grain size distributions of the siltstones and mudstones are illustrated in Text-Fig. 3. The mudstones have a mean quartz grain size of about 0.01 mm while the siltstones have a mean quartz grain size of about 0.05 mm. Bedding type varies from lenticular to wavey bedding. Herring bone cross bedding is not uncommon locally. Shells are well sorted and patchly distributed. About 40% are fragmented and most of the bivalved shells are disarticulated. About 90% of the concavo-convex particles (shells) overlying unbioturbated sediment are orientated concave down. In the bioturbated sediment orientations vary from concave down to concave up. Most isolated particles in this sediment type are orientated concave up. No burrowing bivalves were observed in situ in the facies. Most of the supposedly sessile epifaunal brachiopods (e.g. Salopina, Microsphaeridiorhynchus, Howellella (Fürsich & Hurst, 1974) and motile swimming brachiopods (e.g. Protochonetes (Rudwick, M. personal communication 1978)) occur

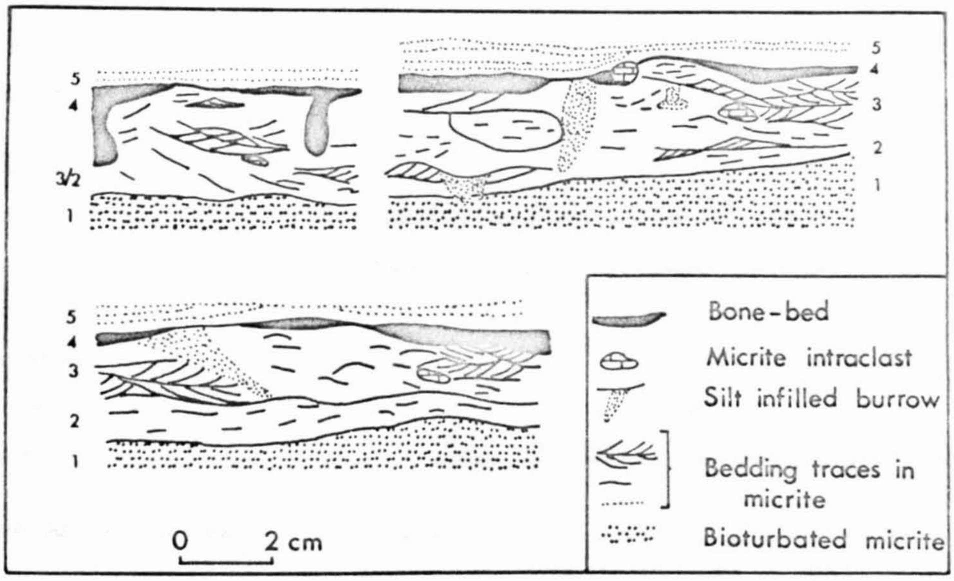
Text-Fig. 3: Quartz grain size distributions and sphericity plots for the Ludford lane section. A key to slide No. is given in Text-Fig. 5. Slides 1-5 are in Facies A, slides 6-7 in Facies B, slides 8-23 in Facies C and slides 24-29 in Facies D.

Grain size (L) in mm is given on the x axis. F = frequency (%) and S = sphericity (values 0-1). The mean sphericity and sphericity range are given for each size grouping. Sphericity is calculated as the shortest axis/longest axis of a grain on the slide.

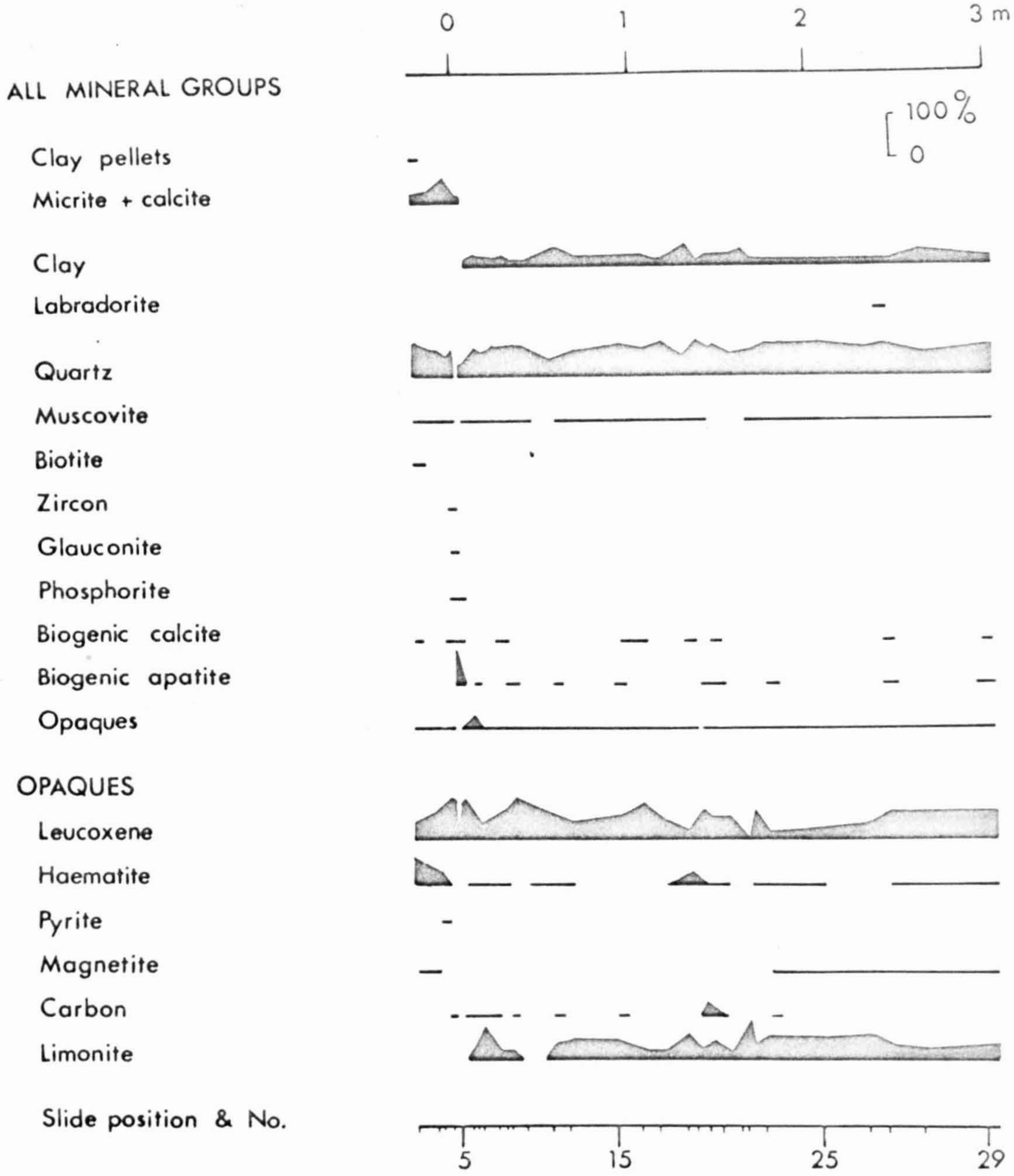


as disarticulated valves. Articulate valves are commonest amongst the species M. nucula, which had a very strong hinge. Since it is difficult to disarticulate a brachiopod with a strong hinge, it could be argued that the presence of such brachiopods provides no real indication as to where an animal lived, as their shells would survive considerable transport (Jones, 1969; Lingwood, 1976a). For example, a transported assemblage of Cerastoderma edule observed by the author in July 1976 just below the high tide mark in the shelly pebble and muddy sand habitat (Antia, 1977) of Sales Point, Bradwell, Essex (G.R. TM 032 087) consisted entirely of dead closed articulated valves, many of which had been reorientated into a 'life orientation' on the surface of the substrate. Details of these shell orientations are given in Table 4.

Ripples present in this facies vary from symmetric crescentic current ripples (wavelength 5 to 20 cm; amplitude 3 to 30 mm) to linguloid and mini ripples. The wavey and lenticular bedded nature of the sediment suggest (Reineck & Singh, 1973) that the facies formed in a region of tidal flow. This is confirmed by the poorly developed herring bone cross bedding present in the sediments (Text-Fig. 4). The mineralogy of the facies is indicated in Text-Fig. 5. Its dominant constituent is quartz occurring as grains varying in diameter from 0.005 to 0.18 mm. The smaller quartz grains tend to be compact, while the larger grains tend to be elongate. Details of the relative elongation (sphericity) of the grains are given in Text-Fig. 3. The smaller quartz grains are apparently unstrained angular and non composite. Some quartz grains greater than 0.1 mm in length are strained, others are composite. Most are angular, though some rare well rounded grains are present. Leucoxene is the most common heavy mineral.



Text-Fig. 4: Traces of vertical sections through the Ludlow Bone-Bed (layer 4) showing herring bone cross bedding in the Whitcliffian micrites (layers 1-3) and the bone-bed infilling burrows in the underlying sediment.



Text-Fig. 5: Mineralogy of the Ludford section B (see Text-Fig. 2).

Table 4. Orientations of dead articulated *Cerastoderma edule* shells at Sales Point, Bradwell, Essex.

Orientation	Number	%
Shells posterior facing upwards	10	23.25
Shells anterior facing upwards	16	37.20
Shells ventral margin facing upwards	12	27.90
Shells dorsal margin facing upwards	5	11.62

Since some of the leucoxene grains contain an ilmenite core, it is possible that much of the leucoxene present may result from the diagenetic replacement of ilmenite by leucoxene after sediment deposition (Hobson, 1960). Micas (both biotite and muscovite) when present tend to occur as both rounded and angular grains frequently containing frayed edges. These grains vary in diameter from 0.08 mm to 0.35 mm. Clays and micritic clays form a large part of the sediment, and show several phases of diagenetic growth. The initial growth appears to have been of platy and honeycomb clays around quartz nuculei, followed by a subsequent microcrystalline coprecipitation of clays and calcite within the 'newly created' sediment pores. At the present time chlorite is the dominant clay (Antia, 1979a; Antia & Whitaker, 1979) though traces of montmorillonite, kaolinite and illite are present.

Within the articulated shells, different diagenetic microenvironments appear to have operated. Most contain a geopetal infill of micrite overlain in some instances by a coarse sparite. Many of the calcareous shells have been replaced by sparite, though some micritic envelopes are present. In the latter instance the micritisation appears to involve either (1) the emplacement of micritic aragonite or high-magnesium calcite in the shell punctae, or (2) a centripetal replacement of whole shells by micrite leaving only scattered shell relics. The process of micritisation is poorly understood (Bathurst, 1975) but could relate to immediate post depositional bacterial activity (Bathurst, 1975, p.391) or later localised diagenetic reactions. The source of the micrite in the sediment is unknown. Among the more probable sources are (1) the diagenetic dissolution and reprecipitation of calcite from shell debris and (2) the reprecipitation of aragonite needles on the sea bed..

Within the facies, sediment type, faunal diversity and composition are variable along a bedding plane surface (Text-Fig. 6). Sample data is presented in Table 5.

An examination of particle size and shape can produce important information regarding the influence of currents and waves on current distribution and strength in the sediment. The CM diagram (Text-Fig. 7) for the facies (calculated after Passega, 1957, 1976) suggests that much of the sediment in the facies originally formed part of a suspension load. Since the effective settling velocity of both clastic and carbonate grains can be calculated, it may be possible to produce an estimate of the effective current strength on the sea bed.

Studies on shell particle settling velocities are rare (e.g. Macklem, 1968; Grubert, 1971; Futterer, 1978a, 1978b, 1978c). However, they have demonstrated that the mathematical functions currently used to calculate the settling velocities of particles (cf. Blatt et al., 1972) are only valid for spherical particles (Futterer, 1978a) and that the effective settling velocities of biogenic particles approximate to (Futterer, 1978c):-

$$s = k\ w/FD \qquad (\text{cm/sec})$$

where s = settling velocity in cm/sec

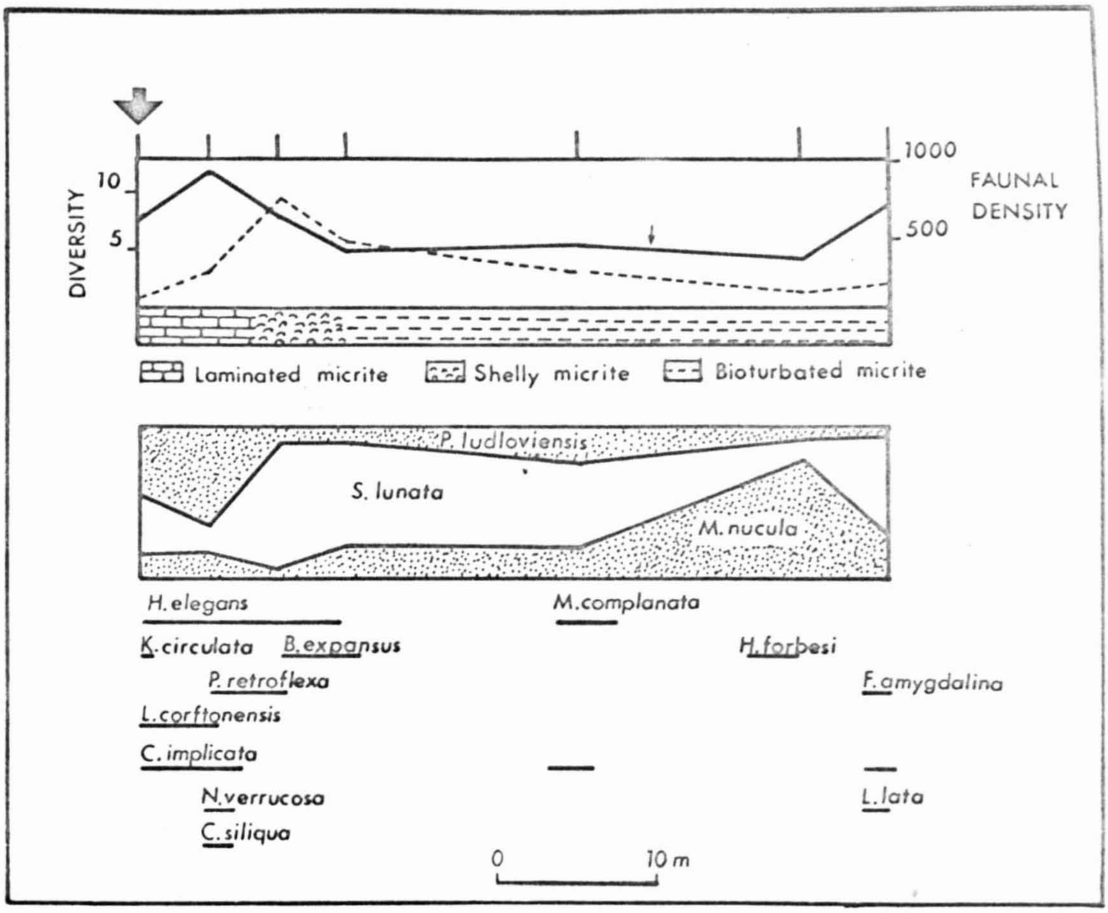
k = proportion factor dependent on particle shape

w = particle weight

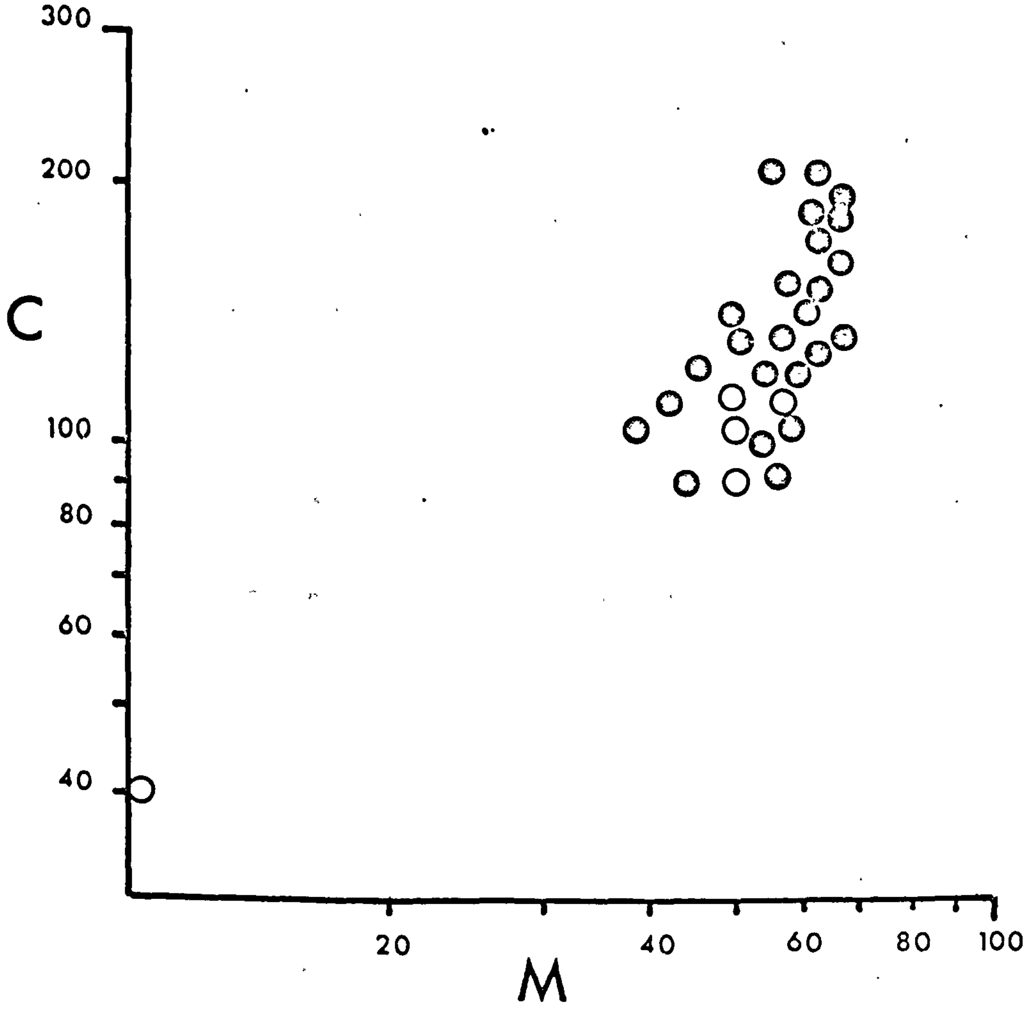
F = effective settling area of the particle

D = density of water

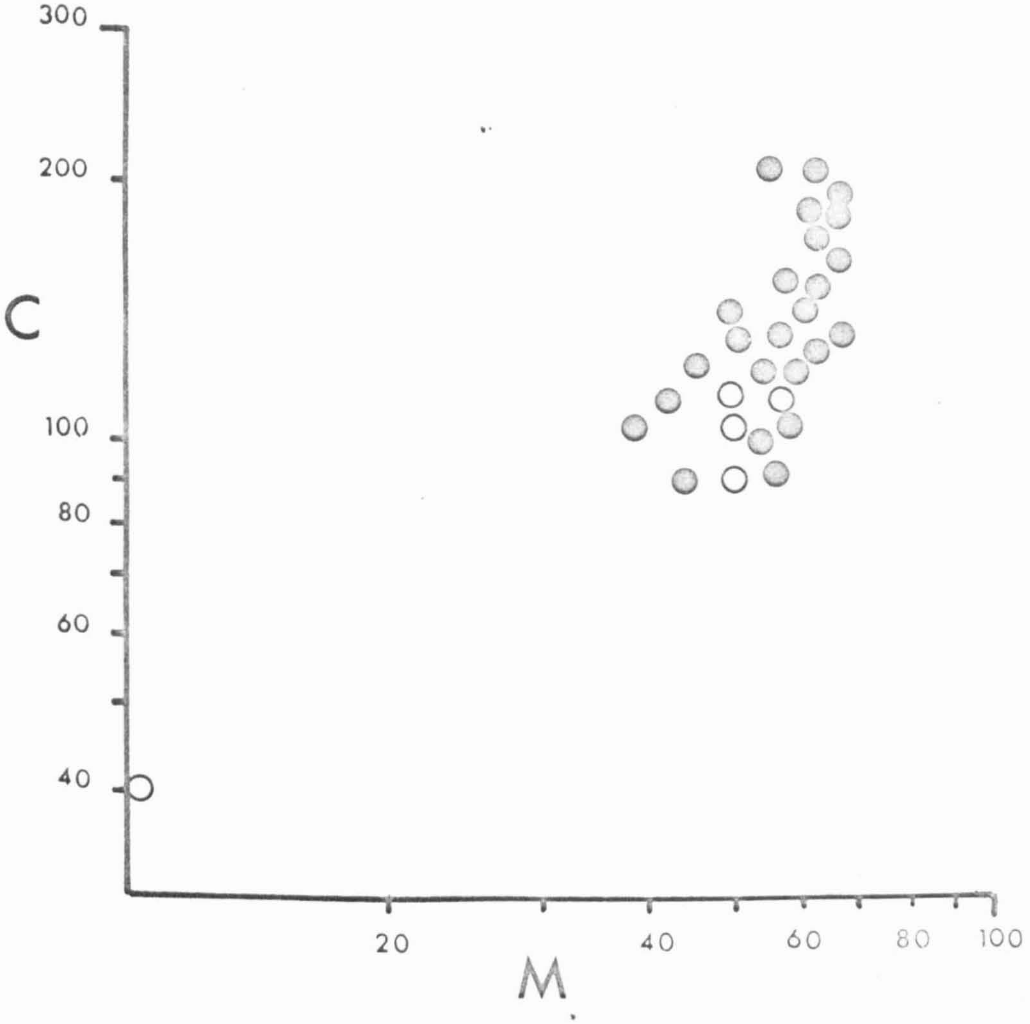
The proportion factor k need not be calculated since Futterer (1978a,c) has demonstrated a direct graphical relationship between the w/F ratio and the settling velocity of



Text-Fig. 6: Variation in sediment type, faunal diversity and faunal composition along a bedding plane surface 14 cm below the Ludford Bone-Bed. Arrow indicate Ludford Corner. Transect is along Whitcliffe Road. The raw data used to compile this diagram is presented in Table 5.



Text-Fig. 7: C/M diagram for the Ludford transect. Open circles are Whitcliffian samples. Others Downtonian samples.



Text-Fig. 7: C/M diagram for the Ludford transect. Open circles are Whitcliffian samples. Others Downtonian samples.

Table 5. Faunal data for the transect illustrated in Text-Fig. 6. The position of Sample 1 is arrowed in Text-Fig. 6, the remainder are indicated by a tick.

	SAMPLE NO.						
SPECIES	1	2	3	4	5	6	7
BRACHIOPODS							
Craniops implicatus	1	8	-	-	1	-	12
Lingula sp. nov.	1	1	-	-	-	-	-
Lingula lata	-	2	-	-	-	-	6
Howellella elegans	1	4	1	3	-	-	-
Microsphaeridiorhynchus nucula	12	22	8	41	35	82	23
Protochonetes ludloviensis	38	163	28	6	57	13	17
Salopina lunata	24	28	624	321	126	17	84
BIVALVES							
Fuchsella amygdalina	-	1	1	-	-	-	2
Modiolopsis complanata	-	-	-	-	1	-	-
Pteronitella retroflexa	-	1	2	-	-	-	4
OTHER MOLLUSCS							
Bucanopsis expansus	-	-	1	1	-	-	-
Hyolithes forbesi	-	-	-	-	-	1	-
OSTRACODS							
Cytherellina siliqua	-	3	-	-	-	-	-
Kuresaaria circulata	1	-	-	-	-	-	-
Nodibeyrichia verrucosa	-	1	-	-	-	-	1
Sample Size	78	234	695	371	220	113	149

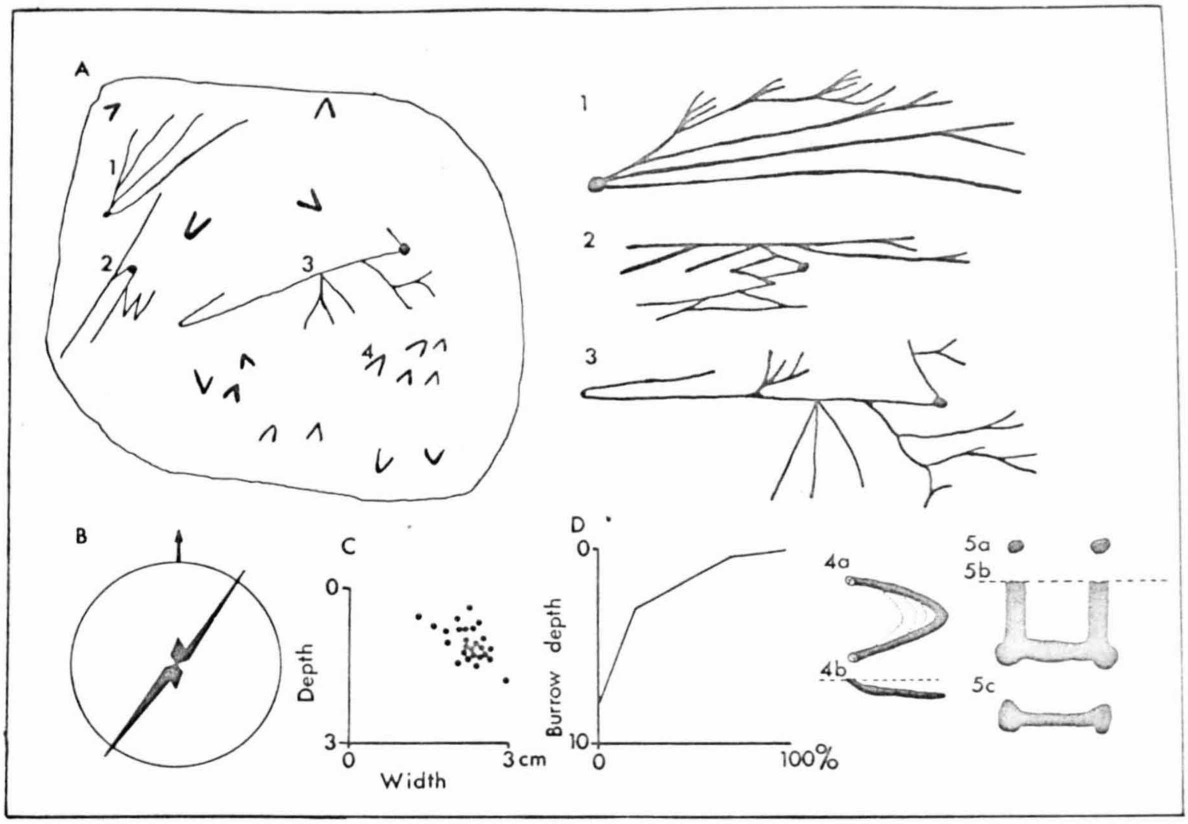
molluscan shells (Bivalves and Gastropods).

The faunal distributions (Fig. 6) show that laterally three species become abundant in turn (P. ludloviensis, S. lunata, and M. nucula) on a single bedding plane. These changes could result from either (1) three distinct clumps of living species with some post-mortem faunal mixing between the individual clumps (Boucot, personal communication, 1978), or (2) from a marked post-mortem mixing and sorting of shells (cf. Lingwood, 1976; Antia, 1977) from differing environments and facies or even within the same facies.

Shells are transported by flotation (Lingwood, 1976), rolling (Futterer, 1978b) and sliding (Futterer, 1978c). The mean grain size of the sediment suggests that its effective settling velocity from suspension was about 10 cm/sec. However, it is possible that the larger non-spherical, elongate grains (0.1 - 0.3 mm) could have been carried by a current of the same magnitude (Komar, 1978).

Trace fossils are abundant in the sediment and can be grouped in three forms (1) vertical burrows - these include Bifungites, Arenicolites and Skolithus (2) oblique burrows - these include Chondrites like burrows (3) horizontal burrows and trails - these include Agrichnium and Dendrotichnium.

The identifications given here are tentative and should not be regarded as absolute. Pye (personal communication 1978) regards Bifungites as a polychaete worm burrow. Text-Fig. 8 illustrates the size distribution of burrows assigned to this species. A bedding plane trace of trace fossils in this facies is given in Text-Fig. 9. Note that the trace fossils indicate the presence of a major NE-SW trending current.



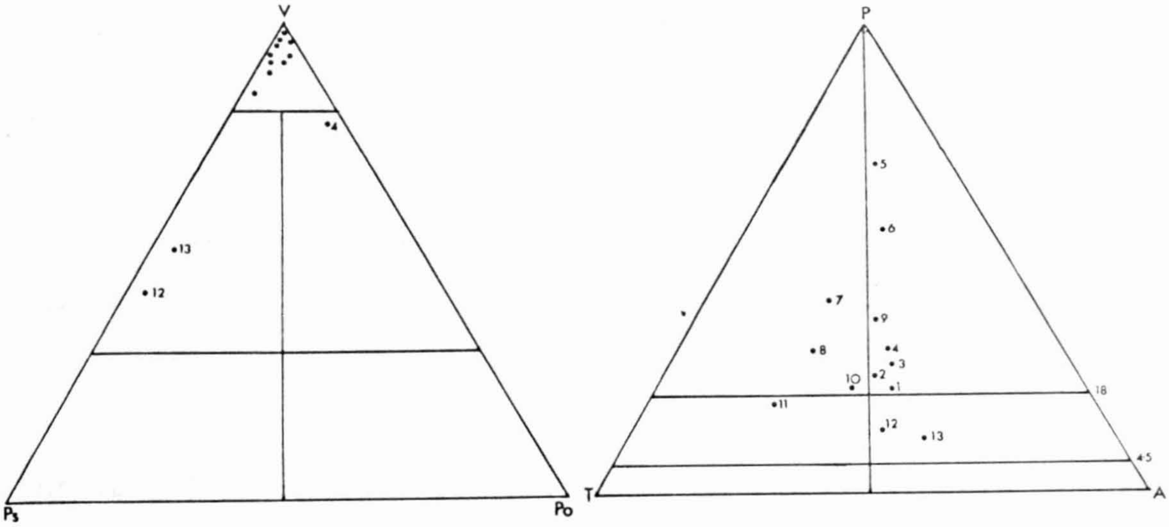
Text-Fig. 8: Trace fossils in Facies A:

(A) Bedding plane trace (25 cm in diameter) of trace fossils 14 cm below the Ludlow-Downton Boundary at Ludford Corner. The four types of trace fossils observed are labelled 1-4 and illustrated. Type 4 is termed here ?Zoophychus sp. Burrow Type 5 is common throughout Facies A, and termed here Bifungites sp.

(B) Axial orientation of ?Zoophychus sp. indicating a NE-SW current orientation.

(C) Plot of burrow depth against burrow width for Bifungites sp.

(D) Plot of Burrow depth against % of burrows reaching that depth of penetration from the sediment surface.



Text-Fig. 9: Composition and classification of Bone-Beds in the Ludford section:

A. Relative proportions of vertebrate remains (V), Phosphatic shells (Ps) and Phosphatic nodules (Po). This graph indicates that most of the bone-beds are lithobonebeds, 4 is pelbonebed, 12 and 13 are biobonebeds (classification after Antia, 1979a).

B. Relative proportions of phosphatic material (P), terregenous clasts (T) and allochems (A) in each Bone-Bed. Bone-Beds 11-13 are subbone-beds (cf. Antia, 1979a). The position of each bone-bed in the section is given in Antia (1979a).

Facies B - Downtonian

The Bone-Bed facies (Allen, 1974a) termed here Facies B, has been extensively described in the literature (Murchison, 1837, 1839, 1859; Elles & Slater, 1906; Stamp, 1923; King, 1934; Allen, 1962, 1974a; Allen & Tarlo, 1963; Antia & Whitaker, 1979; Antia, 1979a etc.). Originally the facies was considered to contain just one bone-bed and was described as 'a gingerbread coloured layer of a thickness of three to four inches dwindling away to quarter of an inch' (Murchison, 1859). More recent work has shown the section to contain a number of bone-beds (Allen, 1974a; Antia, 1979a), none of which are as thick as that described by Murchison. However, it is possible that a thick bone-bed did exist at Ludlow, and has now been removed by geologists etc., as bone-beds elsewhere in the Welsh borderlands exhibit very rapid thickening and thinning within the space of a few metres e.g. Corfton and Aston Munslow (G.R. SO 4965 8535 & SO 512 866).

The basal bone-bed in the facies is considered (Elles & Slater, 1906; Stamp, 1920; Holland et al., 1963; Antia, 1979a) to be the Ludlow Bone-Bed. This bone-bed rests on a rippled silt, containing a crescentic rippled upper surface (wavelength 5 - 10 cm; amplitude 5 - 10 mm). The ripple troughs are bioturbated containing Bifungites burrows infilled with coarse silt and vertebrate debris (Text-Fig. 4). These burrows penetrate the sediment to a depth of 1.5 cm. The absence of a spreite associated with them suggests that they may have been dwelling burrows. Over this sediment surface, burrow densities vary from 35 to 75 Bifungites burrows per square metre. Other burrow types present on this bedding plane surface include Dendrotichnium, Skolithus, Lobichnus and Agrichnium.

Occasional specimens of Goniophora cymbaeformis occur half buried in the sediment on this bedding plane in apparent life orientation (cf. Scott, 1978). These specimens may have been alive when the basal bone-bed was deposited.

The basal bone-bed (The Ludlow Bone-Bed) consists of a thin discontinuous (0 - 6 mm thick) gingerbread coloured vertebrate sand infilling ripple troughs and scour hollows in the underlying sediment. The matrix of this bone-bed consists of a quartz rich micrite. The mean grain size of the quartz grains is about 0.045 mm (Text-Fig. 3). Calcareous shell debris is absent from the layer. However, the larger quartz grains and fish debris in the layer have acted as centres of calcite and micrite growth. This bone-bed is overlain by a thin (3 - 5 cm thick) layer of calcareous grey laminated mudstone containing a shelly brachiopod fauna and casts and moulds of ostracods and molluscs, perhaps suggesting that the ostracods and molluscs had aragonitic skeletons, while the brachiopods had phosphatic calcareous or calcite shells (cf. Bathurst, 1975). Also present in these muds are bedding planes strewn with fish debris (>10 fragments per cm^2) and shell fragments. Some rippled strata and bone-beds are present in this sediment. The top of this mudstone is marked by a thick (< 15 mm) discontinuous rippled bone-bed overlain in some places by a lenticular bedded silt sand sequence containing discontinuous bone-bed horizons. In some places an intervening layer is present consisting of a soft clay containing quartz, biotite and muscovite.

The relative position of each discontinuous bone-bed present in the facies to the facies base noted by Antia (1979a, Table 16, p.145) is listed in Table 6. As already noted, individual bone-beds in the section vary in thickness from 0.5 to 25 mm and are mostly rippled or infill ripple hollows, though some consist of a dense scattering of vertebrate grains on a flat surface. Bone-beds of this latter type have been termed scatter bone-beds elsewhere (Sykes, 1977). All the bone-beds are locally discontinuous, though some can be traced for 30 m laterally along the section.

The individual bone-bed layers are sparitic, micritic and clayey, lithobonebeds, biobonebeds and pelbonebeds (see Text-Fig. 9) and are composed of vertebrate debris, quartz, feldspar, shell, phosphate and clay grains within a diagenetic matrix. The composition of individual bone-beds is variable both laterally and vertically. However, all contain between 5 and 85% phosphate of which between 30 and 95% is fish phosphate. The remaining phosphate consists of phosphatic nodules and phosphatised invertebrate shells.

The chemical composition of the phosphate in the individual bone-beds is variable ranging from a fluorapatite to a carbonate apatite (Antia, 1979a). There also appears to be a relationship between the chemical composition of the phosphatic clasts and the nature of the bone-bed sediment type (Antia, 1979a).

1. Faunal composition

The faunal composition of each bone-bed is outlined in Table 6. Note that at the facies base the fish faunas are dominated by Thelodus parvidens while at the facies top Logania ludlowiensis dominates. This domination could either result from (1) a change in the composition of the fish schools of the sea (Antia, 1979a) or (2) the effects of differential particle size and shape sorting by currents and waves, since the effective

Table 6. Vertebrate (fish scales only) composition of the 13 Bone-Beds observed in the section.

	Bone-Bed No.												
	0	1	2	3	4	5	6	7	8	9	10	11	12
THELODONTS													
Thelodus bicostatus (Hoppe)	0.1	0.3	0.1	-	-	0.1	-	0.7	0.6	-	-	-	-
Thelodus costatus (Pander)	-	-	-	-	0.1	0.1	-	-	-	-	-	-	-
Thelodus pugniformis Gross	0.5	0.7	-	1.8	0.1	0.7	0.3	-	0.6	-	0.3	0.5	0.2
Thelodus trilobatus (Hoppe)	-	2.1	0.1	0.9	1.5	2.0	0.3	5.7	-	1.4	0.3	-	0.6
Thelodus parvidens A.	69.9	82.9	78.0	63.4	51.0	45.8	42.8	28.5	26.3	21.3	7.1	5.5	16.2
Logania ludloviensis Gross	29.3	13.4	21.7	33.2	46.6	51.1	56.2	64.2	71.7	77.2	92.0	93.9	82.5
Katoporus tricavus Gross	0.1	-	-	-	-	-	-	-	0.6	-	-	-	-
Gonioporus alatus (Gross)	-	-	-	0.6	-	-	-	0.7	-	-	-	-	-
ACANTHODIANS													
Nosteolepis sp.	-	0.2	-	-	-	-	0.3	-	-	-	-	-	-
Gomphonchus sp.	-	0.2	-	-	0.4	-	-	-	-	-	-	-	0.2
Sample Size	1432	521	834	331	643	986	322	140	152	136	278	781	431
Height above Ludlow - Downton Boundary (cm)	0	1	3.3	4.9	7.1	8.9	9.1	9.7	10.1	24.2	53.7	110.2	124.9

settling size spherocities and rollability of the two species would be very different. As the facies was deposited during a marine regression, it could be suggested that the upper part of the facies was deposited in a more onshore environment than its lower part. Consequently the differences in clast composition observed could reflect an original depositional sorting of material within the lower part of the intertidal zone..

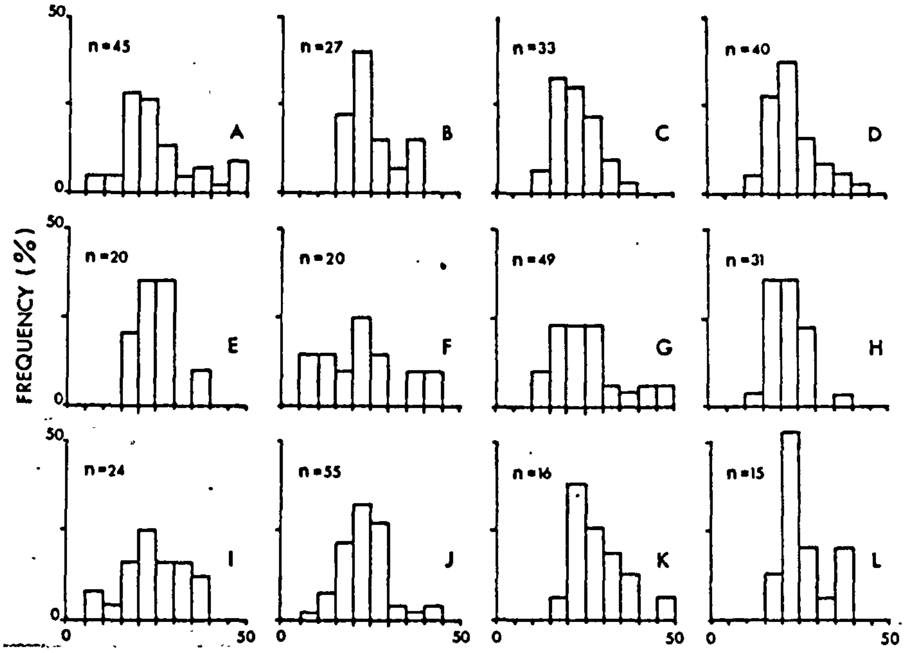
2. Fish remains

Within the bone-beds fish remains are common. Most of the species present have been described or illustrated by Murchison (1858), Gross (1967, 1972), Turner (1973), Antia (1979a) and Antia & Whitaker (1979). The species recorded by the author are listed in Table 6.

Most of the fish remains are unabraded. However, individual grains do show some abrasion features and weathering features, (Antia & Whitaker, 1979; Antia, 1979a) others contain micro-borings (Antia & Whitaker, 1979; Antia, 1979a).

(a) Weathering features

During decomposition vertebrate grains produce a series of distinctive external morphological features. On large grains (e.g. mammalian bones) many of these features are visible to the naked eye. On smaller grains (e.g. Thelodont fish scales) these features only become obvious when examined at high magnigication (i.e. greater than x 200). From this bone-bed facies Antia (1979a) has recorded a number of weathering features and has suggested (Antia, 1979a) that they indicate that the individual bone-beds formed over a very short period of time i.e. within 10 years of the death of the fish constituting the bone-bed (Antia, 1979a).



Text-Fig. 10: Size/frequency histograms of the diameter (x axis) of Algal form B borings on 12 thelodont (*T. parvidens*) scales. Size measurements are in µm.

2. Abrasion features

Thelodont grains are usually complete and show little evidence of abrasive rounding. However, chip marks and abrasion scratches are present on their outer surfaces (Antia & Whitaker, 1979). Some grains have been broken in half during deposition. In such cases the break has developed along cracks parallel to the net radial fibrous structure of the grain (cf. Antia, 1979a). These cracks may be a result of bone weathering processes (Behrensmayer, 1978; Antia, 1979a). Similar abrasion cracks have been recorded (Antia, 1979a) on vertebrate grains from the Muschelkalk Grenzbonebed, the Rhaetic Bone-Bed and the Suffolk Bone-Bed.

Acanthodian spines, scales, teeth and fragments present in the bone-bed also contain abrasion scratches. Fractures produced by abrasive weathering are commonly orientated parallel to the spines axis, though some specimens contain breaks orientated perpendicular to their axis. Other acanthodian fragments are well abraded with fracture surfaces orientated parallel to histological tubes revealing their complex morphology.

3. Microborings

Microborings are abundant on thelodont scales. Two types are present (Antia, 1979a) and have been termed Algal Form A and Algal Form B (Antia, 1979a). Algal Form A consists of small ($<$0.01 mm) diameter tubes, while Algal Form B consists of hemispherical cup shaped hollows on the scales surface (0.005 - 0.065 mm in diameter). Size data pertaining to this latter form is presented in Text-Fig. 10. Similar borings are present on Eifelian and Gèdinnian thelodonts from Iran and France (Material examined in Dr. D. Goujet's collection, Paris), Acrodus fragments from the Muschelkalk Grenzbonebed and on otoliths from the Rockall Bank). The borings also occur on acanthodian spine fragments as either isolated borings on their surface or densely packed in the grooves of the spines. It has been suggested (Antia, 1979a) that the distribution of this species might be controlled by the level of light penetration into the water.

4. Conodonts

Conodonts are a rare constituent of the bone-bed facies and all occur as worn and fragmentary remains. The species present include Ozarkodina confluens, O. eosteinhornensis, Distomodus dubius, Pelekysgnathus dubius, and O. excavata (Aldridge, 1975).

5. Quartz grains

Quartz grains in the bone-beds occur in two size groups. The first has a modal peak of about 0.05 mm and the second a modal peak of about 0.6 mm. Quartz grains in the first category range in size from 0.01 to 0.23 mm and have a negatively skewed, leptokurtosic size distribution (Text-Fig. 3). These grains are generally compact though grains longer than 0.065 mm tend to be elongate (e.g. Text-Fig. 3, Fig. 6). None of the quartz grains examined were composite or strained. Quartz grains in the larger modal group are rare (Antia & Whitaker, 1979). They vary in shape from euhedral crystals to well rounded grains and angular shards (Antia & Whitaker, 1979; Antia, 1979a). Many of the grains contain diagenetic overgrowths. These overgrowths and their order of precipitation during diagenesis have been illustrate and described by Antia & Whitaker (1979), Antia (1979a), who also showed that the quartz grains contain intertidal abrasion features and a silicified microbial flora on their outer surface.

Many of the quartz euhedra present contain abrasion rounded edges and microplates on their outer surfaces (Antia & Whitaker, 1979). Such observations suggest that they have been transported in excess of 20 km from their source, since quartz euhedra can be transported in excess of 16 km in river systems without showing any abrasion chips or rounding features (Mulgrew, personal communication, 1978).

6. Phosphatised invertebrate shell fragments

Phosphatic invertebrate shell fragments are a common constituent of the bone-beds. Their geochemistry has been described by Antia (1979a). Three phosphatised shell species are present as distinctive clasts. They are *Lingula* sp., *Orbiculoidea rugata* and '*Serpulites*' sp. All the invertebrate clasts are fragmentary. In many instances shell abrasion has removed the outer layers of the brachiopod shells to reveal their punctae. The clasts of *Serpulites* sp. occasionally reach 4 cm in length, but more commonly occur as fragments.

7. Phosphatic nodules

Phosphatic nodules present in the facies were originally described as fish coprolites (e.g. Murchison, 1859). They consist of small rounded pellets up to 2 cm in length, which are occasionally bored and frequently nucleate around crinoids and other shell fragments. Many of the nodules are internal moulds (Antia & Whitaker, 1979) of gastropods, monoplacophorans and hyolithids and appear to have been formed by the early diagenetic phosphate replacement of diagenetic clays (Antia & Whitaker, 1979; Antia, 1979a,b). Most of the nodules are rich in limonite, quartz grains and fish scales, and may have formed by the same processes as modern phosphatic nodules on the continental shelf (see Baturin, 1969, 1970, 1971; Burnett, 1974, 1977).

8. Other clast types

For details of the other clast types present in the bone-bed see Antia & Whitaker (1979).

Facies C

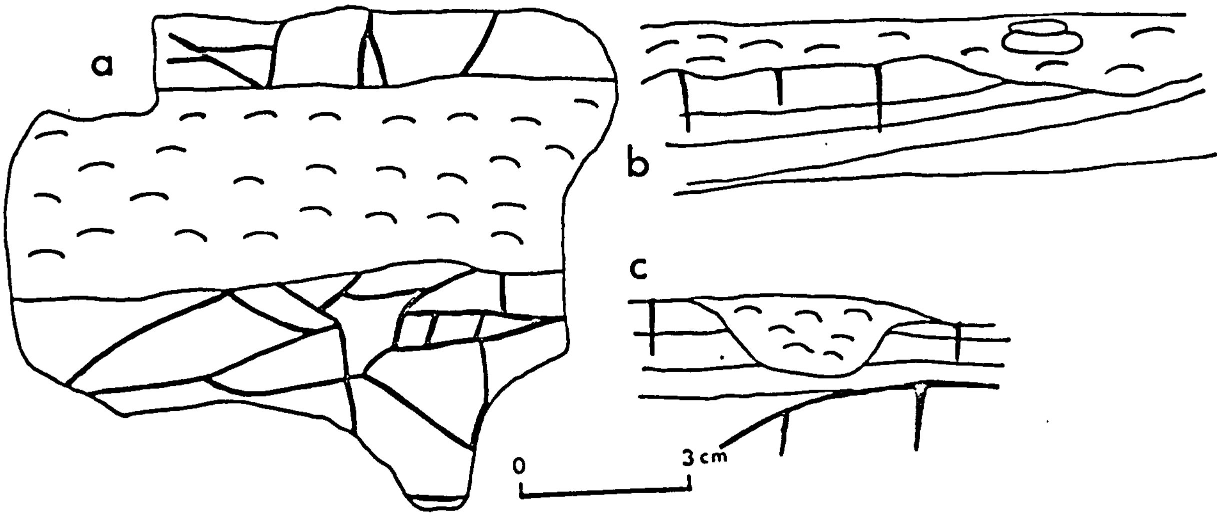
Facies C may be divided into two portions. A lower portion consisting of lenticular bedded mudstones, siltstones and fine sandstones, and an upper portion containing channels and mud-cracks cutting into lenticular and wavey bedded mudstones, silt-stones and sandstones. The transition from the lower to upper portion of the facies is gradual.

At two levels in the section a pale olive green siltstone (0.6 m and 0.3 m above the Ludlow-Downton Boundary) is present. These siltstones are rich in eurypterid segments containing up to 100 segments per metre square bedding plane surface area. The lamination of this siltstone varies from poorly developed wrinkle marks and mini ripple lamination through to crescentic current ripples (wavelength 20 - 30 cm).

The mudstones are commonly rippled and frequently contain streaks on bone sand. Shell debris is fairly common and consists mainly of ostracods (Table 1-3). _In situ_ faunas observed include _Lingula minima_ and _Modiolopsis complanata_. _In situ_ _L. minima_'s are rare occuring in densities of about 1 per 2 m^2 bedding plane surface area. The depth of their burrows from the substrate surface appears to have been in the order of 1.5 to 2 cm. They appear to have preferred the lenticular bedded silts and fine sand environments within this facies. M. complanata occurs in the mudstones as in situ clumps of up to 20 individuals with orientated hinge lines.

In the upper portion of this facies, layers of drifted macerated plant remains are common. These plants belong to Cooksonia sp., Nematophyton, Prototaxites sp. and Pachytheca sp. Most of the sediment in these facies consist of lenticular bedded siltstones and claystones. Locally flat bottomed channels with steep sides (10 - 25 cm deep and 65 - 75 cm wide) are present. Their sediment infill commonly consists of parallel laminated fine siltstones at their base, frequently containing abundant shell and vertebrate debris, which are overlain by cross bedded siltstones and sandstones. This cross lamination consists of both symmetrical and asymmetrical ripple marks and grade upwards into fine siltstones and mudstones.

Allen (1974) compares these channels with the Rinnen of Hantzchel & Reineck (1968). However, they are morphologically similar to the Essex Mud Mound facies described by Davis (1964) and Greensmith & Tucker (1967, 1969, 1975). The channels in the section are separated by 'mounds' some 1 to 6 m apart. The upper surface of these mounds is frequently mudcracked and often contains abundant plant debris. Locally structures similar to gutter casts are present on the mound surfaces. They cut the mudcracks and are infilled with shelly sand (Text-Fig. 11). In the mounds, limonite replaced burrows and trails, limonitised and phosphatised complete internal moulds of Loxonema gregarium and Leodispis barrowsi are present. Mudcracks rarely penetrate to a depth greater than 3 cm and are infilled with fine sand. They have a crack width of between 0.5 and 3 mm. These features



Text-Fig. 11: Mudcracked sediment surface cut by a 'guttercast' infilled with shell debris from the upper part of Facies C:

(a) Plan view showing guttercast cutting through mudcracked sediment.

(b) Longitudinal section along the gutter cast showing that it has an irregular erosive base.

(c) Section normal to the gutter cast axis illustrating its channel-like morphology. Note the presence of a relict mudcracked surface beneath the channel. The mudcracks are all infilled with coarse silt.

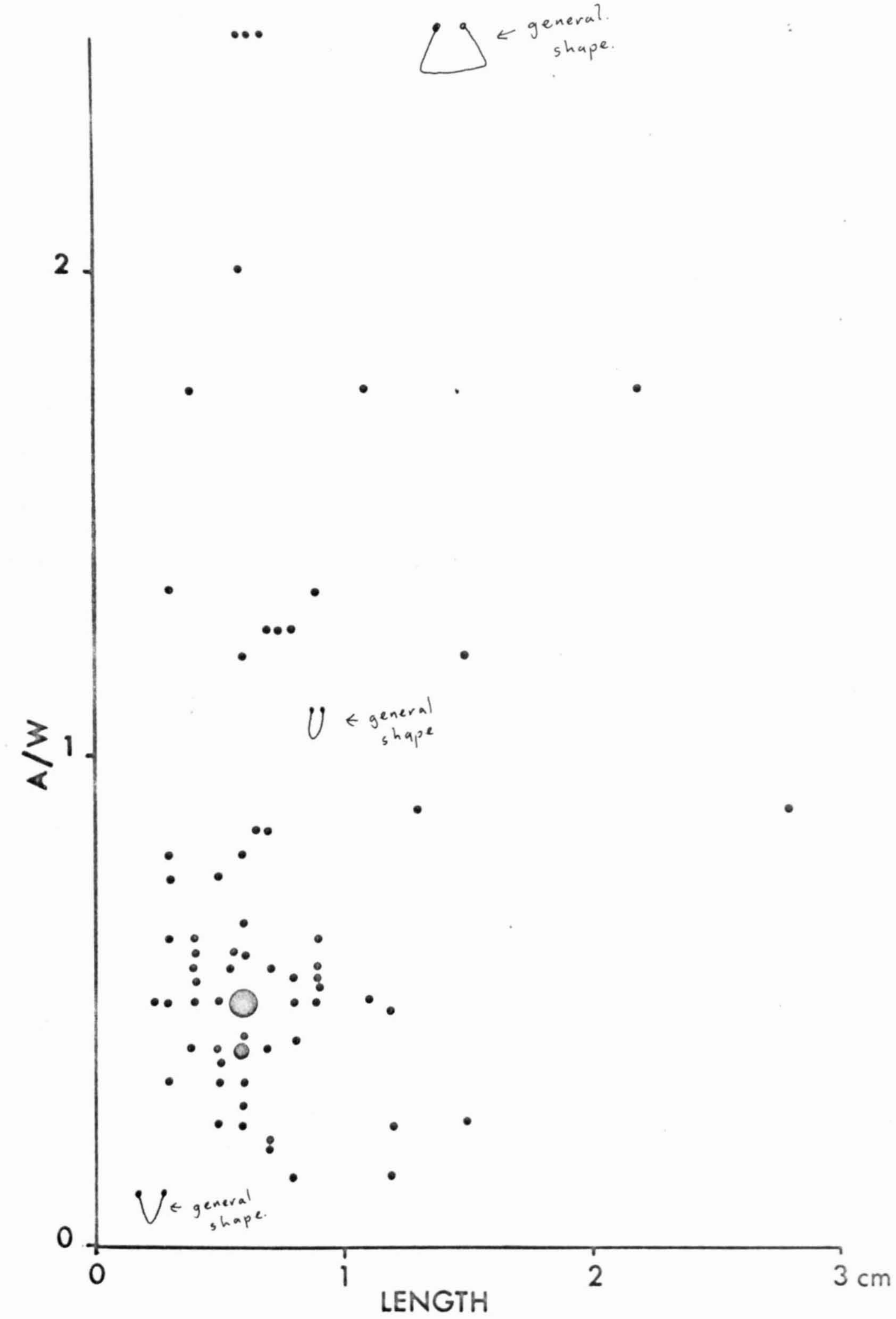
are similar to those present in the Essex Mud Mound topography observed by the author and Greensmith & Tucker (1964, 1976).

The grain size and shape distributions (Text-Fig 3) of the quartz grains indicate an effective settling velocity of between 10 and 15 cm/sec. The calcareous shell fauna of the environment consists of brachiopods, ostracods and molluscs (Table 1-3). Shells of the latter two faunal groups tend to have been replaced during diagenesis by limonite. Some of the ostracod carapaces contain internal moulds of gypsum (e.g. Cytherellina siliqua).

Facies D

The upper 3 m of this section consists of an interbedded sequence of micaceous sandstones and micaceous siltstones. The sandstones occur as trough cross-bedded sand wedges (15 - 35 cm thick), which are locally channelled (Allen, 1974). They merge at their tops into micaceous siltstones containing either well developed parallel lamination or symmetric to asymmetric ripple marks with a wavelength of between 5 and 20 cm. Local erosion surfaces are present at the top and bases of these sand wedges. Allen (1974) has suggested that these sediments may be beach deposits.

Fossils are rare in this facies and occur as fragments of lingulids, ostracods, eurypterids and plants. Locally patches (up to 1 m in diameter) of shell or plant debris are common within the siltstones. Trace fossils belonging to two forms ?Isopodichnus and ?Zoophychus occur infrequently in the siltstones, though locally the latter species occurs in densities which approximate to 800 per m^2 bedding plane surface area. Size and shape measurements for the latter species are given in Text-Fig. 12.



Text-Fig. 12: Plot of ?Zoophychus icho sp. length against posterior width/anterior width. Large circle = 10 observations, median circle=5 observations.

Grain size

Grain size and grain shape are useful parameters which can aid the interpretation of palaeoenvironments. Grain size as measured directly from slides is useless for comparative purposes with maik modern grain size studies because they deal in grain weight or volume. In order to make the slide measurements comparable with modern studies, the mean grain sphericity was calculated for each size frequency unit considered. Where grain sphericity (GS) is calculated as follows

$GS = S/L$

where S = shortest axis of grain

L = longest axis of grain.

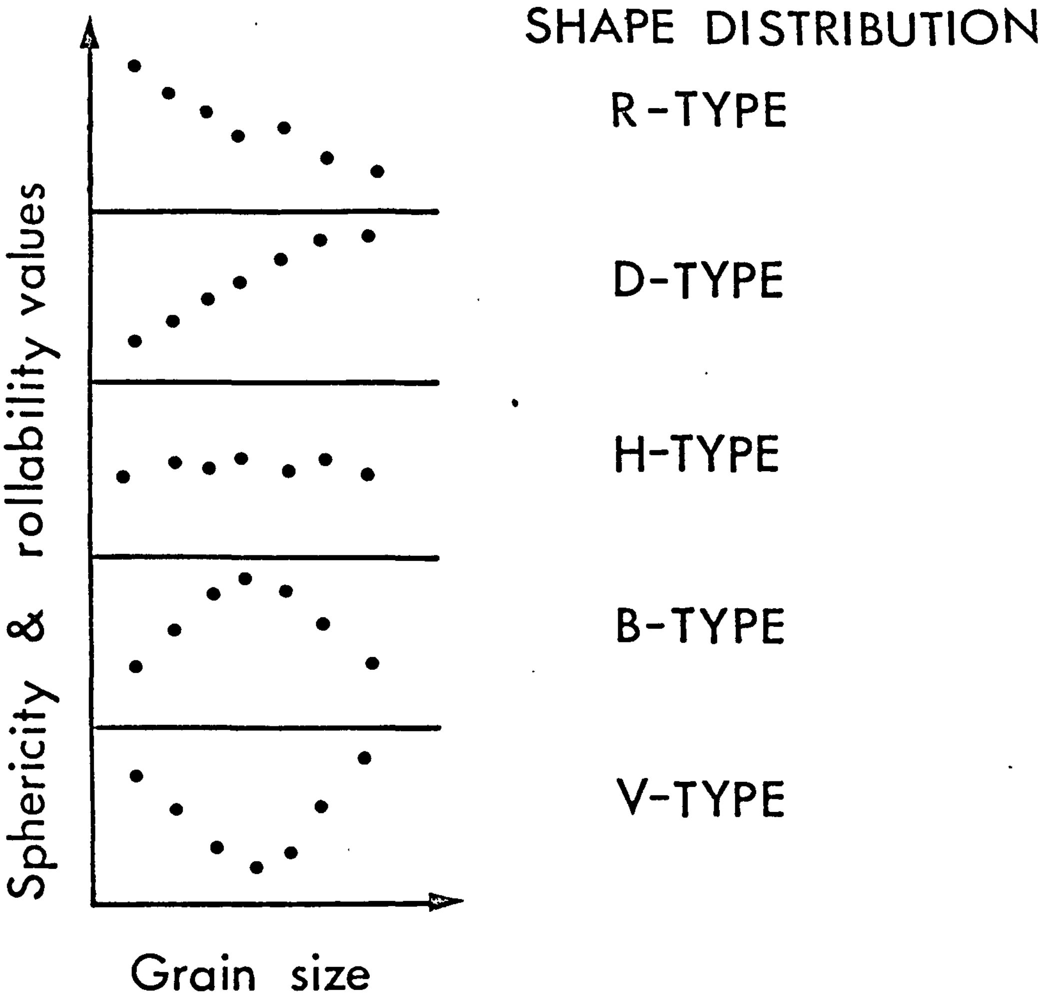
Then for each size interval the mean grain sphericity (MGS) was multiplied by both grain frequency (GF) within the unit and the unit's median size (UMS) to give an effective volumetric frequency (VS).

i.e. $VS = MGS \times UMS \times VS$

The effective volumetric frequencies for each unit were then summed and percentaged.

These percentages are presented in Text-Fig. 3 and may be considered to represent the volumetric distribution of quartz grains of different size frequency elements within the section. The mean grain sphericity and grain sphericity range for each unit is also indicated in Text-Fig. 3.

The latter sphericity points and their variation with grain size within a sample are directly proportional to the equivalent variation in rollability (Winkelmolen, pers. comm. 1979). Consequently a plot of mean sphericity against grain size should (Winkelmolen, pers. comm. 1979) produce similar patterns to a plot of rollability against grain size (Text-Fig.13).



Text-Fig. 13: Shape distribution curves for sphericity and rollability values.

Winkelmolen (1969, p.76-79, 1971, p.708-709) has distinguished five such distribution curves which are illustrated in Text-Fig. 13 and may be interpreted as follows:-

1. R-Type -- These curves are characteristic of accreting environments of diminishing energy conditions. It is most commonly encountered in Dunes, sand/mudflats in tidal regions, beaches and point bar sequences (Winkelmolen, 1969, p.117, 1971, p.709). The beach and sandflat sediments tend to have fairly flat curves, while tidal sediments bordering channels and point bar sediments tend to have steep curves.
2. D-Type -- The D-type curve (Text-Fig. 13) characterises a lag deposit (Winkelmolen, 1971, 709) formed in the tidal channels and in a shallow offshore zone, where sand is gradually moved towards a beach by wave action.
3. H-type -- H-type curves (Text-Fig. 13) indicate that the deposit has been derived from a local source that already contained lag characteristics inherited from earlier depositional events (Winkelmolen, 1969, 79). This type of curve occurs most commonly in offshore sediments (Winkelmolen, 1969, p.117).
4. B-type -- B-type curves (Text-Fig. 13) are most characteristic of river channel deposits (Winkelmolen, 1971, p.709).
5. V-type -- V-type curves (Text-Fig. 13) are indicative of hybrid sediments which arise when there is a difference in strength or duration between alternating tidal currents. Their coarser side is usually a relict lag deposit (Winkelmolen, 1969, p.80, 1971, p.709).

The sphericity distributions in Text-Fig. 3 show R-type curves in slides 1, 2, 9, 6, 12, 14, 15, 16, 17, 18, 19, 20, 21, 24, 25, 27, 28, 29, suggesting that they were deposited in an accreting environment of diminishing energy conditions e.g. a mudflat (cf. Winkelmolen, 1969, 1971). The Ludlow Bone-Bed slide 5 has an H-type curve suggesting that it formed as a lag deposit (cf. Winkelmolen, 1969). H-type or very gently dipping R-type curves are present in the remaining slides. Many of these curves have V-type curves superimposed on an original R-type curve (e.g. slide 4, 6, 7, 15). Such composite curves provide evidence that the Upper Silurian sediments were deposited in a region in which alternating tidal currents varied in strength and duration (cf. Winkelmolen, 1969; 1971).

The gradual dimudation of the slope of the R-type curves from Facies A to Facies D (Text-Fig. 3) supports (cf. Winkelmolen, 1969) the suggestion (Allen, 1979a) that the transition from Facies A-B-C-D represents a regressive intertidal situation in which Facies D may have formed a beach and Facies A an offshore environment.

Palaeoenvironments

The lenticular bedded strata present in Facies A, B and C suggest that they were deposited in a region of tidal flow (cf. Reineck & Singh, 1973). The presence of mud cracks in the upper part of Facies C suggests that it was deposited or formed a temporary erosion surface in the upper part of the intertidal zone (cf. Greensmith & Tucker, 1967; 1976). The sphericity shape curves (Text-Fig. 3) suggest that the sediments were deposited in an accreting environment of diminishing energy conditions e.g. a mudflat.

The distinctive change in mineralogy (Table 6, Text-Fig. 5) at the boundary between Facies A and B is interesting because it implies a geochemical depositional change in the nature of the environment. It suggests that the sediments on the substrate in

Facies A contained oxygenated carbonate rich geochemical micro environments (cf. Krumbein, 1963), while the presence of pyrite framboids (Antia, 1979a) and pyrite deformed spores and acritarchs (Dorning, 1977 personal communication) in Facies B suggests that the depositional subsurface substrates (down to about 40 cm depth below the sediment water interface) in this facies were anoxic and reducing in nature (cf. Berner, 1970; Greensmith & Tucker, 1976). This is in part confirmed by the presence of silicified and phosphatised fungal filaments on the quartz and phosphate grains in this facies (Antia & Whitaker, 1979; Antia, 1979a) because it is unusual for fungi to live on grains buried at a depth of greater than 20 cm below the sediment water interface in an intertidal or a subtidal marine environment (Meadows & Anderson, 1966, 1968). It is probable that the phosphatisation and silicification of the filaments occurred shortly after the deposition of the sediments (Antia & Whitaker, 1979) since studies of marine shelf sediments (e.g. Bates, 1969; Baturin, 1969, 1970, 1971; Berner, 1970; Burnett, 1974, 1977; Elverhøi, 1977; Muller, 1979) have shown that precipitation of pyrite, phosphate and silica can occur within 20 cm of a substrate surface.

Similar silica and phosphate precipitates are absent from Facies C sediments. Quartz grains when present are frequently well rounded and have a frosted exterior showing solution features similar to those present on the rare but well rounded quartz grains of the Bone-Bed facies, perhaps indicating a lateral transport of sediment from a region of Facies C deposition to a region of Facies B deposition. In both Facies C and D authigenic limonite is present. In the former facies authigenic limonite and phosphate nodules are also present indicating reducing conditions of formation (Bray et al., 1968; Greensmith & Tucker, 1976).

The presence of both a geochemical and a sedimentological change at the Facies A - Facies B junction may indicate a major environmental change. Since the overlying Facies C contains mudcracks and Facies B contains intertidal abrasion marks on its quartz grains, it is possible that the bone-bed facies was deposited at a point low in the intertidal zone and that the Facies A - Facies B transition represents an intertidal - subtidal transition.

This interpretation has been confirmed by Richardson & Lister (1969) who recorded a chitinozoan - acritarch flora (indicating marine conditions) from Facies A, and a rare acritarch flora and an abundant spore flora from Facies B and C (indicating intertidal or terrestrial deposition).

Thus the Silurian sea represented by the Ludlovian-Downtonian transition Facies A, B and C may be envisaged as a carbonate rich oxygenated shelf sea containing rippled muds and silts, which merges landward at around the intertidal-subtidal junction into a series of rippled muds and silts containing discontinuous patches (up to 30 m in diameter) of coarse clean vertebrate sand. The remainder of the lower half of the intertidal zone may be envisaged as a series of rippled mud flats merging landwards into a series of runnelled muds (with individual runnels cutting down into previously deposited intertidal mud flat deposits, indicating local changes in the slope of the shoreface from 1 - 2° to 5 - 6° caused by tectonic tilting, sea level oscilations or the effect of a severe storm on the coast line (cf. Greensmith & Tucker, 1967). Since a good mud mound topography is unlikely to be preserved because of its erosive nature, it is probable that the runnel channels observed in the upper part of Facies C constituted the seaward end of a mud mound type complex, where they were more likely to be buried by landward encroachments of the rippled mud facies. The absence of a well developed mud mound topography immediately underlying the beach sands in the section (Facies D interpretation after Allen (1974)), probably results from the temporary nature of a mud mound facies (cf. Greensmith & Tucker, 1975), since it is only developed in order to re-establish a lower angle equilibrium slope on the shoreface. Once this angle has been achieved, the mud mound topography disappears. Such topographies can disappear within 20 years of formation (cf. Davis, 1964; Greensmith & Tucker, 1975).

The uppermost part of the intertidal zone (Facies D) probably consisted of beach sands. Many of the sedimentary structures present in these sands are described and illustrated by Allen (1974). They probably arose from the effect of swash on the beach. The siltstones containing trace fossils may have represented backbeach silt deposition areas. The reoccurrence of both facies types several times may indicate that the encroachment of the land into the sea was both gradual and oscillatory.

Conclusions

This study has examined the sediments (Text-Fig. 2) and faunas (Tables 1-3, 5) of the type section of the Ludlow Bone-Bed and has:-

(1) verified (Elles & Slater's, 1906) observation that the Ludlow Bone-Bed marks the junction between a Ludlovian and a Downtonian fauna. However, some Ludlovian faunal elements (e.g.

Table 7. Mineral abundances across the Ludlow - Downton Boundary at Ludlow.
2a = burrow infill; 5a = -1 - 0 cm below the Ludlow Bone-Bed; 5b = Ludlow Bone-Bed; 5c = 0.2 - 0.5 cm above the Ludlow Bone-Bed. The position of each slide in the section is indicated in Text-Fig. 5. 1 = Clay pellets; 2 = Quartz; 3 = Micrite - calcite; 4 = Shell fragments; 5 = Muscovite; 6 = Opaques; 7 = Biotite; 8 = Fish debris; 9 = Phosphatic nodules; 10 = glauconite; 11 = Zircon; 12 = Clays; 13 = Labradorite. A = Leucoxene; B = Haematite; C = Magnetite; D = Pyrite; E = Carbonaceous debris; F = Limonite.

Slide	MINERALS													OPAQUES					
No.	1	2	3	4	5	6	7	8	9	10	11	12	13	A	B	C	D	E	F
1	2.2	78.6	16.8	0.3	0.9	0.3	0.3	-	-	-	-	-	-	42.0	56.0	2.0	-	-	-
2	-	60.2	32.7	-	5.32	1.7	-	-	-	-	-	-	-	71.2	27.1	1.6	-	-	-
2a	-	80.7	-	-	13.4	5.7	-	-	-	-	-	-	-	10.0	-	-	-	-	-
3	-	56.6	37.5	0.3	1.4	1.8	-	-	-	-	-	-	-	94.2	5.7	-	-	-	-
4	-	37.0	50.7	0.5	3.0	8.6	-	-	-	-	-	-	-	55.7	10.7	-	3.5	-	-
5a	-	59.6	28.0	-	3.0	8.6	-	-	-	0.5	0.5	-	-	83.0	-	-	-	6.4	-
5b	-	-	19.7	-	-	-	-	77.9	4.6	-	-	-	-	-	-	-	-	-	-
5c	-	34.1	23.5	-	3.5	4.7	-	34.1	-	-	-	-	-	94.1	-	-	-	5.9	-
6	-	40.0	-	-	7.9	26.9	-	-	-	-	-	25.1	-	61.6	2.5	-	-	7.8	28.2
7	-	59.5	-	-	5.5	3.9	-	0.2	-	-	-	30.5	-	39.4	9.8	-	-	1.4	49.2
8	-	63.3	-	-	4.7	3.1	-	-	-	-	-	28.6	-	5.3	1.7	-	-	4.0	88.9
9	-	65.3	-	-	1.0	0.7	0.3	-	-	-	-	32.1	-	58.1	6.4	-	-	12.9	22.5
10	-	70.8	-	0.5	3.0	1.5	-	0.5	-	-	-	23.4	-	71.1	4.4	-	-	-	24.4
11	-	69.3	-	-	4.5	3.0	-	1.0	-	-	-	22.1	-	91.3	-	-	-	1.0	7.6
12	-	67.5	-	-	-	0.7	-	-	-	-	-	31.7	-	88.8	1.1	-	-	-	-
13	-	44.6	-	-	1.8	7.5	-	0.6	-	-	-	45.2	-	54.8	1.6	-	-	1.6	41.9
14	-	64.4	-	-	3.1	8.1	-	-	-	-	-	24.3	-	48.9	3.0	-	-	-	47.9
15	-	69.5	-	0.9	0.6	3.0	-	0.6	-	-	-	25.2	-	52.8	-	-	-	3.7	43.4
16	-	69.3	-	0.5	0.5	0.5	-	-	-	-	-	29.1	-	77.9	-	-	-	-	22.7
17	-	76.6	-	-	4.2	1.2	-	-	-	-	-	17.8	-	41.5	3.8	-	-	-	28.5
18	-	47.5	-	0.3	2.4	4.0	-	-	-	-	-	45.6	-	17.6	20.5	-	-	-	61.8
19	-	76.3	-	-	0.9	1.9	-	0.9	-	-	-	19.2	-	65.2	3.0	-	-	-	31.8
20	-	66.8	-	1.0	0.3	1.6	-	0.6	-	-	-	29.5	-	52.5	9.3	-	-	-	38.1
21	-	72.3	-	-	-	1.6	-	0.5	-	-	-	25.4	-	51.8	3.9	-	-	21.7	22.8
22	-	57.9	-	-	1.1	4.5	-	-	-	-	-	38.6	-	10.8	-	-	-	1.2	86.6
23	-	60.9	-	1.4	2.5	1.4	-	-	-	-	-	19.2	-	65.7	2.7	-	-	-	31.5
24	-	73.2	-	-	1.3	0.9	-	0.3	-	-	-	24.1	-	19.3	11.2	1.6	-	6.4	61.2
25	-	78.5	-	-	1.4	0.9	-	-	-	-	-	19.0	-	26.9	9.9	11.3	-	-	51.7
26	-	76.1	-	-	0.2	0.8	-	-	-	-	-	22.7	-	35.5	-	5.7	-	-	55.6
27	-	75.8	-	0.9	1.4	1.9	-	0.7	-	-	-	19.3	0.5	53.4	7.7	1.7	-	-	37.0
28	-	52.6	-	-	4.8	3.8	-	-	-	-	-	38.6	-	58.6	0.4	10.2	-	-	31.1
29	-	61.2	-	14.4	1.6	0.7	-	0.7	-	-	-	21.4	-	32.7	11.8	-	-	-	34.4

Protochonetes ludloviensis) have been shown (Table 3) to continue into the Downtonian;

(2) shown that Ludlow-Downton Boundary marks a mineralogical change carbonate/micrite rich sediments to limonite/clay-rich sediments (Text-Fig. 5, Table 7);

(3) shown that grain size modal peaks throughout the section are in the order of 40 - 80 μm (Text-Fig. 3);

(4) suggested that the grain sphericity curves for the section (Text-Fig. 3) indicate that its sediments were deposited in an accreting environment of diminishing energy conditions, in which alternating tidal currents varied in strength and duration. In some layers (e.g. the Ludlow Bone-Bed) the sphericity curves indicate that sediment was deposited as a lag concentrate;

(5) confirmed Allen's (1974) suggestion that the section can be divided into four sedimentary/environmental facies. The environmental interpretations of each facies may be summarised as follows:-

(a) Facies A - subtidal shallow carbonate mud environment

(b) Facies B - low intertidal/very shallow subtidal mud/silt flat environment containing vertebrate debris sand patches

(c) Facies C - intertidal mudflat deposits

(d) Facies D - high intertidal silt or beach deposits

(6) shown that most of the quartz grains in the section were deposited out of suspension (Text-Fig. 7);

(7) shown that both sediment type and the composition of invertebrate faunas in Facies A are variable along a bedding plane (Text-Fig. 6);

(8) noted that the Ludlow Bone-Bed appears to rest conformably on the underlying Whitcliffe Beds (Text-Fig. 4); and

(9) provided size measurements for three trace fossil species.

The faunal and sedimentary data presented here appears to support the suggestion that the Ludlow Bone-Bed formed as a lag concentrate during a marine regression in a tidal environment. However, it may have been deposited in the littoral or sub-littoral zone.

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References

AEPLER, R. 1974. Der Rhätsandstein von Tübingen-ein Kondensiertes Delta. N. Jb. Geol. Paläont. Abh., vol. 142, pp.113-162.

AEPLER, R. & REIF, W.-E. 1971. Origin of Bone Beds. Abstr. VIII. Internat. Sedimentol. Congr. Heidelberg. p.1.

ALLEN, J. R. L. 1962. Discussion. Q. Jl Geol. Soc. Lond., vol. 118, p.349.

ALLEN, J. R. L. 1974. Sedimentology of the Old Red Sandstone (Siluro-Devonian) in the Clee Hills Area, Shropshire, England. Sediment. Geol., vol.13, pp.73-167.

ALLEN, J. R. L. & TARLO, L. B. 1963. The Downtonian and Dittonian facies of the Welsh Borderland. Geol. Mag., vol. 100, pp.129-155.

ANTIA, D. D. J. 1977. A comparison of diversity and trophic nuclei of live and dead molluscan faunas from the Essex Chenier Plain, England. Paleobiology, vol. 3, pp.404-414.

ANTIA, D. D. J. 1979a. Bone-Beds: A review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering and microbiotac. Mercian Geol. vol. 7, pp.93-174.

ANTIA, D. D. J. 1979b. Authigenic gypsum in marine sediments - a comment. Marine Geol., vol.31, pp.M1-M4.

ANTIA, D. D. J. & WHITAKER, J. H. McD. 1979. A scanning electron microscope study of the genesis of the Upper Silurian Ludlow Bone-Bed. In. W. B. Whalley (ed.) Scanning Electron Microscopy in the study of sediments, pp.119-136.

ARKELL, W. J. 1933. The Jurassic system in Great Britain. Clarendon Press, Oxford, 681pp.

BATHURST, R. G. C. 1975. Carbonate sediments and their diagenesis. Elsievier, 2nd ed., 658pp.

BATURIN, G. N. 1969. Authigenic phosphate concretions in recent sediments of the South West African Shelf. Doklady Earth Sci. Sections, vol.189, pp.227-230.

BATURIN, G. N. 1970. Recent authigenic phosphorite formation on the South West African Shelf. Inst. Geol. Sci. U.K., Rept. No. 70/13, pp.87-97.

BATURIN, G. N. 1971. Stages of phosphorite formation on the seafloor. Nat. Phys. Sci., vol.232, pp.61-62.

BEHRENSMEYER, A. K. 1978. Taphonomic and ecological information from bone weathering. Paleobiology, vol. 4, pp.150-162.

BERNER, R. A. 1970. Sedimentary pyrite formation. Am. Jl Sci., vol. 268, pp.1-23.

BLATT, H., MIDDLETON, G. & MURRAY, R. 1972. Origin of sedimentary rocks. Prentice Hall, New Jersey, 634pp.

BURNETT, W. C. 1977. Geochemistry and origin of phosphorite deposits from off Peru and Chile. Bull. Geol. Soc. Am., vol. 88, pp.813-823.

CALEF, C. E. & HANCOCK, N. J. 1974. Wenlock and Ludlow Marine communities in Wales and the Welsh Borderlands. Palaeontology, vol. 17, pp.779-810.

DAVIS, D. S. 1964. The physical and biological features of the Mersea Flats. Central Electricity Res. Lab. Note. No. RD/L/NI31/164, 14pp.

DENNISON, R. H. 1956. A review of the habitat of the earliest vertebrates. Fieldiana Geol., vol.11, pp.354-457.

DONOVAN, D. T. 1955. Mesozoic. In MacInnes, C. M. & Whittard, W. F. (eds) Bristol and its adjoining countries. Brit. Ass. Adv. Sci., pp.23-28.

DUFFIN, C. J. & GAZDZICKI, A. 1977. Rhaetian fish remains from the Tatra Mountains. Acta Geologica Polonica, vol.27, pp.333-348.

EARP, J. R. 1938. The higher Silurian rocks of the Kerry District, Montgomeryshire. Q. Jl Geol. Soc. Lond., vol.94, pp.125-157.

ELLES, G. L. & SLATER, I. L. 1906. The highest Silurian rocks of the Ludlow District. Q. Jl Geol. Soc. Lond., vol.62, pp.195-220.

ELVERHØI, A. 1977. Origin of framboidal pyrite in clayey Holocene sediments and in Jurassic black shale in the North Western part of the Barents Sea. Sedimentology, vol. 24, pp.591-595.

FREY, W. R., VOORHIES, M. R. & HOWARD, J. D. 1975. Estuaries of the Georgia Coast, U.S.A. Sedimentology and Biology VIII. Fossil and recent skeletal remains in Georgia estuaries. Senckenbergania Marit., vol.7, pp.257-295.

FÜRSICH, F. T. & HURST, J. M. 1974. Environmental factors determining the distribution of Brachiopods. Palaeontology, vol.17, pp.879-900.

FUTTERER, E. 1978a. Untersuchungen über die sink und Transport geschwindigkeit biogener Hartfeile. N. Jb. Geol. Paläont. Abh., vol.155, pp.318-359.

FUTTERER, E. 1978b. Studien über die Einregelung, Anlagerung und Einbettung biogener Hartfeile im Strömungskanal. N. Jb. Geol. Paläont., vol.156, pp.87-131.

FUTTERER, E. 1978c. Hydrodynamic behaviour of biogenic particles. N. Jb. Geol. Paläont. Abh., vol.157, pp.37-42.

GREENSMITH, J. T. & TUCKER, E. V. 1967. Morphology and evolution of inshore shell ridges and mudmounds on modern intertidal flats, near Bradwell, Essex. Proc. Geol. Ass., vol.77, pp.329-346.

GREENSMITH, J. T. & TUCKER, E. V. 1975. Dynamic structures in the Holocene Chenier Plain setting of Essex, England. In Hails, J. & Carr, A. (eds) Nearshore sediment, dynamics and sedimentation, pp.251-272.

GREENSMITH, J. T. & TUCKER, E. V. 1976. Major Flandrian transgressive cycles, sedimentation and palaeogeography in the coastal zone of Essex, England. Geol. Mijnbouw, vol.55, pp.131-141.

GRUBERT, B. 1971. Zur Eignung von Foraminiferen als Indikatoren für Sandwanderung. Dt. Hydrogr. Z., vol.24, pp.1-14.

HÄNTZCHEL, W. & REINECK, H. E. 1968. Fazies - Untersuchungen im Hettangium von Helmstadt (Niedersachsen). Mitt. Geol. St. Inst. Hamb., vol.37, pp.5-39.

HARLEY, J. 1861. The Ludlow Bone-Bed and its crustacean remains. Q. Jl Geol. Soc. Lond., vol.17, pp.542-552.

HOBSON, J. S. C. 1960. The sedimentary petrology of the Downton Castle Sandstone Formation in Wales and the Welsh Borderlands. Ph.D. thesis, University of Birmingham.

HOLLAND, C. H., LAWSON, J. D. & WALMSLEY, V G ~~V. S.~~ 1963. The Silurian rocks of the Ludlow District, Shropshire. *Bull. Brit. Mus. (Nat. Hist.)*, vol.8, pp.93-172.

JUKES-BROWNE, A. J. 1892. *The building of the British Isles*. Geo. Bell & Sons, London, 465pp.

KENDAL, P. F. & WROOT, H. E. 1924. *Geology of Yorkshire*. An illustration of the evolution of Northern England. Hollinck Bros., Vienna, 995pp.

KING, W. W. 1934. The Downtonian and Dittonian Strata of Great Britain and North-Western Europe. *Q. Jl Geol. Soc. Lond.*, vol.90,pp.526-566.

KING, W. W. & LEWIS, W. J. 1912. The uppermost Silurian and Old Red Sandstone of South Staffordshire. *Geol. Mag.*, vol.49, pp.437-443, 484-491.

KOMAR, P. D. 1978. Relative quantities of suspension versus bed-load transport on beaches. *J. Sediment.*, vol.48, pp.921-932.

LAWSON, J. D. 1955. The Geology of the May Hill Inlier. *Q. Jl Geol. Soc. Lond.*, vol.111,pp.85-119.

LINGWOOD, P. F. 1976. *The biostratinomy of some recent Molluscan communities in Liverpool Bay*. Ph.D. thesis, Liverpool University.

McFARLANE, J. M. 1923. *The evolution and distribution of fish*. New York, 564pp.

McKERROW, W. S. 1979. Ordovician and Silurian changes in sea level. *Jl. Geol. Soc. Lond.*, vol.136,pp.137-145.

MAIKLEM, W. R. 1968. Some hydraulic properties of bioclastic carbonate grains. *Sedimentology*, vol.10, pp.101-109.

MAISEY, J. G. 1978. Preservation and prefossilisation of fossil fin spines. *N. Jb. Geol. Palaont. Mh.* (10), pp.595-599.

MEADOWS, P. S. & ANDERSON, J. G. 1966. Micro-organisms attached to marine and fresh-water sand grains. Nature, vol.212, pp.1059-1060.

MEADOWS, P. S. & ANDERSON, J. G. 1968. Micro-organisms attached to marine sand grains. Jl Mar. Biol. Ass. U.K., vol.48, pp.161-175.

MÜLLER, K. J. 1979. Phosphatocopine ostracodes with preserved appendages from the Upper Cambrian of Sweden. Lethaia, vol.12, pp.1-28.

MURCHISON, R. I. 1837. On the fishes of the Ludlow Rocks on Upper Ludlow Beds of the Silurian System. Rep. Brit. Ass. for 1837 Transactions of the sections, p.91.

MURCHISON, R. I. 1839. The Silurian System. J. Murray, London.

MURCHISON, R. I. 1859. Siluria. J. Murray, London.

NEWBERRY, J. S. 1889. The Paleozoic fishes of North America. U.S. Geol. Surv. Mon., vol.16, pp.1-340.

ORTON, E. 1878. The geology of Franklin County. Geol. Surv. Ohio, vol.3,pp.596-646.

PASSEGA, R. 1964. Grain size representation by CM patterns as a geological tool. Jl Sed. Pet., vol.34, pp.830-897.

PASSEGA, R. 1977. Significance of CM diagrams of sediments deposited by suspension. Sedimentology, vol.24, pp.723-733.

PHILLIPS, J. 1848. The Malvern Hills compared with the Palaeozoic districts of Abberlay, Woolhope, May Hill, Tortworth and Usk. Mem. geol. Surv. U.K., vol.2 (1).

REID, C. 1890. The Pliocene deposits of Britain. Mem. Geol. Surv. U.K., H.M.S.O., London, 326pp.

REIF, W.-E. 1969. Bonebeds an der Muschelkalk - Keuper - Grenze in Ostwürttemberg. Dip. Arbeit, Tübingen University. 123pp.

REIF, W.-E. 1971. Zur genese der Muschelkalk - Keuper - Grenz-bonebeds. N. Jb. Geol. Palaont. Abh., vol.139, pp.369-404.

REIF, W.-E. 1974. Profile des Muschelkalk - Keuper - Grenzbereichs im Jagsttal (Trias., Baden-Wurttemburg). Oberrhein. Geol. Abh., vol.23, pp.43-54.

REIF, W.-E. 1976. Sedimentologie und Genese von Bonebeds. Zbl. Geol. Paläont., Part 2., H5/6, pp.252-255.

REINECK, H. E. & SINGH, I. B. 1973. Depositional sedimentary environments. Springer Verlag, New York, 439pp.

RICHARDSON, J. B. & LISTER, T. R. 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and South Wales. Palaeontology, vol.12, pp.261-280.

RICHARDSON, L. 1901. Mesozoic geography of the Mendip Archipelago. Proc. Cotteswold Nat. Fld Club, vol.14, pp.59-69.

RICHARDSON, L. 1911. On the Rhaetic and contiguous deposits of West, Mid and East Somerset. Q. Jl geol. Soc. Lond., vol.67, pp.1-72.

ROMER, A. S. 1955. Fish origins - fresh or salt water? Suppl. to Deep Sea Res., vol. 3, pp.261-280.

SCOTT, R. W. 1978. Approaches to trophic analysis of paleo-communities. Lethaia, vol.11, pp.1-14.

SHORT, A. R. 1904. On some Rhaetic sections in the Bristol district with consideration on the mode of deposition of the Rhaetic Series. Q. Jl geol. Soc. Lond., vol.60, pp.170-193.

SQUIRREL, H. C. 1958. New occurrences of fish remains in the Silurian of the Welsh Borderlands. Geol. Mag., vol.95, pp.328-333.

STAMP, L. D. 1920. Note on the determination of the limit between the Silurian and Devonian Systems. Geol. Mag., vol.57, pp.164-171.

STAMP, L. D. 1923. The base of the Devonian with special reference to the Welsh Borderland. Geol. Mag., vol.60, pp.276-282, 331-336, 367-372, 385-410.

SYKES, J. H. 1977. British Rhaetian Bone-Beds. Mercian Geol., vol.5, pp.39-48.

TUCKER, E. V. 1960. Ludlovian biotite bearing bands. Geol. Mag., vol.97, pp.245-249.

WAGNER, G. 1913. Beitrag zur stratigraphie u. Bildungsgeschichte des oberen Hauptmuschelkalkes u. d. unt. Lettenkohle in Franhken. Geol. u. Palaont. Abh., N.F., 12.

WALMSLEY, U. G. 1959. The geology of the Usk inlier (Monmouthshire). Q. Jl geol. Soc. Lond., vol.114, pp.483-516.

WELLS, J. W. 1944. Middle Devonian bonebeds of Ohio. Bull. Geol. Soc. Am., vol.55, pp.273-302.

WHITAKER, J. H. McD. 1962. The geology of the area around Leintwardine Herefordshire. Q. Jl geol. Soc. Lond., vol.114, pp.319-342.

WHITE, E. I. 1950. The vertebrate faunas of the Lower Old Red Sandstone of the Welsh Borders. Bull. Brit. Mus. (Nat. Hist.) Geol., vol.1, pp.51-67.

WICKES, W. H. 1904. Rhaetic bonebeds. Proc. Bristol Nat. Soc., vol.2, pp.213-225.

WINKELMOLEN, A. M. 1969. Experimental rollability and natural shape sorting of sand. Thesis, Groningen, Holland, 141pp.

WINKELMOLEN, A. M. 1971. Rollability, a functional shape property of sand grains. Jl Sed. Pet., vol.41, pp.703-714.

ADDITIONAL REFERENCES

GROSS,W. 1967. Uber Thelodontier - Schuppen.Palaeontographica, vol.127A,pp.1 -67.

GROSS,W. 1971. Downtonische and Dittonische Acanthodier - reste des Osteegebietes.Palaeontographica,vol.136A,pp.1 - 82.

TURNER,1973. Siluro - Devonian Thelodonts from the Welsh Border lands. Jl. geol.Soc. Lond.,vol. 129,pp. 557 - 584.

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COMMENTS ON THE ENVIRONMENTS AND FAUNAS ACROSS THE LUDLOVIAN-DOWNTONIAN BOUNDARY (UPPER SILURIAN) AT SIEFTON, SALOP

by

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Abstract

A new temporary section across the Ludlovian-Downtonian boundary (Upper Silurian) at Siefton (Nr Craven Arms), Salop, England, is described. The sediments present in the section were deposited in both intertidal and subtidal marine environments. The shelly faunas across the section are recorded and considered to be transported assemblages. Both burrowing and boring trace fossils occur in the presumed subtidal environments. Evidence for a late Whitcliffian marine transgression, following a marine regression is presented.

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During August 1977 a temporary roadside trench produced in the course of extensive road repairs at Siefton (British National Grid Reference SO 475833 - 478835) exposed the Ludlow-Downton boundary (Upper Silurian). The faunas and sediments present in the trench section were recorded and are described here in Tables 1 and Fig. 1. The section observed contained a vertical thickness of 6.14 m of sediment (Fig. 1) and extends from the Upper Whitcliffe Beds (Upper Ludlovian) into the Downton Castle Formation (basal Downtonian),

The first appearance of the ostracod Frostiella groenvalliana is taken to indicate the base of the Downtonian in the section (cf. Martinsson, 1967; Shaw, 1969). This species makes its first appearance in the section about 1.4 m below its top and indicates that the Ludlovian-Downtonian boundary occurs at this point in the section. The fauna (Table 1) above the boundary is of typical Downtonian aspect (cf. Elles & Slater, 1906), while the fauna (Table 1) below contains some species (e.g. Lingula minima and Londinia kiesowi) which are commonly found in the Downtonian (see Elles & Slater, 1906; Shaw, 1969), as well as typical Whitcliffian forms (cf. Holland, Lawson & Walmsley, 1963).

The sediments recorded in this section (Fig. 1) can be assigned to four facies.

Facies A - Lenticular bedded silts and clays (sensu Reineck & Singh, 1973), containing well sorted shell sheets composed almost entirely of a single species. For example one shell sheet contained Pteronitella retroflexa shells covering about 80% of the substrate. These shells had a leptokurtosic size distribution (Fig. 2a). Some wavey bedding (sensu Reineck & Singh, 1973) is also present in the facies. The lenticular bedded nature of the sediments indicates that they were deposited in a tidally influenced environment (Reineck & Singh, 1973, p.101) in which periods of

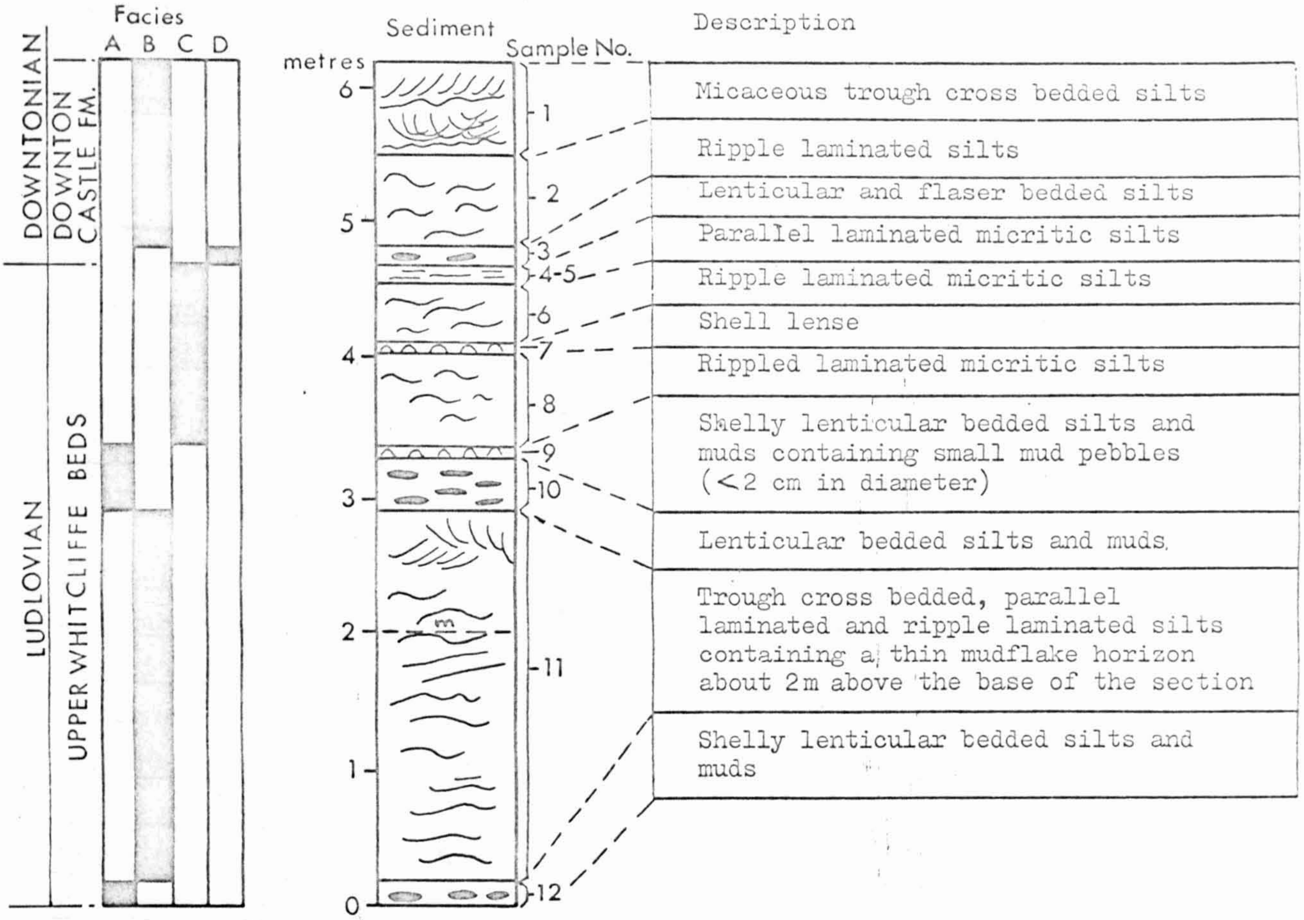


Figure Captions

Fig. 1. Distribution of sediments and facies across the Ludlovian/ Downtonian boundary at Siefton. Sample Nos. refer to the faunal collections in Table 2. An explanation of the facies is given in the text.

Table 1. Fossils across the Ludlow/Downton boundary at Siefton. Numbers indicate the frequency of occurrence of shells and shell fragments. See Fig. 1 for the position of each layer in the section.

SPECIES	DOWNTON				LUDLOW SERIES							
					LAYER							
	1	2	3	4	5	6	7	8	9	10	11	12
Brachiopods												
Craniops implicata (J.de.C Sowerby)	–	–	–	–	–	–	2	–	–	–	–	2
Howellella elegans (Muir-Wood)	–	–	–	–	–	–	4	–	2	–	–	44
Lingula sp.	–	–	–	–	–	–	–	–	–	1	–	–
Lingula minima (J.de C. Sowerby)	82	119	112	–	–	–	–	–	–	–	11	–
Microsphaeridiorhynchus nucula (J. de C.Sowerby)	–	–	–	–	1	2	27	–	13	35	–	18
Orbiculoidea rugata (J. de C. Sowerby)	–	–	1	–	–	–	–	–	–	–	–	1
Protochonetes ludloviensis (Muir-Wood)	–	–	–	–	36	–	305	–	159	303	–	3
Salopina lunata (J. de C. Sowerby)	–	–	–	–	3	–	38	–	24	64	–	36
Bivalves												
Goniophora cymbaeformis (J. de C. Sowerby)	–	–	–	–	–	–	–	–	2	–	–	–
Modiolopsis complanata	2	–	2	–	1	–	–	–	–	–	–	–
Pteronitella retroflexa (Wahlenberg)	–	–	–	–	–	–	–	–	–	1	–	29
Fuchsella amygdalina (J. de C. Sowerby)	–	–	–	–	–	–	–	–	–	9	–	4
Solenomya sp.	–	–	–	–	–	–	–	–	–	–	4	–
Gastropods												
Loxonema gregarium (J. de C. Sowerby)	1	–	–	–	–	2	–	–	–	–	–	–
?*Umbospira helicites* (J. de C. Sowerby)	–	–	1	–	–	–	–	–	–	–	–	–
Cephalopods												
Leurocycloceras sp.	–	–	–	–	–	–	–	–	–	–	–	2
Eurypterids												
Hughmilleria sp. (?)	–	–	–	–	–	–	–	–	–	–	1	–
Pterygotus sp.	–	3	12	–	–	–	–	–	–	–	1	–
Ostracods												
Calcaribeyrichia torosa (Jones)	1	–	–	–	–	–	–	–	–	–	–	–
Cytherellina siliqua (Jones)	1	1	3	–	–	–	–	–	–	–	–	–
Nyhamnella naturalis (Sarv)	–	–	1	–	–	–	–	–	–	–	–	–
Londinia kiesowi (Krause	–	–	9	–	–	–	–	–	–	–	1	–
Frostiella groenvalliana Martinsson	7	–	18	–	–	–	–	–	–	–	–	–
Cavellina sp.	1	–	–	–	–	–	–	–	–	–	–	–
Bryozoans												
Leioclema sp. (colonies)	–	–	–	–	–	–	–	–	–	1	–	–
(zooecia)	–	–	–	–	–	–	–	–	–	362	–	–

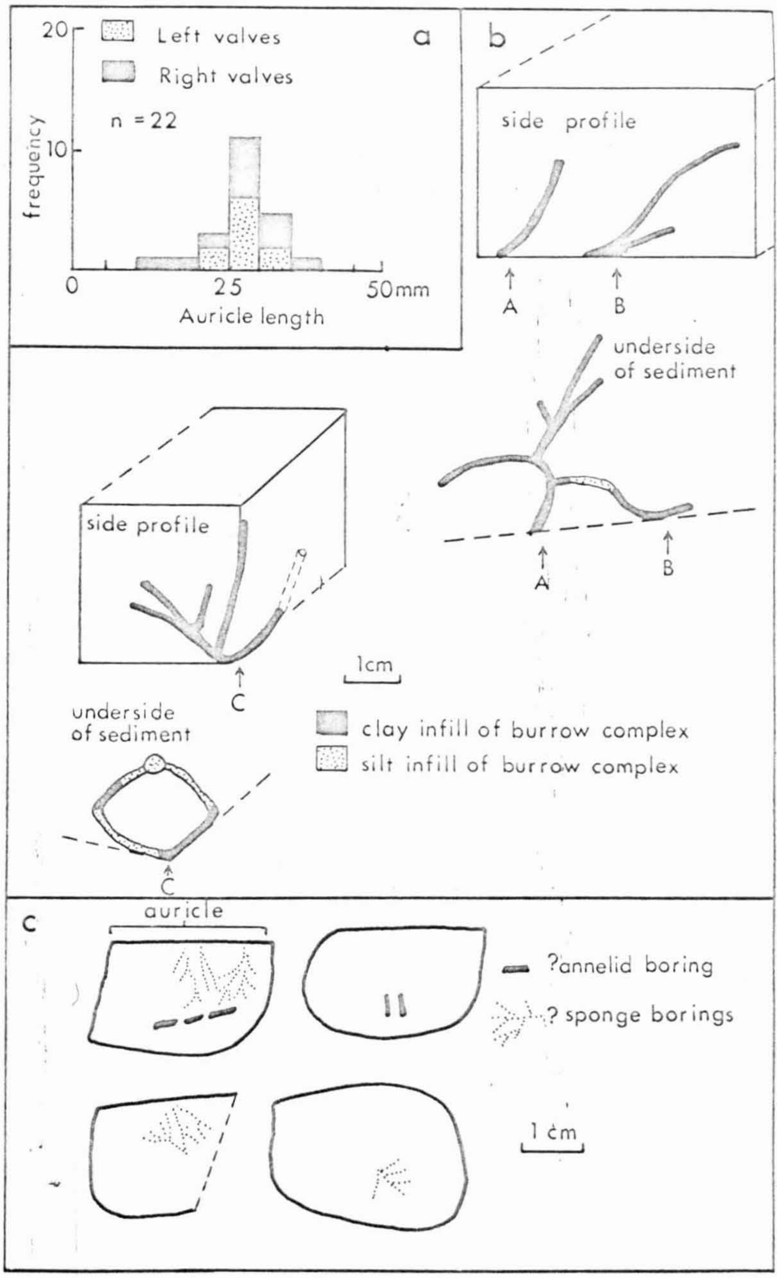
Table 1 (continued)

SPECIES	LAYER											
	1	2	3	4	5	6	7	8	9	10	11	12
Plants												
Gloeotrichia sphaerica (Hooker)	1	5	1	-	-	-	-	-	-	-	-	-
Vertebrates												
Logania ludlowiensis Gross	5	-	5	-	-	-	-	-	-	-	-	-
Thelodus parvidens Ag.	277	8	297	-	-	-	-	-	-	-	-	-
'Onchus' tenuistriatus Ag.	3	-	-	-	-	-	-	-	-	-	-	-
Total fauna counted	381	136	482	-	41	4	376	-	200	775	18	139
Bedding plane surface area examined (m^2)	0.2	0.3	0.1	2	0.5	3	0.03	6	0.07	0.09	7	0.15

tidal currents alternated with periods of quiescent or slack water. The climbing ripple lamination effect produced by the lenticular bedding, contains in-drift ripple laminae (sensu Mckee, 1965) in which the ripple stoss side is absent and its lee side is preserved, suggesting that the suspension load / bed load ratio was low (cf. Jopling & Walker, 1968). The ripple trough/ crest axes were striking at angles of between 200° and 245°. Local erosion surfaces are common and these are frequently densely strewn with concave down orientated shells. The shell cover of the substrate on these layers varies from 65 to 90%.

Frequently the original structure of the sediment has been destroyed by bioturbation. The most abundant trace fossil types can be referred to the ichnogenera ?Chondrites, ?Dendrotichium and ?Lophoctenium. However a number of burrows (Fig. 2b,a) not unlike the three dimensional burrows produced by modern annelids (cf. Ronan, 1977), are present in the facies. These burrows (Fig. 2b,ia) have a burrow diameter of between 1 and 2 mm, a burrow height of between 15 and 30 mm, a burrow complex width of between 10 and 25 mm, a burrow complex length of between 20 and 35 mm and between 4 and 10 terminal shafts. These burrows were probably produced by a deposit feeding 'polychaete worm', 2 to 5 cm in length (M. Pye, personal communication, 1979). It may be that many of the traces doubtfully assigned here to the ichnogenera Lophoctenium, Chondrites and Dendrotichium were formed by these 'polychaetes' during their reworking (for food) of the uppermost 5 - 10 cm of the contemporary sediment substrate. These polychaete burrow complexes occur in densities of between 200 and 350 per metre square of bedding plane surface area.

The high density of the 'polychaete' burrows and the highly bioturbated nature of the sediment, locally destroying all its internal structure indicates (Reineck, 1967) that the sedimentation rate was normally slow and



The ? sponge borings branching pattern is very similar to that of contemporary bryozoans and it is possible that these borings were produced by a bryozoan
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Fig. 2. (a) Size distribution of *Pteronitella retroflexa* on the surface of a shell sheet. Their Left valve/ right valve ratio is 0.76. (b) Side and basal profiles of two complex burrow systems from facies A. (c) Traces of four shells of *P.retroflexa* showing the two types of shell boring. About 65% of the shells had ?sponge borings and 45% had ?annelid borings. All specimens illustrated in this figure are from facies A, layer 12 of the section (see Table 1) and have been deposited in Ludlow Museum.

that little contemporary erosion ocurred. However, both the shell sheets and lenticular bedding indicates that the environment represented by this facies was affected by turbulent conditions. (Reineck & Singh, 1973.) This apparent paradox can be resolved if the sediments were deposited in a subtidal region of slack water currents in which silt lenticles were periodically deposited as a result of unusually strong tides (e.g. spring tides), locally giving the sediment a lenticular bedded appearance. The deposition of the shell sheets could have resulted from either tidal current or storm activities.

Many of the shells in this facies are bored. At the present time two boring types have been recognised. The first consists of discontinuous grooves 2 - 4 mm in length, 0.2 - 0.5 mm in depth and 0.5 - 1 mm in width. These are considered by Ben Akpan (personal communication, 1979) to have been formed by a boring annelid. The second form consists of a branching network of pores (0.2 - 0.4 mm in diameter) interconnected by fine tubes (0.2 - 0.9 mm in length), and may have been produced by sponges (Akpan, personal communication, 1979). The distribution and boring style of these two trace fossil types on some <u>P.retroflexa</u> shells is illustrated in Fig. 2d. A more detailed account of these borings will be presented elsewhere (Akpan & Antia, in prep.).

<u>Facies B</u> - In-phase climbing ripple-laminated (sensu McKee, 1965) fine grained sands and parallel laminated silts containing some erosion surfaces, grading up into trough cross bedded and channelled silts and sands, containing some layers rich in platy mudclasts up to 35 m in length. This facies can be assigned to the Downton Castle Fm. Facies D described by Allen (1974) which is considered (Allen, 1974) to have been deposited in the high intertidal zone.

<u>Facies C</u> - In-phase climbing wave rippled silts with clay drapes, interbedded with parallel laminated silts and shell sheets. Ripple mark axes

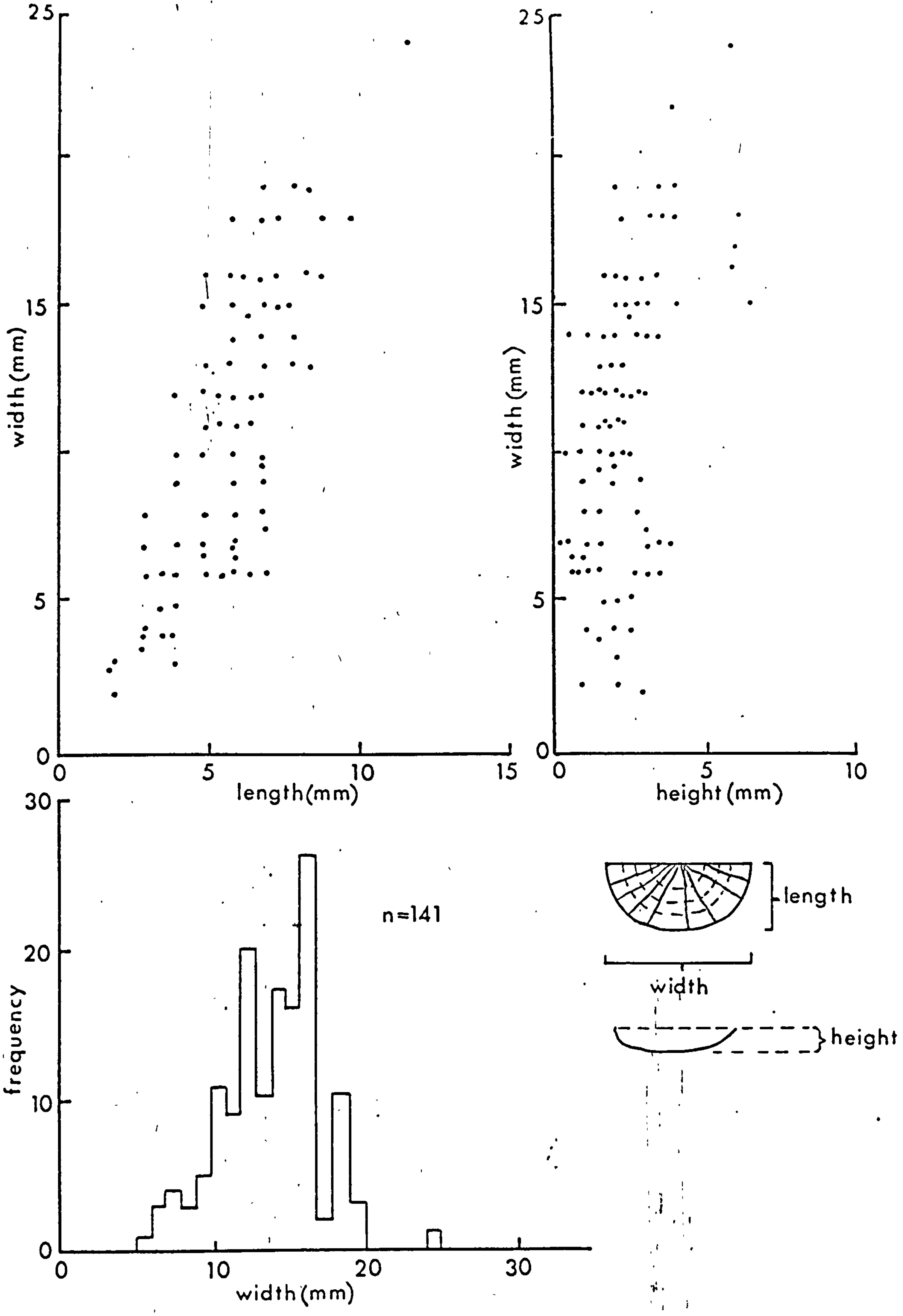

Fig. 3. Size measurement of *Protochonetes ludloviensis* from a shell bed in facies C, layer 7.

are orientated at between 220° and 260° (wavelength 6 - 14 cm, amplitude 6 - 14 mm). Some layers contain interference wrinkle marks (ridge thickness 0.5 - 1.5 mm, wavelength 2.5 - 3 mm, amplitude 0.2 - 0.5 mm, orientation 270° to 350°, shape-asymmetrical to symmetrical with a rounded crustal region). The ripple marks are occasionally asymmetical (depositing current came from the south east) and tend to have well developed bifurcating ripple crests. These asymmetric ripples have stoss side length of 6 - 8 cm, a lee side length of 4 - 5 cm and a slip face of 2 - 3.5 cm. Many of the sediment surfaces contain anti ripplets. Some of the rippled surfaces show load structures at their base. The presence of wrinkle marks suggests that the sediment was formed in an intertidal environment (Singh & Wunderlich, 1978). This is confirmed by the presence of antiripplets, which are formed (Reinek & Singh, 1973) by the capture of wind blown sand on a water saturated sediment surface. They suggest that the wind travelled from the north east to the south west. The strike of these antiripplets is between 270° and 280°. Some rare trails are present on the sediment surfaces. The shell layers appear to have infilled small hollows in the substrate and contain an internal cross laminated structure, and a 'parallel laminated upper surface. Shell size measurements for one shell layer are given in Fig. 3.

Facies D - Interbedded rippled (wavelength 2 - 6 cm, amplitude 3 - 6 mm) and parallel laminated silts containing rare laminae rich in shell debris, phosphate nodules and fish debris. The sediments are probably best assigned to the Downton Castle Formation Facies B, which Allen (1974) and others (Antia & Whitaker, 1979; Antia, 1979a) consider to have been deposited in the lower part of the intertidal zone. The fish debris and phosphate nodule rich layers probably formed as lag concentrates within the intertidal zone (cf. Allen & Tarlo, 1963; Allen, 1974; Antia & Whitaker, 1979; Antia, 1979a).

The phosphate nodules occur as compact rounded grains 4 to 15 mm in length. Similar grains occurring at the top of the Ludlovian Series elsewhere are considered (Antia, 1979a) to have formed within the sediment of a subtidal environment and been subsequently excavated and concentrated in a variety of vertebrate rich sediments. If the phosphate nodules occurring in this facies formed in a subtidal environment, then their presence in presumed intertidal sediments indicates that there was some onshore transport of subtidal material into the intertidal zone. This suggestion is further supported by the presence of subtidal brachiopods (see Calef & Hancock, 1974; Fursich & Hurst, 1974) in the intertidal sediments of facies C. Many recent studies (e.g. D'Anglejan, 1967; Shafer, 1972; Antia, 1977) have demonstrated that fish bones, phosphate nodules and shells can be transported from a subtidal environment into both intertidal and supratidal environments.

The order of facies up the section is A-B-A-C-D-B, suggests that the sequence represents an initial shallowing up sequence from a subtidal environment into an intertidal environment (initial facies A - B transition - see Fig. 1), followed by a small marine transgression (facies B - A transition - see Fig. 1). This marine transgression was followed by continued marine regression resulting in the facies A-C-D-B transitions (see Fig. 1), in which each successive facies represents a shallower subtidal or a more emergent intertidal environment.

The absence of an in situ shelly fauna and the apparent faunal change (Table 1) within the intertidal zone may coincide with either a substrate preference for sandy conditions by lingulids confining them to facies B and D or it may coincide with the change in the chemical nature of the upper

Silurian sea from a carbonate saturated sea to a highly oxygenated, carbonate undersaturated sea which has been described elsewhere (Antia, 1979b). This change might relate to the gradual southward advancement of the fluvial environment whose sediments eventually engulfed the Ludlow - Much Wenlock region during the late Downtonian and early Dittonian (Allen, 1974).

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References

Allen, J. R. L. 1974. Sedimentology of the Old Red Sandstone (Silurian-Devonian) in the Clee Hills area, Shropshire, England. Sedimentary Geology 12, 73 - 167.

Allen, J. R. L. & L. B. Tarlo, 1963. The Downtonian and Dittonian facies of the Welsh Borderland. Geol. Mag. 100, 129 - 155.

Antia, D. D. J. 1977. A cpmparison of diversity and trophic nuclei of live and dead molluscan faunas from the Essex Chenier Plain, England. Paleobiology 3, 404 - 414.

Antia, D. D. J. 1979a. Bone-Beds: A review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering and microbiotas. Mercian Geol. 7, 93 - 174.

Antia, D. D. J. 1979b. Authigenic gypsum in marine sediments - a comment. Marine Geol. 30 (in press). Published in vol.31,pp.M1 - M4.

Antia, D. D. J. & J. H. McD. Whitaker. 1979. A scanning electron microscope study of the genesis of the upper Silurian Ludlow Bone Bed. pp. 119 - 136 In W. B. Whalley (ed.) Scanning electron microscopy in the study of sediments. Geoabstracts Ltd. Norwich.

Calof, C. E. & N. J. Hancock. 1974. Wenlock and Ludlow marine communities in Wales and the Welsh Borderland. Palaeontology, 17, 779 - 810.

D'Anglejan, B. F. 1967. Origin of marine phosphorites off Baja, California. Marine Geol. 5, 15 - 44.

Elles, G. J. & I. L. Slater. 1906. The highest Silurian rocks of the Ludlow District. Jl geol. Soc. Lond. 62, 195 - 220.

Fursich, F. T. & J. M. Hurst. 1974. Environmental factors determining the distribution of brachiopods. Palaeontology 17, 879 - 900.

Holland, C. H., Lawson, J. D. & V. G. Walmsley. 1963. The Silurian rocks of the Ludlow district, Shropshire. Bull. Br. Mus. Nat.Hist. (geol.) 8, 95 -171.

Jopling, A. V. & R. G. Walker. 1968. Morphology and origin of ripple drift cross lamination, with examples from the Pleistocene of Massachusetts. J. Sediment. Petrol. 38, 971 - 984.

Martinsson, A. 1967. The succession and correlation of ostracode faunas in the Silurian of Gotland. Geol. Foren. Stockholm Forb. 89, 350 - 386.

McKee, E. D. 1965. Experiments on ripple-lamination. IN Middleton, G. V. (ed.). Primary Sedimentary structures and their hydrodynamic interpretation. Soc. Econ. Palaeontologists & Mineralogists Spec. Pub. 12, 66 - 83.

Reineck, H. -E. 1967. Paramtor von Schichtung und Bioturbation. Geol. Rundschau. 56, 420 - 438.

Reineck, H. -E. & I. B. Singh. 1973. Depositional sedimentary environments. Springer. Berlin 439p

Ronan, T. E. Jr. 1977. Formation and palaeontological recognition of structures caused by marine annelids. Paleobiology 3, 389 - 403.

Shafer, W. 1972. Ecology and palaeoecology of marine environments. Oliver and Boyd Edinburgh 586p.

Shaw, R. W. L. 1969. Beyrichiacean ostracodes from the Downtonian of Shropshire. Geol. For. Stockh. Forh. 91, 52 - 72.

Singh, I. H. & Wunderlich, F. 1978. On the terms wrinkle marks (Runzelmarken), millimetre ripples and miniripples. Senckenbergiana marit. 10, 75 - 83.

The Ludlow-Downton Series transition (Upper Silurian); at Corfton, Aston Munslow, Shipton, Brockton, Netherton and Lye.

by

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Abstract

Faunal and sediment distributions in seven boundary sections are discussed. A cyclic pattern of sediment modification by crinoids is noted. [illegible]. A major change in the chemistry of the Silurian sea is postulated and its effects on sedimentation and faunas discussed.

Introduction

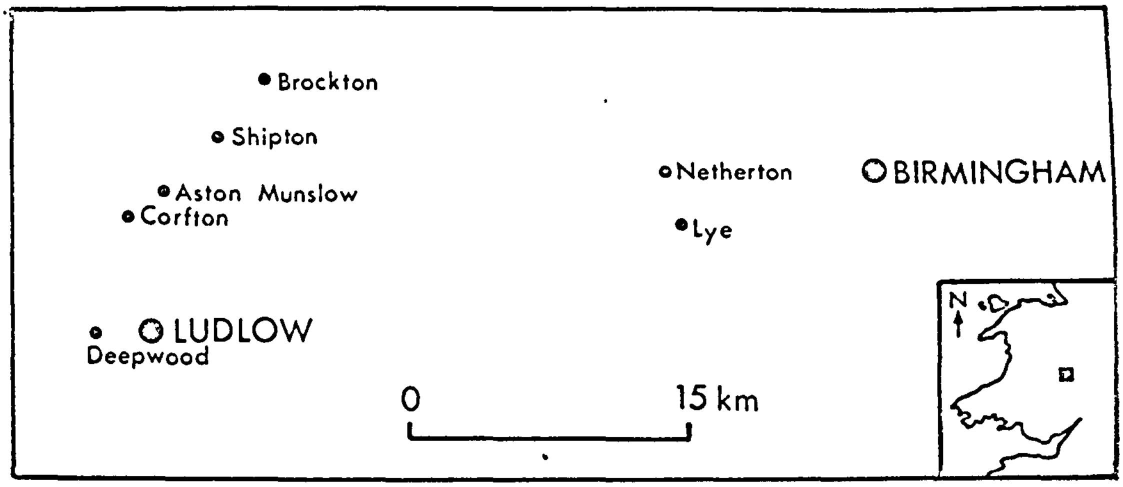
The Ludlovian (Whitcliffian stage) - Downtonian series boundary has been described from two sections in recent years in the Craven Arms-Much Wenlock District (White & Coppack, 1978; Antia, 1979a). The section near Craven Arms at Siefton (Antia, 1979a) demonstrated the presence of Whitcliffian intertidal sediments and a minor transgression within the overall regressive sequence (cf. McKerrow, 1979). The other study (White & Coppack, 1978) showed that the series boundary was marked by a bone-bed which divided a Whitcliffian fauna from a Downtonian fauna. In both sections a carbonate rich sediment containing a Whitcliffian type (cf. Holland _et_ _al_, 1963) brachiopod fauna is found below the boundary and a non calcareous limonite sediment containing a Downtonian type ostracod-bivalve fauna (cf. Elles & Slater, 1906; Shaw 1969) above.

Three explanations for this abrupt change exist. The first suggests that the boundary represents a major unconformity (e.g. Stamp, 1920; 1924) and may be discounted on both sedimentological and palaeontological evidence (Turner, 1973; Aldridge, 1975; Siveter 1978, Allen, 1974a, Antia 1979a, b & c; Antia & Whitaker 1979). The second suggests that the change is related to the change of environment at the boundary from a sequence of subtidal to intertidal sediments. (cf. Allen, 1974a; Antia 1979b; Antia & Whitaker, 1979). However, this is unlikely because the first (Whitcliffian) change from subtidal sedimentation to intertidal sedimentation at Siefton was not marked by a change in faunas and was contained within a sequence of carbonate sediments (Antia, 1979a).

The third and perhaps most likely explanation is that the change in sediment mineralogy and faunas is related to a change in the chemical composition of the Silurian ocean (Antia, 1979c), in which a carbonate saturated sea changed to a carbonate depleted, oxygen rich sea. Such a change could account for both carbonate depletion of Downtonian sediments and the change in faunas at the Ludlow-Downton boundary.

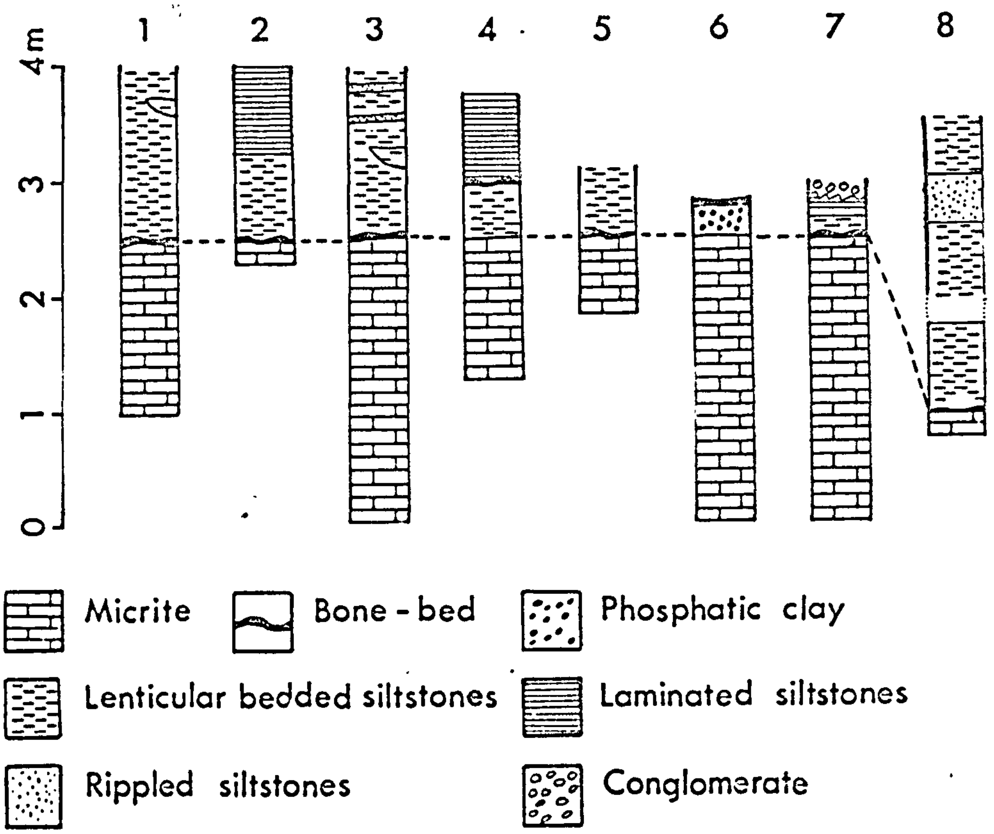
In this study further confirmation of the sedimentological and faunal abruptness of this change is presented from seven sections in the Birmingham and Much Wenlock to Craven Arms area (Fig. 1.) Each section will be dealt with separately.

Fig.1



Location map of the sections examined in this study. Inset map of Wales indicates the relative position of the area studied.

Fig.2



Sediment logs for eight sections across the Ludlow-Downton boundary. 1. Corfton, Sun Inn Car Park; 2. Corfton, lane section; 3. Aston Munslow, Swan Inn Car Park; 4. Shipton; 5. Brockton; 6. Netherton; 7. Lye; 8. Deepwood - Note there is a 3 m break in the section due to poor exposure.

1. Corfton

The Ludlovian-Downtonian transition is exposed in two sections at Corfton. The first is in the Sun Inn Car Park (G.R.SO 497 852) and consists of a series of calcareous lenticular bedded silts and clays containing horizontal burrows and trails infilled with fish debris, glauconitic fecal pellets and coarse silts (Upper Whitcliffe Beds), overlain by two discontinuous layers of rippled vertebrate sand (2 - 25 mm thick) representing the Ludlow Bone-Bed, (Turner, 1973). The sediment immediately above the bone-bed (basal Downton Castle Fm.) consists of rippled silts containing in situ authigenic phosphate nodules and internal limonite moulds of T. helicites.

The overlying silts and clays contain some thin sand sheets and some small flat based channels (30 - 50 cm wide; 5 - 15 cm deep). The distribution of sediments in the section is summerised in Fig. 2. The faunal lists (macrofossils) for the section are presented in Tables 1 and 2.

The Whitcliffe sediments contain some patches of shell gravel (up to 2 m in length, 3 cm thick)) with a symmetrical rippled upper surface (wavelength 20 - 30 cm). Occasional specimens of L. lata and L. corftonensis sp. nov. occur in situ in short burrows containing a base some 2 - 4 cm (Fig. 4) below the apparent syndepositional substrate surface. The fauna contained within these sediments is of typical Whitcliffian aspect (Table 1) and includes S. lunata, ludloviensis, M. nucula, H. elegans, C. implicata, G. cymaeformis, L. corftonensis, L. lata, F. amygdalina, Leioclema sp. Burrows in this sediment are sometimes infilled with glauconitic fecal pellets and thelodont scales. The Bone-Bed (figured on the cover of the Mercian Geologist (1979) vol. 7 pt. 2) appears to rest conformably on the underlying strata, and forms a series of rippled lenses traceable laterally within the section for 2 - 4 m. Both symmetrical and slightly asymmetrical (wavelength, 5-25 cm; amplitude 3-15 mm) ripple marks are present. Some symmetric wave ripples are present. They have a wavelength of 25 - 35 cm and an amplitude of 4 - 6 mm. The fish fauna of the bone-bed is dominated by T. parvidens and L. ludlowiensis (Table 3) and contains numerous phosphatic invertebrate fragments. The bone-bed is a sparitic lithobonebed and

Table 1 Faunal composition of the Whitcliffe Beds at Corfton, Sun Inn section. Sample positions are located with respect to the base of the Ludlow Bone-Bed.

	SAMPLE POSITION (cm)									
SPECIES	0	10	20	30	40	50	60	70	80	90
Brachiopods										
Craniops implicatus (J.de C.Sowerby)		-	-	-	4.7	-	9.2	1.3	1.2	1.5
Howellella elegans (j.de C.Sowerby)		-	33.3	-	-	-	3.7	23.8	32.7	-
Lingula lata J.de C.Sowerby		-	-	-	4.7	8.2	12.0	-	-	-
Lingula sp. nov.		-	-	-	-	-	-	-	-	6.4
Microsphaeridiorhynchus nucula (J.de C.Sowerby)		-	16.6	-	-	-	1.8	0.6	27.2	-
Protochonetes ludloviensis Muir Wood		0.8	-	64.0	90.0	22.9	20.3	0.6	9.2	18.2
Salopina lunata (J.de C.Sowerby)		99.2	50.0	36.0	-	64.5	51.8	35.4	29.0	73.9
Bivalves										
Fuchsella amygdalina (J.de C.Sowerby)		-	-	-	-	-	0.9	-	-	-
Goniophora cymbaeformis (J.de C. Sowerby)		-	-	-	-	2.0	-	-	-	-
Modiolopsis complanata (J.de C.Sowerby)		-	-	-	-	2.0	-	-	-	-
Bryozoan colonies										
Leioclema sp.		-	-	-	-	-	-	0 6	-	-
Number of fossils observed		125	6	25	20	48	108	62	162	23
Bedding plane surface area examined(m^2)		0.8	0.8	0.6	0.9	1.1	1.3	0.4	0.9	2.0

Table 2. Faunal list for the Downtonian at Corfton Sun Inn section. A = Abundant

	HEIGHT ABOVE THE BASE OF THE LUDLOW BONE-BED (cm)																	
SPECIES	0	2	9	10	16	31	39	60	76	88	102	108	118	136	147	161	173	183
Brachiopods																		
Lingula minima J.de C.Sowerby	33·3	1·7	78·5	96·7	7·9	97·9	39·5	-	-	52·5	-	37·0	-	-	-	76·6	-	
Bivalves																		
Modiolopsis complanata (J.de C.Sowerby)	66·6	75·9	7·1	0·9	1·5	-	-	26·9	-	19·6	-	62·9	42·8	38·4	53·3	11·3	-	
Gastropods																		
Cymbularia carinata (J.de C.Sowerby)	-	-	-	-	1·5	9·5	-	-	-	-	-	-	-	-	-	-	-	
Loxonema gregarium (J.de C.Sowerby)	-	10·1	3·5	0·4	-	-	-	3·8	-	-	-	-	-	-	-	-	-	
Turbocheilus helicites (J.de C.Sowerby)	-	0·5	-	-	36·5	-	6·2	15·3	-	-	-	-	-	16·0	-	0·7	-	
Ostracods																		
Cavellina cf. *baltica* Sarv	-	2·3	-	-	-	-	-	-	-	0·2	-	-	-	-	-	-	-	
Cytherellina siliqua Jones	-	-	-	-	-	-	-	-	-	6·4	-	-	-	-	-	0·5	-	
Frostiella groenvalliana Martinsson	-	9·5	-	-	-	-	33·3	7·6	-	15·9	-	-	14·2	3·8	6·7	10·5	-	
Hebellum cf. *tetragonum* (Krause)	-	1·1	3·5	-	-	-	-	-	-	0·2	-	-	14·2	-	-	-	-	
Londinia kiesowi (Krause)	-	2·9	-	-	-	2·0	4·1	-	-	2·1	-	-	-	-	-	-	-	
Lophoctonella sp.	-	-	-	-	-	-	-	-	-	0·2	-	-	-	-	-	-	-	
Nyhamnella cf. *naturalis* Sarv	-	-	-	0·4	-	-	10·4	-	-	0·9	5·7	-	-	-	-	0·2	-	
Fish																		
Gomphonchus tenuistriata(Ag.)	-	-	-	-	30·1	-	2·0	3·8	-	-	-	-	-	-	-	-	-	
Logania ludlowiensis Gross	A	-	-	-	11·1	-	-	-	-	-	-	-	-	6·2	-	-	-	
Thelodus parvidens Ag.	A	-	-	-	-	-	-	7·6	-	-	-	-	-	-	-	-	-	
Other fossils																		
Arabellites sp.	-	-	-	0·9	-	-	-	-	-	-	-	-	-	-	-	-	-	
Calcareous tubes	-	-	-	-	-	-	-	-	-	1·0	-	-	-	-	-	-	-	
Eurypterid fragments	-	-	-	-	-	-	-	3·8	-	-	-	-	-	-	13·3	-	-	
Plant debris	-	-	-	A	-	-	-	-	-	A	94·2	A	A	A	26·6	-	-	
Pachytheca sp.	-	-	7·1	0·4	1·5	-	-	-	-	-	-	-	-	-	-	-	-	
'*Serpulites*' sp.	-	-	-	-	-	-	-	11·5	-	-	-	-	-	-	-	-	-	
?*Zoophychus* sp.	-	-	-	-	-	-	-	19·2	-	0·2	-	-	-	-	-	-	-	
Number of fossils observed	6	168	28	215	63	49	33	26	0	777	35	27	5	26	15	381	0	
Bedding plane surface area examined (m^2)	0·7	0·2	0·4	1·1	1·1	1·9	6·1	10·7	8·2	8·5	3·3	6·6	4·5	3·7	3·5	9·9	1·5	

Table 3. Composition of the Ludlow Bone-Bed (Thelodonts only). 1 = Corfton, 2 = Corfton (lane section), 3 = Aston Munslow, 4 = Shipton, 5 = Lye, 6 = Deepwood.

SPECIES	1	2	3	4	5	6
Logania ludlowiensis Gross	3 86	0 24	22 12	19 94	36 86	3 36
Thelodus costatus (Pander)	-	-	0 88	-	-	-
Thelodus parvidens Ag.	95 76	73 57	76 46	79 75	63 13	96 63
Thelodus pugniformis Gross	-	-	0 53	0 31	-	-
Thelodus trilobatus Gross	0 37	-	-	-	-	-
Number of thelodont scales counted	803	140	565	321	198	208

contains some quartz and mica. Trace fossils are rare, or absent from the sediment though borings are present on the thelodont scales and acanthodian spines.

The Downtonian sediments contain a poor macrofossil and trace fossil assemblage. The former includes typical Downtonian macrofossils (Table 3) like M. complanata, T. helicites, L. gregaria, and L. minima, and the microfossils F. groenvalliana, L. kiesowi, C. siliqua, and N. naturalis. The trace fossils present include ?Pelecepodichnus, Lobichnus, and ?Zoophychus sp. nov.

Also present in the section are good periglacial features (of presumed Quaternary age) deforming the Downtonian silts.

In a nearby lane section (G.R. SO 497850) trough cross bedded sandstones are present. These buff coloured sandstones are poorly exposed and poorly fossiliferous (3 hrs fossil hunting revealed no fossils) and may be analagous with Allen's (1974) Downtonian facies D.

Another section across the Ludlovian-Downtonian boundary (Robertson, 1927) occurs on a farm track situated about half way between Corfton and Diddlebury (G.R. SO 497853). This section consists of rippled Whitcliffian calcareous flags overlain by a rippled discontinuous bone-bed. This bone-bed has been correlated with the Ludlow Bone-Bed (Robertson, 1927) and may be described as a rippled layer (wavelength 20 - 40 cm; amplitude 0.2 - 14 cm) which extends laterally within the section for about 10 m before disappearing. The bone-bed varies laterally in composition from a sparitic-biobonebed to a micritic-biobonebed.

It contains a number of grain types and its composition is described in Table 2. Locally the bone-bed is made of several overlapping rippled vertebrate sand layers resting directly on each other. Many of the features present on the quartz grains in this bone-bed have been illustrated by Antia & Whitaker (1978). They vary from rounded grains to euhedral crystals and have a modal size of about 0.7 mm. Some contain silicified fungal filaments on their outer surfaces, others contain intertidal abrasion features. On some grains silica plastering has resulted in the formation of celtic crosses on the grains surface. Palaeocurrent information for the section is given in Table 5. Note the change in current direction between the Whitcliffian and Downtonian sediments. From the north east in the Upper Whitcliffe Beds to the North-West in the Downtonian. The Downtonian siltstones are mostly parallel laminated with some rippled layers, some containing miniripples and wrinkle marks. A faunal list for the section is given in Table 4 and a sediment log for the section given in Fig. 2. Trace fossils (Fig. 3) are present in the Downtonian sediments taken from the basal metre of the Downtonian. Occasionally at the base of the bone-bed trails and burrows are present. A bedding plane trace of these trace fossils is illustrated in Fig. 3d. The change in ripple index up the section (Table 5 and the presence of wrinkle marks in the Downtonian suggest that the transition represents a change in environment

2. Deepwood: Ludlovian-Downtonian boundary section.

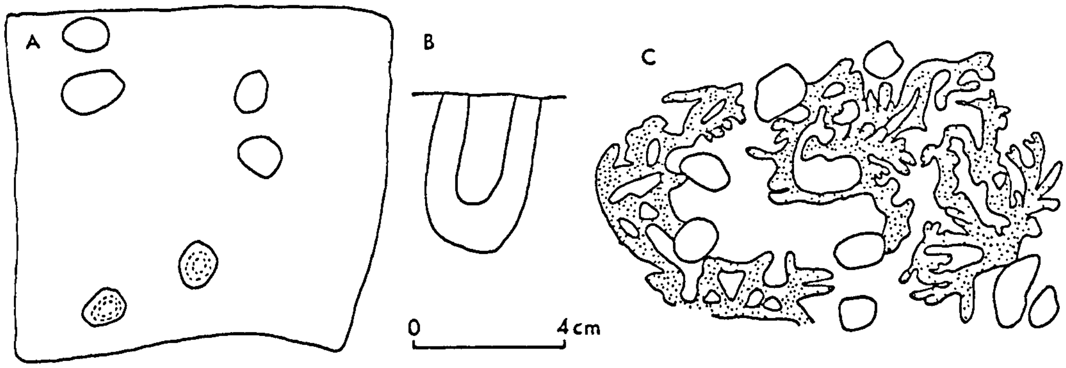
On a forest track near Ludlow an undescribed parastratotype (Holland et al, 1963 section across the Ludlovian-Downtonian boundary is present (G.R. SO 459741). This section consists of two adjacent sections whose sediment distributions are indicated in Fig. 2. The faunas present in the section are documented in Table 6.

3. Aston Munslow: Ludlovian-Downtonian boundary section.

The section in the Swan Inn Car Park (G.R. SO 512866) contains the Ludlow Bone-Bed (Greig et al, 1968; Turner, 1973). The sediments present (Fig. 2) consist of highly bioturbated Whitcliffian calcareous siltstones and mudstones. A number of discontinuous bone-beds (inc. The Ludlow Bone-Bed) and a sequence of Downtonian siltstones and sandstones.

The Whitcliffian sediments are lenticular bedded, containing shell patches on individual bedding planes, calcareous nodules, and thin shelly sub-lithobonebeds. About 1.8 m below the bone-bed horizon is a clay band about 2 cm thick rich in Chlorite. This layer may represent a degraded bentonite (cf. Marsh, 1976). Most of the fauna occurs as disarticulated and fragmented brachiopods (e.g. P. ludloviensis, S. lunata, M. nucula, O. rugata, and H. elegans). The only

Fig. 3

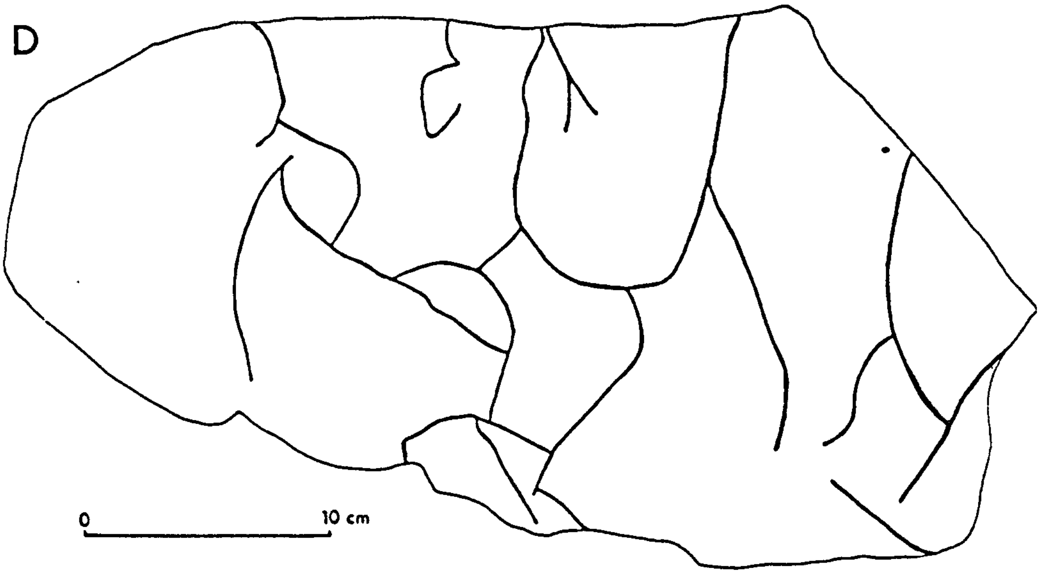


Tracings of trace fossils in Downtonian laminated silts of the Corfton lane section. Two types of trace fossil were observed. The first consisted of U tubes without spreite. The second consisted of a Lobichnus type trace fossil which appeared to be connected to the U tubes.

A. U tubes plan view.

B. U tube vertical sections.

C. Plan view of Lobichnus trace fossils connected to U tubes.



D. Bedding plane trace of trails on the underside of the Ludlow Bone-Bed in the Corfton Lane section.

Table 4. Faunas from the lane section across the Ludlow - Downton Series boundary at Corfton (G.R. SO 497853). A total of 60 kg of rock was processed and shown to contain 631 shells and shell fragments. In the Ludlow Bone-Bed fish remains are expressed in the format ,abundant (A),common (C),present(P).

	SAMPLE POSITION (cm) WITH RESPECT TO THE BASE OF THE DOWNTONIAN										
SPECIES	-10	0	8	9	21	39	43	59	82	128	153
Brachiopods											
Lingula minima	-	-	22.2	77.4	4.3	27.7	18.2	51.4	67.3	83.3	
Lingula sp. nov.	5.5	-	-	-	-	-	-	-	-	-	
Howellella elegans	5.5	-	-	-	-	-	-	-	-	-	
Protochonetes ludloviensis	44.4	-	-	-	-	-	-	-	-	-	
Salopina lunata	27.7	-	-	-	-	-	-	-	-	-	
Bivalves											
Fuchsella amygdalina	5.5	-	-	-	-	-	-	-	-	-	
Modiolopsis complanata	-	-	44.4	16.1	37.4	3.2	-	1.4	13.5	-	
Pteronitella retroflexa	11.1	-	-	-	-	-	-	-	-	-	
Gastropods											
Cymbularia carinata	-	-	-	3.2	1.1	-	-	-	-	-	
Loxonema gregarium	-	-	3.3	3.2	29.7	0.4	6.1	-	1.9	-	
Turbocheilus helicites	-	-	-	-	9.8	-	-	-	15.4	-	
Ostracods											
Cytherellina siliqua	-	-	-	-	-	15.6	27.2	-	1.9	-	
Frostiella groenvalliana	-	-	-	-	3.3	14.8	-	0.7	-	-	
Londinia kiesowi	-	-	-	-	2.2	6.8	-	2.2	-	-	
Fish											
Gomphonchus murchisoni	-	P	-	-	-	-	-	-	-	-	
Logania ludlowiensis	-	C	-	-	-	28.1	-	-	-	-	
Thelodus parvidens	-	A	-	-	3.3	2.4	-	-	-	-	
Other fossils											
Calcareous tubes	-	-	-	-	7.6	0.8	48.4	43.5	-	16.7	
Eurypterid fragments	-	-	-	-	1.1	-	-	-	-	-	
Plant debris	-	-	-	-	-	-	-	-	A	-	

Table 5 Sedimentary data, pertaining to ripple marks in the lane section at Corfton (G.R. SO 497853). OR = orientation,W=wavelength,R.I.=ripple index. Sample positions are given with respect to the base of the Ludlow Bone-Bed.

Sample position (cm)	OR	W	R.I.	Wave ripples	Current ripples	Herring bone lamination
-10 to 0 cm	040 - 050°	25 - 35 cm	20 - 30	-	+	-
0 to 8 cm	040 - 050°	27 - 60 cm	7·5 - 8·2	-	+	-
8 to 9 cm	040 - 050°	12 - 14 cm	6 - 7	-	+	-
9 to 18 cm	130 - 140°	7 - 9 cm	4·5 - 8.3	+	-	+
18 to 21 cm	130 - 140°	1 -1·2 cm	2·5 - 3·5	+	-	-
21 t0 39 cm	-	-	-	-	-	-
39 to 43 cm	130 - 140°	5 - 66 cm	4·5 - 8	+	-	+
43 t0 59 cm	130 - 140°	2 - 3 cm	4·2 - 4·8	+	-	+
59 to 82 cm	130 - 140°	8 - 20 cm	5·5 - 13	+	-	-
82 to 160 cm	-	-	-	-	-	-

Table 6. Faunal list for the Ludlow - Downton Series transition at Deepwood (G.R. SO 459841)

	HEIGHT ABOVE THE BOUNDARY (cm)				
SPECIES	-21	0	155	214	332
Brachiopods					
Lingula lata		7.69	-	-	-
Lingula minima		-	21.87	20.12	19.14
Microsphaeridiorhynchus nucula		7.69	-	-	-
Orbiculoidea rugata		-	-	0.32	-
Protochonetes ludloviensis		46.15	-	-	-
Protochonetes cf. novascoticus(Mclearn)		-	-	0.32	-
Salopina lunata		30.76	-	-	-
Bivalves					
Leodispis barrowsi		-	-	-	0.39
Modiolopsis complanata		-	-	11.36	4.29
Gastropods					
Loxonema gregarium		-	-	0.32	-
Turbocheilus helicites		-	37.50	29.87	0.78
Ostracods					
Cytherellina siliqua		-	6.25	2.27	12.50
Frostiella groenvalliana		-	18.76	18.83	57.42
Hermannia marginata		-	-	0.97	1.95
Londinia kiesowi		-	12.50	10.06	1.17
Other fossils					
Cornulites sp.		7.69	-	-	-
Fish debris		-	+	+	+
Gomphonchus murchisoni		-	3.12	1.29	-
Gomphonchus tenuistriata		-	-	3.57	-
Sclerodus sp.		-	-	0.32	-
Pachytheca sp.		-	-	-	1.94
Number of fossils observed		13	32	308	256
Bedding plane surface area examined (m^2)		0.9	1.4	2.6	1.2

species observed which might be <u>in situ</u> is the boring bryozoan <u>Rhopalonaria</u> sp.

The main bone-bed facies consists of three discontinuous bone-beds varying in thickness from 2 to 60 mm (wavelength 15 - 25 cm; amplitude 5 - 40 mm). All of them occur within a few centimetres of each other (Antia 1979b.) The sediment between them is well bedded (usually parallel laminated, though some cross bedding is present) and contains a rich brachiopod fauna (Table 7). Locally the bone-bed contains carbonate nodules (up to 7 cm in diameter) rich in shell debris and vertebrate material. In the basal bone-bed this shell debris is derived from brachiopods, while in the other bone-beds the debris is derived from loxonemid gastropods.

The sediment immediately above the bone-beds consists of lenticular bedded silts (ripple wavelength 5 - 15 cm) containing a bivalve fauna (Table 7), and in places deep flat based channels up to 1 m wide and 20 cm deep infilled with coarse cross bedded sandstones. The top layers of the channels consist of parallel laminated sandstones strewn with shells and mud pellets. Overlying this channelled sediment is a rubbly micritic layer containing eurypterid debris. This sediment appears to be in the early stages of calcrete formation and may represent a short period of palaeosol formation, possibly of the order of a few hundred years duration (cf. Allen, 1974b).

Immediately overlying this palaeosol is a coarse grained micaceous sandstone sheet (8 cm thick) with a slightly discordant base and a cross laminated internal structure. It is overlain by an alternating sequence of sandstone sheets and olive green mudstones.

4. <u>Shipton: Ludlovian-Downtonian boundary section</u>.

The Ludlovian-Downtonian boundary section (G.R. SO 564918) at Shipton (Robertson, 1927) may be subdivided into three units.

(a) A Whitcliffian unit.

(b) A Bone-Bed unit.

(c) A Downtonian unit.

Sediment distributions in the section are given in Fig. 2. Faunal

Table 7. Faunas across the Ludlow - Downton Series boundary at Aston Munslow. C=Common.

	HEIGHT ABOVE THE BOUNDARY (m)						
SPECIES	-2 00	-1 67	-0 75	0 00	0 06	0 40	1 59
Brachiopods							
Craniops implicatus	-	-	0.70	11.66	-	-	
Lingula lata	11.53	2.66	6.34	0.61	-	-	
Lingula minima	-	-	-	3.50	43.28	82.26	
Lingula sp. nov.	-	1.52	0.17	-	-	-	
Howellella elegans	-	1.52	2.99	2.54	-	-	
Microsphaeridiorhynchus nucula	7.69	4.56	2.46	10.08	-	-	
Orbiculoidea rugata	-	5.32	1.05	2.36	-	-	
Protochonetes ludloviensis	19.23	24.33	26.63	30.43	1.86	-	
Salopina lunata	57.69	50.19	58.02	27.71	-	-	
Bivalves							
Goniophora cymbaeformis	-	-	-	-	0.37	-	
Leodispis cf. *barrowsi*	-	-	-	0.17	1.11	-	
Modiolopsis complanata	-	-	-	2.63	29.85	4.52	
Nuculites ovata (J.de C.Sowerby)	-	-	-	-	0.74	-	
Pteronitella retroflexa	-	-	-	0.17	-	-	
Gastropods							
Cymbularia carinata	-	-	-	0.26	0.74	-	
Loxonema gregarium	-	-	-	1.22	9.70	1.91	
Loxonema obsoletum	-	5.32	-	-	-	-	
Naticopsis sp.	-	0.38	-	-	-	-	
'*Platyschisma*' *williamsi*	-	-	-	0.26	-	-	
Turbocheilus helicites	-	-	-	4.12	5.97	1.04	
Other molluscs							
Hyolithes forbesi	-	0.76	-	0.17	-	-	
Leurocycloceras sp.	-	0.38	0.70	-	-	-	
'*Orthoceras*' sp.	3.84	-	-	0.17	-	-	
Bryozoan colonies							
Rhopalonaria sp.	-	0.38	0.17	0.01	-	-	
Ostracods							
Calcaribeyrichia torosa (Jones)	-	-	-	0.01	-	-	
Cytherellina siliqua	-	1.52	0.52	0.80	1.11	2.26	
Hermannia cf. *marginata* (Keys)							
Londinia cf. *kiesowi*	-	-	-	-	0.37	0.86	
Annelids							
'*Serpulites*' *longissimus*	-	-	0.17	0.26	-	-	
Echinoids							
Round crinoid columnals	-	0.38	-	-	-	-	
Fish							
Gomphonchus murchisoni	-	-	-	0.01	-	-	
Gomphonchus tenuistriata	-	-	-	-	0.37	-	
Sclerodus sp.	-	-	0.17	-	-	-	
Thelodus parvidens	-	-	-	C	1.49	0.34	
Thelodont (*T. parvidens*) skin fragment	-	-	-	-	-	0.34	
Plants							
Plant debris (?*Nematophyton* sp.)	-	-	-	-	-	1.21	
Pachytheca sp.	-	-	-	0.43	1.49	2.60	
Others							
Calcareous tubes	-	-	-	0.01	0.74	1.73	
Glauconitic faecal pellets	-	-	C	C	-	-	
Number of fossils observed	26	263	567	1140	268	575	
Bedding plane surface area examined (m^2)	0.3	0.8	1.1	1.5	1.9	0.8	

Plate 1 (a) Vertically orientated crinoid stem encrusted by *Leioclema* sp. from Shipton (Upper Whitcliffe Beds).

(b) Typical vertically orientated crinoid stem from Shipton (Upper Whitcliffe Beds).

(c) Typical branched plant stem from the Lowest Downtonian of Corfton, Sun Inn Car Park.

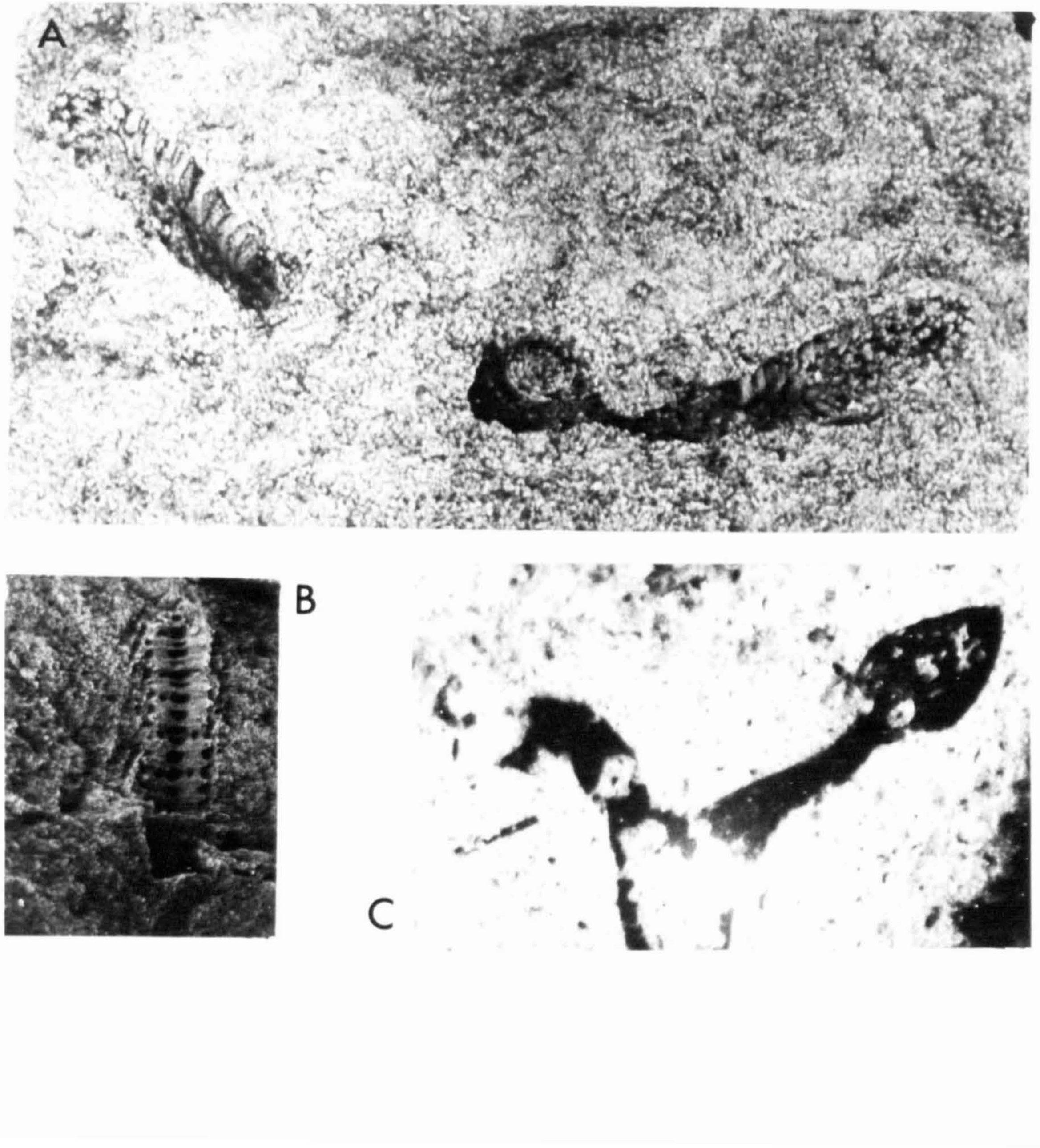
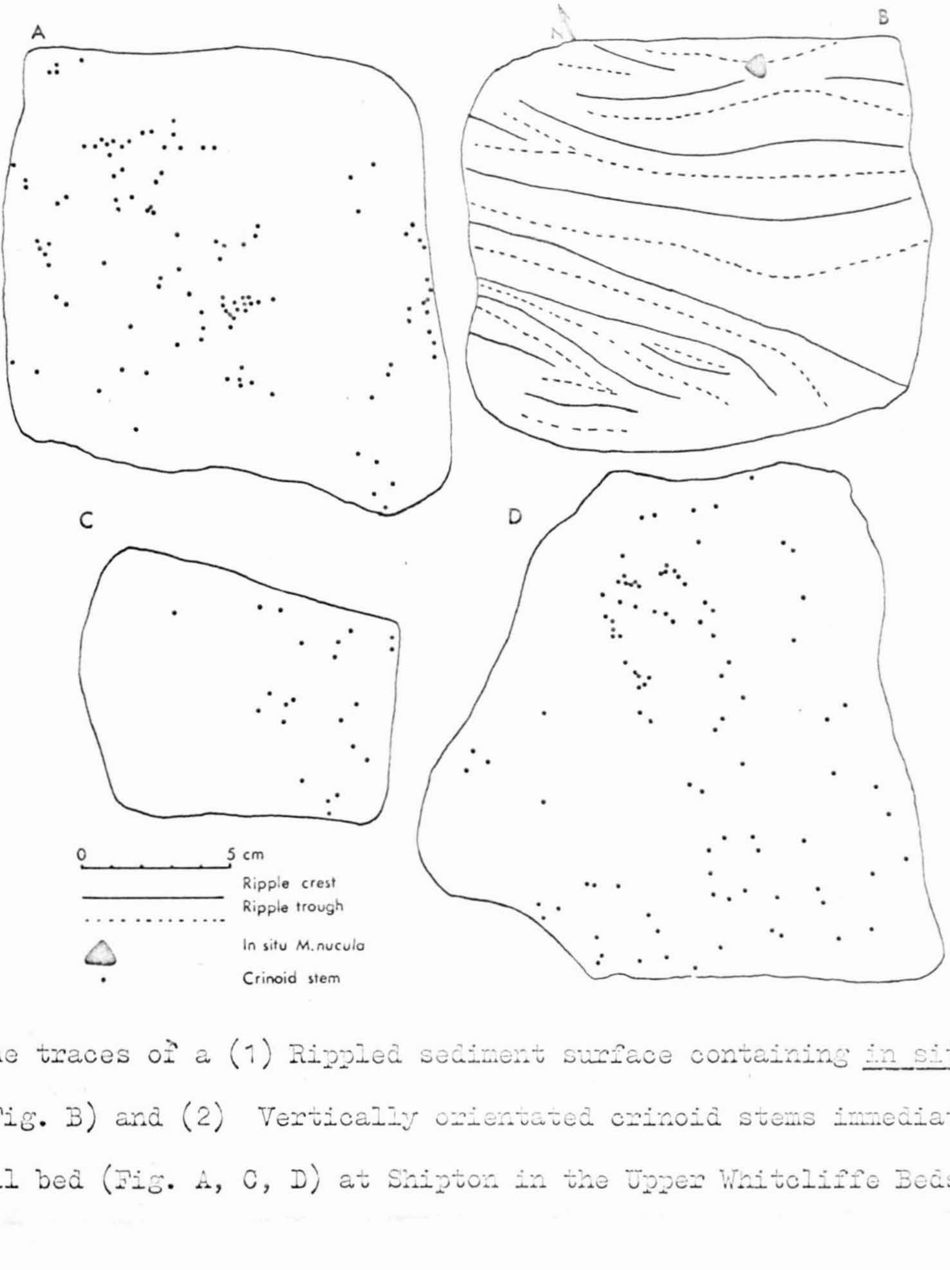
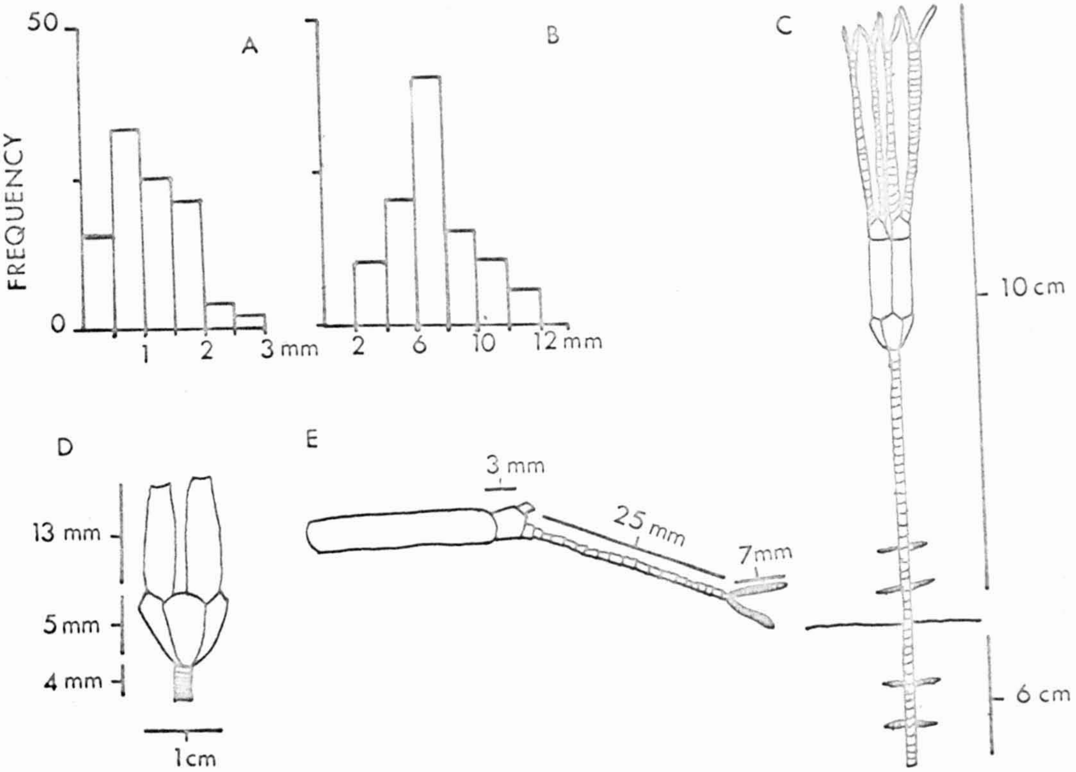

A
B
C

Fig. 4



Bedding plane traces of a (1) Rippled sediment surface containing *in situ* *M. nucula* (Fig. B) and (2) Vertically orientated crinoid stems immediately below a shell bed (Fig. A, C, D) at Shipton in the Upper Whitcliffe Beds.

Fig. 5



Crinoids from the Upper Whitcliffe Beds.

(a) Size/frequency (%) histogram at Shipton of stem width immediately below a Shell Bed (n = 58).

(b) Size/frequency % histogram for the recent Ophiuroid. Ophiocomina nigra's disc width from shelf waters off Cumbrae (n = 200).

(c) Crinoid Cicerocrinus elegans Sollas reconstructed indicating 2-6 cm of stem embedded in the sediment and 8-10 cm high stem + crown above the sediment, based on Ludlow Museum specimens 58/75/132 & 103/73/5.

(d) Detail of basal and radial plates (based on Ludlow Museum specimen 58/75/152). Note that stem illustrated contains 14 columnals.

(e) Detail of a ray (based on Ludlow Museum specimen 58/75/132). The basal auxiliary contains 18 brachials on each arm below the upper auxiliary. Each of the arms above this upper auxiliary contains 12 brachials.

lists for the section are given in Table 8.

The Whitcliffian unit or facies contains a sequence of shell gravels, lenticular bedded and amorphous siltstones and mudstones in an apparent cyclic sequence of sedimentation. The cycle appears to be tripartite starting with the deposition of lenticular bedded siltstones (ripple wavelength is 8 - 30 cm). These siltstones contain an apparent <u>in situ</u> fauna of <u>M. nucula</u> (densities of 10 - 30 per m^2 bedding plane surface area) occurring as isolate specimens (Fig. 4B). Towards the top of these lenticular bedded units vertically orientated crinoid stems start to occur in low densities (10 - 100 per m^2 bedding plane surface area). When the densities of these crinoid stems reach about 1,000 per m^2 the rippled lenticular bedded structure of the sediment disappears and is replaced by an amorphous structure. These vertically orientated crinoid stems (Plate 1b) are cirriferous crinoid holdfasts (cf. Franzen, 1977). They commonly occur in clumps radiating from a common source (Fig. 4), buried 2 - 6 cm below the substrate surface. Some of the stems contain epizoan bryozoan encrustations (Plate 1a).

The density of the vertically orientated crinoid stems at the top of this homogenous unit is frequently in excess of 10,000 stems per square metre of bedding plane surface area. The third part of this cycle consists of a shell band containing crinoid columnals and shell debris with an erosive base, which truncates the crinoid stems. This shell band is conformably overlain by lenticular bedded siltstones enabling the cycle to be repeated. The shell deposits probably result from the effects of a major storm on a shallow sea floor moving shell debris in a normally placid environment. The severity of the storm is indicated by the truncation of the crinoids stems leaving their holdfasts in the sediment. A size frequency graph of the crinoid stem diameters on an erosion surface at the shell gravel amorphous silt junction (Fig. 5a) indicates the presence of few juvenile or elderly forms. Similar size distributions are presented by the ophiuroid <u>Ophiocomina nigra</u> (Fig. 5b) from the shallow (8 m depth) shelf waters off the Island of Cumbrae (Strathclyde) - G.R. NS 155537. In the latter instance the absence of juveniles is caused by the cannabalistic removal of settling spat by

Table 8 Faunal distributions across the Ludlow - Downton Series boundary at Shipton. Sample positions are given with respect to the Downtonian Boundary.

	SAMPLE POSITION (cm)																				
SPECIES	78	58	46	-42	36	34	32	30	24	22	10	0	-12	-24	-36	-48	-60	-62	-102	-103	-113
Brachiopods																					
Craniops implicatus		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.0	-	-
Howellolla elegans		-	-	-	-	-	-	-	-	-	-	-	-	0.6	-	-	-	-	-	-	-
Lingula lata		-	-	-	-	-	-	-	-	-	-	-	33.3	3.4	-	3.8	1.5	2.6	10.8	4.5	-
Lingula minima		46.7	81.0	66.6	3.0	100.0	91.0	46.0	77.0	57.0	55.0	77.0	-	-	-	-	-	-	-	-	-
Lingula sp. nov.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-
Microsphaeridiorhynchus nucula		-	-	-	-	-	-	-	-	-	-	-	16.6	8.2	14.4	15.3	19.0	15.0	7.4	7.5	11.5
Orbiculoidea rugata		-	-	-	-	-	-	-	-	-	-	-	-	3.8	-	-	-	4.4	12.9	-	-
Protochonetes ludloviensis		-	-	-	-	-	-	-	-	-	-	-	-	5.2	2.0	-	4.7	3.5	12.9	11.2	3.8
Salopina lunata		-	-	-	-	-	-	-	-	-	-	-	50.0	25.0	43.7	26.9	19.0	41.5	-	10.0	50.0
Bivalves																					
Fuchsella amygdalina		-	-	-	-	-	-	-	-	-	-	-	-	0.1	-	-	1.5	1.7	-	-	3.8
Goniophora cymbaeformis		-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.7	-	-	9.2	-	-
Leodispis barrowsi		-	-	-	3.0	-	-	-	-	-	-	-	-	-	-	2.7*	-	-	-	-	-
Modiolopsis complanata		5.2	-	-	87.8	-	-	3.8	13.5	10.5	-	5.5	-	-	-	-	-	-	-	-	-
Pterinea tenuistriata		-	-	-	-	-	-	-	-	-	-	-	-	0.1	-	-	-	-	-	-	3.8
Pteronitella retroflexa		-	-	-	-	-	-	-	-	-	-	-	-	0.4	-	5.1	-	1.7	-	0.2	-
Other molluscs																					
Hyolithes forbesi		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.5	-	-	-	-
Leurocycloceras sp.		-	-	-	-	-	-	-	-	-	-	-	-	0.8	2.0	-	3.1	-	-	0.2	3.8
Loxonema gregarium		-	-	-	-	-	-	-	2.7	-	22.2	-	-	-	-	-	-	-	-	-	-
Paraphragmites ibex		-	-	-	-	-	-	-	-	-	-	-	-	0.8	-	-	-	-	-	-	-
Bryozoan colonies																					
Ceramopora sp.		-	-	-	-	-	-	-	-	-	-	-	-	0.1	-	-	-	-	-	-	-
Leioclema sp.		-	-	-	-	-	-	-	-	-	-	-	-	1.2	2.0	-	-	0.8	3.7	0.8	7.6
Ostracods																					
Cytherellina siliqua		-	7.8	-	3.0	-	-	7.6	.3	-	11.1	16.6	-	-	-	-	-	-	-	0.8	-
Frostiella groenvalliana		10.5	-	-	3.0	-	-	30.7	.3	-	-	-	-	-	-	-	-	-	-	-	-
Hebellum cf. tetragonum		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-
Londinia kiesowi		-	7.8	-	-	-	-	-	.3	-	-	-	-	-	-	-	-	-	-	-	-
Neobeyrichia verrucosa		-	-	-	-	-	-	-	-	-	-	-	-	0.7	-	-	-	-	-	1.5	-
Thilipsura sp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-
Fish																					
Gomphonchus murchisoni		-	-	-	-	-	-	-	.3	-	-	-	-	-	-	-	-	-	-	-	-
Logania ludlowiensis		5.2	-	33.3	-	-	4.1	-	.6	21.0	11.1	-	-	-	-	-	-	-	-	-	-
Thelodus parvidens		-	2.6	-	-	-	-	-	-	10.5	-	-	-	7.3	-	-	-	1.7	-	46.1	-
Other fossils																					
Calcareous tubes		5.2	-	-	-	-	4.1	11.5	-	-	-	-	-	-	-	-	-	-	-	-	-
Crinoid columnals		-	-	-	-	-	-	-	-	-	-	-	-	3.8	-	-	-	4.4	12.9	-	-
Crinoid stems		-	-	-	-	-	-	-	-	-	-	-	-	29.6	35.4	43.5	49.2	22.1	33.3	12.2	15.3
Keilorites sp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-
Tentaculites tenuis		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.8	-
Number of fossils observed		19	38	3	33	31	24	26		19	9	18	6	1116	48	78	63	113	54	399	26
Bedding plane surface area examined (m^2)		2.0	1.9	1.4	0.8	1.5	1.7	1.4		1.1	1.6	0.7	0.5	0.6	0.1	0.1	0.1	0.1	0.1	0.1	0.2

Asterixed species abundance is for Nuculites antiquas

The Downtonian sediments consist of an interbedded sequence of buff lenticular bedded rubbly siltstones containing a typical Downtonian fauna (Table [illegible]) and two bone-beds near their base.

the more mature forms already present on the substrate, during their normal filter and suspension feeding activities. Since Silurian crinoids were also filter and suspension feeders (Haugh, 1978) it is possible that the observed (Fig. 5a) absence of juvenile forms could have resulted from the cannabalistic activities of the adults or alternatively their absence could suggest that the entire stems of the juveniles were uprooted during the storm and floated away aided by currents.

The crinoid ?species can be recognised from the stem fauna. One has pentagonal columnals. The other more abundant crinoid stem type has circular columnals and probably belongs to the Whitcliffian species Cicerocrinus elegans Sollas. Crinoid calyxa of this species occur rarely throughout the Whitcliffe Beds, They are always attached to a portion of stem (up to 10 cm in length) which has been broken off from its holdfast, possibly as the result of a storm similar to those whose effects on the substrate have just been described. The morphology of this crinoid species is illustrated in detail in Fig. 5c-e.

← INSERT

5. Brockton: Ludlow-Downton Boundary section.

Opposite (G.R. SO 579939) the Feathers Inn in a largely overgrown bank, the Ludlovian-Downtonian boundary is present (Robertson, 1927). The section (Fig. 2) dug out in August, 1977, had become overgrown by April, 1978. It consisted of a bone-bed facies separating a Whitcliffian-Brachiopod-Bivalve fauna (Table 9) contained within a sequence of calcareous lenticular bedded silts (indicating deposition in a tidally influenced environment) from a sequence of limonitic lenticular bedded and parallel laminate muddy silts containing a Downtonian fauna (Table 10). The Bone-Bed consists of a number of discontinuous (up to 60 cm in length) vertebrate sand lenticles rarely thicker than 5 mm in a lenticular bedded clayey silt. This silt contained a Downtonian fauna (Table 9) including a single specimen of T. helicites. Overlying this silt is a well laminated olive green silt containing both mini ripples and wrinkle marks and few fossils (Table 9 & 10). The sedimentary structures present in this latter sediment type suggest an intertidal mudflat depositional environment (cf. Singh & Wunderlich, 1978).

Table 9. Macrofossils from the Brockton section (opposite the Feathers Inn): Whitcliffian - Downtonian.

SPECIES	WHITCLIFFIAN	DOWNTONIAN
Brachiopods		
Howellella elegans	3.3	-
Lingula minima	-	5
Microsphaeridiorhynchus nucula	13.3	5
Orbiculoidea rugata	1.6	-
Protochonetes ludloviensis	3.3	-
Salopina lunata	60.0	15
Bivalves		
Fuchsella amygdalina	3.3	-
Modiolopsis complanata	6.6	50
Pteronitella retroflexa	6.6	-
Gastropods		
Cymbularia carinata	-	5
Loxonema gregarium	-	15
Turbocheilus helicites	-	5
Other fossils		
'Orthoceras' sp.	1.6	-
'Serpulites' sp.	1.6	-
Number of fossils observed	60	20
Bedding plane surface area examined (m^2)	1.2	3.4

Table 10. Microfossils from the Brockton section:Whitcliffian - Downtonian.

SPECIES	WHITCLIFFIAN	BONE-BED	DOWNTONIAN
Sample size/sediment weight	12/1 kg	493/20 gms	293/ 5 kg.
Gomphonchus tenuistriata	18.1	0·4	2.0
Logania ludlowiensis	54.5	49·2	43.6
Thelodus bicostatus	-	0·2	-
Thelodus parvidens	8.3	34·8	44.3
Thelodus trilobatus	-	0·2	0.3
Orbiculoidea rugata	-	1·4	2.7
Sclerodus sp.	-	0·2	-
'*Serpulites*'sp.	18.1	12·1	5.4

Note (Table 11) that the quartz grains contain crescentic abrasion pits indicating a possible intertidal environment of deposition (Krinsley & Dornkamp, 1973).

6. Netherton - Upper Whitcliffian - Basal Downtonian

The Ludlovian-Downtonian boundary has been described from the Tram Bridge Section at Saltwells (near Netherton, Birmingham - G.R. SO 936874) by King & Lewis (1012). The section they described consisted of 6.6 m of Upper Ludlow sediments overlain by 2.6 m of Downtonian sandstones.

They described the Upper Ludlow sediments as green calcareous sandstones containing thin limestone bands crowded with *P. ludloviensis* (*Chonetes striatella*), *P. minimus*, *M. nucula*, *L. lata*, *L. obsoletum*, *O. rugata*, *S. longissimus*, *C. serpularis* and *F. amygdalina*.

They noted a bone-bed 57.5 cm thick which was divisible into a basal impure limestone (10 cm thick), a calcareous sandstone rich in phosphatic pebbles (23 cm thick) and a bone-bed (3 cm thick) containing *P. ludloviensis*, *H. elegans*, *M. nucula*, *Lingula* sp., *L. obsoletum*, *Pachytheca* sp., *Onchus*, and *Thelodus*. They did not describe the fauna of the Downtonian sediments.

In this study the section was re-examined. It was largely overgrown, exposing only King & Lewis's Bone-Bed and the Upper Ludlow sediments. The section measured is described in Fig2.

The faunal composition of the two major lithological units present in the section is documented in Tables 12 and 13.

It is interesting to note that *Protochonetes minimus* was not recorded in this study, and that if the fauna recorded from the bone-bed facies had been observed at Ludlow it would have assigned to the Whitcliffian Stage (cf. Holland *et al*, 1963).

The mineral composition of the various layers in the measured section are listed in Table 14. Note that the Whitcliffian silts contain a micrite matrix, quartz and muscovite, while the bone-bed facies contains gypsum, haematite, feldspar, phosphorite, quartz, muscovite and clay pellets.

Table 11. Percent frequency occurence of selected surface features on quartz grains from the Brockton section as seen using a scanning electron microscope, based on samples of 50 grains per Unit

FEATURE	WHITCLIFFIAN	BONE - BED	DOWNTONIAN
Rounded outline	56	64	68
Angular outline	44	36	32
Breakage blocks	16	2	0
Euhedral form	2	10	0
Rounded edges	60	70	72
Crescentic chip marks	0	16	6
Impact pits	10	12	18
Etch Pits	12	14	10
Plastered surface	2	2	0
Overgrowths	2	2	8
Grooves and scratches	18	34	42
Cleavage plates	16	26	22

Table 12. Macrofaunas from the Upper Silurian sediments at Netherton.

SPECIES	WHITCLIFFE BEDS	BONE-BED FACIES
Brachiopods		
Lingula lata	0.09	-
Howellella elegans	0.27	-
Microsphaeridiorhynchus nucula	0.73	-
Protochonetes ludloviensis	22.85	1.11
Salopina lunata	59.26	6.66
Molluscs		
Hyolithes forbesi	-	1.11
Fuchsella amygdalina	14.37	-
Loxonema gregarium	-	8.88
Loxonema obsoletum	1.65	-
Other fossils		
Ceratiocaris sp.	-	64.44
Pachytheca sphaerica	-	17.77
Number of fossils observed	1085	90
Bedding plane surface area examined (m^2)	6	1.1

Table 13. Microfossils from the Netherton section. Sample positions are given with respect to the base of the Bone-bed facies. Whitcliffian samples weighed about 2 kg, Downtonian samples about 0.5 kg.

	SAMPLE POSITION (cm)									
SPECIES	-69	-59	-52	0	5	13	14	23	24	31
Foraminifera										
Hyperammina sp.	55.31	6.72	77.03	-	-	-	-	-	-	
Scolecodonts										
Arabellites sp.	38.27	-	0.74	-	-	-	-	-	-	
Oenonites cf. aspersus Hinde	2.12	-	-	-	-	-	-	-	-	
Ostracods										
Cavellina sp.	-	0.30	-	-	-	-	-	-	-	
Brachiopods										
Orbiculoidea rugata	4.25	0.60	-	-	0.57	0.94	-	-	-	
Gastropods										
Loxonema gregarium	-	0.30	-	-	-	-	-	-	-	
Annelids										
'Serpulites' sp.	-	4.28	22.22	2.13	0.43	-	-	-	-	
Crustacea										
Ceratiocaris sp.	-	0.30	-	1.87	1.58	-	-	-	4.55	
Fish										
Gomphonchus sp. (scales)	-	-	-	-	0.86	-	-	-	-	
Gomphonchus murchisoni	-	-	-	0.26	0.28	-	-	-	-	
Katoporus altatus	-	0.60	-	-	0.57	-	-	-	0.12	
Logania ludlowiensis	-	36.69	-	54.54	55.90	46.69	-	75.42	67.98	
Nosteolepis striata Gross	-	-	-	-	0.57	-	-	-	-	
Thelodus bicostata	-	-	-	-	0.14	-	-	-	-	
Thelodus costatus	-	-	-	-	8.64	-	-	-	5.66	
Thelodus parvidens	-	49.23	-	41.17	25.64	51.41	-	24.23	18.10	
Thelodus pugniformis	-	-	-	-	-	-	-	-	0.12	
Thelodus trilobatus	-	0.90	-	-	4.75	0.94	-	0.34	3.44	
Number of fossils counted	47	135	327	374	694	212	-	293	812	

Table 14. Mineral compositions of the sediment as determined by point counting (minimum 1,000 points counted) in the Netherton section.

	SAMPLE POSITION (cm)									
MINERAL	-69	-59	-52	0	5	13	14	23	24	31
Micrite	47.9	43.1	40.5	-	-	46.2	-	-	-	
Quartz	40.3	35.2	55.4	11.7	25.6	39.1	21.4	51.4	45.4	
Shell fragments	0.7	24.48	3.9	0.2	-	0.3	-	-	-	
Opaques	8.0	-	-	-	22.3	0.5	11.8	1.9	-	
Biotite	-	-	-	-	-	-	-	-	0.1	
Muscovite	2.9	0.1	1.2	0.1	0.1	0.2	0.1	-	-	
Clay pellets	-	-	0.1	-	0.6	0.9	0.1	-	-	
Clay matrix + organic debris	-	-	-	86.9	22.3	-	43.1	22.7	26.3	
Fish remains	-	-	-	0.3	11.1	6.7	16.5	11.1	9.9	
Phosphatic pebbles	-	-	-	-	1.9	5.4	0.1	-	1.0	
Gypsum	-	-	-	2.1	-	-	-	-	-	
Haematite	-	-	-	-	15.4	-	6.9	11.2	10.8	
Haematite pellets	-	-	-	-	0.1	-	-	-	-	
Orthoclase	-	-	-	-	0.2	0.3	-	0.8	1.7	
Andesine	-	-	-	-	-	0.1	-	-	-	
Albite	-	-	-	-	-	-	0.6	-	-	
Labradorite	-	-	-	-	-	-	-	0.2	-	
Glauconite	-	-	-	-	-	-	-	-	0.4	
Pores	-	-	-	-	-	-	-	-	4.1	

The section has recently been briefly described by Antia (1979c) and divided into three environmentally significant portions from base to top as follows:-

(1) 2^+m of olive green silts with rippled layers of comminuted shell fragments, which may have formed on an oxygenated $CaCO_3$ saturated sea floor accumulating calcareous shell material on its surface and SO_4^{2-} ions, formed as a result of normal decomposition processes, in the sediment.

(2) 5 cm of gypsum rich black clays, which formed on a relatively stagnant seafloor, during a temporary period in which the chemical and physical properties of the sea changed allowing an influx of oxygen rich bottom waters undersaturated with respect to Ca^{2+} and CO_3^{2-} to sweep the sea bottom, resulting in a calcium carbonate depletion of the underlying sediments and gypsum precipitation in the sediment (resulting from an oversaturation of the sediment porewaters in Ca^{2+} and SO_4^{2-} ions).

(3) 35 cm of silts, clays and sands enriched in phosphatic nodules and fish scales. The basal 10 cm also contains some gypsum. These sediments may indicate a persistence of the oxygen rich (Ca^{2+} and CO_3^{2-} poor) bottom waters. Such a condition would result in a higher primary and secondary plankton production and a higher organic contribution to the sediment. This increased organic contribution is considered to have altered the microenvironments of the subsurface sediment to produce an anoxic environment within a few centimetres of the aerobic sediment/water interface. Within the anoxic organic rich environment, organophosphates are thought to have formed, bound with, and replaced adjacent clays, to form soft phosphatic nodules, which could be excavated and concentrated on the sediment surface.

The abundant fish remains associated with the phosphate nodules may have resulted from an increase in the size of the fish population caused by the higher plankton concentrations of the overlying waters.

Lye: Ludlovian-Downtonian Boundary Section

The overgrown road section (G.R. 929845) at the Hayes, Lye, Birmingham, described by King & Lewis (1912), was examined and the faunas observed are documented in Table 15. Turner (1973) considered the supposed bone-bed horizon present in the section to be younger than the Ludlow Bone-Bed. This bone-bed consists of a quartz sand containing rare vertebrate remains, which is both rippled and discontinuous varying in thickness from 2 - 18 mm. It separates a sequence of Whitcliffian lenticular bedded calcareous silts from a sequence of parallel laminate and Downtonian rippled muddy silts (containing some wrinkle marks). However, the faunas present in the deposit neither confirm nor deny King & Lewis's correlation of this sand layer with the Ludlow Bone-Bed.

DISCUSSION

The Downtonian sediments immediately overlying the Ludlow Bone-Bed appear to be intertidal mudflat deposits (cf. Allen, 1974a ; Facies B). However, the change from carbonate rich Whitcliffian type sediments to limonite rich Downtonian type sediments cannot be attributed solely to the transition from a subtidal through to an intertidal environment, even though pyrite (which would later degrade to limonite) could be expected to occur in the latter environment (Greensmith and Tucker, 1976; Howarth, 1979). This is because studies on shell transport in recent intertidal zones (e.g. Lingwood, 1976; Antia, 1977) have shown that subtidal Whitcliffian brachiopods could be expected to occur abundantly in the Downtonian intertidal zone. This situation was clearly not observed (Tables 3, 4, 6, 7, 8, 9, 12) at the Ludlow-Downton transition, even though it occurs at a subtidal-intertidal transition in the Upper Whitcliffe Beds at Siefton (Antia, 1979a). This latter transition is contained within a sequence of micritic sediments.

Consequently it is suggested here that the Ludlow-Downton transition either represents a period where no onshore transport of shells occurred or alternatively

Table 15. Faunas across the Ludlow-Downton boundary at Lye.

SPECIES	TOP WHITCLIFFIAN	DOWNTONIAN
Brachiopods		
Lingula minima	-	38.4
Microsphaeridiorhynchus nucula	20.9	-
Protochonetes ludloviensis	26.7	-
Salopina lunata	48.8	-
Bivalves		
Fuchsella amygdalina	3.4	-
Plants		
Pachytheca sp.	-	61.5
Number of fossils counted	86	13

that the transition coincides with the postulated (Antia, 1979c) change in sea water composition. The latter hypothesis accounts for the observed change in faunas at the Ludlow-Downton transition and the changes at the boundary from (1) carbonate intertidal to limonitic intertidal sediments at Siefton (Antia, 1979a), (2) carbonate subtidal to limonitic intertidal sediments at Lye, Corton, Aston Munslow, Brockton and Shipton (Fig. 2), and (3) carbonate subtidal sediments to subtidal phosphatic black organic debris rich clays at the boundary at Netherton (Antia, 1979c), Longhope (Lawson, 1954), Priors Frome (Squirrell and Tucker, 1960), and Perton (Gardiner, 1927).

1. The Subtidal Downtonian environment.

Prior to the change in sea water composition the intertidal zone contained (Antia, 1979a) shells of *P. ludloviensis*, *C. implicata*, *H. elegans*, *M. nucula*, *S. lunata*, *M. complanata* and *L. gregarium*. After the change both *M. complanata* and *L. gregarium* became more abundant elements of this fauna, while the thick calcareous shelled invertebrates diminished and disappeared. *L. gregarium* became the dominant gastropod in the subtidal environments (cf. Antia, 1979c, 1979b; and Table 16), while in the intertidal environment the gastropods *C. carinata*, *T. helicites* and *'P'. williamsi* were also present (Tables, 3, 4, 6, 7, 8, 9). The latter species may well have lived in the intertidal environment, while the former species may have lived in the subtidal environment and been swept on shore by currents etc. A similar situation exists at the present time on the Essex Coast, where subtidal black organic rich silts contain a low diversity high density gastropod fauna (cf. Davis, 1965, Barnes & Coughlan 1971, 1972 and Antia, 1977), and the adjacent intertidal mudflat sediments contain a more diverse high density living gastropod fauna which has been enriched by dead gastropod shells transported on shore from an off shore life environment (Antia, 1977).

Other species inhabiting the subtidal environment after the change were the crustacean *Ceratiocaris* sp., the hyolith *H. forbesi* and the inarticulate

Table 16. Composition of phosphatic steinkerns in the black phosphatic clays of the basal Downtonian.

	LOCALITY		
SPECIES	NETHERTON	LONGHOPE	PRIORS FROME
Brachiopods			
Lingula sp.	-	20.0	4.5
Orbiculoidea rugata	17.0	20.0	0.9
Protochonetes sp.	-	-	0.9
Salopina sp.	-	-	1.8
Molluscs			
Bucanopsis expansus	-	-	2.7
Cymbularia carinata	-	-	4.5
Hyolithes forbesi	5.0	30.0	1.8
Loxonema gregarium	83.0	15.0	74.7
Nuculites cf. *ovata*	-	-	0.9
'*Orthoceras*' sp.	-	-	0.9
'*Platyschisma*' *williamsi*	-	-	1.8
Turbocheilus helicites	-	10.0	-
Other fossils			
Crinoid-stems	1.0	-	1.8
Pachytheca sp.	-	-	0.9
'*Serpulites*' sp.	4.0	5.0	-
Tentaculites sp.	-	-	1.8

brachiopods *O. rugata* and *Lingula* sp. The latter three species occur in this environment as phosphatic steinkerns. The common occurrence (Antia 1979c and Table 16) of *H. forbesi* is interesting since the species is a rare element of the underlying carbonate rich silts of the Whitcliffe Beds (cf. Holland *et al*, 1963). However, since hyoliths were probably motile benthic omnivorous deposit feeders feeding on detritus and micro organisms living on or just within the sediment/water interface (Marek & Yochelson, 1976, p77), possessing thin aragonite shells, the postulated environmental change which resulted in (1) a higher plankton productivity in the water column (2) a higher input of organic debris to the sediment and (3) a decrease in the carbonate content of the sea water, meant that (1) the hyoliths food supply increased exponentially with respect to their original population and (2) that there was insufficient Ca^{2+} and CO_3^{2-} ions in the water to allow competitors (cf. Holland *et al* 1963 Watkins, 1978) such as *Nuculites* spp. to grow, but sufficient Ca^{2+} and CO_3^{2-} ions to allow *H. forbesi* to grow up to 12 mm in length. The net result was that *H. forbesi* was presented after the sea water change with virgin territory for which it was admirably adapted. Like most other species in similar circumstances (cf. Valentine 1973) it seized the opportunity and became a dominant element of the fauna (Table 16).

Also contained within these dark muds at Netherton, Longhope and Priors Frome are closed articulated shells of two Lingulid species and *O. rugata* (Table 16) indicating that these species probably lived within or on the muds in which they are found. Neither of the Lingulid species are present in the Whitcliffian carbonate rich micritic sediments, although both may be assigned to typical Downtonian lingulid species, i.e. *L. minima* and *L. cornea*. The former species has also been recorded from the middle Ludlow of Estonia (Hoppe 1931). It is probable that both species had an entire ciliation of the cirri like the modern Lingulid, *L. unguis* as an adaptation to life in a muddy habitat (cf. Chuang, 1956) and a plankton trophic shelled embryo and larvae (cf. Chuang, 1977). It occurs in densities of between 150 and 250 per m^2 area. This figure is comparable with the recent densities of 230 lingulids per m^2 area recorded by Mattox (1955) in subtidal environments. Since the digestive system of brachiopods has remained essentially the same since the Lower Palaeozoic (Steele-Petrovic, 1976, p.433), these Silurian lingulids were probably lophophorate (Rudwick, 1970), ciliary feeders (Chuang, 1956) which fed on dissolved organic substances, bacteria and organic debris derived from the algae and plankton (cf. Steele-Petrovic, 1976). It is interesting to note that modern lingulids contain in their gut the enzymes amylase, sucrase, inulase, ruffinase, maltase, lactase, and methylcettulase (Chuang, 1959; Yokoe and Yasumasu, 1964). These enzymes degrade cellulose (Kristensen, 1972) and the contents of most algae, chrysophyta, euglenoids and bacteria (Meeuse, 1962; Kreger, 1962; Fowden, 1962; White et al, 1968; Kristensen, 1972).

The presence of O. rugata is interesting since Cocks and McKerrow (1978) consider that it lived cemented to the surface of algal fronds. However, Holland (1971) has demonstrated that it cemented to shells resting on the substrate surface. One specimen of the species at Ludlow museum (No. 453794) has two juveniles cemented onto its dorsal valve. Most commonly the species is found nestling on the surface of micritic silts in the Whitcliffian (e.g. Ludlow Museum No. SHRCM G103/73/5). The Downtonian forms are stunted and rarely reach 8 mm in diameter compared with 20 mm in the Whitcliffian. However, its presence on a wide range of substrates in the British Upper Silurian suggests that like its modern relatives its motile planktotrophic shelled larvae (cf. Chuang, 1977) could have settled on aerobic or anoxic substrates at a great range of depths (Mueller, 1861; Simroth, 1897, Yatsu, 1905; Eichler, 1911; Zezina, 1970; Chuang, 1977). It may also have inhabited a wide geographic area. For example a modern discininid Pelagodiscus atlanticus (King) occurs in the Pacific, Indian and Atlantic Oceans (Zezina, 1965; Cooper, 1973) and is known from both the Northern and Southern hemispheres. It has a wide depth tolerance since it has been recorded living at depths of 366 m (Thomson, 1927) and 6160 m (Zezina, 1970). At the present time discininids are found living in phosphatic black clays (D'Angelan, 1967) and are found in association with lingulids (Zezina, 1970).

The higher abundance of Ceratiocaris sp. is not surprising, since crustaceans are common inhabitants of black phosphatic muds at the present time (D'Angelan, 1967).

The higher density of fish remains in the sediment was probably a direct result of the postulated water composition change resulting in higher primary production and reduced biogenic carbonate sedimentation (cf. Antia, 1979c). Similar concentrations of fish debris in the sediment have been associated with increased plankton production and changed sea water chemistry (cf. Malz 1979a, b; Diester-Hauss & Schrader, 1979). The thelodont fish probably fed on plankton and algae in the overlying waters (Antia, 1979b). However, some of the rare toothed acanthodians (e.g. Isanthocanthus kingii) may have been carnivores.

The early Downtonian subtidal environment as presented by the Netherton section consisted of an anoxic organic rich mud with either an anoxic or an oxygenated sediment water interface (cf. Bruce, 1928; Antia & Wood, 1977; Degens et al, 1978). Within this mud both authigenic gypsum and phosphate formed (Antia, 1979c). The glauconite present (Table 13) may be authigenic (cf. Birch, 1979), but could equally well be allochthonous.

This mud contained an infauna of lingulid brachiopods and a sessile epifauna of O. rugata. The motile epifauna of H. forbesi, C. tenuistriata and L. gregarium probably grazed or reworked the sediment surface for food (Marek & Yochelson, 1976; Peel, 1977). Two other invertebrates ('Serpulites' sp. and Conodonts) whose remains are found in the sediments may have been sessile epifaunal filter feeders and motile detritivores respectively. It is interesting to note that the surface of these muds contained some noncalcareous blue green algal sheets in situ.

2. The intertidal Downtonian environment

The Downtonian intertidal environments consisted of a series of intertidal mudflat deposits and beach sands (Allen, 1974a, Antia, 1979 a, b; Antia & Whitaker, 1979). The mudflat deposits had a rippled surface and contained patches of rippled vertebrate sand (bone-beds) and fine quartz sand. The bone-beds probably formed as onshore migrating lag concentrates; similar to the transported shell sheets rich in the subtidal species P. ludloviensis present in the Upper Whitcliffian intertidal zones (Antia, 1979a) and the recent transported shell sheets of subtidal molluscs in modern intertidal environments (Antia, 1977).

They contain some abraded Whitcliffian brachiopod shells, which were probably derived from the local reworking of Whitcliffian sediments (cf. Greensmith & Tucker, 1967). However, most of the fish species and all of the phosphatic invertebrate remains (Table 2) contained within the bone-beds are present in the black clay Downtonian subtidal environment (Table 16) suggesting that a post mortem onshore migration of off shore faunas may have occurred in the Downtonian, and resulted in the formation of the bone-beds. At the present time onshore migrations of offshore faunas are commonplace and can form vast intertidal biogenic clastic deposits covering areas in excess of 5000 km^2 area (e.g. Byrne et al 1959 & Price 1959).

The mudflats contain in situ specimens of the endobyssate bivalve M. complanata and the shallow burrower L. barrowsi. This latter species was probably a rapid burrower adapted for life in shifting sediment (cf. Stanley, 1970). Both species probably had aragonitic shells and were suspension feeders. Other in situ species include the shallow burrower L. minima and the deeper burrower Solenomya sp. Plant debris is locally abundant in the zone and consists of small filaments 2 - 6 mm long and 0.3 - 1 mm wide. Some of these filaments are branched and contain reproductive bodies at the end of the branches (Plate 1c). They may have formed part of the flora in higher parts of the intertidal zone, or may alternatively represent drifted organic debris from a variety of ecological habitats.

The remaining gastropods (Tables 2, 5, 6, 7, 8, 11) probably also lived in the mudlfat environment. T. helicites, 'P'. williamsi and C. carinata were probably algal grazers, while L. gregarium was probably a detritivore (Peel, 1977). It is not known whether the L. gregarium in the intertidal environment is the same species as the one in the subtidal environment as Hannford-Ellis (1978, 1979) has shown that different recent gastropod species belonging to the same genus can have the same external morphology.

Microbial organisms and borings have been recorded from the vertebrate sands (Antia & Whitaker, 1979; Antia, 1979b). Borings on the Thelodont scales . . .

, are more common in the intertidal bone-bed deposits than in the subtidal clays suggesting that either (1) the boring organism preferred to live in the intertidal or (2) reflecting a longer residence time on the sediment surface for the thelodont scales in the bone-beds.

Ostracods are relatively uncommon in both the Whitcliffian micrites (and the Downtonian subtidal black clays (Tables 1, 6, 7, 8, 11, 12), but extremely abundant in the intertidal Downtonian sediments (Tables 2, 6, 7,8, 11, 12). This feature is interesting because it suggests that the presence of Ca^{2+} and/or CO_3^{2-} ions may have adversely affected both their abundance and diversity in the Whitcliffian. Their absence from the Downtonian black clays may be a consequence of (1) a low O_2 water content immediately above the sediment-water interface, (2) poor preservation caused by shell dissolution after death and (3) a high PO_4^{2-} content in the underlying muds. It is interesting to note that many recent ostracods prefer environments containing Ca^{2+} ions in concentrations of 90 - 100 ppm (Delforme, 1971) and that PO_4^{2-} concentrations in excess of 1 ppm adversely affect their diversity and abundance (Delforme, 1971) similar observations have been made with respect to Cl^- and CO_3^{2-} ions (Delforme, 1971; Kaesler, 1975).

Since the average carbonate saturated environment could expect to contain in excess of 600 ppm Ca^{2+} (cf. Bathurst, 1975) it perhaps is not surprising that ostracods are rare in the Upper Whitcliffian environments examined. The low Ca^{2+}, CO_3^{2-} and PO_4^{2-} contents of the Downtonian intertidal zone may have presented a more favourable environment for the ostracods.

If as Antia (1979a) suggests the change in water geochemistry was brought about by the effect of transgressing fluvial fresh water on the Silurian sea then variations in the concentrations of Cl^{2-} ions would probably be a dominant factor in determining the distribution and size of the ostracod faunas (Barker, 1963; Delforme, 1971; Kaesler, 1975). In such a situation pynchnocline could have developed above the sea floor (cf. Degens et al, 1978) and allowed a restricted marine fauna to live on and in the sediment. The organisms living in the overlying waters and adjacent coast may then have been euryhaline and oligohaline forms. However, the evidence of an onshore migration of subtidal biogenic debris from the black clays mitigates against the suggestion of a pynchocline in the early Downtonian sea.

It is interesting to note that the geochemical change in sea water composition affected the Long Mountain at a later time than the Ludlow District (Palmer, 1972). A possible explanation of this is that the geochemical changes in both regions resulted from the effects of two different fluvial systems. In this instance differing chemical conditions could be expected in both environments. Such differing conditions would affect the morphology of individual ostracods and could result in the presence of a number of different morphotypes for the same phenotype (Kaesler, 1975). One such example may be the ostracod Londinia. Three species have been recorded from the basal Downtonian sediments of the Welsh Borderlands. They are L. arisaigensis Copeland, L. fissurata Shaw and L. lata Shaw. Martinson (1967) considered that L. arisaigensis may be intraspecific with L. kiesowi (Krause) and recorded L. cf. kiesowi from the Welsh Borderlands

Siveter (oral communication 1977, 1978) considers L. lata to be intra specific with L. fissurata. The holotype of L. fissurata figured by Shaw (1969) and Siveter (1974, 1978) is morphologically identical to L. kiesowi (Krause) illustrated by Martinsson (1964), it could be suggested that the three British Londinia spp. are morphotypes of the L. kiesowi phenotype. This is the approach which has been adopted in the faunal identifications presented here.

The British Downtonian species L. kiesowi had at least six instars (Fig. 6) with its adductorial sulcal length (z)/height(H) ratio decreasing with increasing age (Fig. 7). The published z/H ratio range for the various Londinia morphotypes is presented in Fig. 7. It is interesting to note that the z/H ratio of the adult can have a wide range and can have a lepto or platykurtosic frequency distribution (Fig. 7).

The z/H ratio range covered by any one Downtonian population of L. kiesowi covers the theoretical z/H ratios of the morphotypes L. arisaigensis, L. lata, and L. fissurata. The observed frequency variation of this ratio in the adult (Fig. 7) may be either a preservation effect or may be a reflection of slightly different chemical concentrations at the two locations examined.

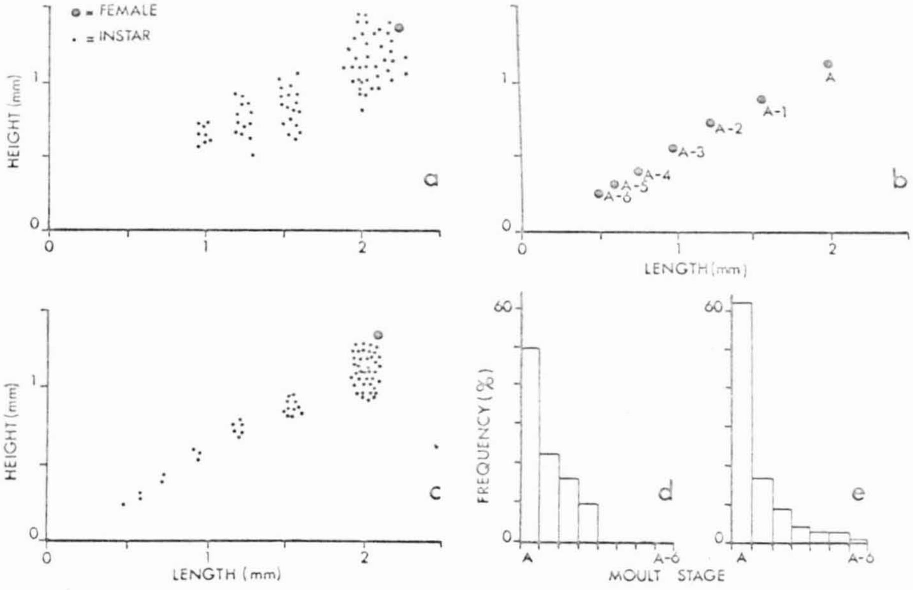
CONCLUSIONS

Faunas and sediments from seven Ludlovian-Downtonian boundary sections have been examined. They appear to support the hypothesis that this boundary coincides with a major change in sea water geochemistry at the end of the Ludlovian (Antia, 1979 a, c)

At the end of the Whitcliffian the sea supported a benthic fauna of sessile articulate brachiopods and other invertebrates on a micrite substrate. The Whitcliffian intertidal fauna was dominated by transported shells belonging to the subtidal environment.

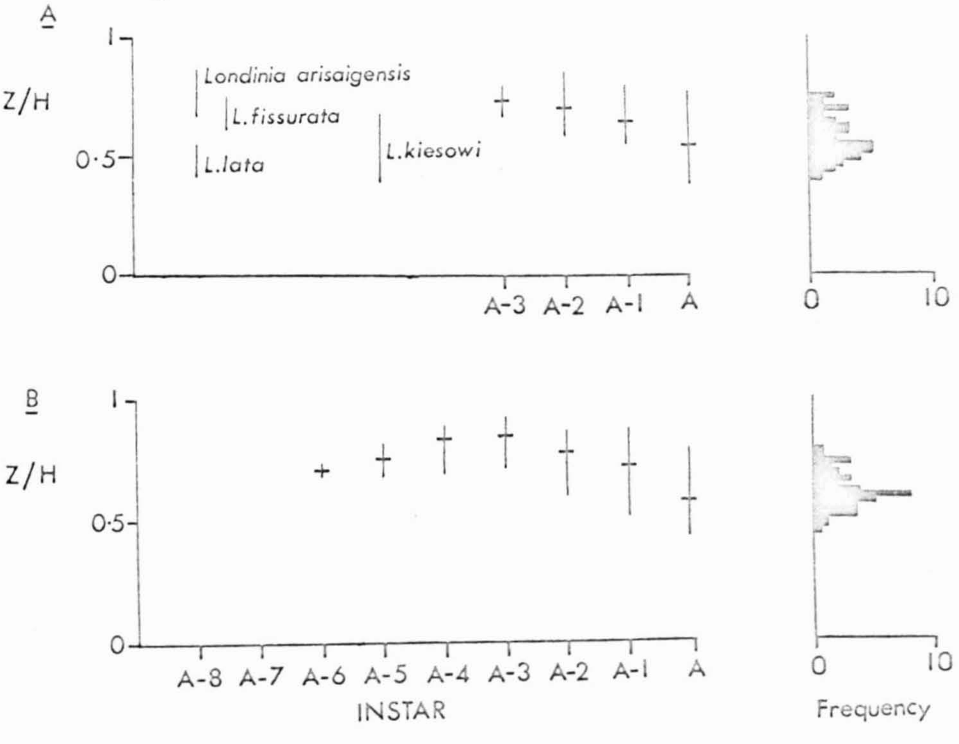
The early Downtonian sea deposited carbonaceous muds supporting a low diversity benthic fauna of inarticulate brachiopods hyoliths and gastropods, and a high diversity necktonic planktonic fauna of fish. The Downtonian intertidal zone supported a benthic fauna of bivalves, gastropods and inarticulate brachiopods and contained vertebrate sands (bone-beds) composed of faunal debris which had been derived from the subtidal environment.

Fig.6



Londonia kiesowi (Krause) (a) Length/height plot for specimens collected from the basal Downtonian at Kerry (G.R. SO 158 847). (b) Probable length/height positions of each instar, (c) length/height plots for specimens collected from the basal Downtonian at Ludlow, (d) Frequency (%) occurrence of each moult stage at Kerry, (e) Frequency (%) occurrence of each moult stage at Ludlow.

Fig.7



Z/H ratios/instar number for Londina kiesowi at (A) Kerry, (B) Ludlow the frequency histograms refer to the ratios frequency distribution on the ? Adult moult.

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REFERENCES

Aldridge, R.J. 1975 The stratigraphic distribution of conodonts in the British Silurian. Jl.Geol.Soc.Lond., 131, 607 - 618.

Allen, J.R.L. 1974a Sedimentology of the Old Red Sandstone (Siluro - Devonian) in the Clee Hills area, Shropshire, England. Sediment.Geol., 12, 73 - 167

Allen, J.R.L. 1974b Studies in fluviatile sedimentation: implications of pedogenic carbonate units, Lower Old Red Sandstone, Anglo-Welsh outcrop. Geol.J., 9, 181 - 208

Antia, D.D.J. 1977 A comparison of diversity and trophic nuclei of live and dead molluscan faunas from the Essex Chenier Plain, England. Paleobiology, 4, 404 - 414.

Antia, D.D.J. 1979a Comments on the faunas and environments across the Ludlow - Downton boundary (Upper Silurian) at Siefton, Salop. Geol.J. vol 14, p 127-134.

Antia, D.D.J. 1979b Bone-Beds: a review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology weathering, and microbiotas. Mercian Geol., 7, 93 - 174.

Antia, D.D.J. 1979c Authigenic gypsum in marine sediments - a comment. Marine Geol., 31, M1 - M4.

Antia, D.D.J. 1979d On the recognition of abrasive rounding versus rounding by cryptocrystalline silica. - a discussion contribution. In W.B. Whalley (ed.) Scanning electron microscopy in the study of sediments. GeoAbstracts, Norwich. pp. 135 - 136

Antia, D.D.J. & Whitaker, J.H.McD. 1979 A scanning electron microscope study of the genesis of the Upper Silurian Ludlow Bone Bed. In W.B. Whalley (ed.) Scanning electron microscopy in the study of sediments. GeoAbstracts, Norwich. pp. 119 - 134.

Antia, D.D.J. & Wood, B.A. 1977 Some aspects of the palaeoecology of the E_1b zone of the Edale Shales (Namurian) in the Edale Valley, Derbyshire. Mercian Geol., 6, 174 - 196

Barker, D. 1963 Size in relation to salinity in fossil and Recent euryhaline ostracodes. J.Mar.Biol.Ass.U.K., 43, 785 - 795.

Barnes,R.S.K. & Coughland,J. 1971 A survey of the bottom fauna of the Blackwater Estuary:1970.Essex Nat., 32 , 263 - 276.

Barnes,R.S.K. & Coughland,J. 1972 The bottom fauna of the Blackwater Estuary. Essex Nat., 33 , 15 - 31.

Bathurst,R.G.C. 1975 Carbonate sediments and their diagenesis. Elsievier,Amsterdam. 658 p.

Birch,G.F. 1979 The nature and origin of mixed apatite/glauconite pellets from the continental shelf off South Africa. Marine Geol., 29 , 313 - 334.

Bruce,J.R. 1928 Physical factors on the sandy beacon.Part III Chemical changes - carbon dioxide concentration and sulphides. J.Mar.Biol.Ass.U.K., 15 ,553 - 563.

Byrne,J.V.,Leroy,D.O.,Riley,C.M. 1959 The chenier plain and its stratigraphy, southwestern Louisiana. Trans.Gulf Coast Ass.Geol.Soc., 9 ,237 - 259.

Chuang,S.H. 1956 The ciliary feeding mechanisms of Lingula unguis (L) (Brachiopoda). Proc.Zool.Soc.Lond., 127 , 167 - 189.

Chuang,S.H. 1959 The breeding season of Lingula unguis. Biol.Bull., 117 , 202 - 207.

Chuang,S.H. 1977 Larval development in Discinisca (Inarticulate B Brachiopod). Amer.Zool., 17 , 39 - 53.

Cooper,G.A. 1973.Verma's Brachiopoda (Recent).Smithsonian Cont. Paleobiol., No.17, 51p.

D'Anglejan,B.F. 1967 Origin of marine phosphorites off Baja, California. Marine Geol., 5 , 15 - 44

Davis,D.S. 1965 A study of the bottom fauna of the Blackwater Estuary:1960 - 1963. Central Electricity Res.Lab. Rep. No RD/L/R1300, 54p.

Degens,E.T.,Stoffers,P.,Golubic,S., & Dickman,M.D. 1978 Varve chronology: estimated rates of sedimentation in the Black Sea Deep Basin. Initial Rep. Deep Sea Drilling Project , 42 , 483 - 488.

Delforme,L.D. 1971 Palaeoecological determinations using Pleistocene freshwater ostracods. Bull.Centre Rech. Pau - SNPA , 6 supl., 341 - 347.

Diester - Haass,L. & Schrader,H.-J. 1979 Neogene coastal upwelling history of northwest and southwest Africa. Marine Geol., 29 , 39 - 54.

Eichler,P. 1911 Die Brachiopoden der Deutschen sued polar expedition 1901 bis 1903. Deutsche Suedpolar - Expedition 1901 - 1903 Bd.12. Zoologie, 4 , 381 - 401.

Fowden,L. 1962 Amino acids and proteins. In Lewin,R.A. (ed.) Physiology and biochemistry of algae.Academic Press, London, 189 - 210.

Franzen,C. 1977 Crinoid holdfasts from the Silurian of Gotland. Lethaia, 10 , 219 - 214.

Gardiner,C.I. 1927 The Silurian Inlier of Woolhope,Herefordshire. Q.Jl.Geol.Soc.Lond., 83 , 501 - 530.

Greensmith,J.T. & Tucker,E.V. 1967 Morphology and evolution of inshore shell ridges and mudmounds on modern intertidal flats, near Bradwell,Essex. Proc.Geol.Ass., 77 , 329 - 346.

Greensmith,J.T. & Tucker,E.V. 1976 Major Flandrian transgressive cycles, sedimentation and palaeogeography in the coastal zone of Essex,England. Geol.Mijnbouw , 55 , 131 - 131 - 141.

Hannaford - Ellis,C.J. 1978 Littorina arcana sp. nov.: a new species of winkle (Gastropoda:Prosobranchia:Littorinidae) J.conch.Lond., 29 , 301.

Hannaford - Ellis,C.J. 1979 Morphology of the oviparous rough winkle; Littorina arcana Hannaford -Ellis,1978, with notes on the taxonomy of the L.saxatilis species complex (Prosobranchia,Littorinidae).J.Conch.Lond., 30 , 43 - 56.

Haugh,B.N. 1978 Biodynamic and phyletic paradigms fo sensory organs in camerate crinoids. Lethaia , 11 , 145 - 174.

Holland,C.H. 1971 Some conspicuous participants in Palaeozoic symbiosis. Sci.Proc.R.Soc.Dublin,Ser.A. , 4 (2) , 15 - 26.

Holland,C.H.,Lawson,J.D., & Walmsley,V.G. 1963 The Silurian rocks of the Ludlow District,Shropshire.Bull.Brit.Mus.(Nat.Hist.) Geol., 8 , 95 - 171.

Hoppe,K. - H. 1931 Die Coelolepiden und Acanthodier des Obersilurs der Insel Osel.Palaeontographica, 76 , 35 - 94.

Howarth,R.W. 1979 Pyrite:Its rapid formation in a salt marsh and its importance in ecosystem metabolism. Science, 203 , 49 - 51

Kaesler,R.L. 1975 Morphology of Cypridopsis vidula (O.F.Muller): variation with environment.Bull.Am.Pal., 65 , 225 - 244.

King,W.W. & Lewis,W.J. 1912 The uppermost Silurian and Old Red Sandstone of South Staffordshire. Geol.Mag., 49 , 437 - 443,484 - 491.

Kreger,D.R. 1962 Cell walls In Lewin,R.A.(ed.) Physiology and biochemistry of Algae. Academic Press, London. pp. 315 - 316.

Kristensen,J.H. 1972 Carbohdrases of some marine invertebrates with notes on their food and on the natural occurrence of the carbohydrates considered. *Mar.Biol.*,**14**,130 - 142.

Lawson,J.D. 1954 The geology of the May Hill inlier. *Q.Jl.Geol.Soc. Lond.*, **111** , 85 - 116.

Lingwood,P.E. 1976 *The biostratinomy of some recent Molluscan Communities in Liverpool Bay*.Ph.D. Thesis,Liverpool University.

Malz,H. 1978a Massengrab fossiler Ohrsteine.*Umschau* **78**,**1**,27 - 28.

Malz,H. 1978b Aquitane Otolithen-Horizonte im Untergrund von Frankfurt am Main. *Senckenberg. Lethaia*,**58**,451 - 470.

Marek,L. & Yochelson,E.L. 1976 Aspects of the biology of the Hyolitha (Mollusca).*Lethaia*,**9**,65 - 82.

Marsh,R. 1976 *Silurian stratigraphy and mineralogy in the Welsh Borderlands and Central Wales*.Ph.D. thesis,Leicester University.

Martinsson,A. 1964 Palaeocope ostracodes from Well Leba 1 in Pomerania.*Geol.Fören.Stock.Förhan.*,**87**, 109 - 138.

Martinsson,A. 1967 The succession and correlation of ostracode faunas in the Silurian of Gotland. *Geol.Fören. Stock.Forhan.*, **89** , 350 - 386.

Mattox,N.T. 1955 Observations on the brachiopod communities near Santa Catalina Is.. *In* *Essays in Natural Sciences in Honor of Capt. Allan Hancock*. Univ. California Press pp. 73 - 86.

McCammon,H.M. 1969 The food of articulate brachiopods. *J.Paeont.*, **43** , 976 - 985.

McCammon,H.M. & Reynolds,W.A. 1972 Implication of the brachiopod lophophore as an organ of nutrient assimilation.*Abst.Geo Geol.Soc.Amer.*, **4** , 587.

McKerrow,W.S. 1979 Ordovician and Silurian changes in sea level. *Jl.Geol.Soc.Lond.*,**136**,137 - 145.

Meeuse,B.J.D. 1962 Storage products. *In* Lewin,R.A.(ed.) *Physiology and Biochemistry of Algae*.Academic Press.Lond. 289 - 314.

Mueller,F. 1861 Die Brachiopodenlarvae von Santa Catharina.*Zweiter Beitrag.Arch.Naturgesch.*,**27**,53 - 56.

Robertson,T. 1927 The highest Silurian rocks of the Wenlock district. *Mem.Geol.Surv.Summ.Prog. for 1926.*,80 - 97.

Peel,J.S. 1977 Systematics and Palaeoecology of the Silurian gastropods of the Arisaig Group,Nova Scotia.Biol.Skr.,21, 89p.

Shaw,R.W.L. 1969 Beyrichiacean ostracodes from the Downtonian of Shropshire.Geol.Fören.Stock.Förhan., 91 , 52 - 72.

Simroth,H.1897 Die Brachiopoden der Plankton-Expedition.Eryeba. Plankton - Exped.,2,3 - 17.

Siveter,D.J. 1974 The superfamily Beyrichiacea (ostracoda) from the Silurian and Devonian systems of Britain. Ph.D.thesis,Leicester University.

Siveter,D.J. 1978 The Silurian. In Bate,R. & Robinson,E.(ed.) A stratigraphical index to British ostracoda.Geol.J. spec. Issue No.8, 57 - 100.

Squirrel,H.C. & Tucker,E.V. 1960 The geology of the Woolhope inlier (Herefordshire).Q.Jl.Geol.Soc.Lond.,116,139 - 185.

Stamp,L.D. 1920 Note on the determination of the limit between the Silurian and Devonian systems.Geol.Mag., 52, 164 - 171.

Stamp,L.D. 1923 The base of the Devonian with especial reference to the Welsh Borderlands.Geol.Mag.,60,276-282,331-336,367-372,385-410.

Stanley,S.M. 1970 Relation of shell form to life habits of the Bivalvia (mollusca).Geol.Soc.Am.Inc.Mem.,125.

Thomson,J.A. 1927 Brachiopod morphology and genera (Recent and Tertiary).New Zealand Board of Science and Art, Manual. No. 7, 388p.

Turner,S. 1973 Siluro-Devonian thelodonts from the Welsh Borderland. Jl.Geol.Soc.Lond.,129,557 - 584.

Valentine,J.W. 1973 Evolutionary paleoecology of the marine biosphere. Prentice-Hall,New Jersey. 510p.

White,A.,Handler,P., & Smith,E.L. 1968 Principles of Biochemistry. McGraw Hill. 1187 p.

White,D.E. & Coppack,B.C. 1978 A new section showing the junction between the Ludlow and Downton Series in the Much Wenlock area,Shropshire. Bull.Geol.Surv.G.B. No.62,25 - 32.

Yatsu,N. 1902 On the development of Lingula anatina. J.Coll.Sci. Tokyo., 17, 1 - 112.

Yokoe,Y. & Yasumasu,I. 1964 The distribution of cellulase in invertebrates.Comp.Biochem.Physiol.,13,323 - 338.

Zezina,O.N. 1965 The distribution of the deepwater brachiopod genus species Pelagodiscus atlanticus (King). Okeanologiya, 5, 345 - 358.

Zezina,O.N. 1970 On the distribution of brachiopods in recent oceans with some reference to the problem of zoogeographical zonation.Paleont.Zhurnal.(2),3 - 17.

ADDITIONAL REFERENCES

Cocks,L.R.M. & W.S.McKerrow 1978. In McKerrow,W.S. (ed.) The ecology of fossils.

Rudwick,M.J.S. 1970. Living and fossil Brachiopods.

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Letter Section

AUTHIGENIC GYPSUM IN MARINE SEDIMENTS — A COMMENT

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In a recent paper, Briskin and Schreiber (1978) noted the occurrence of authigenic tabular gypsum crystals in marine sediments. Their model for its formation suggested that it formed on a relatively stagnant seafloor during a short period in which oxygen-rich bottom waters undersaturated with respect to Ca^{2+} and CO_3^{2-} swept the sea bottom.

They suggest that initially the ($CaCO_3$ saturated) seafloor accumulated calcareous shell material (mainly planktonic and benthic foraminifera) on its surface and SO_4^{2-} ions (formed as a result of normal post-mortem decomposition processes) in the sediment; and that the influx of oxygen-enriched, calcium-carbonate-depleted bottom waters to this seafloor would result in (1) a calcium-carbonate depletion of the sediments and (2) gypsum precipitation in the sediment (resulting from an oversaturation of the sediment porewaters with respect to Ca^{2+} and SO_4^{2-} ions).

If this oxygen-rich bottom water persists for any length of time, a higher primary and secondary planktonic production and hence a higher organic contribution to the sediment should result. This increased organic input may alter the sediment microenvironments to produce an anoxic environment a few centimetres below the aerobic sediment/water interface (cf. Baturin, 1971; Burnett, 1974). Within this anoxic, organic-rich environment it is probable that organophosphates will form (cf. Summerhayes, 1973; Emsley and Hall, 1976) and that these organophosphates will bind with and eventually replace the adjacent clays (Antia and Whitaker, 1978) and form soft phosphatic nodules which can be excavated and concentrated in the sediment (Baturin, 1969, 1971). Also as a result of the higher plankton concentrations, the fish population should increase in size and may leave abundant remains in the sediment (cf. Malz, 1978).

Although Briskin and Schreiber (1978) do not describe this latter phosphatic extension of their model, there is some evidence for it in the geological column.

Near Birmingham in the Dudley Canal section at Netherton (British National Grid Reference SO 936874) there is an Upper Silurian (Whitcliffe Beds, Ludlow Series) sequence which may be described from base to top as follows:

2⁺m	Olive green silts with rippled layers of commutated shell fragments rich in foraminifera (about 2 per g of sediment).
5 cm	Gypsum-rich black clays.
35 cm	Silts, clays and sands enriched in phosphatic nodules and fish scales. The basal 10 cm also contains some gypsum.

The occurrence of the gypsum-rich layer marks three important changes in the faunas and mineralogy of the section (Table I).

(1) Below the gypsum layer the sediment is enriched in calcite, while in the layer and above, clays, quartz and phosphate dominate the sediment and calcite is absent.

(2) The fish fauna and phosphatic nodules become abundant above the gypsum layer.

TABLE I

The Netherton section

	1	2	3
Mineralogy			
Calcite	A	—	—
Quartz	C	C	VC
Chlorite (+ other clays)	—	A	VC
Gypsum	—	FC	R
Phosphate	—	—	VC
Macrofossils			
Fuchsella amygdalina	C*	—	—
Protochonetes ludloviensis	C*	—	—
Salopina lunata	VC*	—	—
Ceratiocaris sp.	—	—	P
Loxonema gregaria	—	—	A
Hyolites forbesi	—	—	FC
Orbiculoidea rugata	—	—	P
Microfossils			
Foraminifera	A	—	—
Ostracods	R	—	—
Vertebrates			
Thelodus spp.	—	VC*	A
Logania ludlowiensis	—	C*	FC—P
Acanthodian scales and spines	—	R*	R
Algae			
Pachytheca sp.	—	—	P
organic debris	—	A	C

1 = olive-green carbonate sediment; *2* = gypsum layer; *3* = phosphatic clays, silts and sands; only the major elements are listed here. *A* = Abundant (>50%); *VC* = Very Common (30—50%); *C* = Common (20—30%); *FC* = Fairly Common (10—20%); *P* = Present (4—10); *R* = Rare (< 4%); * = low density.

(3) The calcareous macroinvertebrate fauna above (as determined from phosphatic casts and moulds) the gypsum layer differs from that below (Table I).

If the expanded Briskin and Schreiber (1978) model is used to interpret these sediments, it could be suggested that:

(1) The olive-green carbonate sediments containing a *Salopina* community fauna (Calef and Hancock, 1974) and a high-density foraminifera assemblage represent a quiet, soft-bottom environment (Fursich and Hurst, 1974) in which the bottom waters were saturated or supersaturated with respect to calcium carbonate.

(2) The gypsum-rich clays contain a rare fauna of fish scales and abundant tabular gypsum crystals in an organic-debris-rich clay. Thin sections show the sediment to be draped over the crystals, suggesting either early in-situ diagenetic growth or predepositional crystal growth. The absence of calcite and presence of gypsum crystals in organic-rich clays may result from a change in the chemistry of the depositional bottom waters to an oxygen-rich, and calcium-carbonate-depleted bottom water; resulting in the solution of calcium carbonate and combination of Ca^{2+} ions (from $CaCO_3$ breakdown) and SO_4^{2-} ions (from the breakdown of biogenic organic debris) to form gypsum. The high concentration of organic debris in the sediment may indicate an increased plankton population and/or a change in chemistry of the sediment porewaters.

(3) The phosphatic sediments contain gypsum and phosphatic nodules in their clay layers and large quantities of fish scales. This sediment might have arisen from a prolonged period of calcium-carbonate-depleted, oxygen-rich waters sweeping the seafloor and removing calcareous debris (by solution). The phosphatic nodules might have formed by the processes already outlined and the fish debris might result from the mortality of fish schools feeding on the plankton (cf. Antia, 1979; Malz, 1978).

If, as has been suggested here, the Briskin and Schreiber (1978) model can result in a marine phosphorite deposit overlying a gypsum deposit, then it may provide an alternative explanation for the genesis of some phosphorites and phosphatic bonebeds to the traditional explanation of formation in regions of upwelling currents (cf. McKelvey, 1967).

ACKNOWLEDGEMENTS

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REFERENCES

Antia, D.D.J., 1979. Bone-beds: a review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering and microbiotas. Mercian Geol., 7(2): 93—174.

Antia, D.D.J. and Whitaker, J.H.McD., 1978. A scanning electron microscope study of the genesis of the Upper Silurian Ludlow Bonebed. In: B. Whalley (Editor), Scanning Electron Microscopy in the Study of Sediments. Geobooks, Norwich.

Baturin, G.N., 1969. Authigenic phosphate concretions in recent sediments of the South West African Shelf. Dokl. Earth Sci. Sections, 189: 227—230.

Baturin, G.N., 1971. Stages of phosphorite formation on the seafloor. Nat. Phys. Sci., 232: 61—62.

Briskin, M. and Schreiber, B.C., 1978. Authigenic gypsum in marine sediments. Mar. Geol. 28: 37—49.

Burnett, W.C., 1974. Phosphorite Deposits from the Seafloor off Peru and Chile. Radiochemical and Geochemical Observations Concerning their Origin. Thesis, University of Hawaii, 164 pp. (unpublished).

Calef, C.E. and Hancock, N.J., 1974. Wenlock and Ludlow marine communities in Wales and the Welsh Borderlands. Palaeontology, 17: 779—810.

Emsley, J. and Hall, D., 1976. The chemistry of phosphorous. Harper and Row, London, 563 pp.

Fürsich, F.T. and Hurst, J.M., 1974. Environmental factors determining the distribution of brachiopods. Palaeontology, 17: 879—900.

Malz, H., 1978. Aquitance Otolithen-Horizonte im Untergrund von Frankfurt am Main. Senckenbergiana Lethaea, 58: 451—471.

Summerhayes, C.P., 1973. Distribution, origin and economic potential of phosphatic sediments from the Agulas Bank, South Africa. Trans. Geol. Soc. Afr., pp. 271—277.

McKelvey, V.E., 1967. Phosphate deposits. U.S. Geol. Surv. Bull., 1252-D: 1—21.

7

The Temeside Bone-Bed: An analysis of its occurrence and environmental significance in the late Silurian - early Devonian marine regression in Wales and the Welsh Borderlands

by

David D. J. Antia

Summary

The type section of the Temeside Bone-Bed in the Ludlow region has been documented and is thought to have been deposited in a high intertidal marine environment. The transition, both sedimentological and faunal, from the top Ludlovian into the higher Downtonian has been examined in the Builth Wells, Kerry, Ludlow and Longmountain districts in order to place the Temeside Bone-Bed in its overall environmental situation.

Some recent ostracods from the intertidal zone of Sales Point, Bradwell, Essex are also discussed.

Introduction

The Temeside Bone-Bed was first recorded at Ludlow (G.R. SO 520 742) by Murchison (c. 1850-1854; 1856) and later by Elles and Slater (1906). This latter paper termed the deposit the Temeside Bone-Bed and suggested that it also occurred at Onibury (SO 457 795) and at Downton (SO 444 742). Since then Turner (1973) has claimed that it is present in the now inaccessible Ludlow Railway cutting section (cf. Murchison 1850-1854; also Text-Fig. 1c) and King and Lewis (1912) have recorded it at Birmingham in now inaccessible canal sections.

In this study the type section of the Temeside Bone-Bed at Ludlow and the nearby section at Onibury are examined, and placed in their environmental setting. The faunas and sediments ranging from the upper Ludlovian into the Temeside Formation (Upper Silurian) near Kerry, the Long Mountain and Builth Wells are also examined in an attempt to determine why the Temeside Bone-Bed is absent from these regions.

The general stratigraphy of the British Upper Silurian is summarised in Table 1, and the region studied indicated in Text-Fig. 2.

Although it is a widely held belief that the Temeside Formation is always present (cf. Robertson, 1927; Allen, 1974a), it appears to be absent at Ludlow, where the Ledbury Formation rests directly on the Downton Castle Formation (cf. Murchison, 1850-1854; Also Text-Fig. 1a) and at Downton (SO 456 742). Here, the Downton Castle Formation consists of micaceous buff sandstones Text-fig 2 pt a,b containing mega-ripples (wavelength 0.5 - 10 m; amplitude 5 - 50 cm) with secondary ripples, interference ripples and sand volcanoes superimposed on their surface (Text-Fig. 3 pt e-i). Small patches of vegetable debris containing Nematophyton sp., Prototaxites sp. and Pachytheca sp. are present in the ripple troughs. The pachythecids are well sorted and dominated by individuals of differing modal sizes in different vegetable patches (Text-Fig. 3 pt c,d) suggesting that they may have been transported into the sandstone environment.

The overlying red clays of the Ledbury Formation appear to rest conformably on the underlying sandstones. They contain no distinct lamination and some

Table 1. The stratigraphy of the British Upper Silurian in the type area (after Elles & Slater, 1906; Holland *et al*, 1963; Copeland, 1964; Kaljo, 1978; Antia, 1979a)

SYSTEM	SERIES	STAGE	FORMATION	ZONES			
				1. Ostracod	2. Conodont	3. *Lingula*	4. Fish
SILURIAN	Downton	Not assigned	Ledbury	*Aparchites* sp.	*Ozarkodina remscheidensis*	*Lingula* cf. *missendenensis*	*Logania* - *Thelodus* - *Hemicyclaspis*
			Temeside	*Hermannia*-*Londinia*	*Ozarkodina eosteinhornensis*	*L. cornea*	*Logania* - *Thelodus*
						L. minima	
			Downton Castle	*Frostiella* - *Londinia*			*Thelodus* - *Logania* - *Gomphonchus*
	Ludlow	Whitcliffe	Upper Whitcliffe Beds	*Calcaribeyrichia torosa*		*L. lata* - *Lingula* sp. nov.	*Thelodus* - *Gomphonchus*
			Lower Whitcliffe Beds	*C. tegula*		*L. lata* - *L. lewisii*	
		Leintwardine	Upper Leintwardine Beds	*Neobeyrichia lauensis*			

Text-Fig. 1. Tracings of 3 unpublished sections, thought to have been produced by Sir R. I. Murchison in about 1852 (ca. 1850-1854) and now deposited in Ludlow Museum.

A. *Ludlow* (G.R. SO 520 742)

The individual sediment layers are given as follows:-

1, 3, 16. Probably red marls - key not given;

2, 4. Yellow shale; 5. Grey grit with *Auchenaspis*, *Cephalaspis*, *Onchus*, *Pterygotus*, *Lingula*. This is the fish band referred to by Murchison (1856) and the ?Temeside Bone-Bed of Elles and Slater (1906); 6. Reddish marl; 7. Red sandstone; 8. Green mudstone; 9. Red mudstone; 10. 3 inch thick grey sandstone; 11, 13. Grey grit; 12. Brown sandstone; 14. Brown sandstone; 15. Brown rubbly micaceous sandstone; 17. Downton sandstone; 18. Ludlow Bone-Bed; 19. Upper Ludlow rock; 20. 6 - 8 feet coarse gravelly deposit.

B. *Onibury* (G.R. SO 455 794)

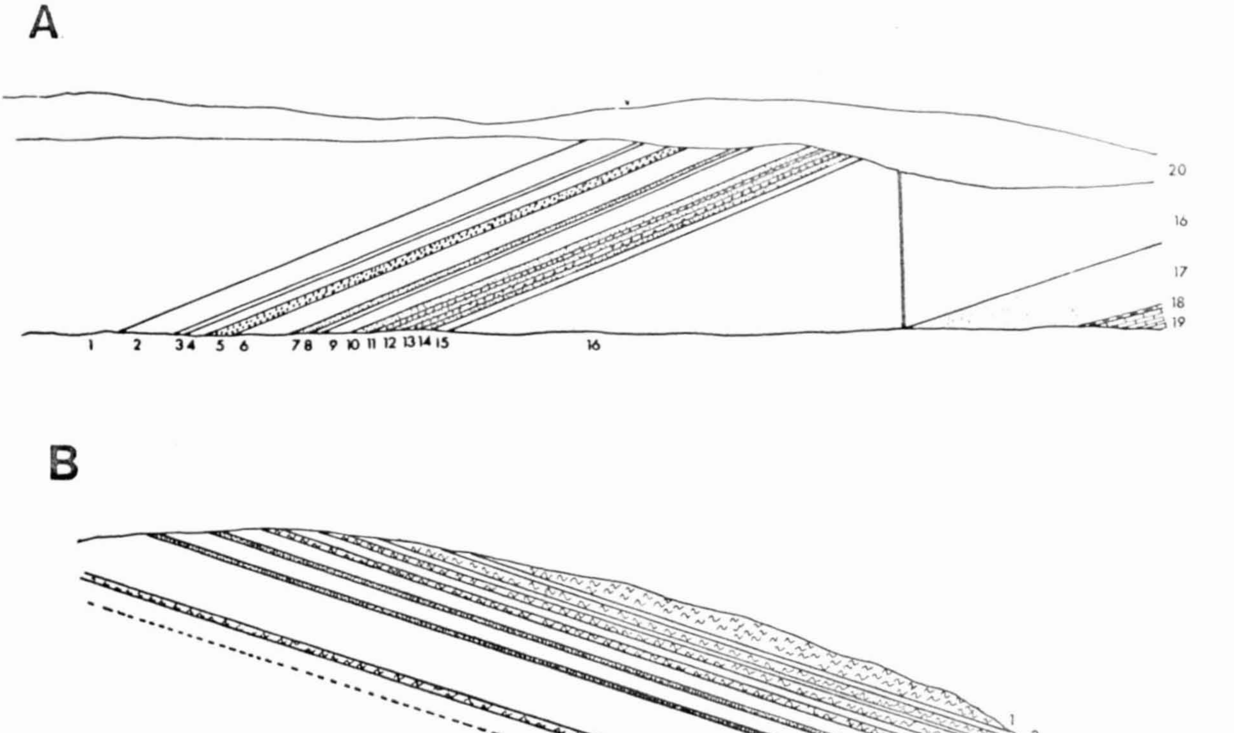
The individual sediment layers are given as follows:-

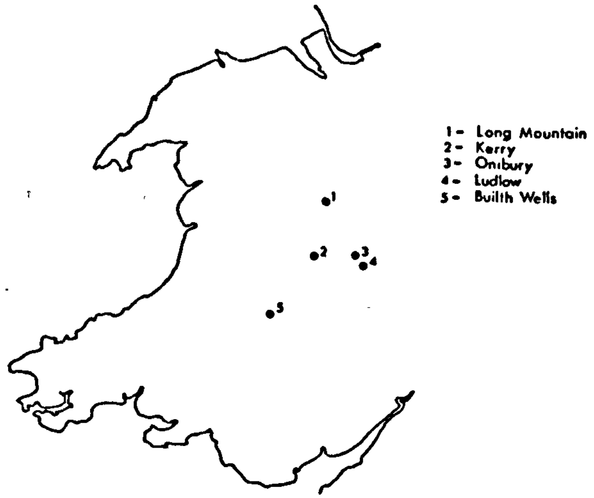
1, 3, 5, 7, 13. Green rubbly shale; 2, 4, 6. Red marl; 8. Brown shale; 9, 11. Grey grit bands; 10, 12, 14. Green shale; 15. This space uncertain (probably red and green marls); 16. Downton sandstone; 17. Ludlow Bone-Bed 2 inches thick; 18. Upper Ludlow rock.

C. *Ludlow Railway cutting*

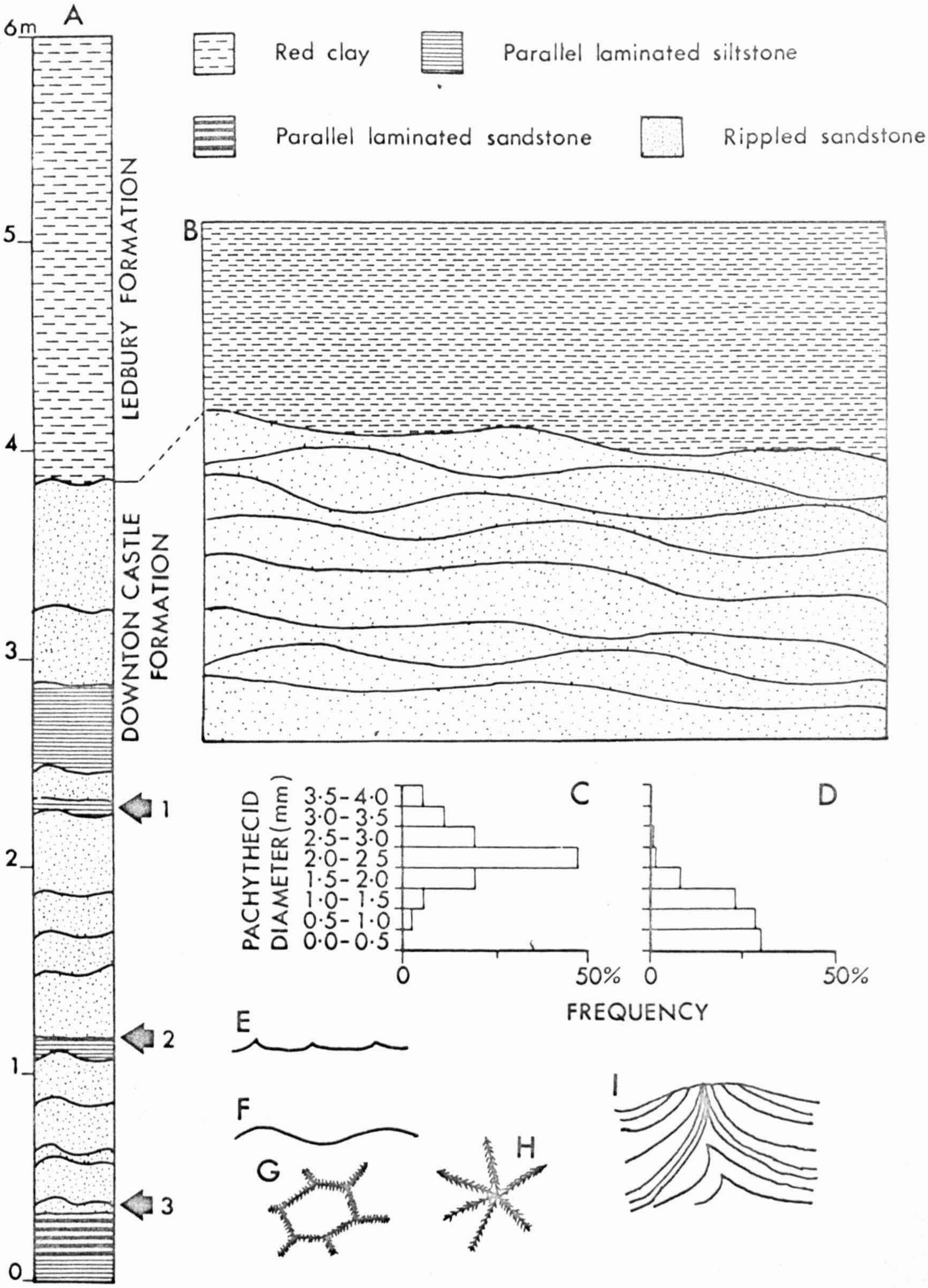
The individual sediment layers are given as follows:-

1, 3, 5, 7, 9, 16. Red marl; 2, 4, 6, 8. Red sandstone; 10. Brown and grey beds (10 feet thick); 11. Yellow sandstone; 12, 15. Green shale; 13. Grit band with *Cephalaspis*, *Auchenaspis*, *Pterygotus*, Eurypterids, *Lingula*, *Lerpiditia* and *Modiola*. This bed may be the Temeside Bone-Bed referred to by Turner (1973); 14. Sandstone band.


A
20
16
17
18
19
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
16
B
1 2 3 4 5 6 7 8 9 10 11 12
18 17 16
15
14 13
C
1 2 3 4 5
16 15 14 13 12 11 10 9 8 7 6
0 20m



Text-Fig. 2. Location map showing the Long Mountain, Kerry, Ludlow, Onibury and Builth Wells.


A
6m
5
4
3
2
1
0
LEDBURY FORMATION
DOWNTON CASTLE FORMATION
1
2
3
Red clay
Parallel laminated siltstone
Parallel laminated sandstone
Rippled sandstone
B
C
D
PACHYTHECID DIAMETER (mm)
3·5-4·0
3·0-3·5
2·5-3·0
2·0-2·5
1·5-2·0
1·0-1·5
0·5-1·0
0·0-0·5
0
50%
0
50%
FREQUENCY
E
F
G
H
I

Text-Fig. 3. The Downton Castle Formation - Ledbury Formation junction at Downton (G.R. SO 456 742).

A. Sediment profile observed in the section. Fossils were recorded at three points in the section (arrowed). At point 1, 623 disarticulated shells and shell fragments of *Lingula minima* were observed in a bedding plane surface area of 1 m^2. Associated with them were 40 specimens of *Pachytheca sphaerica*, whose size distributions are given in Text-Fig. 3.D. At Point 2, 1 fragment of *Lingula minima*, 1 eurypterid fragment, 20 *Prototaxites* sp. fragments, 192 *Pachytheca sphaerica* and 11 *Hostinella* sp. fragments, and 7360 plant fragments (probably derived from *Hostinella*, *Psilophytites*, *Cooksonia* and *Nematophyton*) were recorded in a bedding plane surface area of 368 cm^2. The size frequency distributions of the pachythecids recorded in this layer are given in Text-Fig. 3.C. At Point 3, 48 disarticulated shells and fragments of *Lingula minima*, 1 broken spine of *Gomphonchus tenuistriata* and 9 scales of *Thelodus parvidens*, and 305,008 plant fragments derived from *Hostinella* (20-30%), *Pachytheca* (10-15%), *Psilophytites*, *Prototaxites*, *Cooksonia*, and *Nematophyton* were recorded on a bedding plane surface area of 13864 cm^2. The sediment surface at this point was covered in box ripples (Text-Fig. 3.G) concentrating vegetal debris in their ripple troughs. The diameter of each box varied from 4-6 cm with an amplitude of 0.5 - 1.2 cm. Also present on the sediment surface were sand volcanoes (Text-Fig. 3.H). Across section across one such sand volcanoe is illustrated in Text-Fig. 3.I

The laminated siltstones below

this point contained 3 eurypterid fragments and 1 _Lingula minima_ fragment over a bedding plane surface area of 1 m^2.

B. Sketch of the section showing that the rippled sandstones occur as megaripples (wavelength 3 - 8 m, amplitude 10 - 40 cm). The surfaces of these megaripples are covered in smaller ripples (Text-Fig. 3.E,F,G). Width of sketch about 25 m.

C. Size-frequency distribution of _Pachytheca sphaerica_ at sample point 2. Sample size = 192.

D. Size-frequency distribution of _Pachytheca sphaerica_ at sample point 1. Sample size = 40.

E. Oscillation wave ripples from the surface of a megaripple 85 - 88 cm above the sections base. (Wavelength 35 - 40 cm; amplitude 1.6 - 2.3 cm.)

F. Ripple on the surface of a megaripple, 65 cm above the section base. (Wavelength 55 - 60 cm; amplitude 4 - 7 cm.)

G. Box ripple on the sediment surface at point 3. (Diameter 4 - 6 cm; amplitude 0.5 - 1.2 cm.)

H. Sand volcanoe on the sediment surface at point 3. The centre of this volcanoe has an elevation of 1.8 cm. Its diameter is 3 - 4 cm.

I. Profile through a sand volcano at point 3.

micrite nodules are present.

The criteria used by the author to distinguish between the Ledbury, Temeside and Downton Castle Formations are summarised in Table 2.

1. The type section of the Temeside Bone-Bed

This section was first noted by Murchison (1850-1854; 1856) and later by Elles and Slater (1906). They recorded the sedimentological and faunal succession of the section. Later, Allen (1974a) noted the presence of sand sheets, and Antia (1979a) briefly described the bone-beds in the section.

In this study both the faunas and sediments present in the section are described and some conclusions drawn.

Methods

In the field the section was measured and the various lithologies noted. A continuous sequence of sediment was collected, with 2-3 Kg of sediment removed from each sample point (Text-Fig. 4), for sedimentological and palaeontological analysis. Each layer sampled was examined in the field for macrofossils and their densities recorded. X.R.D. analyses were made to identify the clay minerals (Text-Fig. 5).

After all the sediment had been broken down and examined for fossil moulds casts and traces in the laboratory under a binocular microscope, 1 Kg of sediment from each layer was put in a 40% hydrogen peroxide solution, boiled for 1 hour and left to cool for 3 days. The sediment was then sieved and the residues examined for invertebrate remains, fish and plant debris.

Palaeontology

The fossils recorded from each sampled layer of the section are listed in Tables 3 and 4. The faunas present show a distinct division into two groups. The first (layers 1 - 11) contains an ostracod - foraminifera assemblage (averaging 3 fossils per Kg of sediment). This ostracod fauna contains the ubiquitous marine species Kuresaaria circulata (see Shaw, 1971), Aechimina sp.,

Table 2. Characteristics of the Downton Castle, Temeside and Ledbury Formations (after Allen, 1974a).

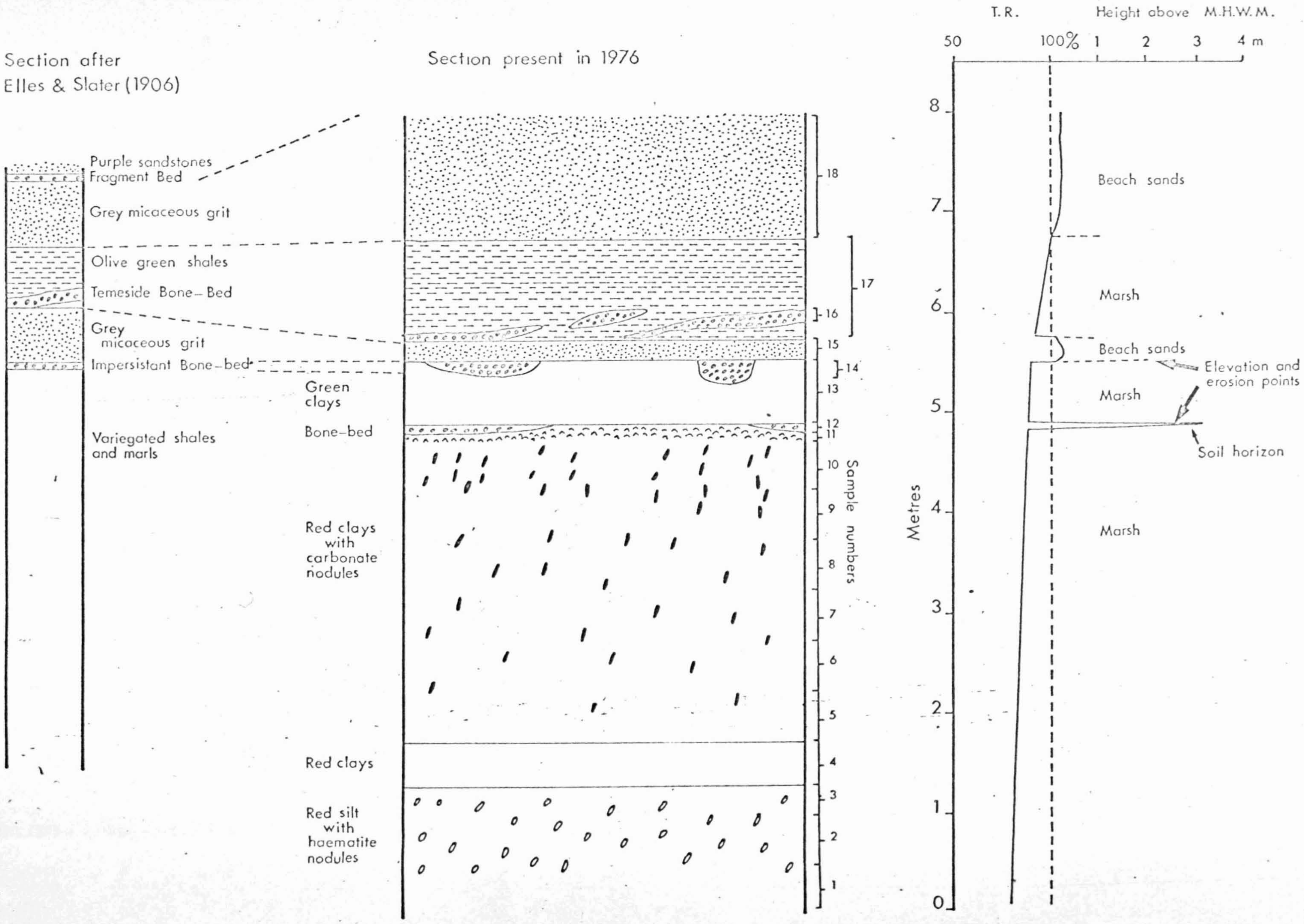
FORMATION	CHARACTERISTICS
Ledbury	Red mudstones and shales with coarse sandstones
Temeside	Olive green mudstones and shales with some sandstones
Downton Castle	Green shales and mudstones with buff yellow sandstones

Table 3. Fauna recorded from layers 1 - 11 at the Teme River Section, at Ludlow. Numbers indicate the number of specimens present in 1 kg. of sediment sampled. A key to the sampled layers is given in Text - Fig. 4.

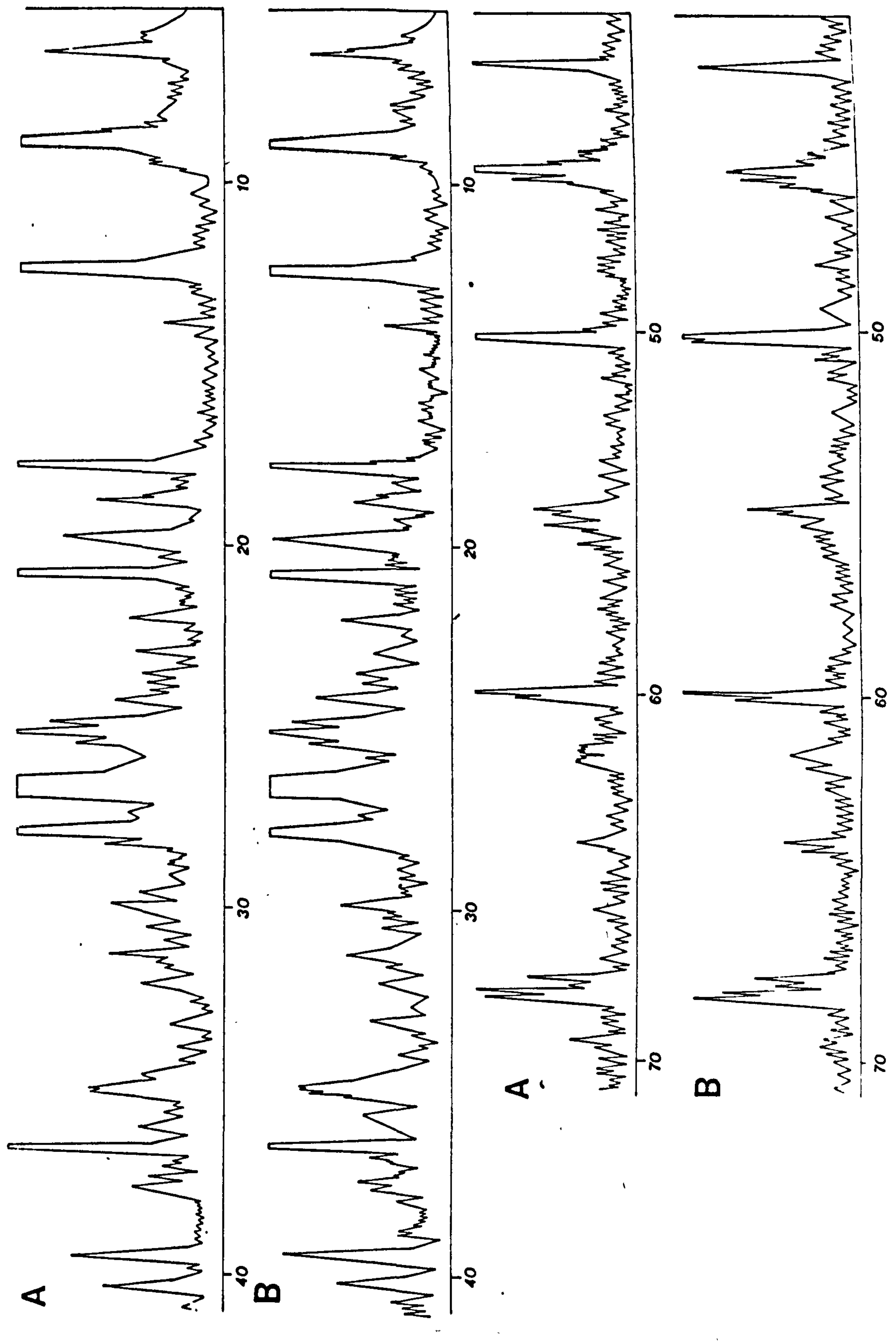
SPECIES	1	2	3	4	5	6	7	8	9	10	11
Ostracods											
Aechimina sp.	-	-	-	-	-	-	-	-	1	-	-
Aparchites sinuatus (Hall)	-	-	-	2	-	-	-	2	9	-	-
Cavellina cf. *plana* Neckaja	-	-	-	-	-	-	-	2	1	1	-
Kuresaaria circulata (Neckaja)	-	-	-	-	-	-	-	-	1	-	-
?*Gotlandella* sp.	-	-	-	-	-	-	-	-	1	-	-
Hermannia cf. *marginata* (Jones)	-	-	-	-	1	-	-	-	-	-	-
Foraminifera											
Hyperamnia sp.	-	3	5	-	-	-	1	-	-	-	1
Brachiopods											
Lingula cornea J.de C.Sowerby	-	-	-	-	-	-	-	3	-	-	1
Fish											
Thelodus parvidens Ag.	-	-	-	-	-	-	1	-	-	1	1

Table 4. Fauna recorded from layers 12 - 18 at the Teme River Section at Ludlow. Numbers indicate the number of specimens present in 1 kg. of sediment sampled. Layer 12 = Bone-bed BK1; Layer 16 = Bone-Bed BK2; Layer 16 = Bone-Bed BK 3 (The Temeside Bone - Bed of Elles & Slater,1906)). A key to the sampled layers is given in Text-Fig. 4.

SPECIES	12	13	14	15	16	17	18
Brachiopods							
Lingula _cornea_ J.de C. Sowerby	-	-	7	-	-	-	-
Lingula cf. _missendenensis_ Straw	-	-	-	2	-	-	-
Fish							
Corvaspis cf. _kingi_ Woodward	-	-	-	-	2	-	-
Cephalaspis spp.	22	-	-	-	61	-	-
Gomphonchus _tenuistriata_ (Ag.)	6	-	3	-	3	-	-
Gomphonchus sp.	2	-	-	-	4	-	-
Logania _cunetea_ Gross	-	-	2	-	-	-	-
Logania _ludlowiensis_ Gross	70	-	90	-	2	-	-
Thelodus _bicostatus_ (Hoppe)	1	-	-	-	-	?	-
Thelodus _parvidens_ Ag.	55	1	15	-	3	-	-
Thelodus _trilobatus_ (Hoppe)	28	-	9	-	2	-	-
Indeterminate fish fragments	40	-	65	-	21	-	-
Foraminifera							
Hyperamnia sp.	-	1	-	-	-	-	-
Plants.							
Pachytheca _sphaerica_ Hooker	2	-	5	-	-	-	-
Plant debris	382	-	643	38	424	-	-
Conodonts							
Ozarkodina _remscheidensis_ (Walliser)	1	-	-	-	-	-	-



Text-Fig. 4. Measured section with interpretation of the Ledbury Formation at Ludlow. T.R. = Tidal Range.



Text-Fig. 5. X.R.D. traces of sampled layers (see Text-Fig. 4) 13 and 10. They indicate that the sediment consists of chlorite clay and some quartz.

Cavellina cf. plana, Hermannia sp. and ?Gotlandella sp. All of the species except Aechimina sp. and Hermannia sp. occurred as carapaces. The latter species occurred as a fragmentary valve, which could possibly be assigned to Hermannina marginata. This genus is considered (Berdan, 1969; Warshauer & Smosna, 1977; Smosna, personal communication, 1978) to have lived in a supratidal or high intertidal environment, but since it occurs as rare fragmentary remains, its presence may not be diagnostic of the environment of sediment deposition.

The low density of the ostracod fauna (Table 3) may help to indicate the nature of the environment, as in modern marine sediments ostracod density decreases through the intertidal zone into the supratidal zone (Table 5). For example, in the Essex mudflats at Sales Point, Bradwell, their density varies from about 8 ostracod carapaces/10,000 cm^3 of surface sediment at or around the mean high water mark to about 2,200 carapaces/10,000 cm^3 of surface sediment at the mean low water mark (see Table 5).

Since 10,000 cm^3 of sediment has a dry weight of between 1.2 and 6 kg in this instance (the variation depends on the original moisture and air content of the sediment), and the carapace densities recorded in the section varied from 0 to 11 specimens per Kg of sediment, it could be suggested that the original carapace density of the sediment was in the region of $<$ 1 to 60 carapaces/10,000 cm^3 of surface sediment, indicating that the sediments were deposited in the intertidal zone, occupying a region somewhere between 85 and 100% of the tidal range (cf. Table 5). However, if marked calcite dissolution has occurred in the sediment during diagenesis, then it is probable that the original carapace densities present in the sediment were higher than those observed. Further details concerning the Sales Point Ostracoda are given in the appendix.

The thelodont scales observed show predepositional weathering features on their outer surface. These features can be assigned to weathering stage 3 (cf. Antia, 1979), and indicate that the specimens may have been drifting on

Table 5. Ostracod carapace densities at Sales Point, Bradwell, Essex, on 18/3/1977, expressed as number per 10,000 cm^3 of sediment surface

Percent of tidal range	0	10	20	30	40	50	60	70	80	90	100
Ostracod Carapace density	2200	2123	1986	1438	1265	894	531	268	134	45	8

the substrate surface for 15 or more years.

The second faunal group (layers 12 - 17) is characterised by abundant organic (plant) and vertebrate debris with some shell fragments of Lingula cornea (cf. Table 4). The presence of a fish fauna rich in ?Corvaspis sp. and various cephalaspids is interesting, since it represents a major change in the vertebrate composition of the sea from a Gomphonchus dominated fauna in the Middle Ludlow to a thelodont dominated fauna in the Upper Ludlow and Lower Downtonian, to a thelodont - cephalaspid fauna in the Upper Downtonian. Elles & Slater (1906) recorded Hemicyclaspis murchisoni (Egert.), Ctenacanthus sp. Hemiaspis sp. and Auchenaspis salteri Egert. from these layers, and the cephalaspid fragments observed may belong to these species. A corvaspid - H. murchisoni fauna has been recorded from the Downtonian of Canada (Broad & Dineley, 1973; Dineley & Loefler, 1976), and suggests a late Downtonian age for this section (Dineley & Loefler, 1976, p.52). The conodont (Table 3) Ozarkodina remscheidensis remscheidensis recorded from layer 12 of this section (Antia, 1979a) indicates (Aldridge, personal communication, 1978) a possible lowest Gedinnian age for this layer.

The sediments

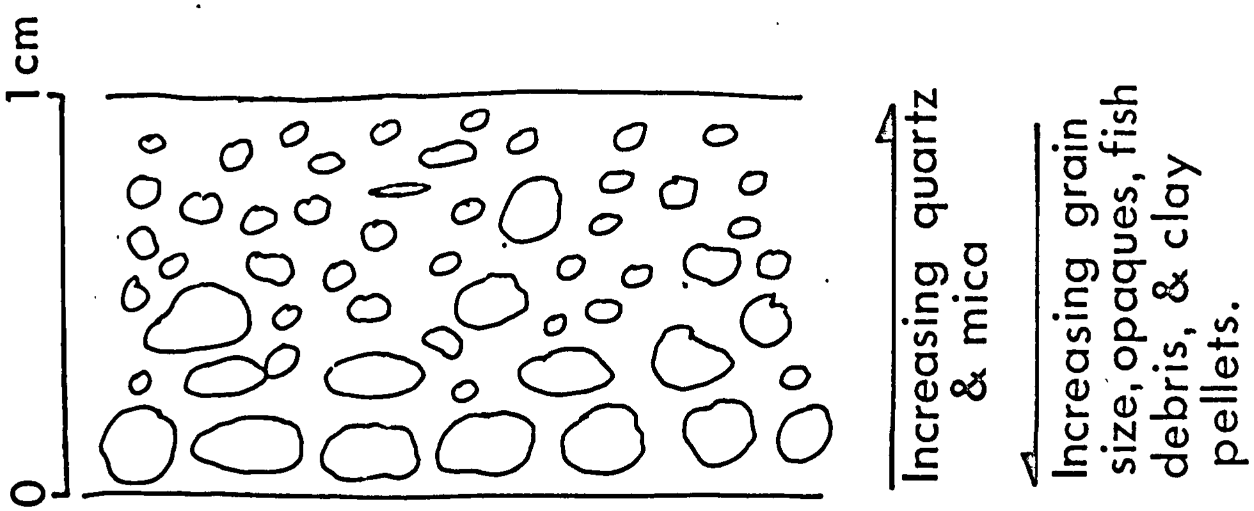
In the field the section is divisible into 2 parts. The lower part (layers 1 - 11) of the section consist of a sequence of red silts while the upper part of the section consists of a sequence of green clays and sandstones (layers 12 - 18).

Selected layers from the section were examined in thin section and point counted. The point counts indicate that the lower part of the section is comprised principally of clay (identified as chlorite by X.R.D. analysis (Text-Fig. 5)), micrite and quartz. The grains are all heavily coated in haematite giving a red colouration to the sediment sequence. In the sieved residues examined for the palaeontological part of this study, rare topaz grains (up to 3 mm in diameter) and marcasite grains are present (both grain types were identified by D. S. Weedon and N. Holgate). The upper part of the section contained green clay sequences which were similar to the underlying clays, quartz rich sandstones and a bone-bed. In the latter deposit there was an apparent graded sequence of mineral deposition which is illustrated in Text-Fig. 6. Grain size distributions of the quartz grains in some of the layers in the section are indicated in Text-Fig. 7.

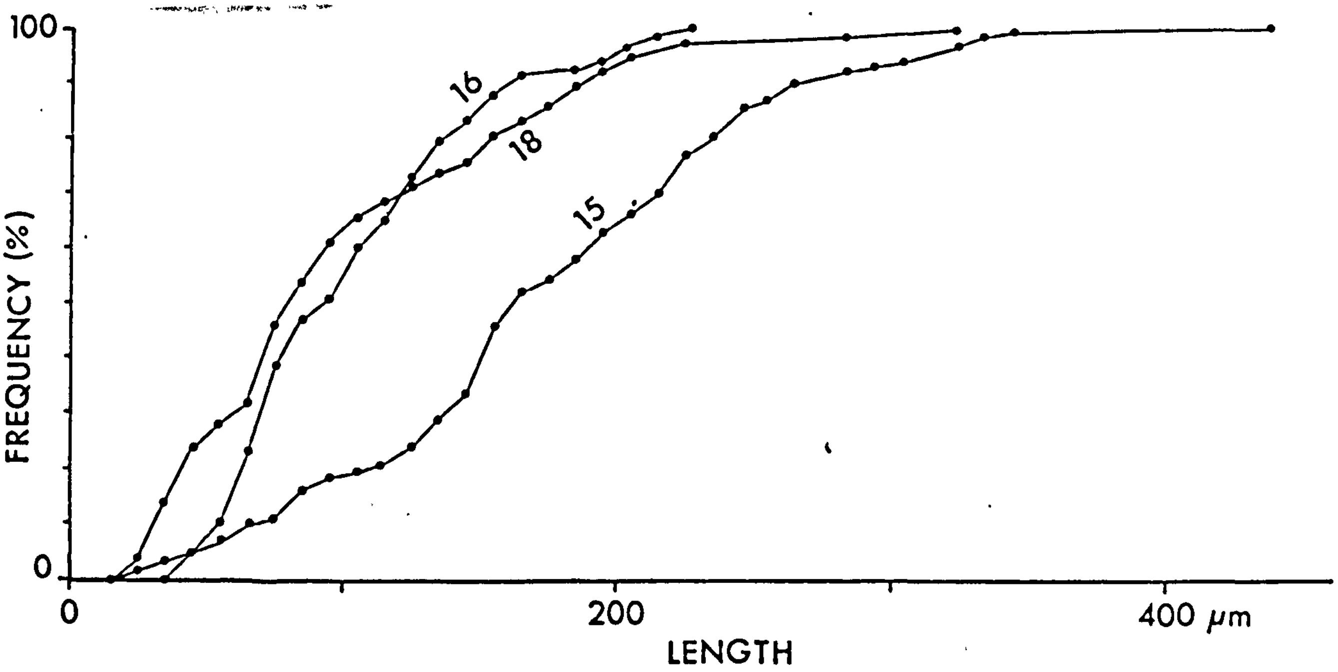
Environment of formation (Layers 1-11)

Layers 1-11 of the section can be described from base to top as a basal red silt clay unit with reduction spots (layers 1 to 4) overlain by 3 m of carbonate rich red clays (layers 5 to 11). These sediments are thinly bedded (laminae 1 - 2 mm thick) with wavy, slightly discordant laminae of poorly sorted muddy silt and clay laminae. Similar bedding has been observed by Greensmith et al. (1973), Greensmith & Tucker (1967, 1976) and Reineck & Singh (1973), in supratidal marsh sediments. If this is a correct interpretation, then the thin discontinuous bone-bed rich in plant debris (layer 12), resting on top of the red clays, may represent a plant debris-vegetal mud similar to those found on the surface of many marsh deposits (cf. Jardine, 1963; Reineck & Singh, 1973).

If the layers 1 - 11 are marsh sediments, then they would contain authigenic pyrite (Reineck & Singh, 1973; Greensmith & Tucker, 1976), which would be subsequently oxidised to limonite (Greensmith & Tucker, 1976; p.137). Prolonged oxidation of the sediment would result in the formation of haematite (Czyscinski et al., 1978). Consequently, red beds formed in a supratidal marsh environment have no palaeoclimatic significance since sulphide bearing sediments are found around the globe (Kawelec, 1973). Similarly, iron for pyrite formation is derived in situ (Howarth, 1979) and oxidised to haematite in its basin of deposition (Berner, 1970). However, the presence of haematite suggests a prolonged period of oxygenation by oxygenated waters shortly after the sediments deposition and may indicate a relative drop in sea level (Czysciniski et al.,



Text-Fig. 6. Graded sequence observed in the bone-bed infilled channels indicating the distribution of minerals and grain size.



Text-Fig. 7. Grain size distributions of three layers in the type section of the Temeside Bone-Beds. The layer numbers indicated on the grain size distributions corresponds to the layer numbers in Text-Fig. 4.

1978).

Confirmation of this suggestion is indicated by the presence of superimposed caliche structures on the red bed sequence. These caliche structures may be described with respect to the section as follows:-

1. The basal layers of the section (layers 1 - 4) contain no calcite, but do contain abundant haematite and haematite nodules (Plate 1, Fig. 1).
2. Micrite starts to appear about 3 m below the oxidised/reduced layer interface (layer 11/12 boundary), as small micrite pipes infilling small cracks and fissures (Plate 1, Fig. 3) grading up the section into vertical micrite pipes and glaebules up to 20 cm in length (Plate 1, Fig. 4). These pipes become very common in parts of the section and culminate in the formation of a calcareous nodular mudstone (Plate 1, Fig. 2) rich in pipes which destroy all evidence of primary bedding.

This situation in which the original unaltered host sediment is enclosed by micritic carbonate crusts to produce minor in situ brecciation at its top with subsurface micrite stringers and pipes underneath, has been recorded and described in detail from thick (1 - 3 cm) caliche sequences in the Welsh Borderlands by Allen (1974b) and in Barbados by Harrison (1977). They occur where caliche profiles have been developed on and within a host substrate (Harrison & Steinen, 1978; p.389).

In the sediment immediately above the red beds micrite is absent, suggesting that the sediment illustrated in Plate 1, Fig. 2, represents the 'crust' of a caliche profile. The overlying plant debris rich bone-bed (layer 12) has an erosive contact with the red bed sequence and infills a scour hollow on the upper surface of the red beds.

The subareal exposure and subsequent caliche development of the supratidal sediments described here might not be the result of a simple marine regression, in which the environments changed from marine conditions in the Ludlow through to supratidal conditions in the Downton Series, but could result from a complex marine regression, containing minor transgressive phases

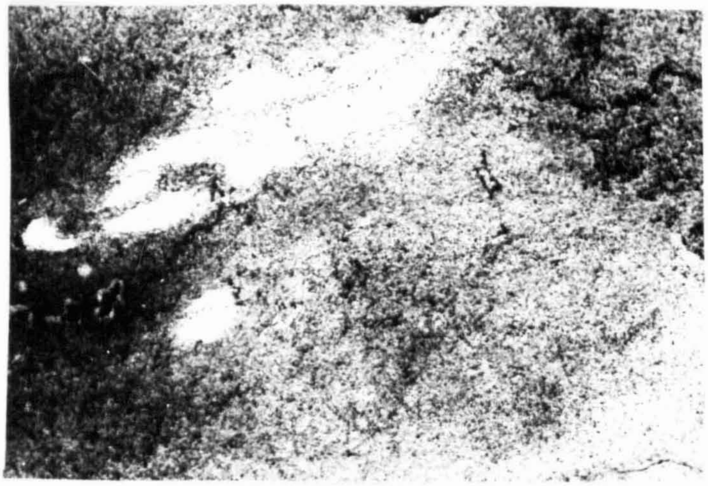
Plate 1, Fig. (1) Haematite nodules (white) in red clays at Ludlow in the Ledbury Formation. (negative print.) (x 8)

(2) Calcareous nodular red clays at Ludlow in the Ledbury Formation, Ludlow. (negative print.) (x 4)

(3) Micrite pipes infilling small cracks (black) in red clays in the Ledbury Formation at Ludlow. (negative print.) (x 4)

(4) Micrite pipe from the red clays of the Ledbury Formation at Ludlow. (x 1)

(5) Plant remains on a bedding plane in the Temeside Formation at Wallop Hall, including ?*Cooksonia* sp. and *Hostinella* sp. (x ½)



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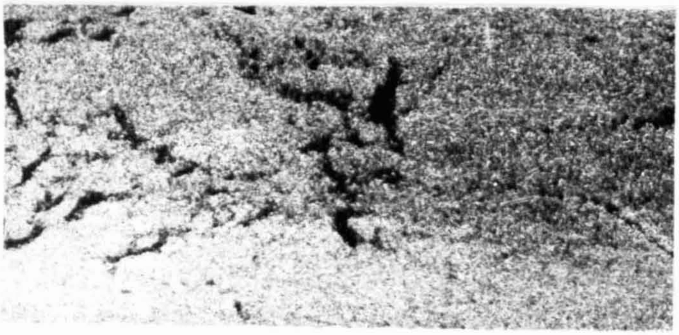

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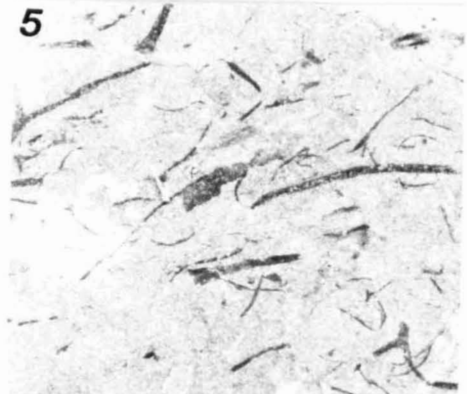

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within the overall regression cycle. Consider the following:-

1. In the Temeside and Ledbury Formations, caliche crusts have been superimposed onto intertidal and supratidal sediments (Allen, 1974a,b).
2. In the supratidal sediments of this section the upper surface of the crusts are scoured and their laminae are discordant with those of the overlying sediment, suggesting a difference in the depositional dip of the two sediments.
3. The presence of micrite subsurface stringers extending down to 3 m below the subarael surface (i.e. the caliche crust), implies a drop in relative sea level of at least that much. Otherwise the sediment pores would have been filled with fresh or marine phreatic waters, precluding any possibility of vadose diagenesis and resultant caliche formation (Harrison & Steinen, 1978; p.394).
4. The presence of caliche horizons with fabrics indicated (Plate 1, Fig. 1-4) here and described by Allen (1974a,b), clearly indicate the presence of gravitational vadose waters, and prove that exposure above the phreatic lense (water table) must have occurred (cf. Gile <u>et al</u>., 1966; Goudie, 1973; Allen, 1974b; Harrison, 1977; Harrison & Steiner, 1978).
5. The presence of haematite in the sediment suggests a period of prolonged oxygenation by percolating warm (10 - 30°C) oxygenated water (Norris, 1969; Czyscinski <u>et al</u>., 1978; Setlow, 1978). The oxidation may have been contemporaneous with the relative uplift of the sediment since the haematite is absent from sediments deposited after the formation of the caliche crust in the section.

These observations provide unequivocal documentation of a relative drop in sea level of about 3 m during the deposition of the Ledbury Formation. The prolonged subareal exposure of the sediments may have lasted as long as 1000 years (cf. Allen, 1974b). The presence of caliche rich sediment indicates a relatively warm climate (mean temperature greater than 6°C, Blatt <u>et al</u>., (1973)) and a rainfall of less than 75 cm/year (Blatt <u>et al</u>., 1973). Field examination of the carbonate crust suggests that it may have developed within the top 10 cm of soil, thus indicating that the actual rainfall was probably in the order of 20 - 40 cm/year (cf. Jenny & Leonard, 1934). The presence of a caliche crust *does not* provide evidence for a seasonal rainfall (Woodrow *et al*., 1973; Goudie, 1973) in the British Upper Silurian as suggested by Allen (1974 a, b).

The haematite nodules in the base of the section (Plate 1a, layers 1-3) may have formed as ferricretes (cf. Goudie, 1973). It is, however, more probable that both they and the haematite in the red beds (layers 1-11) formed by the intrastratal alteration of ferromagnesium silicate grains pyrite and authigenic iron bearing minerals (cf. Walker, 1976; Waugh, 1978) by perculating oxidising pore waters (Czyscinski *et al*., 1978; Waugh, 1978). Many of the biotite grains in these sediments have been heavily impregnated in crystalline haematite between their cleavage laminae (cf. Walker, 1976; Walker *et al*., 1978; Waugh, 1978). Some of the clays in these sediments possess no crystalline form and occur as grain coatings, suggesting (cf. Crone, 1974; Walker, 1976; Walker *et al*., 1978; Waugh, 1978) that they have mechanically infiltrated the sediment. However, other clays in the sediment have a definite crystalline structure (Plate 2, Fig. 3) which may have formed during later sediment diagenesis (cf. Waugh, 1978) or shortly after sediment deposition (Ospipov and Sokolov, 1978).

Environment of formation (Layers 12 - 18)

This part of the section contains three vertebrate rich clay horizons (layers 12, 14, 16) which have been described as bone-beds (Elles & Slater, 1906; Antia, 1979). Layer 16 was described as the Temeside Bone-Bed, and layer 14 as an impersistent bone-bed (Elles & Slater, 1906, p.204-205). The presence of a discontinuous clayey sub-bone-bed infilling scour hollows (layer 12) on the surface of the calcrete crust of the red beds may mark a change from a non-marine to a marine environment. The presence of mud balls, highly abraded and weathered fish scales, comminuted shell fragments and algal plant debris suggest a possible depositional site within the supratidal zone (cf. Antia, 1979a). Similar supratidal bone-beds are found in the British Rhaetic and Carboniferous where they mark the onset of a marine transgression (Richardson, 1911; Nickless et al., 1976; Marshall, 1978). The overlying green clays containing slightly discordant parallel laminae may have been deposited in a supratidal marsh environment similar to those of the underlying red beds (cf. Greensmith et al., 1973; Greensmith & Tucker, 1976). Cut into these clays are two channels (15 x 20 cm and 10 x 35 cm), one of which is flat based. They contain an apparent mineralogical cyclothemic sequence of sedimentation which may be described as follows:-

(1) A basal lag rich in heavy minerals, grey clay pellets (up to 1 cm in diameter) and fish debris.

(2) This grades up into a quartz rich layer and then into a quartz and mica rich layer. This cycle summarised in Text-Fig. 6 suggests that the sediment was deposited from either a density current or from a sediment laden current gradually decreasing in strength over a short period of time (a few hours!). The order of settling suggests that the vertebrate grains were denser than the quartz grains at the time of deposition. Such an observation could be explained only if the vertebrate remains were second cycle (Reif, 1969, 1971, 1976) - i.e. had been reworked after they had been deposited in an older sediment and been diagenetically enriched in phosphate.

The vertebrate remains are black in colour, highly weathered (see Antia, 1979a) and highly abraded. An X.R.D. analysis of these grains shows that they are made of a pure carbonate apatite, while the vertebrate remains in the underlying red beds are a translucent yellow colour suggesting that they might be made of a fluorapatite enriched in organic debris (cf. Antia, 1979a). Similar colour variations have been recorded elsewhere in the geological column on fish debris, but not interpreted (e.g. the Triassic; see Sykes & Simon, 1979). The most likely explanation for the highly corroded worn and weathered nature of these fish scales, which appear opaque black in all three bone-beds, is that they have been eroded out of the underlying red beds and have been redeposited in the vertebrate lags in which they are now found (cf. Reif, 1971, 1976), suggesting that the Layer 12/Layer 11 boundary may represent a disconformity of several thousand years, and that an unknown amount of sediment may have been removed. It is interesting to note that the conodont specimen was unworn, and had a translucent fresh appearance suggesting that it might be a contempory fossil of bone-bed BK1 age, unlike the fish which were almost certainly reworked from an older sediment (cf. Reid, 1890; Reif, 1969, 1971; Frey et al., 1975).

Overlying these channels and clays is a sand sheet containing a micaceous quartz sand and some cross bedding (Layer 15). Also present in the sandstone are layers of plant debris. Diagnostic environmental features were not observed in this sandstone. Its quartz grain size distribution is given in Text-Fig. 7. The quartz grains include composite igneous grains, highly strained grains (often with biotite inclusions) and unstrained grains.

The overlying clays containing Bone-Bed BK3 are olive green and contain parallel and slightly discordant laminae. They are overlain by rippled sandstone (Layer 18) which may represent a supratidal sand deposit related to a beach environment (cf. Allen, 1974a).

Environmental Summary

An environmental interpretation of the section is given in Text-Fig. 4.

Boreholes through modern Flandrian sediments suggest that marsh sediments can accrete at a rate of about 1 mm a year (e.g. Greensmith & Tucker, 1976). From this figure a chronology of events can be determined for the section.

1. Lagoonal marsh deposition (Layers 1 - 11) for at least 4,730 years. If an appreciable amount of sediment has been removed between the type Layer 11 and Layer 12 were deposited, it is possible that the period of lagoonal marsh deposition may have been appreciably longer, possibly in the order of 10 - 15,000 years.
2. This period of deposition was followed by a period of elevation, to at least

3 m above sea level, and a period of caliche and haematite formation which lasted for some ?500 - 1500 years.

3. The subsequent ?marine transgression deposited ?lagoonal marsh sediments for about 6000 years.
4. For some reason this marsh deposition ceased and a channelled surface was developed. These channels and the erosion surface were then transgressed by a sand sheet (possibly a beach ridge (Allen, 1974a)).
5. Over the next 250 years marsh accretion continued and eventually buried the sand sheet. This marsh accretion continued for the next 1,100 years before being buried by another beach ridge.

Consequently, it can be suggested that the sediments observed in the section may represent some 10,000 - 15,000 years of sediment accretion, contain some erosive surfaces and may contain an unconformity at the junction of Layers 11 and 12. This junction represents a possible contender for the Silurian-Devonian Boundary in Britain.

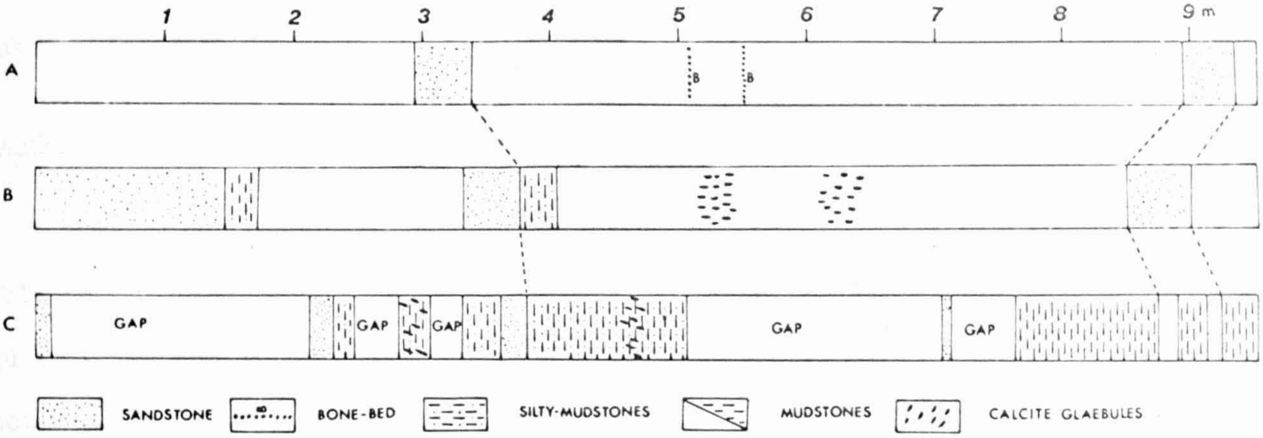
2. The Onibury Section (G.R. SO 455 794)

The Onibury section was first recorded by Murchison (1850-1854; Also Text-Fig. 1) and later by Elles and Slater (1906) who recorded the Temeside Bone-Bed in the section. Later, Shaw (1969) recorded a rich ostracod fauna in the bone-bed and Allen (1974a, p.133) documented the sediments present in the section, without recording a bone-bed. The sediment sections recorded by Elles and Slater (1906), Allen (1974a) and the author are presented in Text-Fig. 8.

In this study both the faunas and sediments present in the section are described and some environmental conclusions drawn.

Methods

The section was measured and the various lithologies present noted. A continuous sequence of sediment was collected with 2 - 3 kg of sediment removed

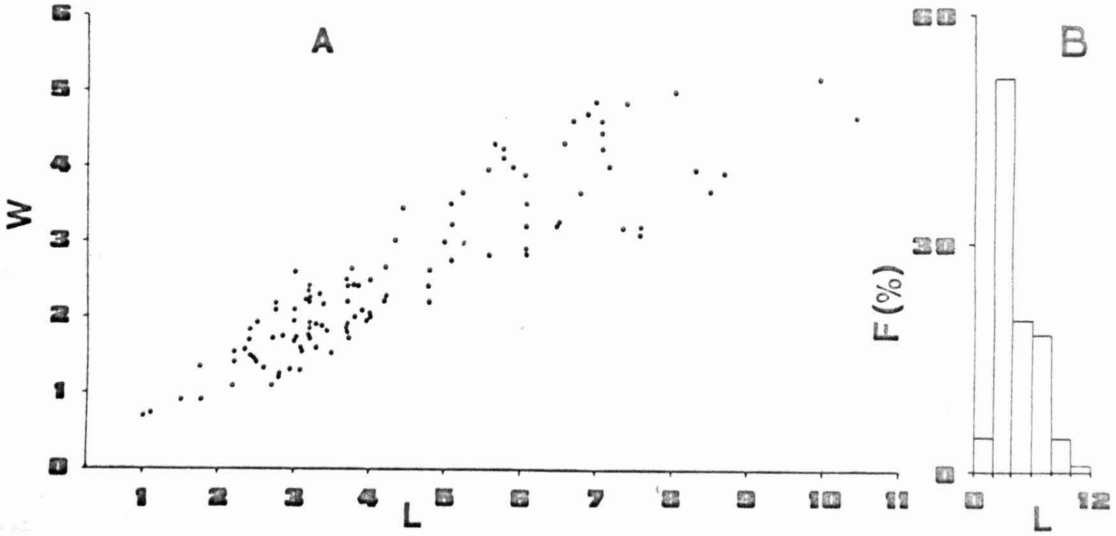


Text-Fig. 8. The Temeside Beds at Onibury:-

A. Section after Elles & Slater (1906);

B. Section after Allen (1974a);

C. Section present in 1976.



Text-Fig. 9. (a) Length (L)/height (W) scattergram for Cytherellina cf. siliqua.

(b) Length (L)/frequency (F) histogram for C. cf. siliqua.

from each sample point. The sediment was broken down and examined for fossil moulds and casts in the laboratory under a binocular microscope.

Palaeontology

The fossils recorded from each sampled layer of the section are listed in Table 6. The brachiopods Lingula cornea and L. minima occurred both in situ and as disarticulated transported valves and fragments. Most of the ostracods occurred as isolated valves. However, some species (e.g. L. kiesowi and C. cf. siliqua) occur as carapaces and probably lived in the environment in which they are now found (cf. Oertli, 1971, also appendix 1). The species C. cf. siliqua is the same as the species C. cf. siliqua figured by Shaw (1971) and deposited in the Institute of Geological Sciences in London. A length/height scattergram for this species is presented in Text-Fig. 9. The eurypterid occurred as both fragments and segments in association with abundant transported plant debris. The fish debris in the section consisted of Gomphonchus murchisoni Ag., Thelodus parvidens Ag., T. trilobatus Hoppe and Logania ludlowiensis Gross, and occurred as isolated spines and scales in the sediment. Fish debris did not occur in sufficient abundance so as to constitute a bone-bed (sensu Antia, 1979a, p.94-98). The bone-bed recorded by Elles and Slater (1906) is currently not exposed in the section (cf. Text-Fig. 8).

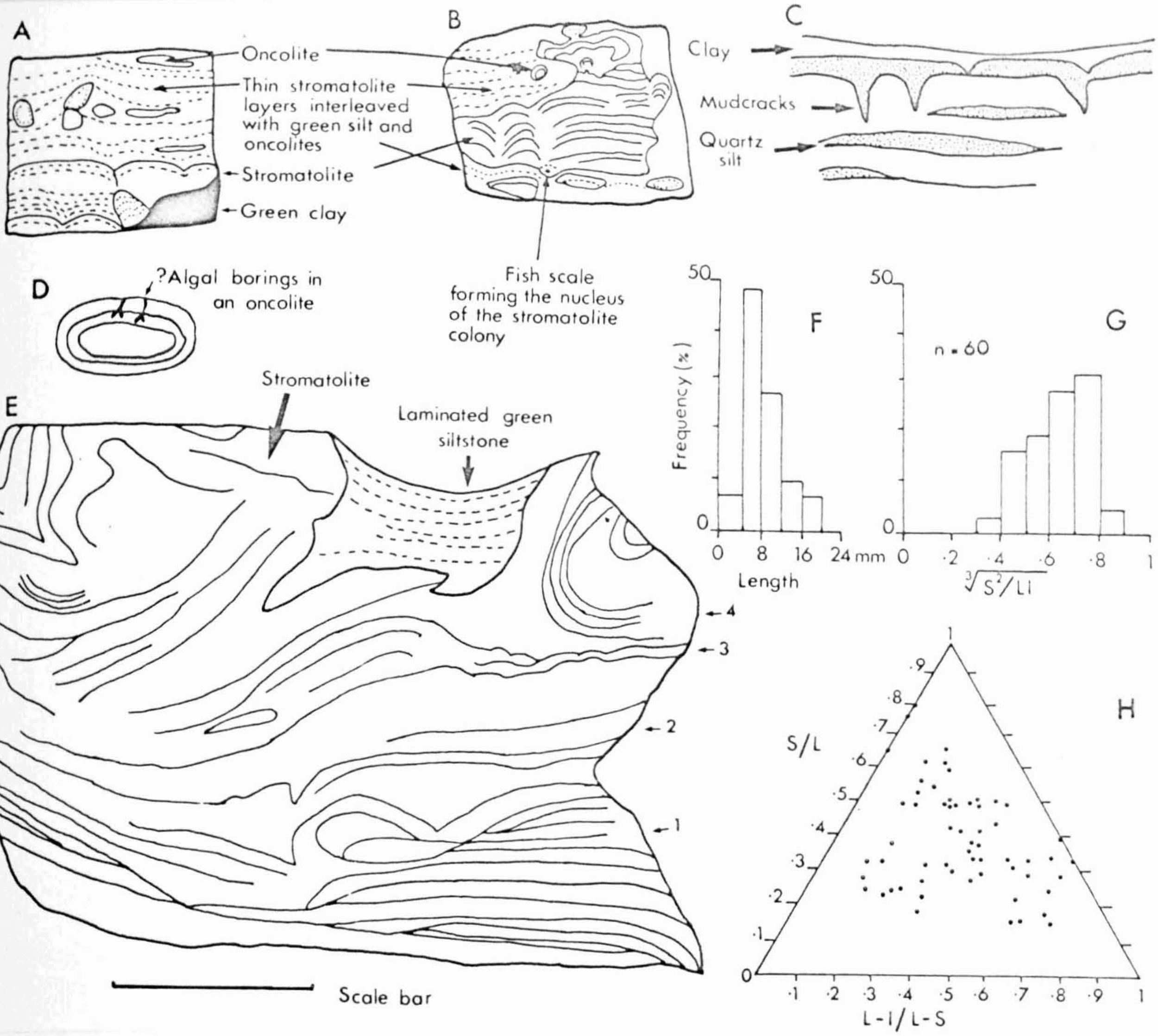
Sediments

The sediments in the section (Text-Fig. 8) vary from a biotite rich quartzite to olive green mudstones containing carbonate nodules (Allen, 1974a; p.133) and mudcracks (Text-Fig. 10c). These sediments and their environmental significance are described in Text-Fig. 8.

Allen (1974b) considers the carbonate nodules in this section to be pedogenic. However, some of these nodules are bored (Text-Fig. 10D) and contain an internal lamination (Text-Fig. 10A,B,C). This lamination can either consist of concentric rings or of wavy laminae and domes, and suggests (cf. Allen,

Table 6. Faunas from the Onibury Section (Temeside Formation). The relative position of each fossiliferous sample is given with respect to the base of the section, illustrated in Text - Fig. 8c. p=Present

SPECIES	0	282	370	390	405	434	515	964
	SAMPLE POSITION (cm)							
Brachiopods								
Lingula cornea	-	23	54	21	95	133	25	
Lingula minima J.de C. Sowerby	-	2	-	-	-	2	-	
Ostracods								
Cytherellina cf. *siliqua*	-	3	10	883	3	10	5	
Frostiella bicristata Shaw	-	8	-	1	1	-	-	
Frostiella groenvalliana Martinsson	-	-	-	-	1	-	-	
Londinia kiesowi Krause	-	31	-	87	11	-	6	
Hermannia marginata (Keys)	-	1	-	-	-	-	3	
Other fossils								
Eurypterid fragments	-	p	-	-	-	-	p	
Leodispis barrowsi Reed	-	2	-	-	-	-	-	
?*Kionoceras* sp.	-	1	-	-	-	-	-	
Pachytheca sp.	-	-	-	-	1	-	1	
Plant debris	-	p	-	-	-	-	p	
Thelodont scales	-	-	-	-	-	-	81	
Sample size in Kg of sediment	2	3	1·8	1	3	5	11	



Text-Fig. 10. Sediments at Onibury:-

A. Stromatolitic carbonate sediments showing incipient cracks on the upper surface of the stromatolite. Those cracks probably arose from areal exposure of the stromatolite in a supratidal or intertidal zone (cf. Bathurst, 1975, p.219) and may have been responsible for the slight doming at the top of the stromatolite (cf. Bathurst, 1975, p.219). Interleaved with the green silt sediment are thin carbonate bands, which may have formed thin algal mats on the sediment surface. The oncolites present in the sediments may both represent bits of larger stromatolites which were broken off during storms and later redeposited in the sediment and small motile accreting stromatolites similar to those described by Schäfer and Stapf (1978). Scale bar = 4 cm :

B. Domed laminar stromatolite growing on a siltstone containing stromatolite laminae and oncolites. The irregular dome structure on the stromatolites upper surface surrounded by silt (arrowed) probably represents the growth of younger lamina over the upturned edges of older desiccated laminae (cf. Bathurst, 1975, p.221). Scale bar = 4 cm.

C. Mudcracks in olive green clays draped by brown quartz silt containing plant debris, eurypterid fragments and ostracodes. Scale bar = 2 cm.

D. Algal oncolite containing characteristic concentric ring structure (cf. Shäfer and Stapf, 1978) and algal borings. Scale bar = 5 mm.

E. Micrograph tracing of an algal stromatolite. Note the original domed paired laminae, (1) were over grown to produce a sequence of horizontal laminae, (2) these were later replaced by a single dome structure, (3) subsequence disiccation of the stromatolite surface was followed by recolonisation of the surface by algal domes separated by laminated green siltstones, (4) scale bar = 1 cm. Illustrated in Plate 2a.

F. Size/frequency histogram for the oncolites

G. Effective settling sphericity/frequency histogram for the oncolites

H. Sphericity form diagram for the oncolites

1974a; Harrison and Steinen, 1978) that the nodules are not pedogenic concretions, and are probably stromatolites and Oncolites (cf. Bathurst, 1975). Although the original internal structure of these nodules has been replaced by sparite, it is possible to note that many of these stromatolites (e.g. Plate 2, Fig. 1, 2) consisted of horizontal laminae (Plate 2, Fig. 1, 2; Text-Fig 10A, B), which locally changed into dome shaped structures surrounded by mud (e.g. top of Plate 2a, Text-Fig. 10E). Similar structures to those recorded here in Plate 2a, b and Text-Fig. 10A, B. E, have been recorded in modern intertidal and supratidal environments (Kendall and Skipwith, 1968; Davis, 1970). Interbedded with some of these stromatolites are quartz rich silt sheets which are similar to the storm deposits interbedded with modern stromatolites (Davis, 1970).

The oncolites/stromatolite fragments are well sorted (Text-Fig. 10F,G) and vary from a platy to an elongate to a compact shape, and frequently contain quartz grain or fish scale nuclei (e.g. Text-Fig. 10B). Associated with these nodules are rare lerpiditid ostracods Hermannia sp. Similar algal-leperditid ostracod associations have been interpreted as indicating that the leperditids fed on the blue green algae forming the carbonate nodules (Warshauer and Smosna, 1977, p.478). Similar feeding relationships exist between ostracods and non-calcareous algae exist at the present time (Whatley and Wall, 1975).

The presence of in situ lingulids, algal stromatolites, mudcracks and lenticular bedded sediment in the section suggests that its sediments were deposited in an intertidal or shallow subtidal environment (cf. Paine, 1969; Reineck and Singh, 1973; Allen, 1974a). The sandsheets in the section may be chenier deposits (Allen, 1974a, p.134). Although such an interpretation seems plausible (cf. Bernard and Le Blanc, 1965; Greensmith and Tucker, 1967, 1969), transported shells and shell fragments which are abundant in many modern chenier sand sheets (Greensmith and Tucker, 1967; Antia, 1977) are absent. Consequently, it is possible that they represent subtidal or intertidal (beach) sandsheets.

Plate 2, Fig. (1) Stromatolites in the Temeside Beds at Onibury. (x 3)

(2) Stromatolites in the Temeside Beds at Onibury. (x 3)

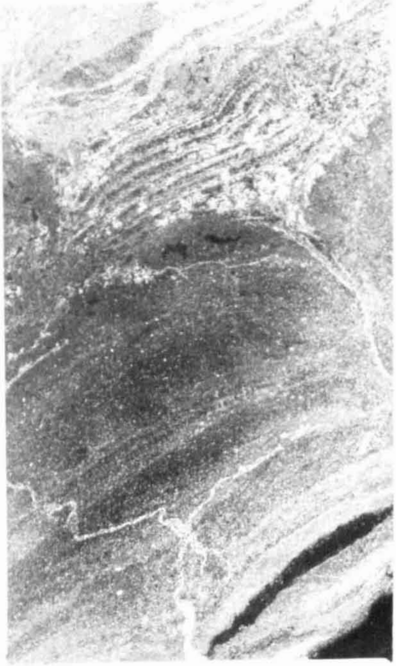
(3) Clays in the Ledbury Formation (red beds) at Ludlow. (x 1000)

(4) Burrows in a sandstone sheet at Builth Wells (locality 2, Text-Fig. 19). (x 2)

(5) *Hermannia phaseola* from the Temeside Formation at Wallop Hall. (x 3)

(6) *H. marginata* from the Temeside Formation at Wallop Hall. (x 3)

(7) *Bifungites* sp. from the Downtonian of the Kerry district.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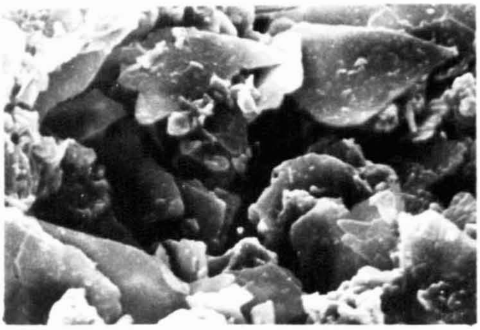
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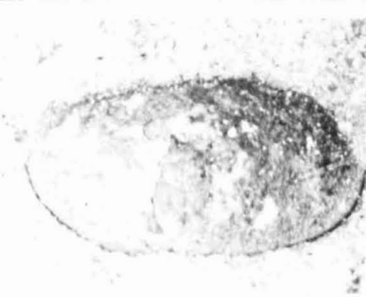
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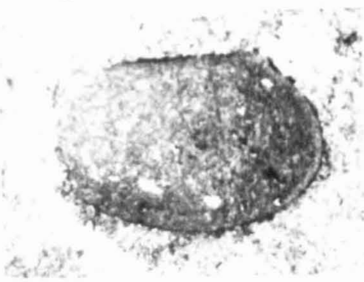
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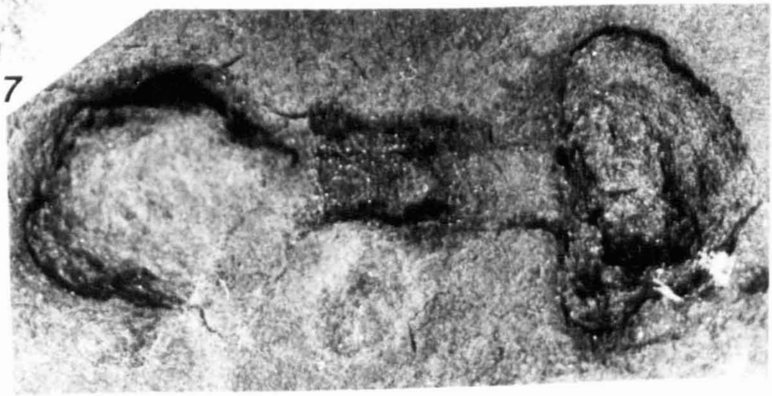
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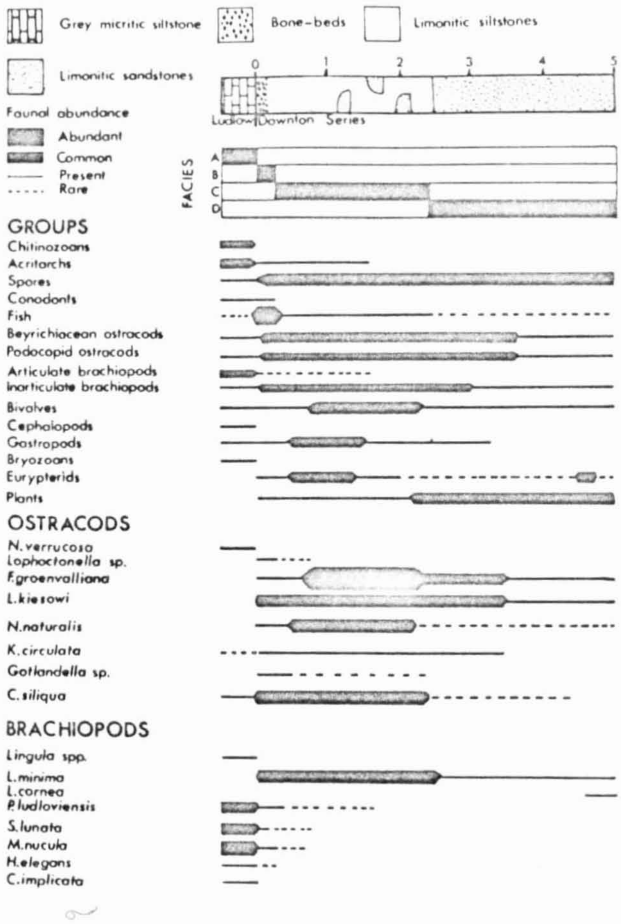
The Temeside Bone-Bed in an environmental context

The Ledbury Formation in which the Temeside Bone-Bed occurs was deposited during a general marine regression which started in the early Ludlovian (McKerrow, 1979, p.139) and continued through the Downtonian into the earliest Devonian of Wales and the Welsh Borderlands (Allen, 1974a). Traditionally the Ludlovian has been divided into a basin and shelf region (cf. Holland and Lawson, 1963; Watkins and Berry, 1977; Cherns, 1977 etc.). The basin is characterised by thick sediment pile (Holland and Lawson, 1963) containing a diverse fauna of necktonic species and a rare but very diverse benthic fauna, while the shelf is characterised by an abundant low diversity benthic fauna (cf. Holland, 1959; Holland et al., 1963; Jones, 1969; Calef, 1972, 1973; Calef and Hancock, 1974; Hancock et al., 1974; Watkins, 1978, 1979; Cherns, 1977) which may be facies controlled in its distribution (Hurst and Watkins, 1977). The junction between shelf and basin is rapid (about 15 km wide) occurring over the Church Stretton fault zone (Stamp, 1918; Holland and Lawson, 1963), and is marked by a series of submarine canyons (Whitaker, 1962, 1968, 1974, 1976a,b; Cherns, 1977). This distinction into shelf and basin has been present since the Ordovician (Cave and Davies, 1976; Hurst et al., 1978).

However, at the close of the Ludlow Series the distinction between shelf and basin sediments disappeared and was replaced by a sequence of carbonate depleted limonite and haematite enriched sandstones, siltstones and clays containing a molluscan-ostracod fauna (c.f. Stamp, 1923; Cave and White, 1972; Holland, 1957; Lawson, 1954, 1955). This transition was virtually instantaneous in most localities e.g. Siefton (Antia, 1979c), in others e.g. Ludlow (cf. Fig. 11) the transition was more gradual with rare Ludlovian fossils continuing into the Downtonian. It has been suggested (e.g. Allen, 1974; Antia, 1979a) that this transition represents a change from marine through to non-marine and fluvial sediments in the Ledbury Formation and overlying Ditton Group.

The general palaeogeography and the environmental changes from the Upper Ludlow into the Ledbury Formation will be discussed here in order to place the



Text-Fig. 11. Faunal distributions across the Ludlow-Downton Boundary at Ludlow (scale in m) showing the distribution of sediments, major faunas and facies:-

Facies A = subtidal tidally influenced environment

Facies B = intertidal muddy sandflats

Facies C = intertidal mudflats

Facies D = high intertidal - supratidal, beach siltstones and back beach lagoonal siltstones.

Note the continuation of some subtidal Whitcliffian faunas into the intertidal Downtonian.

Temeside Bone-Bed in its regional and local significance.

1. Palaeolatitudes

During the Upper Silurian the Welsh Borderlands were situated between 15° and 37° south of the earth's rotational equator (Roy, 1972; Creer, 1973; Allen, 1974a). This is indicated by the presence of calcretes in the British Upper Silurian and Devonian (Allen, 1973, 1974a,b). The continuation of these calcretes throughout the upper Silurian and the Devonian (Lotze, 1964; Allen, 1974b) has led some observers (e.g. Friend & House, 1964; Allen, 1974a) to suggest by analogy with tropical to subtropical landscapes from the Quaternary (cf. Goudie, 1973) that the Welsh Borders remained for most of the Devonian and for at least the upper part of the Silurian within an arid zone situated some 15° to 37° south of the earth's rotational equator.

However, it has been noted (Heckel, pers. com. 1978) that the earth's rotational pole was situated between 10° and 25° to the south of the earth's magnetic pole during most of the Devonian. Since the position of the Welsh Borderlands, with respect to the earth's rotational pole, has remained unchanged throughout the upper Silurian and early Devonian (Allen, 1974a) and was situated 25° south of the earth's magnetic equator (Briden et al., 1973a,b), it could be suggested that either (1) the earth's magnetic and rotational poles were nearer to each other in the Silurian than in the Devonian or (2) that the earth's global arid zone extended up to 60° south of the earth's magnetic equator during the upper Silurian.

2. Palaeoclimates

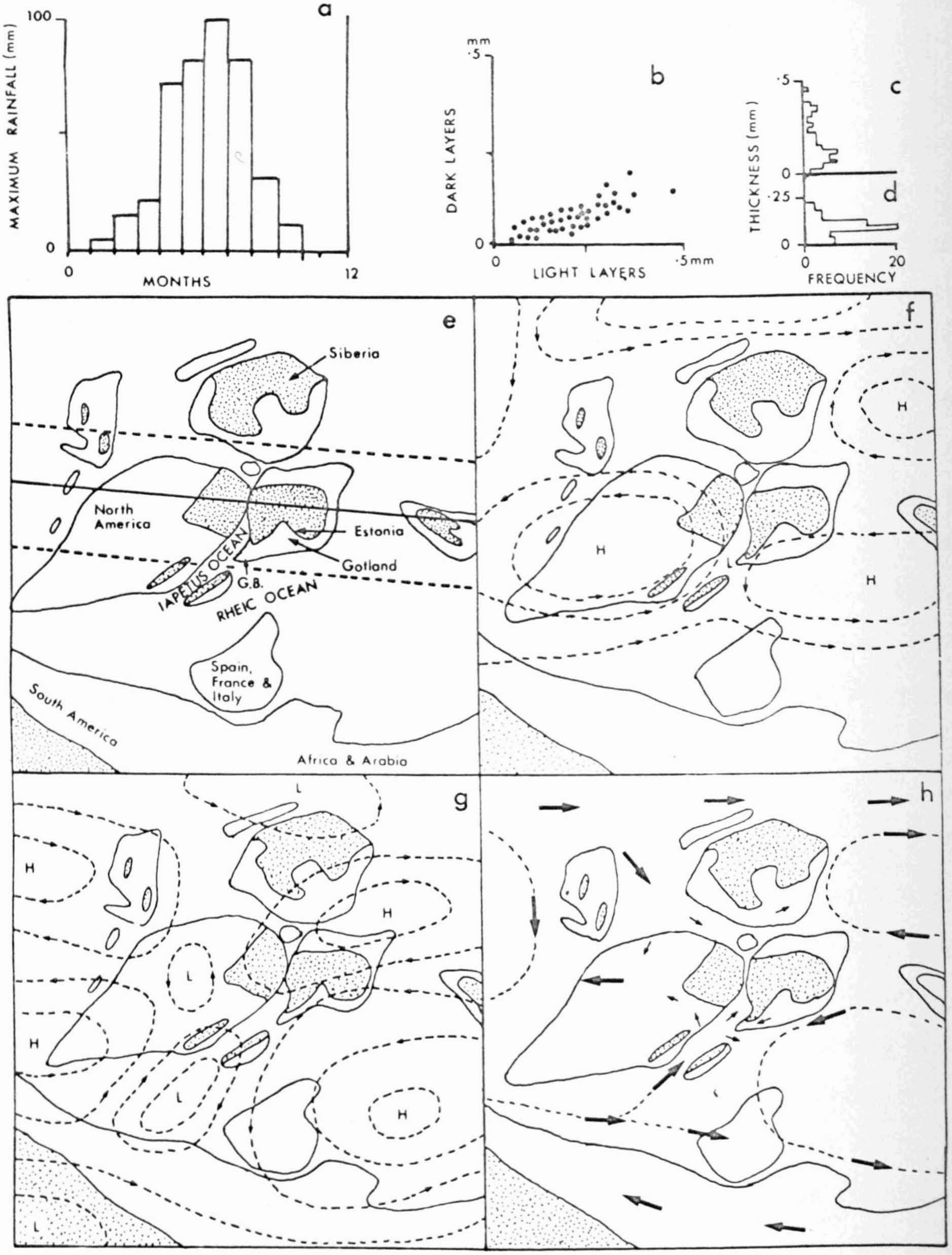
At the present time no systematic palaeoclimatic studies have been made of the Welsh Borderlands during the Whitcliffian and Downtonian. However, the rhythmites present in the lower Ludlovian (Atkins, pers. com., 1979) and the Whitcliffian (Atkins and Antia, 1979) suggest that the climate was seasonal, with a wet season alternating with a dry season (Reineck & Singh, 1973; Atkins pers. com., 1979). The calcretes present in the Ledbury Formation suggest (Allen, 1974a) that the climate was warm to hot (mean annual temperature 16 - 20°C) with a seasonally distributed rainfall (mean annual rainfall in the range 100 - 500 mm (Allen, 1974a): probable mean annual rainfall 200 - 400 mm. The absence of ferricretes (Allen, 1974a) suggests (Goudie, 1973) that the maximum monthly rainfall was less than 25% of the mean annual precipitation (i.e. less than 50 - 100 mm). A histogram illustrating the typical 'monthly' precipitation that could be expected if the rainfall was seasonal is indicated in Text-Fig. 12a.

Support for this notion of a seasonal climate is given by the rhythmites present in the lower part of the Whitcliffian (Atkins and Antia, 1979). Their dark 'winter' laminations have a very narrow size range (Text-Fig. 12b,c) and their light 'summer' laminations have a broad size distribution spread, implying that the summer months represented a period of increased sediment deposition which varied in intensity and duration from year to year.

3. Wind directions

At the present time little is known about palaeowind directions in the British upper Silurian. However, Antia (1979c) has recorded some antirippled-like structures on sediments which were probably deposited as part of a Whitcliffian intertidal mudflat at Siefton. These structures suggest that the wind came from the north.

This wind direction supports the hypothesis outlined by Ziegler et al. (1977) that the dominant wind direction affecting the Welsh Borderlands during the Silurian was from the north throughout the year (see Ziegler et al., 1977, fig. 3 & 4). However, they note that this type of wind pattern would result in a moist summer in the Welsh Borderlands and a humid winter, with the region being an area of low pressure during the summer and medium pressure during the winter. The most probable atmospheric circulation patterns for both the winter and summer are illustrated in Text-Fig. 12d,e,f. These circulation patterns have been modified after Ziegler et al. (1977) and show the relative position of


a
MAXIMUM RAINFALL (mm)
100
0
MONTHS
12
b
mm
·5
DARK LAYERS
LIGHT LAYERS
·5 mm
c
d
THICKNESS (mm)
·5
·25
FREQUENCY
20
e
Siberia
North America
Estonia
Gotland
IAPETUS OCEAN
G.B.
RHEIC OCEAN
Spain, France & Italy
South America
Africa & Arabia
f
H
L
g
h

Text-Fig. 12. a. Schematic representation of annual maximum rainfall distribution in the British Upper Silurian.

b. Plot of thickness of light (?summer) layers against dark (?winter) layers for rhythmites from near Kerry.

c. Size/frequency distribution of light layers from rhythmites near Kerry.

d. Size/frequency distribution of dark layers from rhythmites near Kerry.

e. Relative distribution of oceans, land (stippled) equator (straight line) and 25° N and S latitudes (dashed lines) in the Upper Silurian (modified after Ziegler, <u>et al</u>., 1977).

f. Hypothetical summer atmospheric circulation over the Globe during the Upper Silurian. (Modified after Ziegler <u>et al</u>., 1977.)

g. Hypothetical winter atmospheric circulation over the Globe during the Upper Silurian. (Modified after Ziegler <u>et al</u>., 1977.)

h. Ocean circulation patterns during the Upper Silurian. (Modified after Ziegler <u>et al</u>., 1977.)

high and low pressure areas in both the mid winter and mid summer months.

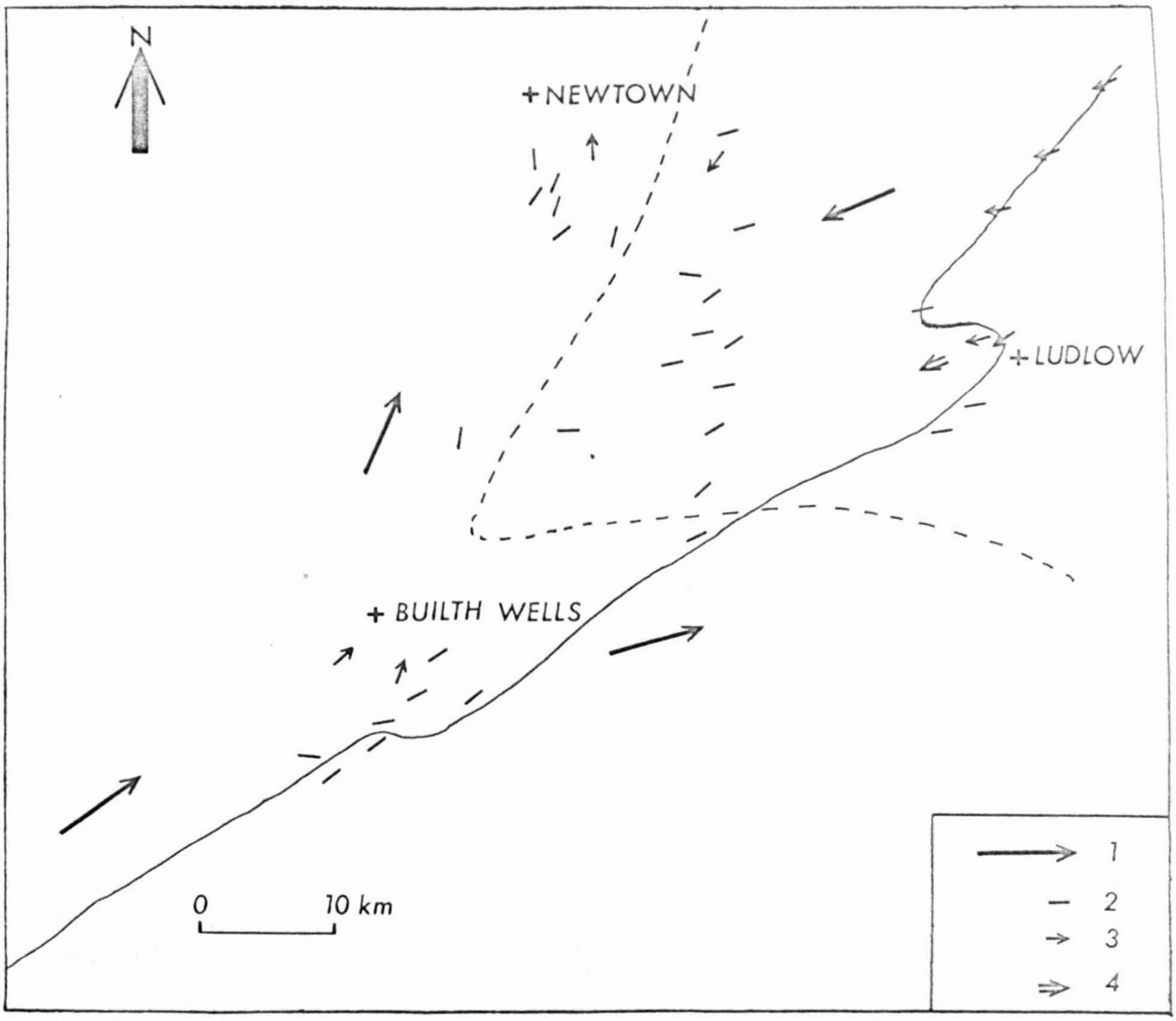
4. Palaeocurrents

Some palaeocurrent studies of the upper Whitcliffian and Downtonian have been made (e.g. Hobson, 1960; Bailey & Rees, 1973; Allen, 1974a). However, these studies (summarised in Text-Fig. 13 for the Whitcliffian) have tended to deal with small areas, and have not tried to relate these palaeocurrents and associated sediments to the larger more global picture of ocean current circulation. As can be seen in Text-Fig. 12, the Welsh Borderlands were situated at a point in between the western edge of the Rheic ocean and the eastern margin of the Iapetus ocean. During the Ludlovian the Welsh Borderlands were separated from the Iapetus ocean by a land mass extending across from Pembrokeshire over most of Ireland (cf. Holland, 1969; Sanzen & Baker, 1973). Shelf sedimentation on the eastern margin of the Iapetus Ocean resulted in the deposition of carbonate silts in the Upper Wenlockian (Watkins, 1978b) and early Ludlovian (Holland, 1969) of Western Ireland (Dingle Peninsula). In the upper Ludlovian these carbonate sediments were replaced by a red bed sequence which Holland (1969, p.302-303) interprets as having formed in a variety of intertidal and fluviatile environments, suggesting that the Irish - Welsh land mass was expanding westwards during the upper Ludlovian into the Iapetus Ocean.

The southern end of this land mass probably allowed some mixing of the northward moving Iapetus Ocean currents (Ziegler <u>et al</u>., 1977) and the southward flowing currents of the Rheic Ocean (Norman, 1963; Ziegler <u>et al</u>., 1977).

The overall palaeogeography of the Welsh Borderlands at the close of the Ludlow series and early Downtonian is indicated in Text-Fig. 14.

The transition from marine sedimentation in the upper Ludlow through to the Temeside Formation in the basin at Kerry, the north western shelf in the Long Mountain, the southern shelf at Builth Wells and the eastern shelf at Ludlow will be described separately in order to determine why the Temeside Bone-Bed was deposited in the Ludlow district but not elsewhere.



Text-Fig. 13. Palaeocurrents over the Welsh Borderlands during the uppermost Ludlovian. (Modified after Bailey & Rees, 1973; Whitaker, 1962

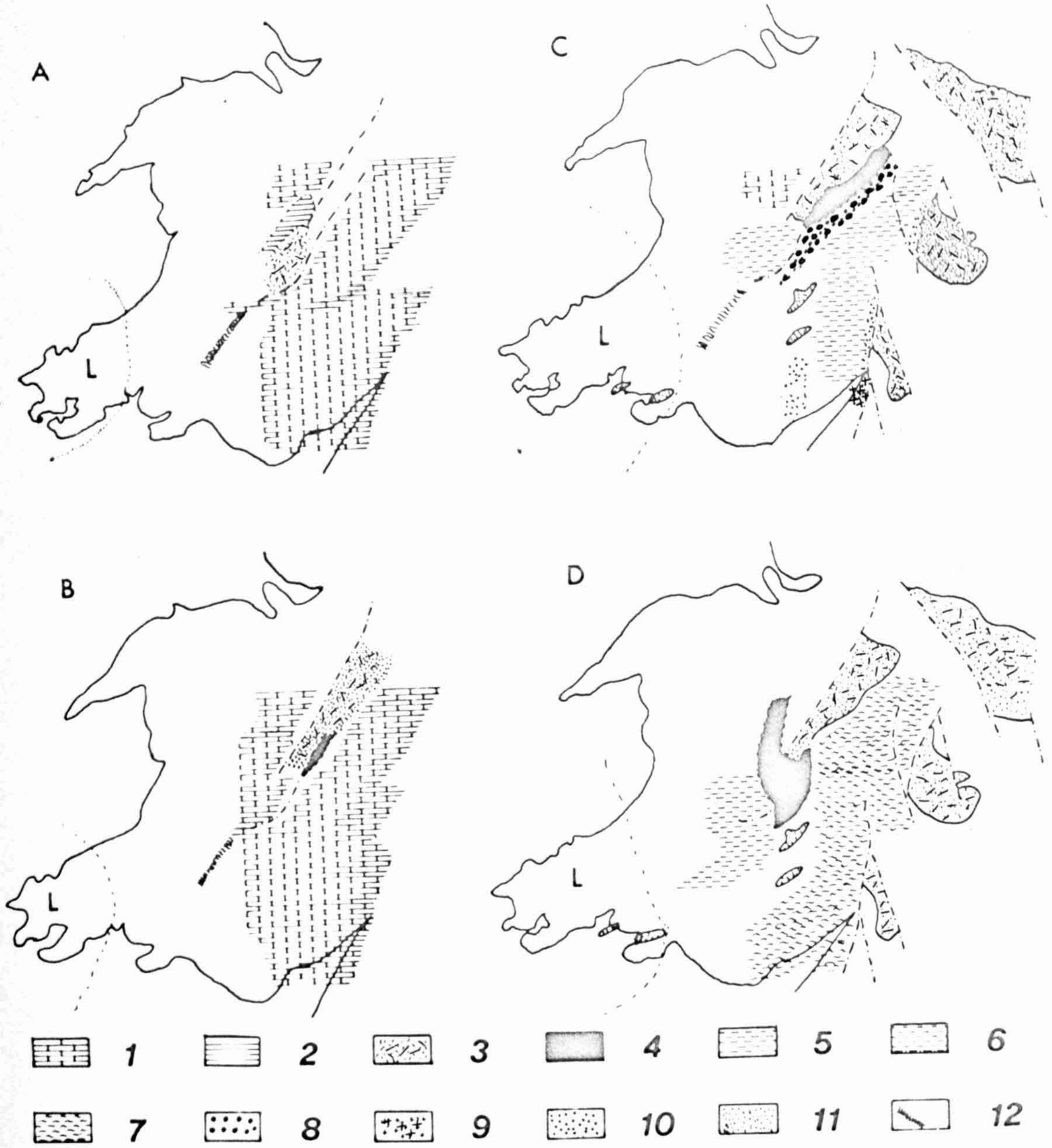
1. Major palaeocurrent trends

2. General current lineation

3. Measured palaeocurrent direction

4. Submarine canyon

Dashed line separates northward from southward flowing currents.



Text-Fig. 14. Ludlovian and Downtonian palaeogeographies:-

(a) Basal Whitcliffian - note presence of deep fault bounded basin surrounded by shelf sediments.

(b) Top Whitcliffian - note that general uplift has resulted in intertidal deposition on the eastern margin of the Longmyndian Precambrian block and the removal of the Ludlovian basin.

(c) Basal Downtonian - note (1) carbonate shelf sedimentation on the western side of the Longmyndian block, (2) carbonate depleted shelf sedimentation in the old Ludlovian basin, (3) an enlargement of the intertidal zone on the eastern margin of the Longmyndian block, (4) the development of a N-S trending strip of subtidal phosphatic clays bounded on both sides by quartz rich sublithobonebeds and lithobonebeds on the eastern side of the Longmyndian block, and (5) that this band of phosphatic clays grades into phosphorites at its southern extremity.

(d) Middle Downtonian - about the time the Temeside Bone-Bed was deposited. Note (1) intertidal sedimentation on the southern and western margins of the Longmyndian Block, (2) shelf sedimentation of siltstones and sandstones in the old Ludlovian basin and southern margins in the Cennen valley contain an articulate Brachiopod fauna (Appendix 2), (3) high intertidal/supratidal and fluvial Red Bed deposition in Usk contain an articulate Brachiopod fauna (Walmsley, 1959).

The Precambrian blocks indicated probably formed land areas or positive regions of no sediment deposition which were gently rising through the Downtonian. The erosion surface indicated in Wales probably persisted from the early Whitcliffian into the basal or middle Downtonian (cf. Potter & Price, 1965; Siveter, 1974; Squirrell & White, 1978).

Key to symbols:-

1 = Carbonate Shelf sea sedimentation; 2 = Mega-varves and Turbidite sedimentation; 3 = Rhythmite and Turbidite basinal sedimentation; 4 = Intertidal sediments; 5 = Subtidal phosphatic clays; 6 = Subtidal shelf siltstones and sandstones; 7 = Supratidal, high intertidal and fluvial red beds; 8 = Lithobonebeds; 9 = Phosphorites; 10 = Quartz rich sublithobonebeds; 11 = Rising Precambrian massifs; 12 = Erosion surface; L = Land.

Compiled after Allen, 1974a; Antia, 1979a,b,c; Sanzen-Baker, 1972; Bailey & Rees, 1972; Cave & White, 1972; Squirrell & White, 1978; Lawson, 1955; and about 30 other articles, papers and theses, some of which are listed in the Bibliography.

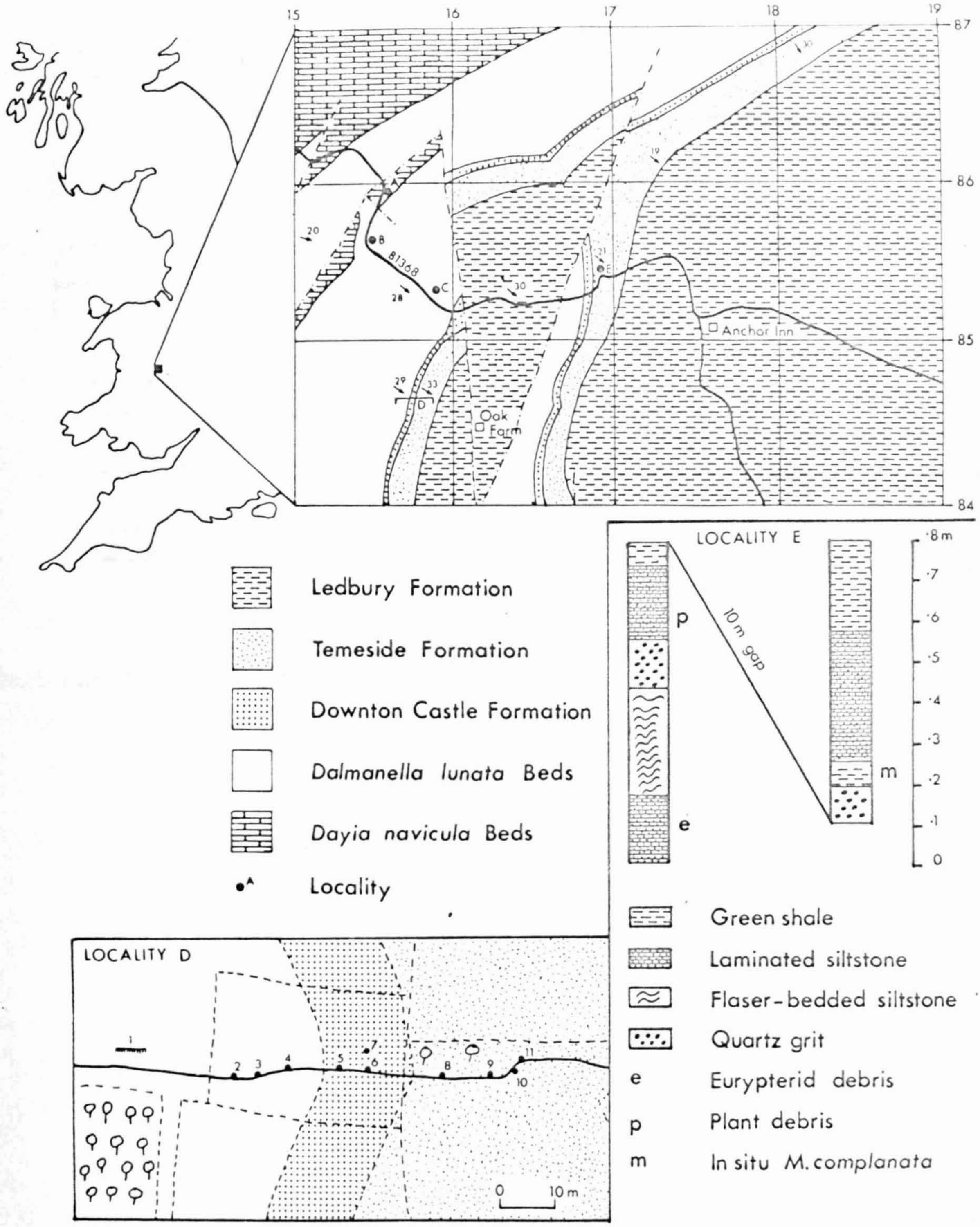
1. The Kerry region

The region studied and sample localities are indicated in Text-Fig. 15. The sediments observed have been mapped by Earp (1938) and may be described as follows:-

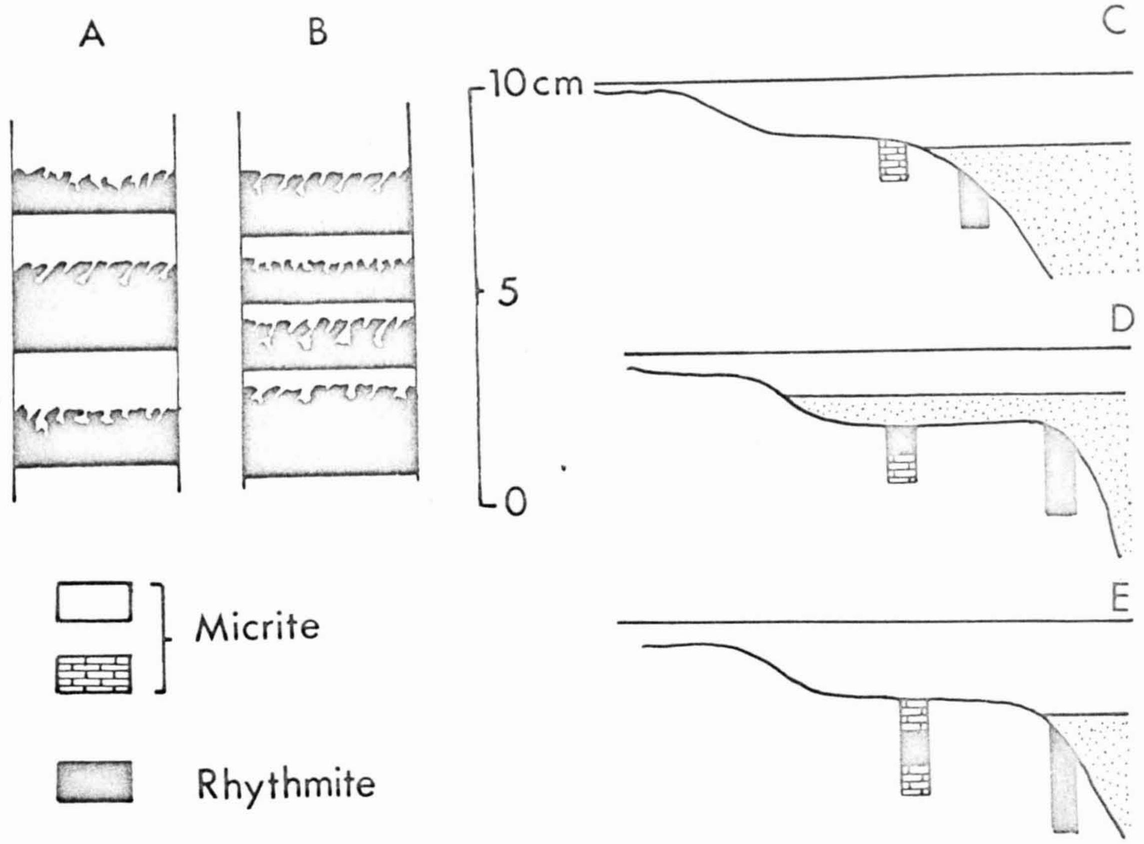
(a) Dayia navicula Beds (Lower Whitcliffian, Locality A)

The Dayia beds may be described as bioturbated grey micrites (1 - 10 cm thick) containing a low density monospecific assemblage of articulated ?in situ brachiopods belonging to the species Dayia navicula (density of 62.4 articulated ?in situ D. navicula's per m^2 bedding plane surface area: 10 m^2 examined), alternating with well laminated grey clay/silt rhythmites containing no fauna (6 m^2 bedding plane surface area examined). The upper surface of these rhythmites are occasionally burrowed by burrows extending down into them from the overlying micrites (Text-Fig. 16). These rhythmites also contain layers rich in limonite specks (originally pyrite framboids?).

At the present time similar sediment structures are produced as a direct result of an oscillating thermohaline stratification of the water body (Degens and Stoffers, 1976; Degens et al., 1978). It is known that the Ludlovian basin (Holland and Lawson, 1963) in which Kerry is situated, had a stratified water body (Cherns, 1977). The contrasting environments above and below the pycnocline differed in oxygen and hydrogen sulphide content (Cherns, 1977) and other chemical parameters. The carbonate system is particularly sensitive, in that $CaCo_3$ may precipitate above and dissolve below the interface (Degens et al., 1978, p.507). Consequently regions on the margin of a basin may be affected by minor depth fluctuations in the position of the pycnocline resulting in the deposition of megavarves similar to those recorded in this study (Text-Fig. 16). The carbonate fraction of the megavarve is deposited while the pycnocline is lowered (Text-Fig. 16C). A subsequent upward migration of the pycnocline would kill off the extant marine community and result in anoxic rhythmite deposition at this point (Text-Fig. 16d). A later downward migration of the pycnocline would allow the deposition of carbonates (Text-Fig. 16e) and the recolonisation of the region



Text-Fig. 15. Geological map of the Kerry district with insets of (1) minor localities within Locality D and (2) the sediment section at Locality E.



Text-Fig. 16. (a) Megavarves in the Dayia navicula Beds at Locality A, Text-Fig. 15.

(b) Megavarves from the Black Sea D.S.D.P. borehole 379A, Section 60-2(after Degens et al., 1978). Note their similarity to the Ludlovian megavarves in Text-Fig. 16a.

(c) Stratified water body with an oxygenated upper zone and anoxic (stippled) lower zone depositing micrite and rhythmites above and below the pycnoline respectively.

(d) A raising of the pycnocline establishes euxinic rhythmite depositing conditions in the shallower part of the basin.

(e) A subsequent lowering of the pycnocline establishes oxic micrite depositing conditions, supporting a benthic infauna in the shallower parts of the basin.

Repetitions of this cycle (Text-Fig. 16 c-e) will result (Degens et al., 1978) in the deposition of megavarves and could account for the megavarves in the Dayia navicula Beds (Text-Fig. 16a).

by a soft bodied infauna and epifauna. Subsequent changes in the relative position of the pycnocline would result in the deposition of the sediments observed in the *Dayia* Beds.

The *Dayia* Beds are overlain by the *Dalmanella lunata* Beds (Earp, 1938). The latter name is retained here and not updated to *Salopina lunata* Beds in order to conform with current stratigraphic procedure (cf. Hedberg, 1976; Lawson, 1979a,b).

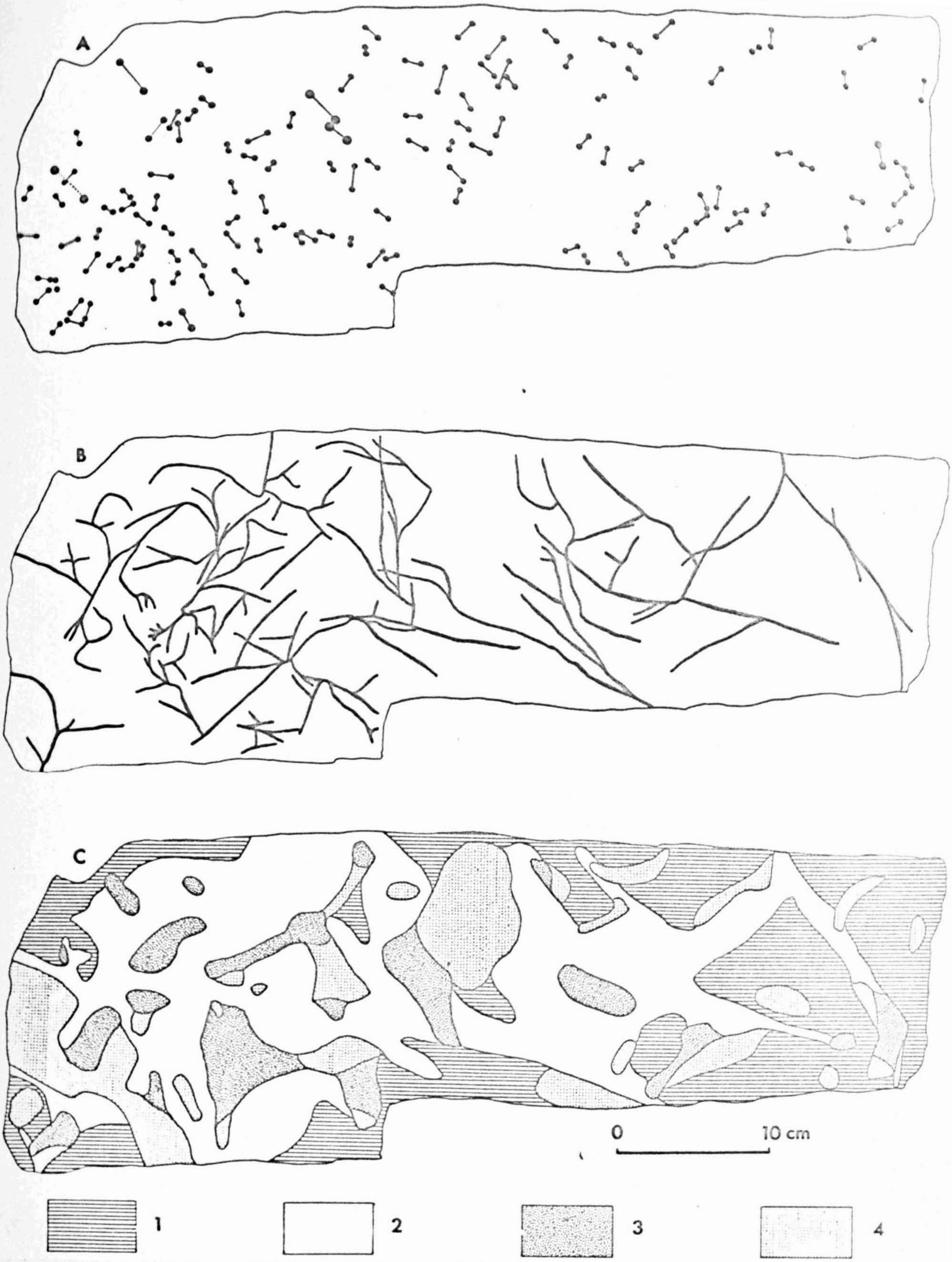
(b) The *Dalmanella lunata* Beds

The *Dalmanella lunata* Beds may be described as a sequence of megavarves and rhythmites similar to those present in the *Dayia* Beds without *Dayia navicula* with interspersed distal turbidites (5 - 15 cm thick) frequently containing transported shells at their base. For example, one turbidite layer contained the following fossils, *Salopina lunata* (n = 58; 55.7%), *Protochonetes ludloviensis* (n = 6; 5.7%), *Microsphaeridiorhynchus nucula* (n = 4; 3.8%), *Fuchsella amygdalina* (n = 1; 0.9%), *Murchisonia corallii* (n = 1; 0.9%) and round crinoid columnals (n = 34; 32.6%) in a 3 m^2 area over its base. The relative thickness of the individual light and dark layers of the rhythmites is indicated in Text-Fig. 12 b,d. The uppermost *Dalmanella lunata* Beds are exposed near Oak Farm, Kerry (Text-Fig. 15). Here they consist of symmetric current rippled sediments (wavelength 5 - 11 cm; amplitude 5 - 8 mm; Ripple index 10 - 22) containing a typical Whitcliffian fauna (Table 7). The overlying sediments consist of micrite sheets in more silty micrites containing shells at their base (Table 7). The overlying sediments (Text-Fig. 15, Locality D5 - 7) are current rippled and parallel laminated bioturbated limonite rich silts containing dense shell sheets enriched in *T. helicites* and *M. complanata*. These Beds have been termed the *Platyschisma* Beds by Earp (1938) and others.

Two types of trace fossil are common on these sediments. The first assigned here to the genus *Bifungites* sp. (Plate 2, Fig. 7) occurs in densities of up to 850 individual burrows to a metre square. Bedding plane surface area (Text-Fig. 17) in which individual burrows are oriented (Text-Fig. 18a) and

Table 7. Faunas recorded from locality D at Kerry. The position of each sample site is indicated in Text - Fig. 15.

	SAMPLE SITE										
SPECIES	1	2	3	4	5	6	7	8	9	10	11
Brachiopods											
Craniops implicatus (J.de C. Sowerby)	7·5	5·8	-	-	-	-	-	-	-	-	-
Lingula cornea	-	-	12·5	-	-	0·4	-	-	0·4	-	3·3
Microsphaeridiorhynchus nucula (J.de C.Sowerby)	-	-	-	5·0	-	-	-	-	-	-	-
Orbiculoidea rugata (J.de C.Sowerby)	-	5·8	-	-	-	-	-	-	-	-	-
Protochonetes ludloviensis Muir Wood	25·0	23·5	-	65·0	-	-	-	-	-	-	-
Salopina lunata (J.de C.Sowerby)	65·0	52·9	-	15·0	-	-	-	-	-	-	-
Molluscs											
Bucanopsis expansus (J.de C.Sowerby)	2·5	-	-	5·0	-	-	-	-	-	-	-
Leodispis barrowsi	-	5·8	12·8	-	0·0	3·0	62·1	-	77·0	-	6·6
Modiolopsis complanata J.de C.Sowerby	-	-	-	-	57·3	14·1	7·3	14·0	8·3	66·6	86·6
Solenamya sp.	-	-	-	-	-	-	6·3	-	-	-	-
Turbocheilus helicites (J.de C. Sowerby)	-	-	-	-	-	67·8	-	-	-	-	-
Ostracods											
Cytherellina siliqua Jones	-	-	5·1	10·0	-	-	1·0	-	-	-	-
Frostiella groenvalliana	-	-	-	-	-	-	-	0·7	-	-	-
Hermannia marginata	-	5·8	53·8	-	3·7	6·4	14·7	3·7	3·1	33·3	-
Hermannia phaseola (Jones)	-	-	-	-	-	1·7	5·2	5·9	5·9	-	-
Londinia kiesowi	-	-	2·5	-	38·8	1·2	-	71·1	1·5	-	3·3
Lophoctonella sp.	-	-	-	-	-	-	1·0	-	-	-	-
Other fossils											
Eurypterid fragments	-	-	2·5	-	-	2·5	-	-	-	-	-
Fish skin (T.parvidens)	-	-	-	-	-	-	-	-	0·4	-	-
Gomphonchus murchisoni (Ag.)	-	-	10·2	-	-	-	-	-	0·4	-	-
Logania ludlowiensis	-	-	-	-	-	2·5	2·1	-	5·5	-	-
Thelodus parvidens	-	-	-	-	-	-	-	4·4	0·4	-	-
Number of fossils observed	40	17	39	20	1068	233	95	135	253	3	30
Number of kg. of sediment processed (ca.)	7	5	7	5	8	2	2	2	2	2	3

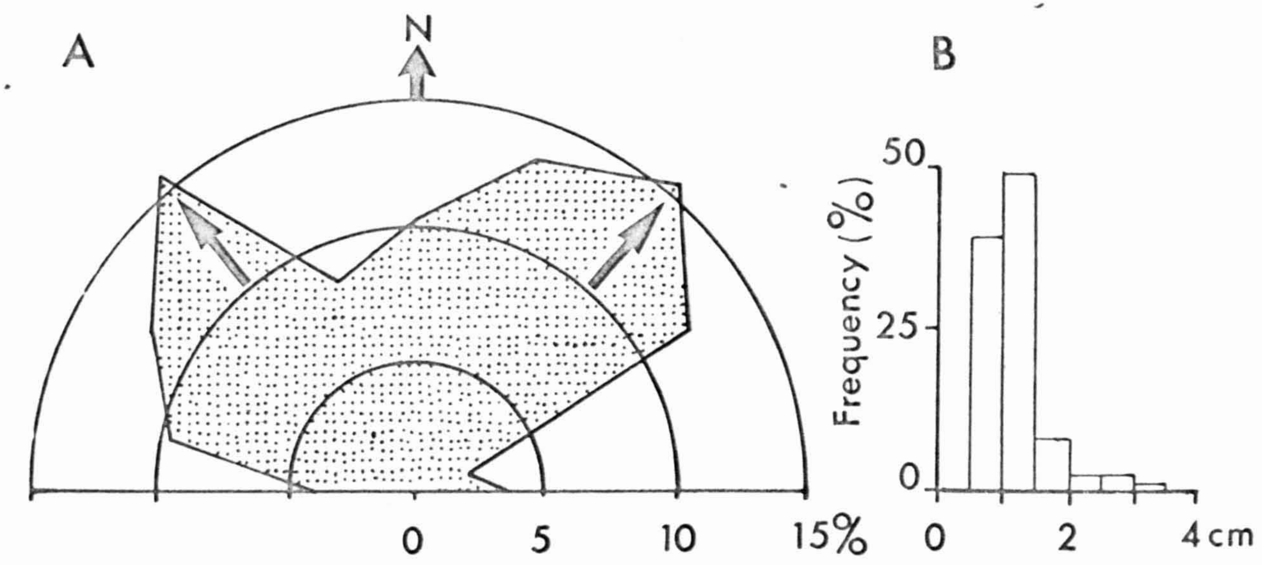


Text-Fig. 17. (A) *Bifungites* sp. burrows from the Downton Castle Formation (at Kerry, Locality D/7 - Text-Fig. 15) on a bedding plane.

(B) Other trails on the same bedding plane.

(C) Distribution of trace fossils on the bedding plane:-

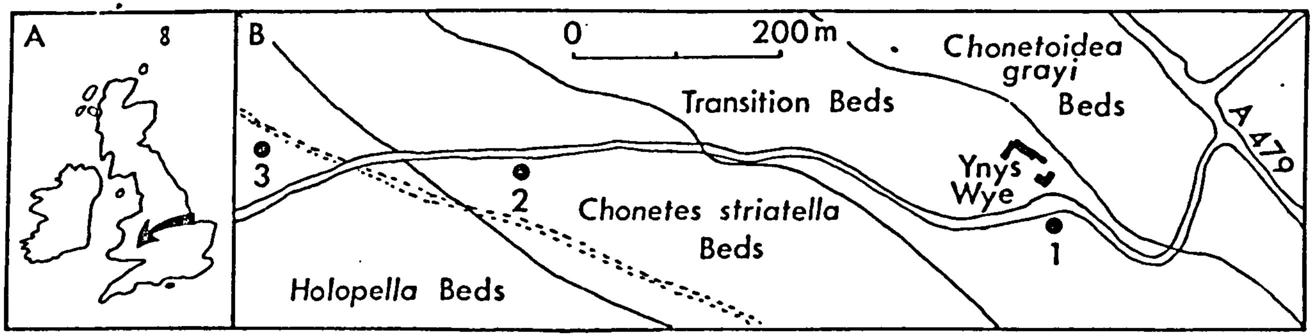
(1) No trace fossils
(2) Trails only
(3) *Bifungites* + trails
(4) *Bifungites* only



Text-Fig. 18. *Bifungites* burrows from the Downton Castle Formation (Locality D/7) at Kerry:-

(a) Orientation. Note Bimodal orientation.

(b) Length/frequency distributions of the same burrows.



Text-Fig. 19. Sampled localities in the Builth region.

have the size distribution indicated in Text-Fig. 18b. They were dwelling burrows which were probably produced by a suspension feeding polychaete or arthropod (Pye pers. com. 1979).

These sediments are overlain by the Temeside Formation (the Green Downtonian of Earp, 1938) which consists of micaceous siltstones and coarse sandstones containing some large calcareous concretions. The faunas present in these sediments are documented in Table 7.

Another section through the Green Downtonian (Text-Fig. 15) contains some plant debris, a eurypterid fragment and a single in situ specimen of M. complanata.

2. The Builth region

In the Builth region the transition from the top Ludlovian into the Temeside Formation has been documented by Straw (1937) near Ynys Wye Farm (Text-Fig. 19). In this study a quarry in each of Straw's three (Whitcliffian) uppermost Ludlow units were examined. The overlying Temeside Formation is poorly exposed and was only seen as small blocks of unfossiliferous green siltstone. The sampled exposures are indicated in Text-Fig. 19.

(a) Transition Beds (?basal Whitcliffian)

The transition beds are exposed in a small quarry opposite Ynys Wye Farm (Text-Fig. 19). They consist of shelly rippled, bioturbated siltstones containing a benthic fauna of articulate brachiopods (e.g. Dayia navicula, Salopina lunata, Microsphaeridiorhynchus nucula and Protochonetes ludloviensis), bivalves, bryozoans and ostracods. The observed fauna is indicated in Table 9.

(b) Chonetes striatella Beds (?Middle Whitcliffian)

The quarry in the Chonetes striatella Beds indicated in Text-Fig. 19 consists of dark siltstones with unfossiliferous fine grained rippled sandstone sheets (up to 8 cm thick) containing trace fossils (Plate 2d). The observed fauna is indicated in Table 8.

(c) Holopella Beds (?Upper Whitcliffian)

The Holopella Beds consist of dark siltstones containing minor slump

Table 8. Faunas from the Builth District. Locality positions are indicated in Text-Fig.20: 3a indicates fauna from a shelly layer; 3b indicates a fauna from poorly fossiliferous muddy siltstones. 4 is a fauna from the Lower Whitcliffe Beds of the Long Mountain.

	LOCALITY				
SPECIES	1	2	3a	3b	4
Brachiopods					
Craniops implicatus	0.09	-	0.74	-	-
Dayia navicula (J.de C.Sowerby)	4.07	-	0.29	-	-
Microsphaeridiorhynchus nucula	6.89	3.04	3.37	22.85	7.40
Orbiculoidea rugata	-	-	0.10	-	-
Protochonetes ludloviensis	70.58	86.58	7.80	5.71	11.11
Salopina lunata	1.06	0.40	47.40	8.57	7.40
Bivalves					
Fuchsella amygdalina (J.de C.Sowerby)	-	2.03	-	-	-
Goniophora cymbaeformis (J.de C.Sowerby)	0.48	0.81	-	-	-
Modiolopsis sp.	-	0.40	-	-	-
Nuculites antiquas (J.de C.Sowerby)	0.58	1.21	1.56	8.57	-
Paracyclas sp.	-	-	0.52	14.28	-
'Pterinea' tenuistriata (McCoy)	0.09	-	-	-	-
Pteronitella retroflexa (Wahlenberg)	-	-	0.07	-	-
Cephalopods					
Kionoceras angulatum (Wahlenberg)	0.09	-	-	-	-
'Orthoceras' sp.	0.19	1.21	0.29	-	44.44
Paraphragmites ibex (J.de C.Sowerby)	0.09	0.40	-	-	-
Other Molluscs					
Bucanopsis expansus	0.19	-	-	-	-
Loxonema obsoletum (J.de C.Sowerby)	-	-	0.81	11.42	-
Hyolithes forbesi (Sharpe)	0.58	-	-	-	-
Ostracods					
Calcaribeyrichia tegula Siveter	0.38	-	-	-	-
Cytherellina siliqua	0.09	-	0.52	-	11.11
Hebellum cf.tetragonum	-	-	0.07	-	-
Hermannia cf. marginata	-	-	0.89	11.42	-
Kuresaaria circulata	0.38	-	1.40	-	7.40
Lophoctonella sp.	-	-	-	-	7.40
Bryozoan colonies					
Ceramopora sp.	-	0.20	0.07	11.42	-
Leioclema sp.	1.35	0.20	-	-	-
Rhopalonaria sp.	-	-	0.07	-	-
Fish					
Gomphonchus murchisoni	-	-	0.07	-	-
Logania ludlowiensis	-	-	0.07	-	-
Nosteolepis sp.	-	-	0.07	-	-
Thelodus parvidens	-	-	0.14	-	-
Other fossils					
Round crinoid columnals	11.65	3.04	36.23	5.71	-
Number of fossils observed	1030	498	1344	35	27
Number of kg of sediment processed (ca.)	3	2	4	5	77

structures (crinkle marks), vertically orientated crinoid stems, and rippled buff fine grained sandstone sheets containing layers of commutated shell debris at their bases. The faunas of these two sediment types are indicated in Table 8.

The overall impression obtained from this vertical transect through the Whitcliffian was that (1) brachiopod diversity decreased up the sequence, (2) the overall environment changed from an aerated benthic environment of shelly siltstones supporting a soft bodied benthic infauna in the Transition Beds through to a more segregated environment in the Chonetes striatella Beds where sand sheets (?storm deposits) alternated with bioturbated dark siltstones containing shell patches. These sandstones contain escape burrows and have been burrowed into from the overlying sediment surface (Plate 2, Fig. 4).

The overlying Holopella Beds contained bioturbated dark siltstones containing slump structures and an in situ fauna of crinoids also sandstone sheets with shell debris bases indicating that the environmental conditions which had developed in the Chonetes striatella Beds continued into the Holopella Beds.

Unfortunately the contact between the Holopella Beds and the overlying sediments of the Temeside Formation is not exposed at the present time and the exposures seen of the Temeside Formation were too scanty to allow proper environmental interpretations to be drawn concerning the relationship between the marine top Ludlovian sediments and the overlying 'Downtonian' Temeside Formation in the Builth region.

3. Long Mountain

The transition from the Whitcliffian (top Ludlovian) into the Downtonian Downton Castle Formation and Temeside Formation has been observed (Austin, 1925; Palmer, 1972) near Wallop Hall. In this study faunal collections were made from the Whitcliffian sediments and Temeside Formation at Wallop Hall.

(a) Lower Whitcliffian (= Causemountain Formation of Palmer, 1972)

These sediments are exposed in a quarry 500 m south of Wallop Hall (S.J. 331 307) and consist of irregularly bedded, shaley - massive, muddy siltstones with a poorly developed rhythmite type carbonate sedimentation, similar to the basinal Whitcliffian sediments (Chonetes striatella Beds) of Kerry. The fauna is rare consisting largely of scattered fragmentary nektonic species (e.g. orthoconic nautiloids). However, at the base of the more crystalline carbonate rich bands (?distal turbidite bands) shell debris belonging to benthic species (e.g. brachiopods and molluscs) is present. A faunal list for this quarry is given in Table 8. The environment of deposition is considered here to be similar to that seen in the Chonetes striatella Beds at Kerry.

(b) Upper Whitcliffian/Downtonian Boundary (= Wallop Hall Formation of Palmer, 1972)

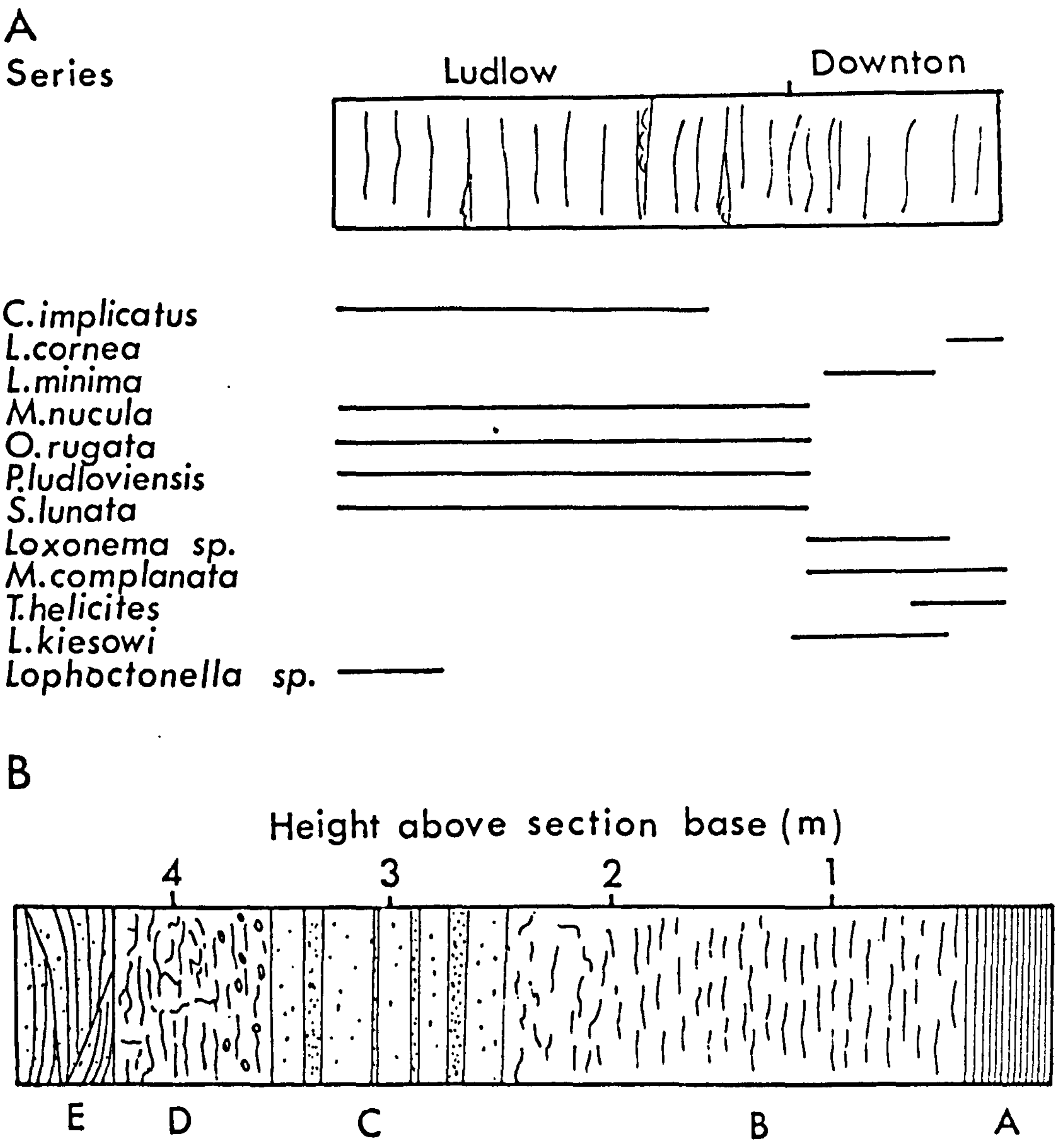
The Whitcliffian/Downtonian Boundary is contained within the Wallop Hall Formation of Palmer (1972). The lower part of this member which may be equated with the upper Whitcliffe Beds at Ludlow consists of poorly fossiliferous hard calcareous non-turbiditic coarse siltstones - fine sandstones (2 - 10 cm thick) with planar and/or current ripple laminae. Generally they are well sorted but may show grading in the form of shelly soles with an abundant current derived fauna including characteristic shallow water Whitcliffian brachiopods. The calcareous siltstones become more abundant towards the middle of the Formation with richly fossiliferous shelly soles. The interbedded shaley micaceous siltstones also become increasingly fossiliferous with some laminae covered in sorted shell assemblages and vertebrate debris (composed of thelodont denticles). This sediment sequence is present (e.g. Palmer, 1972, p.150) at Wallop Hall (S.J. 331 307) and contains an abrupt transition from Whitcliffian to Downtonian faunas within a shallow water marine carbonate siltstone. The distribution of faunas and sediments in this section is illustrated in Text-Fig. 20.

(c) The Temeside Formation

The Temeside Formation can be seen in Wallop Hall quarry (S.J. 331 307) where it consists initially of a sequence of silty parallel laminated mudstones containing an abundant flora (Plate 1, Fig. 5) which grades up into a sequence of mudcracked and wrinkle marked blocky micaceous muddy siltstones containing dense sheets of transported bivalve and ostracod shell debris which are overlain

Table 9 Faunas from the Temeside Formation at Wallop Hall. Sample positions are given with respect to the base of the section illustrated in Text-Fig.20. An additional 10 samples totaling about 30 kg of rock were made from the section. However, they proved to be unfossiliferous.

	SAMPLE POSITIONS				
SPECIES	0·3m	1·1m	1·6m	2·2m	3·0m
Brachiopods					
Lingula _cornea_	15·62	-	0·39	5·76	5·88
Bivalves					
Leodispis _barrowsi_	15·62	5·55	74·71	56·73	21·58
Modiolopsis _complanata_	-	72·22	8·04	5·76	-
Solenamya sp.	-	-	-	3·84	-
Ostracods					
Cytherellina _siliqua_	6·25	-	-	0·96	-
Hermannia _marginata_	-	-	5·74	5·76	11·76
Hermannia _phaseola_	43·75	19·44	3·06	12·50	25·49
Londinia _kiesowi_	3·12	2·77	1·53	-	5·88
Lophoctonella sp.	-	-	-	1·92	-
Other fossils					
Eurypterids	-	-	-	-	11·76
Gomphonchus _murchisoni_	12·50	-	0·39	-	5·88
Logania _ludlowiensis_	-	-	5·36	6·73	11·76
Nosteolepis sp. (Fish skin)	3·12	-	0·39	-	-
Thelodus _parvidens_	-	-	0·39	-	-
Number of fossils counted	32	36	261	104	51
Number of kg of sediment processed	3	4	5	3	6



Text-Fig. 20. (A) Faunas across the Ludlovian - Downtonian Boundary at Wallop Hall (after Palmer, 1972).

(B) Sediments in the Temeside Formation at Wallop Hall:- A = Silty mudstones; B = Blocky-micaceous muddy siltstones; C = Interbedded flaggy siltstones and micaceous fine grained sandstones; D = Blocky-rubbly silty mudstones with calcareous pellets; E = Cross bedded fine grained sandstones.

by a sequence of alternating parallel laminated siltstones and fine sandstones with micaceous laminae and weathered calcareous pellets (0.5 - 2 cm in diameter - ?Oncolites), containing both Lingula cornea and Leodispis barrowsi in situ. These sediments are overlain by first a sequence of rubbly muddy siltstones containing weathered calcareous pellets and then a sequence of cross bedded fine grained sandstones. The observed sediment log is given in Text-Fig. 20. The Lerpiditid ostracods observed are illustrated in Plate 2, Fig. 5, 6, and the fauna recorded is listed in Table 9. The sediments in this section probably represent a low energy accreting mudflat environment at its base, passing up into higher intertidal or even back beach lagoonal muds and 'beach' sandstones (cf. Allen, 1974).

Although the overlying Ledbury Formation was not seen, it has been described (Palmer, 1972) as a red bed sequence of conglomeratic, micaceous fine grained sandstones interbedded with micaceous muddy siltstones containing a fauna of Lingula cornea, Hermannia sp. and rare small bivalves.

4. Ludlow

The transition from the top marine Ludlovian into the Downtonian Ledbury Formation in the Ludlow district has been intensively studied by both the author and other researchers (e.g. Elles & Slater, 1906; Holland et al., 1963; Allen, 1974a).

These studies have recognised nine sedimentary facies.

The stratigraphic position of each facies is shown in Text-Fig. 21. Each facies may be described as follows:-

(a) Rhythmite facies (e.g. G.R. SO 487 712)

Parallel laminated carbonate silts containing 7 - 15 alternations of light (carbonate rich) and dark silt laminae in a 1 cm vertical section. Local erosion surfaces are present and are usually covered with abundant shell debris, frequently forming sheets 3 - 15 mm thick. These shell sheets are considered to have formed as storm deposits (Hurst & Watkins, 1977). The laminae resemble the rhythmites described by Seibold (1955, 1958) and others (see Reineck & Singh, 1973). They are considered here to represent the deepest water environment seen. They are considered by analogy with modern rhythmites to represent a water depth of between 40 and 600 m (Seibold 1955, 1958; Byrne & Emery, 1960; Calvert, 1964).

(b) Rippled carbonate silt facies (e.g. G.R. SO 487 712)

Shelly rippled carbonate silts interbedded with parallel laminate silts, containing local slumps and channels. Shell laminae are common. Bioturbation and a shelly infauna are common.

The transition from this environment to the underlying rhythmite environment is gradual. With an initial influx of bioturbating organisms succeeded by the development of ripples and deposition of some fine grained rippled sand sheets. This environment appears to be less stagnant than the rhythmite environment and probably represents a slightly shallower environment in which both the coarse sands and shell sheets were deposited by storms (Watkins & Berry, 1977). The depth represented by this facies was probably within the range -25 to -100 m O.D. (cf. Allen, 1970; Reineck & Singh, 1973; Antia, 1979a).

(c) Scoured Rippled Carbonate facies (e.g. G.R. SO 508 741)

Shelly rippled laminated silts containing alternating clay and shelly silt lenticles, local scour channels, shell gravel megaripples, shell sheets, rippled sand sheets, local slumping, some parallel laminate storm deposited silts. These sediments probably formed below surf base (ca. 10 m depth) and above wave base (ca. 30 - 50 m depth)(cf. Allen, 1970; Reineck & Singh, 1973).

(d) Lenticular bedded silt facies (e.g. G.R. SO 512 742)

Lenticular bedded calcareous clays silts and shell sheets (cf. Reineck & Singh, 1973). These sediments are thought (Allen, 1970; Antia, 1979a,b; Antia & Whitaker, 1979) to have been deposited in a shallow subtidal environment within 15 m of the low water mark (i.e. above surf base) (cf. Allen, 1970; Reineck & Singh, 1973).

(e) The Bone-Bed facies (e.g. G.R. SO 512 742)

The bone-bed environment may be described as a lenticular bedded sequence of clays, silts, fine sands and vertebrate coquina. It has been described in detail by Antia (1979a) and Antia & Whitaker (1979) and is considered (Allen, 1962, 1974; Allen & Tarlo, 1963; Antia, 1979a, Antia & Whitaker, 1979) to have been deposited within the lower part of the intertidal zone as a series of lag concentrates on a mudflat environment.

(f) The Rippled Mudflat facies (e.g. G.R. SO 512 742)

Lenticular bedded clays, silts and sands, with some rippled sand sheets and rare bioturbation. The sediments of this environment have been described by Allen (1974) and Antia (1979a) and are thought to have formed in the lower part of intertidal environment.

(g) Mud mound facies (e.g. G.R. SO 512 742)

This environment consists of a series of channels (up to 1.2 m wide, 0.3 m deep and 10$^+$ m in length) cut into lenticular bedded silts and infilled with shell debris, silts, sands and muds. The associated mounds often have mud cracks and plant debris on their upper surfaces, and contain limonitised shells and burrows. Similar environments have been recorded in the highest parts of the intertidal zone by Greensmith & Tucker (1967).

(h) Beach sand facies (e.g. SO 512 742).

Series of megaripples and dunes which are locally channelled and trough cross bedded and contain local parallel laminate paper silts. They contain no acritarchs (Richardson & Lister, 1969) and were probably deposited as beach sands (Allen, 1974). Local plant debris horizons are common. Details of one section exposing this environment are given in Fig. .

(i) Back beach clay facies (e.g. G.R. SO 521 741)

Overlying the beach sands are a series of red clays, locally parallel laminated, containing soil horizons. They are considered (Allen, 1974; Antia, 1979a) to represent a series of back beach, high intertidal to supratidal sediments and marine sediments.

Palaeontology

Each of these environments was sampled by the author in the Ludlow District. Samples consisted of 2 - 80 cm thickness of sediment throughout each section. The faunas of each unit (ca. 140 individuals per sample) were converted into percentages. The units were then grouped into environments. The percentages of each species in each environment were summed. These summed percentages (SP) for each species in a given environment were then divided by the number of unit samples (N) collected from the environment to obtain an expected mean value (EMV) of the abundance of each species in the environment. i.e.

$$\text{EMV} = (\text{SP} / \text{N})$$

The values of EMV were used to calculate the rarefied diversity of the calcareous invertebrate faunas in each environment.

The ranked abundances of each species in each environment is indicated in Table 10. Also indicated in this table are the modal environment and range of environments each species present. The total sample size used in compiling this table is about 85,000 fossils. Details of their distribution in the individual sections examined will be presented elsewhere.

Diversity

Almost all studies of the Whitcliffe Beds show that their diversity decreases towards their top (e.g. Holland et al., 1963; Hurst & Watkins, 1977; Watkins, 1978a). This diversity change has been measured in this study using the rarefaction index. This index measures the diversity of different sized collections at a common sample size. The diversity values were calculated using the formula (see Heck et al., 1975, Antia, 1977):-

$$E(s) = s - \sum_{i=1}^{s} (1 - N_i/N)^n$$

$E(s)$ = species richness (diversity), N_i = species population size for $i = 1....s$, N = total number of individuals, s = number of species, n = required sample size.

Table 10 Ranked faunal distributions from 9 palaeoenvironments in the Ludlow District. A key to the palaeoenvironments is given in the text. M.E. = Modal environment, R = The range of environments in which an individual species is present

	PALAEOENVIRONMENT										
Species	1	2	3	4	5	6	7	8	9	M.E.	R
Brachiopods											
Aegeria grayi	8	33	-	-	-	-	-	-	-	1	1 - 2
Atrypa recticularis	17	34	-	-	-	-	-	-	-	1	1 - 2
Craniops implicatus	6	31	17	5	13	-	-	-	-	4	1 - 5
Dayia navicula	12	5	-	-	-	-	-	-	-	2	1 - 2
Howellella elegans	22	37	-	6	23	-	-	-	-	4	1 - 5
Isorthis sp.	32	17	-	-	-	-	-	-	-	2	1 - 2
Lingula sp. nov.	-	-	16	7	18	-	-	-	-	4	3 - 5
Lingula cornea	-	-	-	-	-	-	-	13	2	9	8 - 9
Lingula lata	41	15	19	4	14	-	-	-	-	4	1 - 5
Lingula lewisii	14	36	-	-	-	-	-	-	-	1	1 - 2
Lingula minima	-	-	-	-	1	3	2	4	-	5	5 - 8
Lingula cf. *missendenensis*	-	-	-	-	-	-	-	-	5	9	9
Microsphaeridiorhynchus nucula	2	2	2	3	6	-	-	-	-	1 - 3	1 - 5
Orbiculoidea rugata	27	20	6	10	-	-	-	-	-	3	1 - 4
Protochonetes ludloviensis	5	1	3	2	10	-	-	-	-	2	1 - 5
Salopina lunata	1	3	1	1	4	-	-	-	-	1,3,4	1 - 5
Shagamella ludloviensis	25	-	-	-	-	-	-	-	-	1	1

Shaleria ornatella	18	-	-	-	-	-	-	-	-	1	1
Sphaerirhynchia wilsoni	27	-	-	-	-	-	-	-	-	1	1
Bryozoan colonies											
Ceramopora sp.	15	9	17	-	-	-	-	-	-	2	1 - 3
Leioclema sp.	7	7	11	-	25	-	-	-	-	1,2	1 - 5
Rhopalonaria sp.	-	50	-	16	30	-	-	-	-	4	2 - 5
Bivalves											
Cardiola docens	-	10	-	-	-	-	-	-	-	2	2
Fuchsella amygdalina	9	4	5	11	-	-	-	-	-	2	1 - 4
Goniophora cymbaeformis	-	18	13	8	25	-	-	-	-	4	2 - 5
Grammysia sp.	-	40	-	-	-	18	-	-	-	6	2 - 6
Leodispis barrowsi	-	-	-	-	-	-	-	-	10	9	9
Modiolopsis complanata	-	-	-	19	9	2	4	2	-	6,8	4 - 8
Modiolopsis sp.	-	37	-	-	-	-	-	-	-	2	2
Nuculites antiquas	-	23	-	-	-	-	-	-	-	2	2
Nuculites ovata	20	24	-	19	25	-	-	-	-	4	1 - 5
Pterinea lineata	-	43	-	-	-	-	-	-	-	2	2
'Pterinea' tenuistriata	-	19	20	18	22	-	-	-	-	4	2 - 5
Pteronitella retroflexa	37	29	-	15	24	-	-	-	-	4	1 - 5
Solenomya sp.	-	42	19	-	-	13	-	11	-	8	2 - 8
Gastropods											
Cyclonema coralliii	37	28	-	-	-	-	-	-	-	2	1 - 2
Cymbularia carinata	-	-	-	-	-	15	-	-	-	6	6
Liospira sp.	37	47	-	-	-	-	-	-	-	1	1 - 2
Loxonema conicum	-	-	15	-	29	-	-	-	-	3	3 - 5
Loxonema gregarium	-	44	-	-	8	8	8	-	-	5 - 7	2 - 7
Loxonema obsoletum	-	12	-	12	21	15	-	-	-	2,4	2 - 6
Murchisonia sp.	-	41	-	-	-	-	-	-	-	2	2
Naticopsis cf. trevorpatriciorum	-	26	-	-	-	-	-	-	-	2	2
'Platyschisma' williamsi	-	-	-	-	19	17	-	-	-	6	5 - 6
Turbocheilus helicites	-	-	-	-	7	5	6	6	-	6	5 - 8
Cephalopods											
Kionoceras angulatum	25	21	-	-	-	-	-	-	-	2	1 - 2
'Orthoceras' sp.	23	6	9	-	-	-	-	-	-	2	1 - 3
Paraphragmites ibex	40	25	22	-	-	-	-	-	-	3	1 - 3
Other molluscs											
Bucanopsis expansus	-	27	-	119	-	-	-	-	-	4	2 - 4
Hyolithes forbesi	35	22	15	14	-	-	-	-	-	4	1 - 4
Trilobites											
Calymene sp.	10	-	-	-	-	-	-	-	-	1	1
Encrinuris sp.	16	44	-	-	-	-	-	-	-	1	1 - 2
Annelids											
Arabellites sp.	35	35	10	-	-	-	-	-	-	3	1 - 3
Keilorites sp.	-	-	4	-	-	-	-	-	-	3	3
'Serpulites' longissimus	13	11	7	-	-	-	-	-	-	3	1 - 3
Spirorbis lewisii	-	39	-	-	-	-	-	-	-	2	2
Ostracods											
Amygdalina sp.	50	-	-	-	-	-	-	-	-	1	1
Aparchites sinuatus	-	-	-	-	-	-	-	-	1	9	9
Aechimina sp.	-	-	-	-	-	-	-	-	6	9	9
'Beyrichia' sp.	20	16	-	-	-	-	-	-	-	2	1 - 2
Calcaribeyrichia tegula	-	14	-	-	-	-	-	-	-	2	2
Calcaribeyrichia torosa	-	-	22	-	13	-	-	-	-	5	3 - 5
Cavellina sp.	29	-	-	-	-	-	-	-	-	1	1
Cavellina cf. plana	-	-	-	-	-	-	-	-	4	9	9
Cavellina primaria	32	51	-	-	-	-	-	-	-	1	1 - 2
Cytherellina siliqua	8	30	12	16	5	7	5	3	-	8	1 - 8
?Gotlandella sp.	-	-	-	-	-	-	-	-	6	9	9
Hebellum tetragonum	4	13	-	-	17	9	9	-	-	1	1 - 7
Hebellum triviales	29	-	-	-	-	-	-	-	-	1	1
Hermannia cf. marginata	-	-	-	-	19	-	-	-	6	9	5 - 9
Frostiella groenvalliana	-	-	-	-	2	1	1	1	-	6 - 8	5 - 8
Kuresaaria circulata	11	48	22	-	15	12	-	12	6	9	1 - 9
Londinia kiesowi	-	-	-	-	3	4	3	5	-	5,7	5 - 8
Lophoctonella sp.	-	-	-	-	25	-	-	-	-	5	5
Neobeyrichia lauensis	19	-	-	-	-	-	-	-	-	1	1
Neobeyrichia sissica	32	-	-	-	-	-	-	-	-	1	1
Nodibeyrichia verrucosa	-	-	-	9	16	-	-	-	-	4	4 - 5
Nynamella sp.	29	50	-	-	12	9	9	-	-	6 - 7	1 - 7
Primitia mundula	-	-	-	-	-	14	-	-	-	6	6
Scaldianella simplex	3	8	-	-	-	-	-	-	-	1	1 - 2
Other fossils											
Calcareous tubes	-	-	-	-	-	10	7	7	-	7 - 8	6 - 8
Coral colonies	-	32	-	-	-	-	-	-	-	2	2
Cornulites sp.	25	-	-	23	23	-	-	-	-	4 - 5	1 - 5
Crinoid columnals	-	44	21	-	-	-	-	-	-	3	2 - 3
Hyperamnia sp.	-	-	-	-	-	-	-	-	2	9	9
Ozarkodina sp.	26	48	-	-	-	-	-	-	-	1	1 - 2

The diversity values were standardised to a sample size of 100 individuals and calculated for each environment. These diversity values (Text-Fig. 21) show that there is a general decline in diversity through the Whitcliffian and into the Downtonian in both trace fossil and calcareous faunas. The distinctness of the faunas in each environment was determined using the distinctness index (d) calculated as:-

$$d = s/st$$

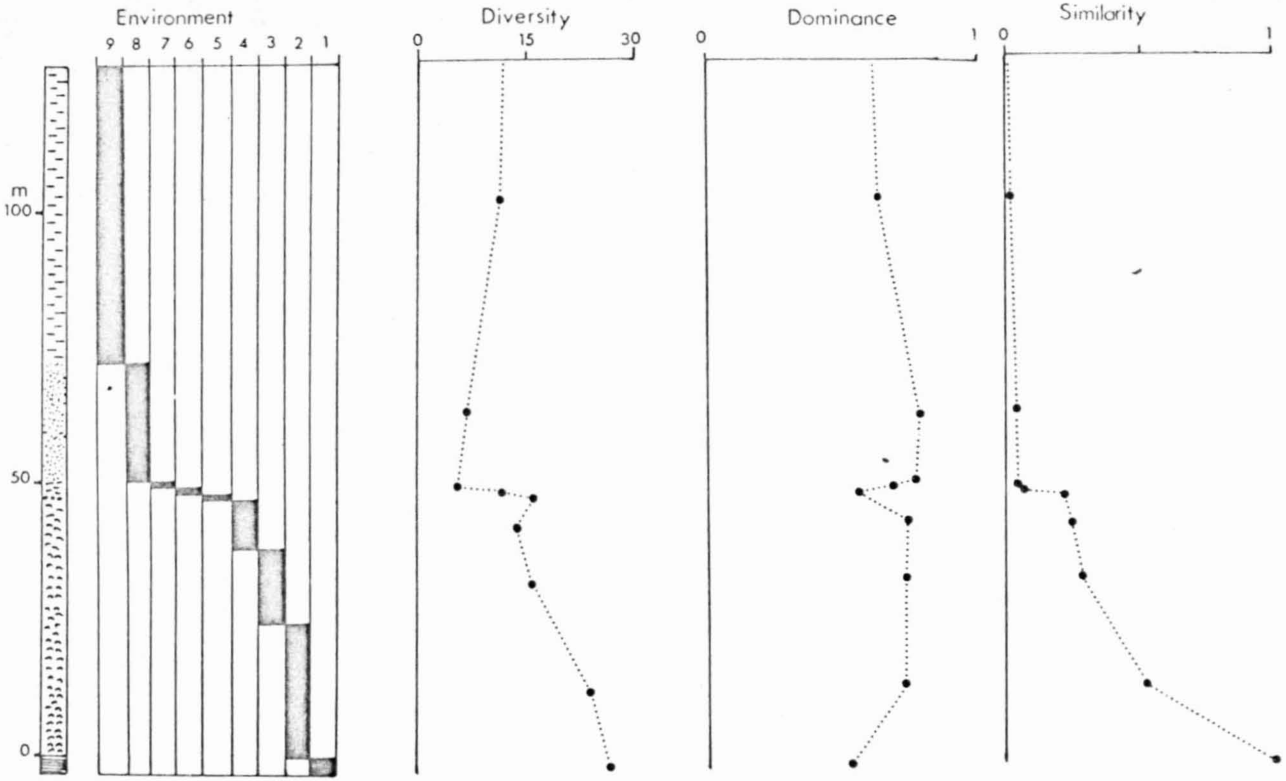
where s = the number of species the two assemblages have in common and st = the total number of species present in the two assemblages.

The results were plotted graphically in Text-Fig. 21, showing the similarity of each environment to **environment 1.**

The graph of faunal diversity (Text-Fig. 21) shows that the change in diversity can be related to environment. For example, (Table ~~12~~ 10) some groups (e.g. bryozoa) are confined to the presumed subtidal environments. Others groups contain vastly different faunas in the intertidal and subtidal environments (e.g. the Brachiopods). The general trend appears to an increase in diversity with increasing depth (Text-Fig. 21). Similar observations have been noted in recent oceans (Sanders, 1968; Sanders & Hessler, 1969; Bosch, 1971). It has also been demonstrated (Antia, 1977) that gross changes in the diversity of a live calcareous fauna are echoed by changes in the diversity of the dead fauna. However, the out of situ dead shell fauna will have a higher diversity than the living calcareous shelled fauna because post mortem shell transport frequently introduces exotic species into an environment (Antia, 1977).

Palaeoenvironmental significance of the Temeside Bone-Bed

The Temeside Bone-Bed appears to have formed as a lag channel deposit in back beach lagoonal muds at Ludlow, during a long and gradual marine regression in which a diverse fauna of subtidal benthic species diminished in diversity and was replaced by a low diversity fauna. Throughout the marine regression faunal dominance appears to have increased (Text-Fig. 21) reflecting the changing



Text-Fig.21. . Sediment environments,diversity,faunal dominance and similarity distributions in a vertical section through the Upper Ludlow and Downtonian sediments in the Ludlow region. 0 m = Base of the Lower Whitcliffe Beds. Ludlow - Downton Boundary is at the base of environment 5. Faunal dominance is calculated as the abundance of the two most abundant species.

environmental conditions from a relatively stable low stress rhythmite type environment through to the relatively unstable high stress intertidal environments of the Downtonian. The gradual nature of this transition, resulting presumably from a fairly constant slow uplift of the Ludlow region, coupled with an inflow of fresh nutrients derived from the southward migrating fluvial systems which covered the area in the Dittonian (Allen, 1974), provided a gradual stability and improvement of the overlying waters.

This improvement and stability undoubtedly allowed a rich planktonic and nektonic fauna (e.g. fish) to develop, resulting in the eventual deposition of bone-beds in the intertidal zone (e.g. The Ludlow Bone-Bed).

In the Kerry and Long Mountain regions the general uplift was more rapid (cf. Holland & Lawson, 1963; Cherns, 1977; McKerrow, 1979) and resulted in a major rapid environmental change in the top Ludlovian from comparatively deep water basinal Whitcliffian sediments through to shallow shelf and intertidal sediments containing little fish debris. The faunas and sediments in the Temeside Beds at these localities varied greatly in lithology and fauna to the sections observed at Onibury containing the Temeside Bone-Bed. These differences are probably a direct consequence of the variations, speed and magnitude of the environmental change from marine to non-marine conditions in the basinal and shelf areas of the Ludlovian sea (cf. Holland & Lawson, 1963). It is interesting to note that (1) vertebrate debris rich horizons developed in the basal Downtonian of the Long Mountain and (2) the magnitude of environmental change was less than that at Kerry over a similar time period.

In the Builth region poor exposure did not allow the transition from top Ludlovian to Temeside Bone-Bed bearing strata to be studied completely. However, the gradual change to more basinal type sediments through the Whitcliffian may suggest that in this region the sea was deepening during the top Ludlovian. It is not clear at the present time how the Downtonian sediments relate to the Whitcliffian sediments in this region.

However, the major point to emerge from this study is that Bone-Beds like the Temeside Bone-Bed only appear to have formed in high intertidal to back beach sediments in regions where the marine regression has been both slow and constant.

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REFERENCES

ALLEN,J.R.L. 1962. Discussion. *Q.Jl.Geol.Soc.Lond.*, vol.118, pp.349.

ALLEN,J.R.L. 1970. *Physical processes of sedimentation.* Allen and Unwin,London. 248 pp.

ALLEN,J.R.L. 1973. Compressional structures (patterned ground) in Devonian Pedogenic Limestones. *Nature Phys.Sci.*, vol. 243,pp.84.

ALLEN,J.R.L. 1974a. Sedimentology of the Old Red Sandstone (Siluro - Devonian) in the Clee Hills Area, Shropshire,England. *Sediment.Geol.*,vol.12,pp. 73 - 167

ALLEN,J.R.L. 1974b. Studies in fluviatile sedimentation: implications of pedogenic carbonate units,Lower Old Redsandstone,Anglo - Welsh outcrop.*Geol.J.*, vol. 9,pp.181 - 208.

ALLEN,J.R.L. & TARLO,L.B. 1963. The Downtonian and Dittonian facies of the Welsh Borderlands. *Geol.Mag.*,vol.100,pp.129 - 155

ANTIA,D.D.J. 1977. A comparison of diversity and trophic nuclei of live and dead molluscan faunas from the Essex Chenier Plain,England.*Paleobiology*,vol.3,pp.404 - 414.

ANTIA,D.D.J. 1979a.Bone-Beds:A review of their classification, occurrence,genesis,diagenesis,geochemistry, palaeoecology,weathering, and microbiotas. *Mercian Geol.*, vol.7,pp.93 - 174.

ANTIA,D.D.J. 1979b. Authigenic gypsum in marine sediments - a comment. *Marine Geol.*,vol. 31, pp. M1 - M4.

ANTIA,D.D.J. 1979c. Comments on the environments and faunas across the Ludlow - Downton boundary (Upper Silurian) at Siefton,Salop. *Geol.J.* vol 14 p. 127 -134

ANTIA,D.D.J. & WHITAKER,J.H.McD. 1979. A scanning electron microscope study of the genesis of the Upper Silurian Ludlow Bone Bed. *In* W.B.Whalley (ed.) *Scanning electron microscopy in the study of sediments.* GeoAbstracts,Norwich. pp. 119 - 136.

ATKINS,D.R. & ANTIA,D.D.J. 1979. Discussion contribution to a paper by J.K. Legatt. *Jl.Geol.Soc.Lond.*

AUSTIN,J.E. 1925. Notes on the Highest Silurian rocks of the Long Mountain.*Proc.Geol.Ass.Lond.*,vol.36,pp.381-382.

BAILEY, R.J. & REES, A.I. 1973. A magnetic fabric study of the late Whitcliffian (U.Silurian) siltstones from the Welsh Borderland. Geol.J., vol. 8, pp.179 - 188.

BATHURST, R.G.C. 1975. Carbonate sediments and their diagenesis. Developments in sedimentology No.12. Elsevier,A Amsterdam. 658p.

BERNARD, H.A. & Le BLANC, R.J. 1965. Resume of Quaternary Geology of the Northwestern Gulf of Mexico. In Wright, H.E. & Frey, D.G. (ed.). The Quaternary of the United States. Princeton Univ. Press. Princeton, N.J. pp. 137 - 185.

BERNER, R.A. 1970. Sedimentary pyrite formation. Am.Journ.Sci., vol. 268, pp.1 - 23.

BLATT, H., MIDDLETON, G. & MURRAY, R. 1972. Origin of sedimentary rocks. Prentice - Hall. New Jersey.

BOESCH, D.F. 1971. Distribution and structure of benthic communities in a gradient estuary. Ph.D. dissertation. Virginia Inst. Marine Sci., Virginia.

BRIDEN, J.C., MORRIS, W.A., & PIPER, J.D.A. 1973. Palaeomagnetic studies in the British Caledonides, VI Regional and global implications. Geophys.J.R.Astron.Soc., vol.34, pp.107 - 134.

BROAD, D.S. & DINELEY, D.L. 1973. Torpedaspis, a new Upper Silurian and Lower Devonian species of Cythaspididae (Ostracodermi) from Artic Canada. Bull.Geol.Surv.Canad., vol.222, pp.53 - 90.

BYRNE, J.V. & EMERY, K.O. 1960. Sediments of the Gulf of California. Geol. Soc.Am.Bull., vol.71, pp.983 - 1010.

CALEF, C.E. 1972. Palaeoecological and stratigraphical studies of the Ludlow in Wales and the Welsh Borderlands. Unpublished Ph.D. thesis. Oxford University.

CALEF, C.E. 1973. Diversity and density of Brachiopods across the shelf in Upper Silurian (Ludlow) times. Geol.Soc.Am.Ann.Meet.Abstr. p.465.

CALEF, C.E. & HANCOCK, N.J. 1974. Wenlock and Ludlow communities in Wales and the Welsh Borderland. Palaeontology, vol.17, pp.7779 - 810.

CALVERT, S.E. 1964. Factors affecting distribution of laminated diatomaceous sediments in the Gulf of California: A symposium. Marine Geology of the Gulf of California, Memoir., vol.3, pp.311 - 330.

CAVE,R. & WHITE,D.E. 1972. The exposures of Ludlow rocks and associated beds at Tites Point and near Newnham,Gloucestershire.Geol.J.,vol.7,pp. 239 - 254.

CHERNS,L. 1977. The Palaeoecology of the Lower Leintwardinian (Upper Silurian) of the Welsh Borderlands and Wales. Ph.D. thesis, Glasgow Univ..

COPELAND,M.J. 1964. Stratigraphic distribution of Upper Silurian Ostracoda,Stonehouse Formation,Nova Scotia.Bull.Geol.Surv.Canad.,vol.117,pp.1 - 13.

CREER,K.M. 1973. A Discussion of the arrangement of palaeomagnetic poles on the map of Pangea for epochs in the Phanerozoic.In.D.H. Tarling (ed & Runcorn,S.K.(eds.) Implications of continental drift to the earth sciences.Academic Press, London.vol.1,pp.47 - 76.

CRONE,A.J. 1974. Experimental studies of mechanically infiltrated clay matrix in sand. Geol.Soc.Am. Abst. with Programs, vol. 6, p.701.

CZYSCINSKI,K.S., BYRNES,J.B., & PEDLOW III,G.W. 1978.In situ red bed development by the oxidation of authigenic pyrite in a coastal depositional environment.Palaeogeogr.Palaeoclimato. Palaeoecol., vol.24,pp. 239 - 246.

DAVIES,W. & CAVE,R. 1976. Folding and cleavage determined during sedimentation. Sediment.Geol., vol.15,pp.89 - 134.

DAVIS,G.R. 1970. Algal - laminated sediments,Gladstone Embayment,Shark Bay,Western Australia. Am.Ass. Petrol.Geol.Mem.,vol.13,pp.169 - 205.

DEGENS,E.T. & STOFFERS,P. 1976. Stratified waters - a key to the past. Nature, vol. 263,pp. 22 - 27.

DEGENS,E.T., STOFFERS,P., GOLUBIC,S., & DICKMAN,M.D. 1978. Varve chronology:estimated rates of sedimentation in the Black Sea. Int. Rep. Deep Sea Drilling Project., vol. 42,pp. 499 - 508.

DINELEY,D.L. & LOEFLER,E.J. 1976. Ostracoderm faunas of the Delforme and associated Siluro - Devonian formations,North West Territories,Canada. Spec.Papers Palaeont. No. 18,pp. 1 - 214.

EARP,J.R. 1938. The higher Silurian rocks of the Ludlow District.*Q.Jl.Geol.Soc.Lond.*,vol.96,pp.125 - 157

ELLES,G.L. & SLATER,I.L. 1906. The highest Silurian rocks of the Ludlow District. *Q.Jl.Geol.Soc.Lond.*, vol.62, pp. 195 - 221.

FREY,W.R., VOORHIES,M.R., & HOWARD,J.D. 1975. Estuaries of the Georgia Coast U.S.A. sedimentology and biology VIII. Fossil and Recent skeletal remains in Georgia estuaries. *Senckenbergiania Marit.*, vol.7,pp.257 - 295.

FRIEND,P.F. & HOUSE,M.R. 1964. The Devonian period. *Q.Jl.geol.Soc.Lond.*, vol. 120S,pp.233 - 246.

GILE,L.H., PETERSON,F.F., & GROSSMAN,R.B. 1966. Morphological and genetic sequences of carbonate accumalation in dessert sands. *Soil.Sci.*, vol. 101,pp.347 - 360.

GREENSMITH,J.T.,& TUCKER,E.V. 1967. Morphology and evolution of inshore shell ridges and mud mounds on modern intertidal flats near Bradwell,Essex. *Proc. Geol.Ass.*,vol.77,pp. 329 - 346.

GREENSMITH,J.T. & TUCKER,E.V. 1969. The origin of Holocene shell deposits in the Chenier Plain Facies of Essex(Great Britain).*Marine Geol.*, vol. 7,pp. 403 - 425

GREENSMITH,J.T. & TUCKER,E.V. 1976 Major Flandrian transgressive cycles, sedimentation and palaeogeography in the coastal zone of Essex,England. *Geol.Mijnbouw* vol. 55,pp. 131 - 141.

GREENSMITH,J.T., BLEZARD,R.G., BRISTOW,C.R., MARKHAM,R., & TUCKER,E.V. 1933. The estuarine region of Suffolk and Essex. *Geol.Ass.Guide* No.12,41p.

GOUDIE,A. 1973. *Duricrusts in tropical and subtropical landscapes*.Clerendon Press,Oxford.

HANCOCK,N.J., HURST,J.M., & FURSICH,F.T. 1974. The depths inhabited by Silurian brachiopod communities. *Jl.geol.Soc.Lond.*, vol. 130,pp.151 - 156.

HARRISON,R.S. 1977. Caliche profiles:indicators of near surface subaerial diagenesis,Barbados, West Indies. *Bull.Canad.Petrol.Geol.*,vol.25,pp.123 173.

HARRISON,R.S. & STEINEN,R.P. 1973. Subaerial crusts , caliche profile, and breccia horizons:Comparison of some Holocene and Mississipian exposures surfaces,Barbados and Kentucky. Geol.Soc.Am.Bull.,vol.89,pp.385 - 396.

HECK,K.L., BELLE,G.V., & SIMBERLOFF,D. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. *Ecology*,vol.56,pp. 1459 - 1461.

HEDBERG,H.D.(ed.) 1976. *International stratigraphic guide.* Int. subcommision on stratigraphic classification.Wiley,New York. 200p.

HOBSON,J.S.C. 1960. *The sedimentary petrology of the Downton Castle Sandstone Formation in Wales and the Welsh Borderland.*Ph.D.thesis, University of Birmingham.

HOLLAND,C.H. 1959. The Ludlovian and Downtonian rocks of the Knighton District,Radnorshire.*Q.Jl.geol.Soc.* Lond.,vol.114,pp. 449 - 482.

HOLLAND,C.H. 1969. The Irish counterpart of the Silurian of Newfoundland.*Am.Ass.Petrol.Geol.Mem.*, vol.12, pp.298 - 308.

HOLLAND,C.H. & LAWSON,J.D. 1963. Facies patterns in the Ludlovian of Wales and the Welsh Borderland. *Geol.J.*,vol.3,pp.269 - 288.

HOLLAND,C.H., LAWSON,J.D. & WALMSLEY,V.G. 1963. The Silurian rocks of the Ludlow District,Shropshire. *Bull.Br.Mus.(Nat.Hist.) Geol.*, vol. 8,pp.95 - 171.

HOWARTH,R.W. 1979. Pyrite: its rapid formation in a salt marsh and its importance in ecosystem metabolism. *Science*, vol. 203,pp.49 - 51.

HURST,J. & WATKINS,R. 1977. Community parallelism in Caradoc (Ordovician) and Ludlow (Silurian) clastic sediments in the Welsh Borderlands,England. *J.Paleont.*, vol. 51 (2S part III),pp. 15 - 16.

HURST,J.M., HANCOCK,N.J. & McKERROW,W.S. 1978. Wenlock stratigraphy and palaeogeography of Wales and the Welsh Borderland.*Proc.Geol.Ass.* vol. 89,pp.197 - 226.

JARDINE,W.G.	1963. Pleistocene sediments at Girvan, Ayrshire. Trans.Geol.Soc.Glasgow, vol.25,pp.4 - 16
JENNY,H. & LEONARD,C.D.	1934. Functional relationships between soil properties and rainfall. Soil Sci., vol.38, pp. 363 - 381.
JONES,M.D.	1969. The palaeogeography and palaeoecology of the Leintwardine Beds of Leintwardine, Herefordshire. M.Sc. thesis,Leicester University.
KALJO,D.	1978. The Downtonian or Pridolian from the point of view of the Baltic Silurian. Eesti,N.S.V., Tead.Akad.Toim. 27,Koide Geol. (1)p.5 - 10
KAWELEC,A.	1973. World distribution of acid sulphate soils.References and map. In Dorst,H(ed.) Acid Sulphate Soils. Proc. Int. Symp. Acid Sulphate Soils 13 - 20 August 1972. Wageningen. The Netherlands. Int. Inst. Land Reclamation and Improvement. Wageninggen. pp. 293 - 295.
KENDALL,C.G. & SKIPWITH,P.A.D'E.	1968. Recent algal mats in a Persian Gulf lagoon. J.Sed.Pet., vol.38,pp. 1040 - 1058.
LAWSON,J.D.	1954. The Silurian succession at Gorsley (Herefordshire). Geol.Mag., vol.91,pp.227 - 237
LAWSON,J.D.	1955. The Geology of the May Hill inlier. Q.Jl.geol.Soc.Lond.,vol.111,pp.85 - 116.
LAWSON,J.D.	1979a. Stability of stratigraphical nomenclature. Newsl.Stratigr. vol.7,pp.159 - 165.
LAWSON,J.D.	1979b. Fossils and Lithostratigraphy. Lethaia, vol.12,pp. 189 - 191.
LOTZE,F.	1964. The distribution of evaporites in time and space. In Nairn,A.E.M. (ed.) Problems in Palaeoclimatology. Interscience, New York. pp. 491 - 509.
MURCHISON,R.I.	1850 - 1854. Unpublished sections. In Ludlow Museum.
MURCHISON,R.I.	1856. On the Bone Beds of the Upper Ludlow Rock and of the base of the Old Red Sandstone Rep.Brit.Ass.Adv.Sci. for 1856. pp. 70 - 71.
McKERROW,W.S.	1979. Ordovician and Silurian changes in sea level. Jl.geol.Soc.Lond., vol.136,pp.137 - 145.

NICKLESS,E.F.P., BOOTH,S.J., & MOSLEY,P.N. 1976. The celestite resources of the area North - East of Bridtol. Inst. Geol.Sci. Mineral Ass. Rept. 25, 84p.

NORMAN,T.N. 1963. Silurian (Ludlovian) Palaeocurrent directions in the Lake District area of England.Bull.Geol.Soc.Turkey, vol.8,pp.27 - 54.

NORRIS,R.M. 1969. Dune reddening and time. Jl.Sed. Pet., vol. 39, pp. 7 - 11.

OERTLI,H.J. 1971. The aspect of ostracode faunas - A new tool in petroleum sedimentology. Colloquium on the paleoecology of ostracodes. In. Oertli,H.J. (ed.) Publie Soc. Nat.Petroles. d'Aquitaine, vol.5 (suppl.) Bull.Centre. Recherches Pau - SNPA Pau,France.

OSPIPOV,V.I. & SOKOLOV,V.N. 1978. Microstructures of recent clay sediments examined by Scanning Electron Microscopy. In Whalley,W.B. (ed.) Scanning electron microscopy in the study of sediments. GeoAbstracts,Norwich. pp. 22 - 40.

PAINE,R.T. 1970. The sediments occupied by Recent lingulid brachiopods and some palaeoecological implications.Palaeogeogr.Palaeoclimat.Palaeoecol vol. 7,pp. 21 - 23.

PALMER,D.C. 1972. The geology of the Long Mountain, Montgomeryshire and Shropshire.Ph.D. thesis, Trinity College, Dublin.

POTTER,J.F. & PRICE,J.H. 1965. Comparative sections through rocks of Ludlovian - Downtonian age in the Llandovery and Llandeilo districts.Proc.Geol.Ass.,vol.76, pp. 379 - 402.

REID,C. 1890. The Pliocene deposits of Britain. Mem. Surv.U.K.,H.M.S.O. 326p.

REINECK,H.E. & SINGH,I.B. 1973. Depositional sedimentary environments. Springer Verlag.New York. 439p.

REIF,W.-E. 1969. Bonebeds an der Muschelkalk-Keuper Grenze in Ostwurttemberg. Dip.Arbeit. Tübingen University. 123p.

REIF,W.-E. 1971. Zur genese der Mushelkalk-Keuper-Grenzbonebeds.N.Jb.Geol.Palaont.Abh.,vol.139, pp. 369 - 404.

REIF,W.-E. 1976. Sedimentologie und Genese von Bonebeds. Zbl.Geol.Palaont.TeilIII,H5/6,pp.252 - 255.

RICHARDSON,J.B. & LISTER,T.R. 1969. Upper Silurian and Lower Devonian Spore assemblages from the Welsh Borderland and South Wales.Palaeontology,vol.12,pp.201 - 252

RICHARDSON,L. 1911. On the Rhaetic and contiguous deposits of West,Mid, and East Somerset. Q.Jl.geol.Soc.Lond. vol.67,pp. 1 - 72.

ROBERTSON,T. 1927. The highest Silurian rocks of the Wenlock District. Mem.Geol.Surv.Sum.Prog. for 1926.,pp. 80 - 97.

ROY,J.L. 1972. A pattern of rupture of the eastern North American - Western European Palaeoblock. Earth Planet.Sci.Lett.,vol.14,pp.103 - 114.

SANDERS,H.L. 1968. Marine benthic diversity: a comparative study. Am.Mid.Nat.,vol.102,pp.243 - 282.

SANDERS,H.L. & HESSLER,R.R. 1969. Ecology of the deep sea benthos.Science vol.163,pp.1419 - 1424.

SANZEN-BAKER,I. 1972. Stratigraphical relationships and sedimentary environments of the Silurian - Early Old Red Sandstone of Pembrokeshire. Proc.Geol.Ass.,vol.83,pp.139 - 164.

SCHAFER,A. & STAPF,K.R.G. 1978. Permian Saar-Nahe Basin and Recent Lake Constance (Germany):Two environments of lacustrine algal carbonates. Spec.Publs.Int. Ass. Sediment.,vol.2,pp.83 - 107.

SEIBOLD,E. 1955. Rezente Jahresschihtung in der Adria. Nues Jahrb.Geol.Palaont.Mon. pp.11 - 13.

SEIBOLD,E. 1958. Jahreslagen in sedimenten der mittleren Adria. Geol.Rundschau.,vol.47,pp.100 - 117.

SETLOW,L.W. 1978. Age determination of reddeded coastal dunes in Northwest,Florida,U.S.A. by use of scanning electron microscopy. In Whalley,W.B. (ed.) Scanning electron microscopy in the study of sediments .GeoAbstracts.Norwich.pp. 283 - 305.

SHAW,R.W.L. 1969.Beyrichiacean ostracodes from the Downtonian of Shropshire.Geol.För.Stock.Förh., vol.91,pp.52 - 72.

SHAW,R.W.L. 1971.Ostracoda from the Underbarrow Kirkby Moor and Scout Hill Flags (Silurian) near Kendal,Westmorland.Palaeontology,vol.14,pp.595-611

SIVETER,D.J. 1974. *The superfamily Beyrichiacea (Ostracoda) from the Silurian and Devonian Systems of* Britain. Ph.D.thesis Leicester University.

SMITH,A.G., BRIDEN,J.C. & DREWRY,G.E. 1973. Phanerozoic world maps.*Spec.Pap.Palaeont.* No. 12, pp. 1 - 42.

SQUIRRELL,H.C. & WHITE,D.E. 1978. Stratigraphy of the Silurian and Old Red Sandstone of the Cennen Valley and adjacent areas south-east Dyfed,Wales.*Rept.Inst.Geol.Sci.*,No.78/6

STAMP,L.D. 1923. The base of the Devonian with special reference to the Welsh Borderlands.*Geol.Mag.*, vol.60,pp.276 - 282,331 - 336,367 - 372,385 - 410.

STRAW,S.H. 1937. The higher Ludlovian rocks of the Builth district.*Q.J&Ggeol.Soc.Lond.*,vol.93,pp.406 - 456.

WALKER,T.R. 1976. Diagenetic origin of continental red Beds. *In* Falke,H.(ed.) *The continental Permian in central,west and south Europe.* Reidel, Dordrecht-Holland,pp.240 - 282.

WALKER,T.R., WAUGH,B. & CRONE,A.J. 1978. Diagenesis in first cycle desert alluvium of Cenozoic age,South-western United States and North-western Mexico.*Geol.Soc.Am.Bull.*,vol.89,pp. 19 - 32.

WATKINS,R. 1978a. Bivalve ecology in a Silurian Shelf environment.*Lethaia*,vol.11,pp.41 - 56.

WATKINS,R. 1978b. Silurian marine communities west of Dingle,Ireland.*Palaeogeog.Palaeoclimat.Palaeoecol.* vol.23,pp. 57 - 78.

WATKINS,R. 1979. Benthic community organization in the Ludlow Series of the Welsh Borderland. *Bull.Brit.Mus.(Nat.Hist.)Geol.*,vol.31,pp.175 - 280.

WARSHAUER,S.M. & SMOSNA,R. 1977. Palaeoecological controls on the ostracode communities in the Tonoloway Limestone (Silurian)Pridioli) of the Central Appalachians.*In* Loffler,H. & Danielpol,D.(eds.) *Aspect of ecology and zooGeography of recent and fossil ostracoda.* Elsievier,pp.475 - 485

WAUGH,B. 1978. Diagenesis in continental Red Beds as revealed under the scanning electron microscope: a review. *In* Whalley,W.B.(ed.) *Scanning electron microscopy in the study of sediments*.GeoAbstracts, pp.329 - 346.

WHITAKER,J.H.McD. 1962. The geology of the area around Leintwardine.Q.Jl.geol.Soc.Lond.,vol.118, pp.319 - 351.

WHITAKER,J.H.McD. 1968. New light on old canyons. Petros,vol.7, pp.19 - 24.

WHITAKER,J.H.McD. 1974. Ancient submarine canyons and fan valleys.In Dott,R.H.jn. & SHAVER,R.H.(eds.) Modern and ancient Geosynclinal sedimentation. Soc.Econ.Pal.Min.Spec.Pub. No.19,pp.106 - 125.

WHITAKER,J.H.McD. 1976a. Geology of the area around Leintwardine Herefordshire. In Whitaker,J.H.McD.(ed.) Submarine canyons and deep sea fans, modern and ancient. Benchmark papers in Geology No.24, pp.286 - 299.

WHITAKER,J.H.McD. 1976b. Ancient submarine canyons and fan valleys. In Whitaker,J.H.McD. (ed.) Submarine canyons and deep sea fans,modern and ancient. Benchmark papers in Geology No 24,pp.316 - 330.

ZIEGLER,A.M., HANSEN,K.S., JOHNSON,M.E., KELLY,M.A., SCOTESE,C.R. & VAN DER VOO,R. 1977. Silurian continental distributions, Palaeogepgraphy,Climatology,and Biogeography. Tectonophysics, vol.40,pp.13 - 51.

Appendix 1

On the distribution of Recent live and dead ostracod faunas from the intertidal zone of Sales Point, Bradwell, Essex.

Aims

To determine whether or not an assemblage of dead ostracods from a number of intertidal mudflat environments is representative of the live fauna of the same environments.

Location

Sales Point, Bradwell, Essex was chosen because the sequence of environments present in a transect from the low water mark to the high water mark (Greensmith & Tucker, 1967; Antia, 1977), closely resembles the postulated sequence of environments present in the Downtonian which culminate in the deposition of the Temeside Bone-Bed (see Allen, 1974a; Antia & Whitaker, 1979; Antia, 1979a).

Material

All the ostracod material examined in this study has been deposited with Ludlow Museum.

Methods

On the 19th March 1977 the habitats on the prograding muddy coastline of the river Blackwater's estuary mouth, recorded by Antia (1977), were sampled for Ostracoda - see Text-Fig. 1. Samples consisted of a 400 cm^2 area of sediment collected to a depth of 1 cm. Sample locations are given in Appendix 1, Text-Fig. 1.

In the laboratory the sediment was stained with Bengal Rose for living tissue and broken down in hydrogen peroxide and hot water, prior to sieving,

Appendix 1.

(a) Location map of the Blackwater Estuary.

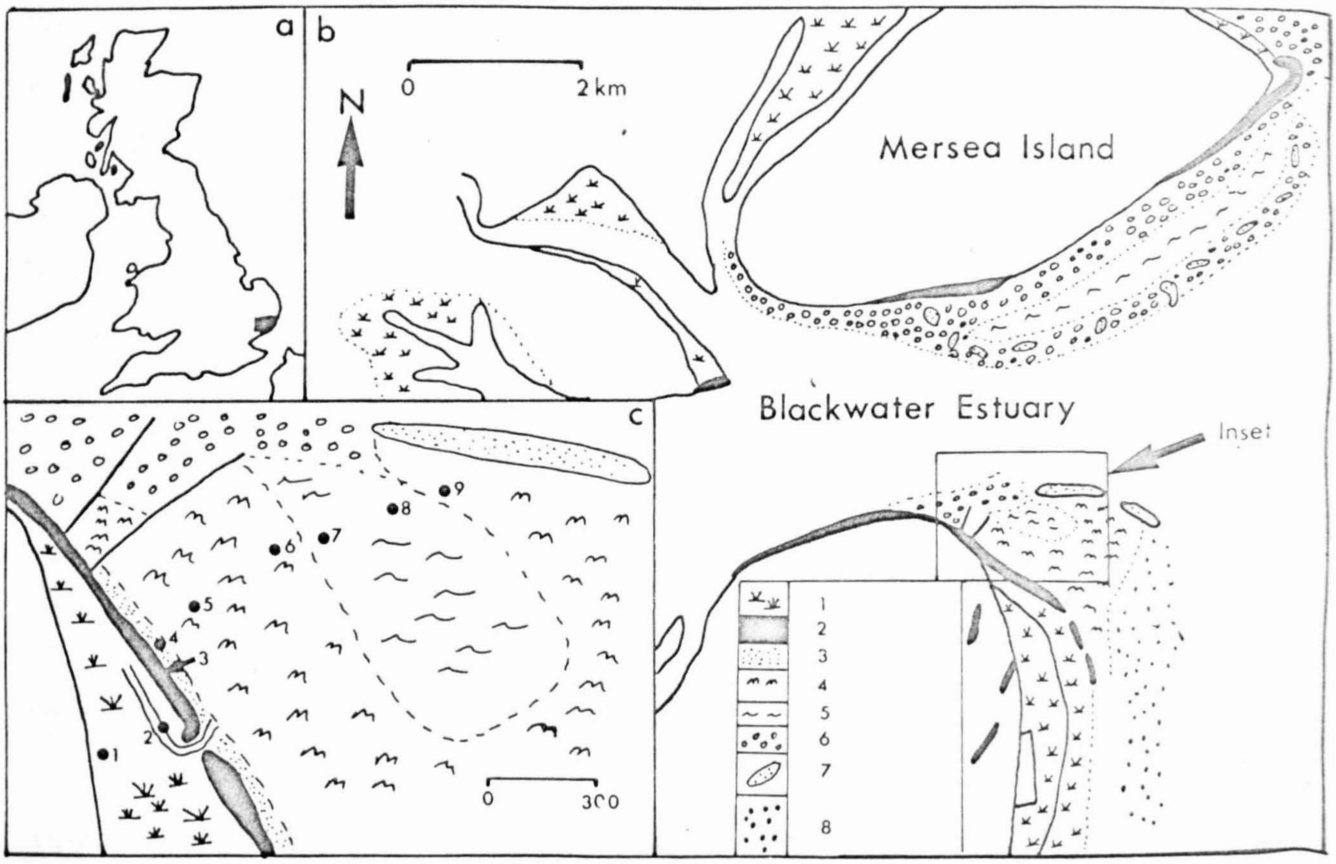
(b) The mouth of the Blackwater Estuary showing sediment distribution and position of sketch map (c).

(c) Sketch map of the Sales Point area indicating sample localities and numbers.

Key to sediment types:-

(1) Salt marsh; (2) Chenier sands; (3) Shell, pebble and muddy sand; (4) Mud mounds; (5) Rippled muds; (6) Silt and gravel; (7) Offshore gravel banks; (8) Sand deposits.

Fig.1.



sorting and counting of the ostracods. An ostracod was recorded as live if it contained its limbs, head and thorax and was stained by the Bengal Rose.

The rank order abundances of the live and dead faunas and their trophic nuclei are presented in Table 1. The trophic nucleus is used here to identify those species which numerically form 80% of the fauna (Neyman, 1966). The composition of the dead faunas is tabulated in Table 2.

Faunal distributions

A total of eight species were recorded in the intertidal zone. Abundances and distributions through the zone are illustrated in Tables 1 and 2. The relative diversity of the live fauna varies from 1 species in the highest salt marsh to 6 species in the lowest mud mounds. A similar diversity change may be observed for the dead faunas where for the same habitats, the change is from 2 to 7 species.

In general among the larger ostracod species (e.g. Cythere lutea) there is little difference between the rank placings of the live and dead faunas (Table). However, the smaller species (e.g. Leptocythere pellucida) show a marked depletion in the dead faunas with respect to their rank placings in the live faunas (Table 1), thus suggesting that either (1) some sedimentological sorting and reworking of the dead shells has occurred, (2) differential destruction of some forms has occurred, thus enriching the fauna in the more robust forms, or (3) that the smaller species have only recently colonised the area. In view of the general stability of the environment, the presence of marked sedimentological sorting and reworking of the sediments in the intertidal zone (Greensmith & Tucker, 1967; Greensmith, 1977; Antia, 1977), and the great abundance of these smaller species in the live fauna, it seems likely that a combination of (1) and (2) has contributed to the differences observed in the rank placings of the live and dead faunas.

The commonest species in the live faunas of the lower Salt Marsh and upper intertidal zone (Table 1) was Cythere lutea. Although this species dominates

Appendix 1,Table 1. Rank order distribution table of the Ostracod faunas at Sales Point.
The position of each locality is given in Appendix 1, Text - Fig. 1.
(L) = live fauna,(D)= dead fauna.

SAMPLE LOCATION NUMBER		*Carinocythere* cf. *carinata*	*Cythere lutea*	*Pontocythere elongata*	*Heterocythereis* cf. *albomaculata*	*Leptocythere pellucida*	*Loxochoncha rhomboidea*	*Urocythere* sp.	ENVIRONMENT
1	(L)	-	-	-	-	1	-	-	Upper Salt Marsh
	(D)	-	1	-	2	-	-	-	
2	(L)	-	1	-	-	2	-	3	Lower Salt Marsh
	(D)	-	1	-	2	3	5	4	
	(L)	-	1	-	3	2	-	-	Lower Salt Marsh - Runnel floor
	(D)	4	1	-	2	-	-	3	
3	(L)	-	-	-	-	-	-	-	Chenier ridge
	(D)	4	1	3	2	-	-	-	
4	(L)	-	1	-	-	2	-	-	Shelly,pebbly,muddy sand.
	(D)	-	1	4	2	5	6	3	
5	(L)	-	1	3	-	2	-	-	Mudmounds (Upper surface) in the higher part of the intertidal zone
	(D)	-	1	3	2	4	-	-	
	(L)	-	1	-	-	2	-	-	Mudmounds (Channel floor) in the higher part of the intertidal zone
	(D)	-	2	3	1	4	-	-	
6	(L)	-	2	-	-	1	-	3	Mudmounds (Upper surface) in the middle part of the intertidal zone
	(D)	-	1	-	2	-	3	-	
	(L)	-	2	-	-	1	4	3	Mudmounds (Channel floor) in the middle part of the intertidal zone
	(D)	-	1	-	2	-	-	3	
7	(L)	-	2		3	1	4	-	Rippled muddy sands
	(D)	-	1	4	2	5	6	3	
8	(L)	5	2	1	-	3	-	4	Rippled muddy sands
	(D)	-	1	2	5	-	4	3	
9	(L)	-	3	2	4	1	5	6	Mudmounds (Upper surface) in the lower part of the intertidal zone
	(D)	6	1	2	3	4	5	-	
	(L)	-	1	3	-	2	-	-	Mudmounds (Channel floor) in the lower part of the intertidal zone
	(D)	-	1	3	4	5	2	-	

APPENDIX 1,Table 2. Distribution of dead ostracods at Sales Point Bradwell,Essex. A key to the locality numbers is given in Appendix 1,Text-Fig.1. R refers to runnel infill,C refers to channel infill.

a) Cythere lutea

	LOCALITY												
% valves	1	2	2R	3	4	5	5C	6	6C	7	8	9	9C
Paired	-	10.6	5.2	1.3	2.8	13.4	9.2	43.8	2.7	11.5	12.2	13.5	18.8
Left	9.0	31.8	31.2	30.1	40.1	35.0	31.8	23.0	38.9	21.8	21.9	37.8	28.3
Right	9.0	36.9	15.6	19.2	28.0	30.8	27.2	28.1	44.4	46.2	39.0	37.8	30.1
Fragments	82.0	21.2	46.9	49.3	28.9	20.7	31.8	5.1	14.0	20.5	26.8	10.8	22.6

b) Carinocytheres cf. carinata

% valves	1	2	2R	3	4	5	5C	6	6C	7	8	9	9C
Paired	-	-	-	-	-	-	-	-	-	-	-	-	-
Left	-	-	-	-	-	-	-	-	-	-	-	100.0	-
Right	-	-	100.0	-	-	-	-	-	-	-	-	-	-
Fragments	-	-	-	100.0	-	-	-	-	-	-	-	-	-

c) Pontocythere elongata

% valves	1	2	2R	3	4	5	5C	6	6C	7	8	9	9C
Paired	-	-	-	-	-	28.7	-	-	-	-	-	-	-
Left	-	-	-	-	33.3	28.5	-	-	-	33.3	47.0	46.6	50.0
Right	-	-	-	-	-	42.8	-	-	-	-	35.2	40.0	30.0
Fragments	-	-	-	100.0	66.6	-	100.0	-	-	66.7	17.6	13.3	20.0

d) Loxochoncha rhomboidea

% valves	1	2	2R	3	4	5	5C	6	6C	7	8	9	9C
Paired	-	-	-	-	-	-	-	-	-	-	-	-	-
Left	-	-	-	-	100.0	-	-	-	-	33.3	-	57.1	55.0
Right	-	-	-	-	-	-	-	-	-	-	100.0	28.5	45.0
Fragments	-	100.0	-	-	-	-	-	-	-	66.7	-	14.2	-

e) Leptocythere pellunica

% valves	1	2	2R	3	4	5	5C	6	6C	7	8	9	9C
Paired	-	-	-	-	-	-	-	-	-	-	-	-	-
Left	-	-	-	-	100.0	100.0	100.0	-	-	25.0	-	50.0	60.0
Right	-	50.0	-	-	-	-	-	-	-	-	-	25.0	20.0
Fragments	-	50.0	-	-	-	-	-	-	-	75.0	-	25.0	20.0

f) Heterocytheries cf. albomaculata

% valves	1	2	2R	3	4	5	5C	6	6C	7	8	9	9C
Paired	-	-	11.1	-	-	-	-	-	-	-	-	11.8	-
Left	-	23.5	44.4	40.0	55.0	37.5	36.8	57.1	72.4	-	-	41.1	71.4
Right	-	70.5	44.4	50.0	35.0	31.3	36.8	7.1	21.2	-	100.0	35.2	-
Fragments	100.0	5.9	-	10.0	10.0	31.2	26.3	35.7	6.4	100.0	-	11.8	28.5

g) Urocythere sp.

% valves	1	2	2R	3	4	5	5C	6	6C	7	8	9	9C
Paired	-	-	-	-	-	-	-	-	-	-	-	-	-
Left	-	50.0	100.0	-	77.7	-	-	-	50.0	-	100.0	-	-
Right	-	-	-	-	22.3	-	-	-	50.0	80.0	-	-	-
Fragments	-	50.0	-	-	-	-	-	-	-	20.0	-	-	-

the dead faunas (Table 1), it is perhaps worth noting that dead articulated valves of the species (minus internal animal) were only found in the habitats inhabited by the species in life (cf. Fig. 2 & Table 2). Leptocythere pellunica was the dominant species in the live faunas of the highest salt marsh and the mud mound habitats (Table 1, Fig. 2). As already noted, the species is grossly under-represented in the dead faunas. Presumably its inability to withstand sedimentological transport (i.e. thin shell and ?weak hinge) accounts for the absence of paired valves in the dead fauna (Table 2). Hemicytheris elongata formed the dominant species in the live faunas of the rippled mud habitat, and a minor component of the mud mount faunas (Table 1).

The reasons for the distribution of each of these three common species in the live faunas may lie in their general morphology. For example, the thin shelled small species, Leptocythere pellunica dominates habitats which are of a protected 'low' energy nature such as the highest salt marsh and lower mud mounds. The more robust smooth cylindrical species Pontocythere elongata, which is almost devoid of ornamentation is commonly found in perhaps the most rigorous environment of the intertidal zone, the rippled mud habitat, and is presumably best adapted to a shifting silt environment. Cythere lutea dominates the faunas of the upper mud mounds (Fig. 2) in its angular robust thick shelled form (Plate 2). It is well adapted to the coarse grained often shelly nature of this 'high energy' habitat. It is also interesting to note that the mud mound surfaces in this region contain a rich algal growth.

Dead valve ratios, articulation and fragmentation

Dead ostracods occurred as either paired articulated valves, single valves, or fragments (Table 2). Table 2 illustrates the proportional distribution of articulated, fragmented, and single valves for each species in each habitat.

Table 2 shows that the relative proportion of paired articulated valves is a function of the environment. For example, Cythere lutea contains a higher proportion of paired valves on the surface of the lower marsh and higher mud mounds than in the adjacent channels and runnels (Table 2) presumably because the valves are more likely to be disarticulated by the constant movement in them of sediment. As can be seen from the comparative abundance of left and right valves (Table 2), some sorting of the disarticulated carapaces must have occurred. The proportion of shell fragments for the commoner dead shell species Cythere lutea and Heterocytheris cf. albomaculata increases to a maximum in the highest intertidal zone, presumably because whole valves were too heavy to be transported into the highest salt marsh habitat. The proportion of fragments in the channels and runnels is higher (Table 2) than in the adjacent mounds, presumably reflecting the high proportion of reworking channel infill undergoes.

Shell abrasion

In general the surface of the live shells are relatively free from abrasion. However, some 'live' carapaces of Pontocythere elongata show abrasive etch marks. The dead ostracod valves may be unworn or show surface pitting. Some of the surface ornament pits have provided microhabitats for epipsammic diatoms.

Conclusions

In this study eight species were recorded from 9 sample stations (Appendix 1, Text-Fig. 1) across the intertidal zone at Sales Point, although none of the commoner species were recorded at a single sample station. Cythere lutea was commonest in the upper part of the intertidal zone (Fig. 2, Table 1). Pontocythere elongata was most abundant in the mid intertidal zone in the rippled mud habitat, while Leptocythere pellunica was commonest in the very highest and middle - lower parts of the intertidal zone.

Neither the relative abundances or rank distributions of the dead fauna (Table 1) accurately reflect the composition of the live fauna, though a reasonably accurate representation can be obtained on a presence - absence basis.

Regions of high sediment movement (i.e. channel infill) tend to contain a high proportion of disarticulated and fragmented carapaces in their dead faunas, when compared to the surrounding substrate.

Many of the valves and carapaces are worn, some while the animal was alive, and may be colonised by encrusting epipsammic diatoms.

Appendix 2

Pridiolian marine fossils from the supposedly upper Leintwardinian (Ludlovian) Cennen Beds of the Cennen Valley. By D. R. Atkins & D. D. J. Antia.

Aims

To demonstrate that the supposedly (Squirrell & White, 1978) Upper Leintwardinian Cennen Beds of the Cennen Valley are of Downtonian (Pridiolian) age.

Material

Sample collected by D. R. A. from the lowermost fossiliferous sediments of the Cennen Beds, about 0.56 m above the base of the unit, in the Cennen Valley. Section exposed in the A 476 road cutting (G.R. SN 6102 1906) 4 km south-west of Llandeilo, Dyfed, Wales.

Methods

The samples (ca. 1 kg) collected by D.R.A. were examined by D.D.J.A. for fossils under a binocular stereomicroscope.

Fauna recorded

The following species were observed in the sample (actual numbers present are given in brackets):-

BRACHIOPODS

Craniops aff. *implicatus* (J. de C. Sowerby), (17); *Lingula cornea* J. de C. Sowerby (1); *Microsphaeridiorhynchus* sp. (17); ?*Orbiculoidea* sp. (1); *Protochonetes* cf. *missendensis* Straw or *P.* cf. *novascoticus* Mclearn (7);

Salopina aff. *lunata* (J. de C. Sowerby) (28); ?*Brachyzga* sp.* (1).

BRYOZOANS

Ceramopora sp. (1); *Leioclema* sp. (11).

OSTRACODS

Frostiella groenvalliana Martinsson (6); ?*Frostiella* sp. (115); *Frostiella* cf. *bicristata* Shaw (1); *Londinia kiesowi* (Krause) (8); *Hermannia* cf. *marginata* (Jones) (2); ?*Nyhamnella* sp. (1).

OTHER FOSSILS

Orthoceras sp. (2); *Kionoceras* sp. (2); Pterinoid (1); ?*Hormotoma* sp. (3); *Hyolithes* cf. *forbesi* (Sharpe) (1); ?*Modiolopsis* sp. (1); *Tentaculites* sp. (6); *Gomphonchus murchisoni* (Ag.) (6); Round crinoid columnals (77).

Faunal conclusions

The ostracod species *F.* cf. *bicristata*, *F. groenvalliana*, *L. kiesowi* and *H.* cf. *marginata* indicate a Downtonian (Pridiolian) age for the Cennan Beds (cf. Elles & Slater, 1906; Martinsson, 1967; Siveter, 1974, 1978; Shaw, 1969, 1971). This age reassignment is supported by the presence of articulate brachiopods of upper Downtonian and lowest Devonian aspect (e.g. *P.* cf. *missendensis* and ?*Brachyzga* sp.).

Implications

The implications of this interpretation of the fauna are (1) the unconformity at the base of the Cennen Beds stretches from the Lower Leintwardinian (cf. Squirrell & White, 1978, p.15) into the Downtonian and not as Squirrell & White (1978, p.15) suggest into the Upper Leintwardinian, (2) The Tilestones of Potter & Price (1965) and Squirrell & White (1978) which rest unconformably on the Cennen Beds, may be of Middle to highest Pridolian (Silurian) or Lowest Gedinnian (Lower Devonian) age, although they themselves lack any diagnostic fossils, (3) Marine conditions prevailed into the Downtonian in South Central

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* The asterixed brachiopod was identified by Dr. C. J. Burton.

Wales, and (4) No sediments representing the Upper Ludlow Series are present in the Cennen Valley.

Additional References

MARTINSSON, A. 1967. The succession and correlation of ostracod faunas in the Silurian of Gotland. Geol. For. Stockholm. Forh. vol. 89, pp.350-386.

SIVETER, D. J. 1978. The Silurian. In Bate, R. & Robinson, E. (eds) A stratigraphical index of British Ostracoda. Geol. J. Spec. Issue. No. 8, pp.57-100.

ADDITIONAL REFERENCES (Appendix 1)

GREENSMITH, J.T. 1977. Carbonate bodies in Essex marshlands. *Geol. Soc. Lond. Newsletter*, vol.6, p.27.

NEYMAN, A.A. 1966. Limits to the application of trophic group concept in benthonic studies. *Oceanol. Akad. Sci. U.S.S.R.*, vol.7, pp.149 - 155.

PRIDOLIAN (UPPER SILURIAN) MARINE FOSSILS FROM THE SUPPOSEDLY UPPER LEINTWARDININAN (LUDLOVIAN) CENNEN BEDS OF THE CENNEN VALLEY,DYFED,WALES.

l.c. Sir, In a recent paper Squirrell & White (1978) suggested that the Cennen Beds of the Cennen Valley,Dyfed,Wales, are of Upper Leintwardinian age. However, a sample collected by D.R.A. from the lowermost fossiliferous sediments of the Cennen Beds in the Cennen Valley, 0.56 m above the base of the unit, contains fossils which indicate that the Cennen Beds are of Pridolian age. The sampled section is exposed in the A 474 road cutting (G.R. SN 6102 1906) 4 km south west of Llandeilo, Dyfed,Wales.

The following species were observed in this sample (the actual number of fossils assigned to each species identified in the sample is indicated in brackets):-

BRACHIOPODS

Craniops aff. implicatus (J.de C.Sowerby),(17);Lingula cornea J. de C.Sowerby,(1); Microsphaeridiorhynchus sp., (17); ?Orbiculoidea sp.,(1); Protochonetes cf. missendenensis Straw, [illegible],(7); Salopina aff. lunata (J.de C.Sowerby),(28); ?Brachyzga sp. (1); - This latter species was identified by Dr C.J.Burton.

OSTRACODS

Frostiella groenvalliana Martinsson,(6); ?Frostiella sp.,(115); Frostiella cf. bicristata Shaw,(1); Londinia kiesowi (Krause),(8); Hermannia cf. marginata (Keys),(2); ?Nyhamnella sp.,(1).

OTHER FOSSILS

Ceramopora sp.,(1);Leioclema sp.,(11); 'Orthoceras' sp.,(2); Kionoceras sp.,(2);Pterinoid,(1); ?Hormotoma sp.,(3); Hyolithes cf. forbesi (Sharpe),(1); ?Modiolopsis sp.,(1); Tentaculites sp., (6); Gomphonchus murchisoni (Ag.),(6); Round crinoid columnals, (77).

The ostracod species F.bicristata,F.groenvalliana,L.kiesowi, and H. cf.marginata indicate a Downtonian (Pridolian) age for the Cennen Beds (cf. Elles & Slater,1906;Martinsson,1967; Shaw,1969;1971;Siveter,1974 (Ph.D. thesis,Leicester University), 1978). This age reassignment is supported by the presence of l.c. articulate brachiopods of Upper Downtonian and lowest Devonian aspect (e.g. P.cf. missendenensis and ? Brachyzga sp.). a ?

The implications of this interpretation of the fauna are:-

1. The unconformity at the base of the Cennen Beds stretches from the Lower Leintwardinian (Squirrell & White,1978,p.15) into the Downtonian and not into the Upper Leintwardinian as Squirrell & White,1978,p.15) suggest. l.c. u/
2. The Tilestones of Potter & Price (1965) and Squirrell & White (1978) which rest unconformably on the Cennen Beds may be of middle to highest Pridolian (Silurian) or lowest Gedinnian (Lower Deyonian) age although they themselves lack any diagnostic fossils.
3. Marine conditions prevailed into the Downtonian in South Central Wales.
4. No sediments representing the upper part of the Ludlow Series are present in the Cennen Valley.

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References

Elles,G.L. & Slater,I.L. 1906. The highest Silurian rocks of the Ludlow District. Q.Jl.geol.Soc.Lond.,62,195 - 221. ? ref

Martinsson,A. 1967. The succession and correlation of ostracode faunas in the Silurian of Gotland. Geol.För. Stock. Förh., 89, 350 - 386.

Potter,J.F. & Potter,J.H. 1965. Comparative sections through rocks of Ludlovian - Downtonian age in the Llandovery and Llandeilo district. Proc.Geol.Ass.Lond.,76,379 - 402.

Shaw,R.W.L. 1969. Beyrichiacean ostracodes from the Downtonian of Shropshire. Geol.För.Stock.Forh.,91,52 - 72.

Shaw,R.W.L. 1971. Ostracoda from the Underbarrow Kirkby Moor and Scout Hill Flags (Silurian) near Kendall, Westmorland. Palaeontology, 14 , 595 - 611.

Siveter,D.J. 1978. The Silurian.Geol.J.spec.Issue No. 8, 57 - 100.

Squirrell,H.C. & White,D.E. 1978. Stratigraphy of the Silurian and Old Red Sandstone of the Cennen Valley, and adjacent areas, south - east Dyfed,Wales.Rept.Inst.Geol.Sci.,No.78/6.

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Comments on Spirobis lewisii (Polychaeta : Serpulidae)

by

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Abstract

Habitat preferences, growth and size distribution in an Upper Silurian population of *Spirabis lewisii* from Ludlow, U.K. are discussed.

Spirorbis lewisii J. de C. Sowerby is a very rare upper Silurian fossil which has only been recorded encrusting on the surfaces of orthoconic nautiloids (Murchison, 1839, 1859; Holland, 1971). An examination of some 50,000 shells from the Whitcliffe Beds (Whitcliffian, upper Ludlovian, upper Silurian) in the Ludlow region, under a binocular microscope revealed the presence of three spirorbid encrusted shell fragments. All three shells were collected from the Lower Whitcliffe Beds, of Mortimer Forest (British National Grid Reference SO 48887113) near Ludlow, England, and have been deposited with the Institute of Geological Sciences, London.

The three shells are orthoconic nautiloids which have been encrusted on their exterior. Two specimens are fragments of Michelinoceras bullatum (J. de C. Sowerby) (2 and 3 cm in length; containing 2 and 6 specimens of S.lewisii respectively) the other is a specimen of Michelinoceras centrale (Barrande), 4.5 cm in length, containing 104 specimens of S.lewisii. These encrusting spirorbids form the data base for this paper.

1. Habitat preferences

It has been demonstrated (Knight-Jones, 1951, 1953; Knight-Jones & Knight-Jones, 1977; Daly 1978a), that modern spirorbids have distinct habitat preferences. For example Spirorbis spirobis (L)'s preferred habitat is the fronds of algae belonging to the species Fucus serratus L. (Daly, 1978a). Similar observations have been made for other encrusting organisms (cf. Havilecek, 1972). The absence of S.lewisii encrusting on non-cephalopod shells suggests that the species may have had a habitat preference for cephalopod shells.

The spirorbids encrusting on M.centrale appear to be arranged in lines parallel to the orthocone's growth lines in which the initial spirorbid tube as aligned parallel to the longitudinal axis of the orthocone (deviation of ± 5°) and faced towards the orthocone's anterior. Within any one line or train of spirorbids the mean distance between the centre of the individual spirorbids is 1.7 mm (minimum distance observed is about 1.4 mm, maximum distance is about 3 mm). Individual trains are arranged at spacings of 2.8 - 3.3 mm (mean 3.1 mm : 7 trains of spirorbids were observed on the specimen). These trains completely encircle the circumference of the orthocone.

Similar trains of spirorbids aligned parallel to the growth lines of both bivalves (Trueman, 1942) and orthocones (Holland, 1971) have been interpreted as indicating that they were colonised while alive, and that the spirorbid spat fall was episodic.

All the spirorbids on the three orthocone fragments were aligned with their initial tube aligned parallel to the orthocone's longitudinal axis and facing forwards, and on one specimen as trains parallel to the shell growth lines and encircling it. These observations suggest that the settling spirorbid larvae migrated to the anterior end of the orthocone because it offered the most favourable site for colonisation (cf. Knight-Jones, 1951) and aligned themselves accordingly. The presence of spirorbid trains completely encircling the orthocone suggests that it was very definitely alive or floating when colonised (Seilacher, 1960; Meischner, 1968). The presence of a number of regularly spaced spirorbid trains suggests that the orthocone was alive when colonised by S.lewisii with each train representing a separate spat fall. (Trueman, 1941; Holland, 1971). The unencrusted shell between each pair of trains represents the growth of the orthocone during the period between two successive spat falls.

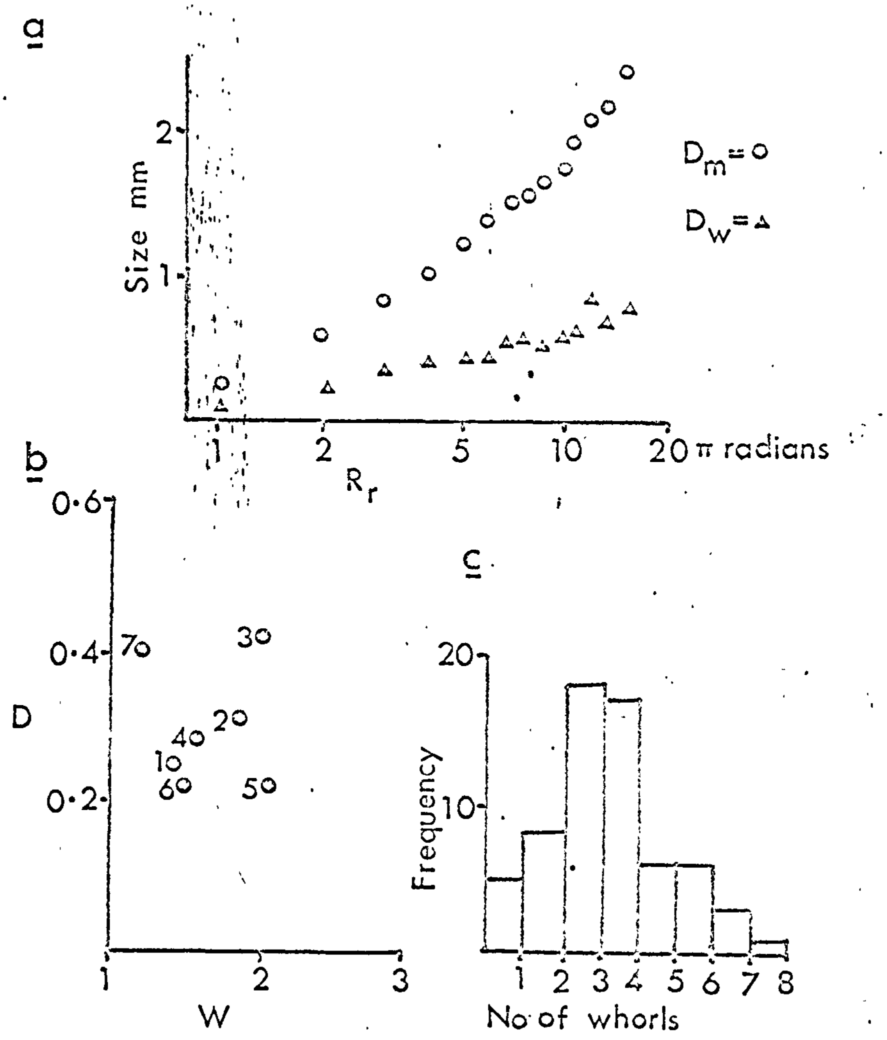

Figure Caption

Fig. 1.

(a) Aperture diameter (D_W) and maximum shell diameter (D_m) plotted against $Log_{(e)}$ solid angle (θ) of spiral. expressed as π radians.

(b) Plot of Whorl Expansion Rate (w) against Distance (D) of generating curve from the axis (see Raup 1966, 1967 for theory)

(c) Size frequency histogram of frequency (numbers) against Number of whorls.

Table ~~1~~. Mean value and varian~~ts~~ce ~~for~~ of D_m, D_w and R for *Spirorbis lewisii*

	D_m	D_w	R
Mean	1.412 mm	0.452 mm	7.64
Variance	0.374	0.036	19.78

2. Growth

At the present time few growth studies of spirorbid shells exist (e.g. Daly, 1978b). Since spirorbids consist of planispiral coiled shells, their growth can be described using the same parameters, which are used to describe spiral growth patterns in cephalopods, gastropods and bivalves (see Raup, 1966, 1967; Raup & Chamberlain, 1967; McGhee, 197[illegible]). In order to illustrate growth in S.lewisii the following measurements were made using a binocular microscope fitted with a micrometer. (1) The maximum diameter (D_m), (2) the maximum radius (D_r), (3) the aperture width (D_w), (4) the minimum radius of the spirorbid tube (D_z). The geometry of the spiral was defined in terms of its solid angle of rotation (R_r) with respect to its beginning, which was taken as a line across the open posterior end of the first tube constructed after metamorphosis. The initial point = 0π radians, the first $\frac{1}{2}$ whorl = 1π radians, the first whorl = 2π radians, the second whorl = 4π radians and so on.

A direct plot (Fig. 1a) of D_m against $\mathrm{Log}_e R_r$ and D_w against $\mathrm{Log}_e R_r$ was made. Their statistics are presented in Table 1. Both plots indicate that S.lewisii had an allometric pattern of growth. A similar pattern of growth has been noted for the modern spirorbid S.spirorbis by Daly (1978b).

The mean D and W values were calculated and graphically plotted for each new whorl (Fig. 1b); where $D = |D_r - D_w| / D_r$ and $W = (D_r/D_z)^2$. This graph (Fig. 1b) shows (cf. Raup, 1966, 1967) that S.lewisii like modern spirorbids (Daly, 1978b) assumed an involute growth form. The advantages of an involute growth form for spirorbids have been summarised by Daly (1978b).

3. Population age structure

The age pyramid for the population of S.lewisii on the specimen of M.centrale (Fig. 10) has the distributional shape of a species producing many young with a comparatively stable population (cf. Clapham, 1971; Antia & Wood, 1977). However, if the orthocone was encrusted by S.lewisii while it was alive, then it is unlikely that the population observed would present an accurate representation of mortality in the species, because the orthocone was fragmented prior to its burial in the sediment, and presumably spent a considerable length of time rolling about on the sea bed. This rolling may have dislodged many of the spirorbids on its surface (cf. Daly, 1978b) resulting in some size biasing of the age pyramid.

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References

ANTIA, D. D. J. & WOOD, B. A. 1977. Some aspects of the Palaeoecology of the E_1b zone of the Edale Shales (Namurian) in the Edale valley, Derbyshire. Mercian Geol. 6, 179-196.

CLAPHAM, W. B. 1971. Natural Ecosystems, New York.

DALY, J. M. 1978a. The annual cycle and the sort term periodicity of breeding in a Northumberland population of Spirorbis spirorbis (Polychaeta: Serpulidae). J. Mar. Biol. Ass. U.K. 58, 161-176.

DALY, J. M. 1978b. Growth and fecundity in a Northumberland population of Spirorbis spirorbis (Polychaeta : Serpulidae). J. Mar. Biol. Ass. U.K. 58, 177-190.

HAVLICEK, V. 1972. Life habit of some Ordovician inarticulate brachiopods. *Vestnik ustred ust geol.* 47, 229-233.

HOLLAND, C. H. 1971. Some conspicuous participants in Palaeozoic symbiosis. *Sci. Proc. R. Soc. Dublin.* Ser. A. 4 (2), 15-26.

KNIGHT-JONES, E. W. 1951. Gregariousness and some other aspects of settling behaviour of *Spirorbis*. *J. Mar. Biol. Ass. U.K.* 30, 201-222.

KNIGHT-JONES, E. W. 1953. Decreased discrimination during settling after prolonged planktonic life in the larvae of *Spirorbis borealis* (Serpulidae). *J. Mar. Biol. Ass. U.K.* 32, 337-345.

KNIGHT-JONES, P. & KNIGHT-JONES, E. W. 1977. Taxonomy and ecology of British Spirorbidae (Polychaeta). *J. Mar. Biol. Ass. U.K.* 57, 453-499.

McGHEE, G. R. 1978. Analysis of the shell torsion phenomenon in the Bivalvia. *Lethaia*, 11, 315-330.

MEISCHNER, D. 1968. Perniciose Epokie von *Placunopsis* auf *Ceratites*. *Lethaia* 1, 156-174.

MURCHISON, R. I. 1839. *The Silurian System*. Murray. London.

MURCHISON, R. L. 1859. *Siluria*. Murray. London.

RAUP, D. M. 1966. Geometric analysis of shell coiling: general problems. *J. Paleont.* 40, 1170-1190.

RAUP, D. M. 1967. Geometric analysis of shell coiling: Coiling in ammonoids. *J. Paleont.* 41, 43-65.

RAUP, D. M. & CHAMBERLAIN, J. A. 1967. Equation for volume and the centre of gravity in ammonoid shells. *J. Paleont.* 41, 566-574.

SEILACHER, A. 1960. Epizoans as a key to ammonoid ecology. *J. Paleont.* 34, 189-93.

TRUEMAN, A. E. 1942. Supposed commensalism of Carboniferous Spirorbids and certain Non-marine Lamellibranchs. *Geol. Mag.* 79, 312-320.

10

POSSIBLE DISPERSAL MECHANISMS ACCOUNTING FOR ANOMALOUS OCCURRENCES OF THE LOWER PALAEOZOIC BRACHIOPOD *SCHIZOCRANIA*

by

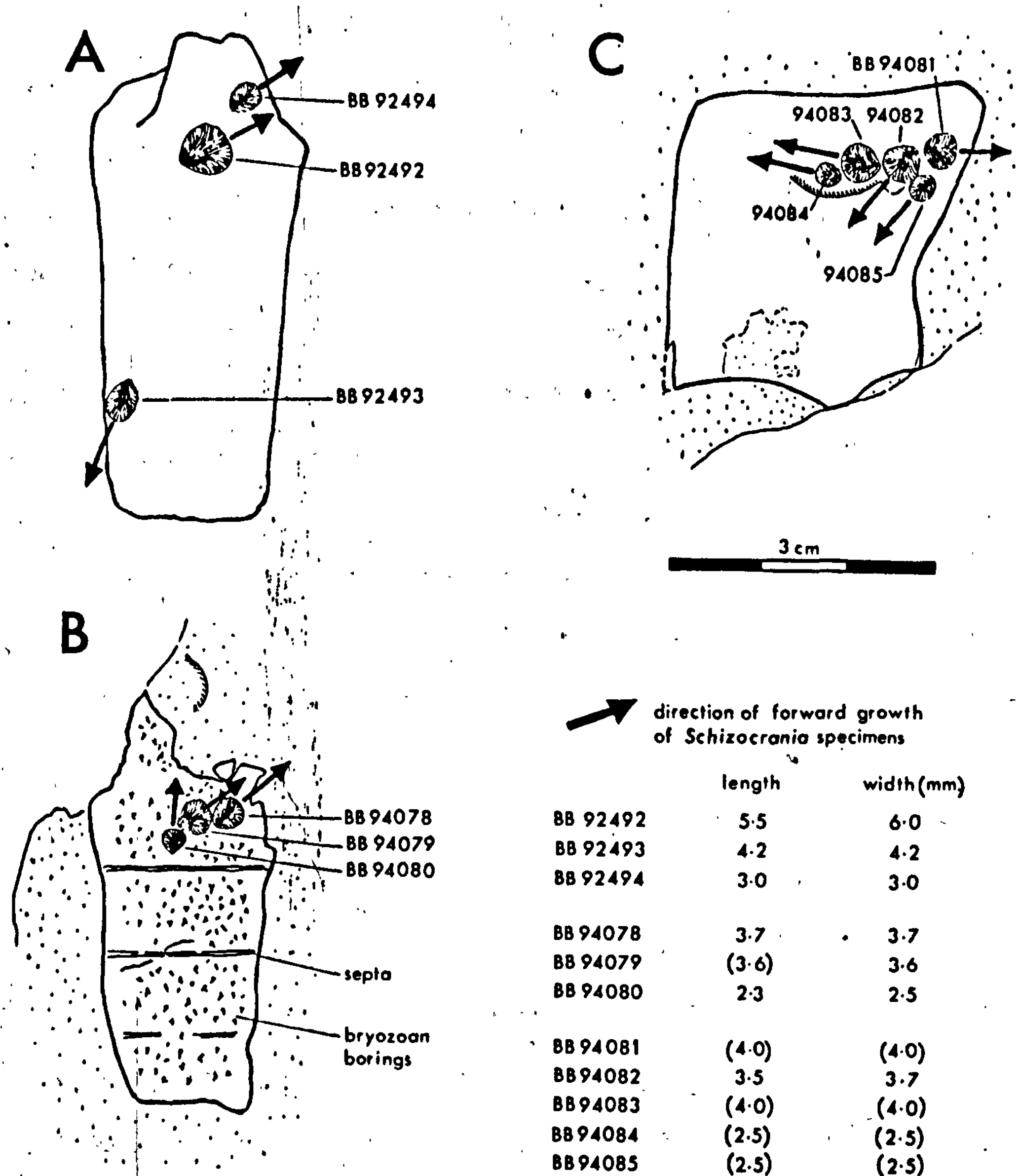
Martin G. Lockley & David D.J. Antia

Abstract Rare occurrences of Ordovician and Silurian species of the inarticulate brachiopod *Schizocrania* (Trematidae) in facies where they are not normally indigenous is explained by illustrating that the orthoconic cephalopod shells to which these inarticulates are attached may have drifted considerable distances prior to their deposition and entombment in onshore sediments.

Introduction During the course of respective studies of an Upper Llanvirn, Ordovician (MGL) and a Whitcliffian, Silurian (DDJA) succession in the Anglo Welsh region, the authors independently noted rare occurrences of orthocones with *Schizocrania* attached to both the inner and outer walls of their body chambers; in both cases the entombing clastic sediments are of a coarse arenaceous type associated with demonstrably shallow-water facies assemblages which include transported shell deposits and disconformities (Williams 1953 and Antia 1979a).

Since the Anglo Welsh *Schizocrania* usually occur abundantly only in argillaceous offshore sediments we consider that, although they are predictably rare in these onshore sediments, some explanation must be sought for their association in significant numbers with the orthocones to which they are attached. Havlicek (1972 p.230) reported that the Upper Ordovician trematid *Ptychopeltis incola* ferner from Bohemia .."lived attached only to the shells of orthocone nautiloids"; he also noted its ancestor *P. hornyi* Havlicek sometimes encrusted orthocones. This intriguing example of apparent host-specific relationships may be paralleled elsewhere amongst the trematidae (e.g. *Schizocrania*) by similar associations between host and encruster. This possibility is considered here.

MATERIAL The Upper Llanvirn orthocone, represented by an incomplete, poorly preserved internal mould (diameter ca. 18 mm) of unknown taxonomic affinity, was recovered from calcareous benthos-dominated, arenaceous shell beds in the upper part of the Flags and Grits Member of the Ffairfach Group exposed at Coed Duon,



	length	width (mm)
BB 92492	5·5	6·0
BB 92493	4·2	4·2
BB 92494	3·0	3·0
BB 94078	3·7	3·7
BB 94079	(3·6)	3·6
BB 94080	2·3	2·5
BB 94081	(4·0)	(4·0)
BB 94082	3·5	3·7
BB 94083	(4·0)	(4·0)
BB 94084	(2·5)	(2·5)
BB 94085	(2·5)	(2·5)

Explanation of Figure 1

Scale drawings of Schizocrania encrusted orthoconic nautiloids from Upper Llanvirn strata exposed near Llangadog, Mid Wales (A) and from Lower (B) and Upper (C) Whitcliffe strata exposed near Ludlow, Salop. All Schizocrania specimens have British Museum numbers and are depicted by the same diagramatic representation regardless of which side of the orthocone mould they appear attached to; length width measurements, listed bottom right, should be regarded as only approximate where bracketed.

3 km south of Llangadog, Dyfed (Grid Ref. SN 709 256) where it lay parallel to bedding. The specimen shows three specimens of Schizocrania cf. saloniensis Williams attached to the inner surface of the cephalopod body chamber with their brachial valves all facing inwards (Fig. 1A). The entire circumference of the orthocone mould is visible with the Schizocrania specimens showing no obvious preference for any particular attachment site although two of the specimens are orientated sub-parallel to each other near the anterior end.

The Whitcliffian orthocones are represented by two poorly preserved fragmentary internal moulds of Orthoceras sp. (diameters ca. 20 mm and 30 mm respectively) from the Lower Whitcliffe Beds of Mortimer Forest, south of Ludlow (Grid Ref. SO 497725) and the Upper Whitcliffe Beds near Broadstone Farm (SO 544900). The older specimen (Fig. 1B) is extensively bored by bryozoa and has three specimens of Schizocrania striata Sowerby attached to the anterior part of its external surface. The specimens all occur closely adjacent to each other on the exposed section of the orthocone mould which faces downward from the undersurface of a bedded unit; relative to the final entombment position of the orthocone the Schizocrania specimens occur on its "underside" and following the dissolution of the cephalopod shell have become impressed onto the preserved mould. The younger (Upper Whitcliffian) orthocone has five poorly preserved specimens of S. striata attached to the inner surface of its body chamber; the specimens are aligned transversely, parallel to the phragmacone edge (Fig. 1C).

All eleven of the Schizocrania specimens, found in association with these orthocones, exhibit only their convex brachial valves facing away from the cephalopod shell surface. Schizocrania is known to attach to substrates by its flat pedicle valve (Rowell in Williams et al. 1965 p.H283). However, it is a recurrent empirical observation that pedicle valves are exceptionally rare, being either altogether absent from assemblages or hidden from view beneath the brachial valve; indeed S. saloniensis Williams (1974 p.44) was until recently (Lockley and Williams personal observation) known only from its brachial valve.

The three orthocone specimens shown in Figure 1 indicate that the posterior edge of the phragmacone was the preferred encrustation site for all but one of the *Schizocrania* specimens. The orientation of these *Schizocrania* inside the phragmacone and on the shell exterior is apparently not random since all adjacent shells are alined with their umbones pointing in approximately the same direction (i.e. transverse or oblique to the orthocones' long axis).

General Observations The orthocones may have been encrusted (A) whilst they were alive and mobile, (B) whilst dead and floating, (C) whilst dead and semi bouyant, being washed around on the sea floor, (D) whilst dead and settled on the sea floor and, finally, (E) whilst being reworked. In each case a different pattern, density, composition and diversity of encrusting faunas may be expected.

Schizocrania is ornamented by numerous radial capillae (Williams 1974 p.44) each of which, according to Williams & Rowell *in* Williams *et al*. (1965 p.H81), would support a setal follicle at the commissure. Both the *Schizocrania* species discussed here exhibit similar capillae densities at the same growth stage (i.e. 10-12 per mm, 5mm anteromedianly of the dorsal umbones).

Observations by Chuang (1968, 1977) and Sudarson (1969) on discinid (Discinisca) larvae indicate that these forms have exceptionally well developed principle setae. In contrast to those "benthic" larvae which usually have 3-4 pairs of setae when attachment takes place, "there may be a prolonged larval stage ... with chaetae increasing in number to facilitate floatation" (Sudarson 1969 p.65). The characteristic high density of capillae in *Schizocrania* therefore might well indicate that it had a prolonged "planktonic" larval stage. If this was the case such larvae would have a potentially wide dispersal range likely to bring them into contact with a greater number of potential attachment sites.

According to Trueman (1942), Seilacher (1954, 1960, 1968) Meischner (1968) and Holland (1971), few encrusting species are completely indifferent to the slope of their substrate and so often show definite preferred growth directions; after attachment forms like bivalves and brachiopods cannot usually adjust growth directions to compensate for a change in substrate orientation (Seilacher 1960 p.189).

Clearly in the case of brachiopod larvae encountering a living orthocone only the external surface would present an obvious potential attachment site whereas during the post mortem drifting phase and subsequent depositional phases the internal wall of the body chamber would also be readily available once remnants of soft tissue had perished. In either case the inherent conical to tubular shape of the typical orthocone would present a uniformly curved surface whose slope depended primarily on the disposition of the orthocone itself.

Knight-Jones (1951, 1953) and Daly (1978) note that spirorbid larvae are host specific and will detach themselves from an unsuitable substrate or move around seeking the optimum location; they will also attach to the inner surface of gastropod shells already occupied by hermit crabs (Knight-Jones & Knight-Jones 1977). These observations are of particular interest since Trueman (1942) and Holland (1971) respectively note examples of alined fossil spirorbids encrusting on Carboniferous bivalves and Whitcliffian orthocones which were presumed to be living.

Clearly once an orthocone has lost its bouyancy and has come to rest on the sea floor it provides a potential attachment site for a variety of essentially "benthic" encrusters. Although it may be hard to establish whether pelagic larvae attached to an orthocone prior to or after its descent to the sea floor, it is less difficult to identify benthonic encrusters which are known primarily in association with true benthos. Lines of evidence which suggest a benthic encrustation phase are as follows: Firstly, according to Meischner (1968) and Seilacher (1960), random growth directions and distribution of attachment sites amongst ammonoid encrusters suggest that the host already lay on the sea floor. Secondly, Lower Palaeozoic cephalopods are commonly encrusted by various bryozoa which encrust and bore a wide range of benthic brachiopod and bivalve species, e.g. Rhopalonaria sp. and Ceramopora sp. (Whitcliffe Beds). A Soudleyan (Caradoc) orthocone from the Allt Ddu Formation, south of Bala (Grid Ref. SH 924267), which is heavily encrusted externally by bryozoa, has been deposited by one of us (MGL) in the National Museum of Wales (N.M.W. 79.5G. Map locality no. 771); Hunterian Museum specimen S25114 a/b of Kionoceras filosum (Sowerby) from the lower Bringewood Beds of the Leintwardine area (Grid Ref. SO 413752) also has bryozoa encrusting the phragmacone edge. Similarly Caradoc cephalopods from Minuntion, near Girvan (Hunterian Museum nos. S25129/1-3), are encrusted externally by bryozoa with small subconical shells, cf. *Archinella* sp., on both internal and external surface of the phragmacone; these Monoplacophorans could be considered homeomorphic with their modern relatives (Filatova *et al.* 1969) and possibly with the modern benthic herbivorous gastropod *Acmaea* (Voigt 1977). The authors note Whitcliffian examples of orthocones with two phases of encrustation, i.e. an earlier *Spirobis* phase and a later superimposed benthic, bryozoan phase. Further examples of benthic borers which affect both orthocones and benthic shells include the Upper Ludlovian (Whitcliffian) calcibicavicales (i.e. sponges and annelids, Antia 1979b). Holland (1971) recorded two Silurian examples of articulate brachiopods apparently directly attached to orthocones by their pedicles and we have noted that N.M.W. specimen 27.110 G.393 of *Orthoceras* from the Ordovician (Llandeilo) of North Wales also has an inarticulate brachiopod, of uncertain taxonomic affinity, externally attached.

Interpretation of orthocone encrustation patterns

Holland (1971) and Havlicek (1972) respectively have favoured the interpretation that articulate and inarticulate brachiopods attached to living orthocones. We consider that although this may have been true for brachiopods with an inferred epiplanktonic mode of life, e.g. *Sericoidea* and *Aegiria* (Bergstrom 1968) and possibly the setiferous trematid *Schizocrania*, found normally in deep water facies, it is unlikely that *Microsphaeridiorhynchus nucula*, referred to by Holland (1971), would have attached to nektonic orthocones since such rhychonellids are normally considered to have been gregarious, living pedicly attached to firm substrates (Fursich & Hurst 1974). Similarly the occurrence of orthocones encrusted by bryozoans such as *Ceramopora*, which encrusts a wide variety of benthic invertebrates, is almost certainly indicative of encrustation whilst the orthocone was on or near the sea bed.

Since modern spirorbids are known to be host specific and capable of seeking a preferred attachment site and orientation, it is almost certain that the occurrence of fossil spirorbids alined along the growth margins of orthocones (Holland 1971) indicates a similar relationship. This may mean that the alinment of *Schizocrania* specimens noted here (Fig. 1) could be indicative of a similar host specific relationship. This contention tends to be supported by our observation that the Anglo-Welsh Schizocrania have not been found attached to any other host organisms; it would also offer possible explanations for the virtual absence of pedicle valves, which could have either remained attached to a host when the brachial valve disarticulated, or become obscured during fossilization by the substrate to which they may have been attached. Indeed, in the light of the present limited evidence, the possibility that they were also attached to an algal substrate (cf. Bergstrom 1968) cannot be overlooked.

The occurrence of Schizocrania on the internal surface of the body chambers of the Llanvirn and Upper Whitcliffian specimens indicates that encrustation would not have taken place before the post mortem drifting phase following the decay of the mantle lining the body chamber and not after the infilling stage of the phragmacone during its depositional history. The Lower Whitcliffian orthocone however could have been encrusted at any one of a number of stages in its history as a live or dead mobile organism. Since the Schizocrania are attached to its underside they must have settled and had time to grow prior to its final entombment in this position.

Distribution of Schizocrania

The Llanvirn orthocone and Schizocrania discussed here are the only representatives of these taxa known from the predominantly arenaceous and rudaceous Ffairfach Group of the Llandeilo area. Since S. salopiensis is well known from penecontemporaneous, argillaceous successions elsewhere in South Wales and the Welsh Borderlands (Williams 1974 and Bassett et al. 1974 p.9) where the fauna is dominated, or exclusively represented by neritic and pelagic faunas (i.e. trilobites, graptolites and cephalopods), it is reasonable to assume that the unique (or "exotic") Ffairfach occurrence may have resulted from the drifting or migration of a stray cephalopod beyond the normal limits of its indigenous environment.

Similarly Schizocrania striata is rare in the Whitcliffe Beds of the Ludlow region where it constitutes only about 0.01 to 0.005% of the total fauna with specimens occurring in a fragmentary condition and a random orientation. It is more commonly found in unbioturbated, parallel-laminated, alternating light and dark siltstones (rhythmites) of deeper water facies (e.g. Upper and Lower

Leintwardinian Beds, Holland *et al.* 1963, p.154 and Lawson 1973, p.274) and is recorded only rarely in shallow water bioturbated siltstones (Facies β *sensu* Antia 1979). In this case, therefore, again it seems possible that the Whitcliffian cephalopods drifted into inshore deposits from an offshore source.

Post mortem drifting of modern cephalopods is a well known phenomenon; House (1973) and Kennedy & Cobban (1976) refer to data which indicates that dead *Nautilus* shells drift for hundreds or even thousands of kilometres. Similarly Hewitt & Pedlay (1978) note that "At the present day *Spirula* frequently drifts inshore from its oceanic habitat", whilst the cuttle bones of *Sepia* may float for years, presumably being less likely to sink than to drift ashore.

Williams (1969 p.143) discussed the potential range of larval dispersal and its bearing on brachiopod migrations during the Ordovician. Clearly his suggested range of up to 250 km might be only a fraction of the potential range which might be considered for brachiopods capable of encrusting live or drifting orthocones. In view of the fact that the Llanvirn occurrence of *Schizocrania* reported here is at least as old as any hitherto known record of the genus in the Anglo Welsh region (Williams 1974 p.45; Bassett et al. 1974 p.9), consideration must be given to the potential importance of "orthocone drifting" as a mechanism contributing to brachiopod dispersal.

Trematid hosts

Encrusting Trematidae such as *Schizocrania*, *Drabodiscina* and *Ptychopeltis* appear to be host specific. *S. salopiensis*, *S. striata* and *P. incola* have hitherto only been observed attached to orthoconic nautiloids presumed to have been alive or floating at the time of their encrustation. Other members of the family, e.g. *Ptychopeltis hornyi* Havlicek and *Drabodiscina grandis* Barrande, are commonly attached to conularids which are considered by Havlicek (1972) to have been mobile during life and the American species *Schizocrania filosa* Hall is almost invariably attached to the brachiopod *Rafinesquina* (Foerste 1924, Cooper 1956 & Rowell *in* Williams *et al.* 1965). With respect to trematid-nautiloid associations, it is intriguing to note that Titus and Cameron record *S. filosa* only in their deep water *Geisonoceras* (Orthocerida) community. Since Dr. R.A. Hewitt and Mrs. Evans (*pers. comm.* 1979) inform us that they know of no Silurian or Ordovician examples of cephalopod encrustation by brachiopods other than those reported here, we conclude that although the examples discussed here are rare they are none the less reminiscent of the appararent host specific relationships noted above.

Conclusions

Faunal associations with abundant Schizocrania in the Ordovician and Silurian of the Anglo Welsh region are almost invariably confined to argillaceous deep wate facies where species of the genus are represented almost exclusively by assemblage of brachial valves. Such exceptionally disproportionate valve ratios, which have never been adequately explained or investigated, are considered to result from the probable encrustation relationships inferred above which might account for the obscuring or removal of pedicle valves.

Known associations between trematid encrusters and hosts such as those reported here and elsewhere (e.g. Havlicek 1972 and Rowell in Williams et al. 196 point to some form of host specific relationship between representatives of this family and other larger invertebrate hosts. Whether such relationships could be termed symbiotic, commensal or parasitic is unclear since, although an encrusting trematid would neither obviously incapacitate or benefit a living host, we currently lack evidence which conclusively demonstrates that hosts were encrusted during life. With respect to this issue, however, we can establish that encrustation of orthocones, which may in some cases have begun during their life, often began no earlier than the post mortem drifting phase, and may have continued or begun at a time when the orthocones were resting or rolling on the sea floor. Since encrustation of these orthocones could not have taken place when they were in their final entombment position (i.e. with at least partially grown Schizocrania attached to the under and inner sides of their sediment filled pragmacones), the stage at which encrustation occurred is narrowed to the middle part of the orthocones pre-entombment history.

Although these considerations theoretically allow for considerable scope in the interpretation of "probable time of encrustation" several factors point to its early occurrence in the orthocones life and post mortem history. 1. The encrusting Schizocrania noted here are not known to attach to other skeletal components within the deposits from which they were recovered and therefore are likely to have settled preferentially on orthocone shells. This is further supported by the high density of Schizocrania on these shells; their apparent clustering and orientation towards the anterior of the phragmacone (on both its inner and outer surfaces) suggests that the orthocone was probably colonized whilst it was floating, since such ordered organization and alinment of these small colonies is reminiscent of patterns observed elsewhere on bouyant host organisms (cf. Seilacher 1954, 1960 & 1968; Holland 1971; Havlicek 1972).

2. Since both Schizocrania and its nautiloid hosts are normally indigenous to sparsely fossiliferous, low diversity offshore facies, it is probable that encrustation occurred in an offshore region well before the orthocones finally became entombed in more diverse, fossilferous, onshore facies. This inference is supported by the observation that the setiferous Schizocrania may well have been adapted to a prolonged larval stage which would have enhanced its chances of encountering a suitable encrustation site, e.g. an orthocone or other indigenous organism. If this were the case and Schizocrania even occasionally encrusted orthocones in a manner analagous to the attachment of epiplanktic aegeromenids to bouyant organisms noted by Bergstrom (1968), then the combined effect of nautiloid mobility during life (e.g. migration) and drifting after deat would offer an explanation for occurrences such as those noted here and point to potential brachiopod dispersal mechanism.

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References

Antia, D.D.J. 1979a. Bone-beds: A review of their classification, occurrence genesis, geochemistry, ecology, diagenesis, weathering and micro-biotas. Mercian, Geol. 7(2), 93-174, 6 pls.

——— 1979b. Comments on the environments and faunas across the Ludlovian Downtonian (Upper Silurian) boundary at Scafton, Salop. Geol. J.

Bassett, D.A., Ingham, J.K. and Wright, A.D. (Eds). 1974. Field excursion guide to type and classical sections in Britain. (Ordovician System Symposium, Birmingham 1974). The Palaeontological Assoc. London. pp.66

Bergstrom, J. 1968. Some Ordovician and Silurian Brachiopod Assemblages. Lethaia. 1. p.230-237.

Chuang, S.H. 1968. The larvae of a discinid (Inarticulata, Brachiopoda). Biol. Bull 135, 263-72.

——— 1977. Larval development in Discinisia (Inarticulata, Brachiopoda). Amer. Zool. 17, 139-53.

Cooper, G.A. 1956. Chazyan and related brachiopods. Smithson. Misc. Coll., Washington, 127, 1-1245, pls.1-169.

Daly, J.M. 1978. The annual cycle and the short term periodicity of breeding in a Northumberland population of Spirorbis spirorbis (Polychaeta: Serpolidae). J. Mar. Biol. Ass. UK. 58, 161-176.

Filatova, Z.A., Sokolova, M.N. and Levenshteyn, R.Ya. 1969. A find of a mollusk of the Cambrian to Devonian Class Monoplacophora in the North Central Pacific. Dokl. Akad. Nauk. Earth Sci. Sect. Vol. 185, p.187-9

Foerste, A.F. 1924. Upper Ordovician faunas of Ontario and Quebec. Mem. Ge Surv. Canada. 138, p.1-255, pls.1-66.

Fursich, F.T. and Hurst, J.M. 1974. Environmental factors determining the distribution of brachiopods. Palaeontology 17, p.879-900.

Havlicek, V. 1972. Life habit of some Ordovician inarticulate brachiopods. Vestnik ustred ust geol. 47. 4. 229-233.

Hewitt, R.P. and Pedley, H.M. 1978. The preservation of the shells of Sepia in the Middle Miocene of Malta. Proc. Geol. Ass. 89(3), 227-237.

Holland, C.H. 1971. Some conspicuous participants in Palaeozoic symbiosis. Sci. Proc. R. Soc. Dublin, Ser. A. 4(2), 15-26.

Holland, C.H., Lawson, J.D. and Walmsley, V.G. 1963. The Silurian rocks of the Ludlow district, Shropshire. Bull. Brit. Mus. (Nat. Hist.), Geol. 8, 95-171.

House, M.R. 1973. An analysis of Devonian Goniatite distributions. Spec. Pap. Palaeont. 12, 305-317.

Kennedy, W.J. and Cobban, W.D. 1976. Aspects of Ammonite Biology and Biostratigraphy. Spec. Pap. Palaeont. 17, 1-94.

Knight-Jones, E.W. 1951. Gregariousness and some other aspects of the settling behavious of Spirorbis. J. Marine Biol. Ass. UK. 30, 201-222.

——— 1953. Decreased discrimination during settling after prolonged planktonic life in the larvae of Spirorbis borealis (serpulidae) J. Mar. Biol. Ass. UK. 32, 337-345.

Knight-Jones, P. and Knight-Jones, E.W. 1977. Taxonomy and ecology of British Spirorbidae (Polychaeta). J. Mar. Biol. Ass. UK. 57, 453-499.

Lawson, J.D. 1973. Facies and faunal changes in the Ludlovian rocks of Aymestrey, Herefordshire. Geol. J. vol. 8, Pt. 2, 247-278.

Meischner, D. 1968. Perniciöse Epökie von Placunopsis auf Ceratites. Lethaia, Vol. 1, 156-74.

Seilacher, A. 1954. Okologie der triassischen Muschel Lima lineata (Schloth.) und ihrer Epöken. N. Jh. Geol. Paleont. Mh. 163-183.

——— 1960. Epizoans as a key to Ammonoid Ecology. J. Palaeont. 34, 189-93.

——— 1968. Swimming habits of Belemnites - recorded by boring Barnacles. Palaeogeog. Palaeoclimatol. Palaeoecol. 4, 279-285.

Trueman, A.E. 1942. Supposed Commensalism of Carboniferous Spirorbids and Certain Non-marine Lamellibranchs. Geol. Mag. 79, p.312-313.

Sudarson, A. 1969. Brachiopod larvae from the west coast of India. Proc. Ind. Acad. Sci. 68B, 59-68.

Titus & Cameron. 1976. Fossil Communities of the Lower Trenton Group (Middle Ordovician) of Central and North Western New York State. J. Paleont. 50, 1209-25.

Voigt, E. 1977. On grazing traces produced by the radula of fossil and recent gastropods and chitons. In Crimes, T.P. and Harper, J.C. (Eds). Trace fossils 2 Geol. J. Spec. Issue No. 9, p.335-345.

Williams, A. 1969. Ordovician faunal provinces with reference to brachiopod distribution in Wood, A. (Ed.). The Pre-Cambrian and Lower Palaeozoic rocks of Wales. Univ. of Wales Press, Cardiff.

——— 1974. Ordovician Brachiopods from the Shelve district, Shropshire. Bull. Brit. Mus. (Nat. Hist.) Geol. Supp. 11, 1-163, pls.1-28.

Williams, et al. in Moore, R.C. (Ed.). 1965. Treatise on invertebrate palaeontology Part H. Brachiopoda. Univ. Kansas Press.

Williams, A. 1953. The geology of the Llandeilo district, Carmarthenshire. Q. Jl. geol. Soc. Lond. 108, 177-208.

11

Thelodontites corftonensis gen. et sp. nov. : A new trace fossil species from the British Silurian, Ludlow Bone-Bed

by

David D. J. Antia

ABSTRACT

A new Silurian trace fossil Thelodontites corftonensis Antia is described. This ichnospecies occurs as borings on fish debris in the Ludlow Bone-Bed. In this paper its size distribution apparent substrate preferences and densities are described. Trace fossils which may be referable to the genus Thelodontites have also been observed on recent otoliths and carbonate debris and on fish debris in the West German Muschelkalk Grenzbonebed.

INTRODUCTION

In two recent papers and an abstract (Whitaker and Antia, 1978; Antia and Whitaker, 1979; Antia, 1979a) borings on thelodont fish scales from the Ludlow Bone-Bed have been recorded and illustrated. The purpose of this note is to describe these borings in greater detail from five Ludlow Bone-Bed localities (Fig. 1).

Two types of borings have been recorded from fish scales in the Ludlow Bone-Bed and they are illustrated in Plate 1, fig. a, c, e. They have been termed Algal Forms A and B by Antia (1979a). A third form of boring is present on the biogenic clasts and is confined entirely to phosphatised shells of '<u>Serpulites</u>' sp. (Plate 1 fig. B). However, both this boring and Algal form B are rare components of the ichnofauna of the Ludlow Bone-Bed. In contrast Algal form A is abundant (Table 1). This later trace fossil is assigned here to the new ichnogenus and ichnospecies <u>Thelodontites</u> <u>corftonensis</u>.

SYSTEMATIC DESCRIPTION

<u>Thelodontites</u> gen. nov.

Type species	<u>Thelodontites</u> <u>corftonensis</u> gen. et sp. nov.
Derivation of name.	After the group of vertebrates on which the boring was first recognised (see Antia and Whitaker, 1979)
Diagnosis	Cup shaped depression on a grain surface less than 0.2 mm in diameter
Known stratigraphic range of the genus.	Upper Silurian to Recent (see Antia and Whitaker, 1979; Antia 1979a)
Remarks	The genus is similar to <u>Myzostomites</u> Clarke, 1921, p.58 (cf. Hantzschel, 1975) and the circular parabolic

Plate 1. A. *Gomphonchus tenuistriata* fragment with *T.corftonensis* borings in its grooves.(Distance between adjacent grooves = 250 - 300 microns).

B. Borings on a phosphatised fragment of *Serpulites* sp. (Boring diameter = 10 - 15 microns)

C. Holotype of *T.corftonensis* (arrowed) on the illustrated (Plate 1A) specimen of *G.tenuistriata* .

D. Recent *Thelodontites* boring (diameter 30 microns) from Sales Point,Bradwell,Essex.

E.Algal form B boring of Antia(1979a) on a *Thelodus parvidens* scale.Note the weathering stage 1 cracks (cf.Antia,1979a) - diameter of borings = 10 - 15 microns.

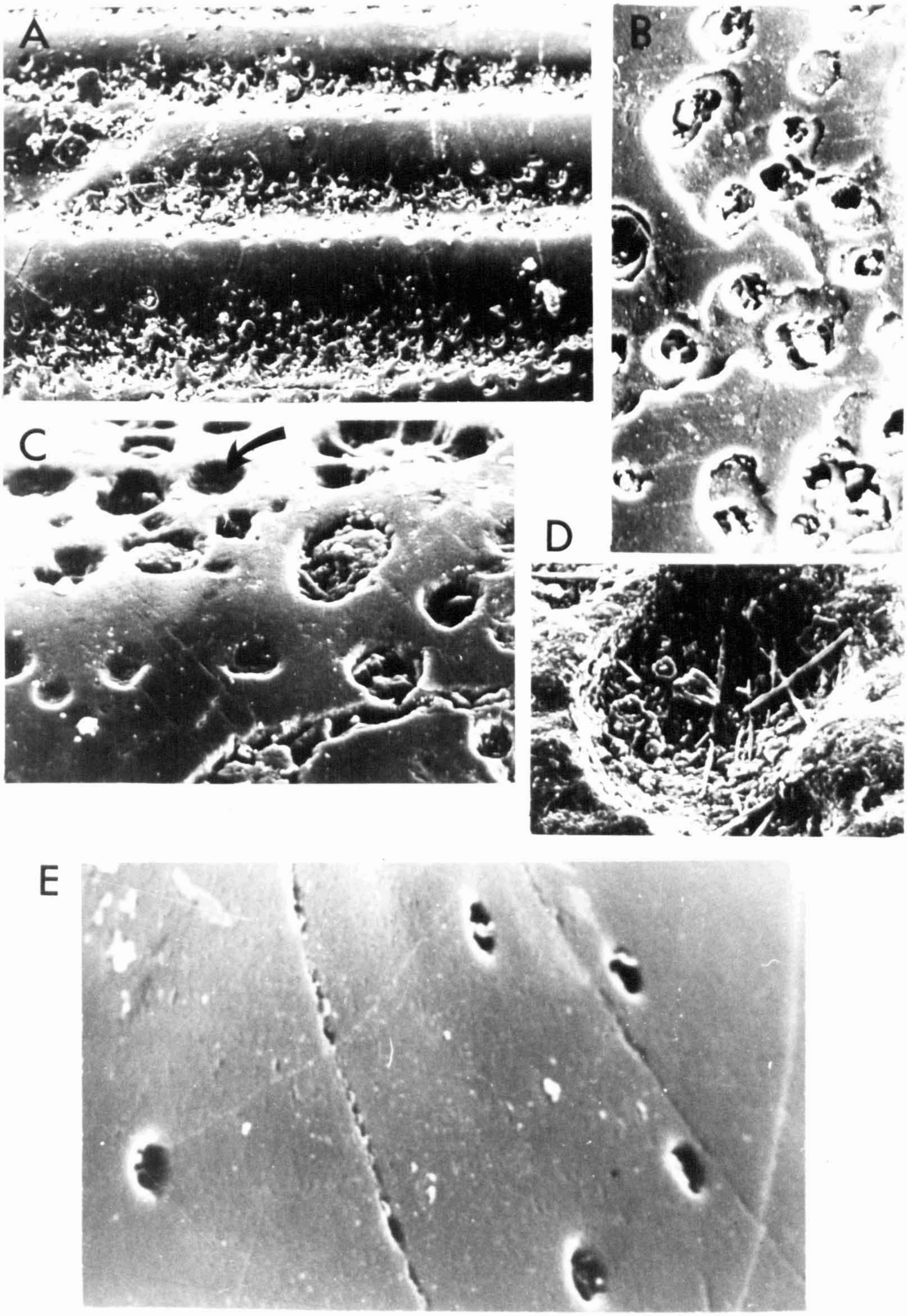
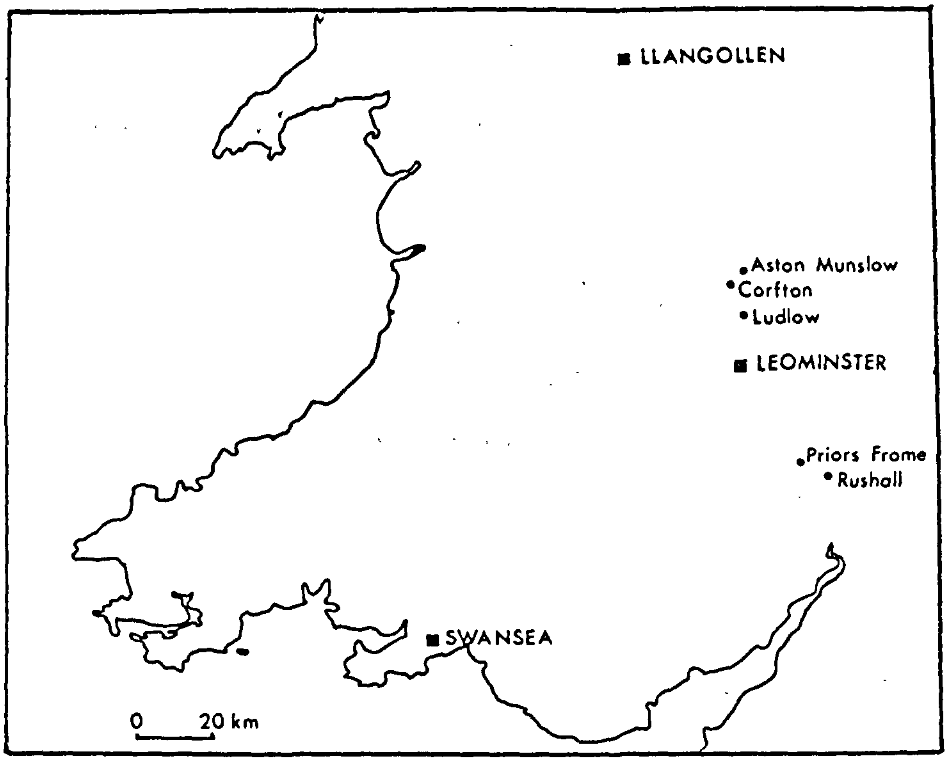

A
B
C
D
E

Table 1. Densities of <u>Thelodontites corftonensis</u> on scales of <u>Thelodus parvidens</u> Ag.

No. of <u>T.corftonensis</u> per scale	Rushall	Priors Frome	Ludlow	Corfton
0	84.95	94.71	59.90	29.40
1- 5	7.16	1.98	18.20	20.50
6-10	4.50	1.95	10.98	14.10
11-15	1.84	0.52	6.66	8.40
16-20	0.51	0.39	4.33	8.10
21-25	0.20	0.26	2.89	5.90
26-30	0.20	0.33	0.86	2.20
31-35	0.20	0.19	0.86	3.20
36-40	0.10	0.06	0.57	2.20
41-45	0.10	-	0.28	2.60
46-50	0.10	0.06	-	0.59
51-55	0.10	-	-	0.59
56-60	-	-	-	0.14
61-65	-	-	-	0.44
66-70	-	-	-	0.44
71-75	-	-	-	0.14
76-80	-	-	-	-
81-85	-	-	-	0.29
86-90	-	-	-	-
91-95	-	-	-	-
96.100	-	-	-	-
Mean No. Borings per scale	1.18	0.56	4.39	10.84



Text Fig. 1.

Location map showing the five Ludlow Bone Bed sites visited during the course of this study. The British National Grid References of the localities are given as follows:

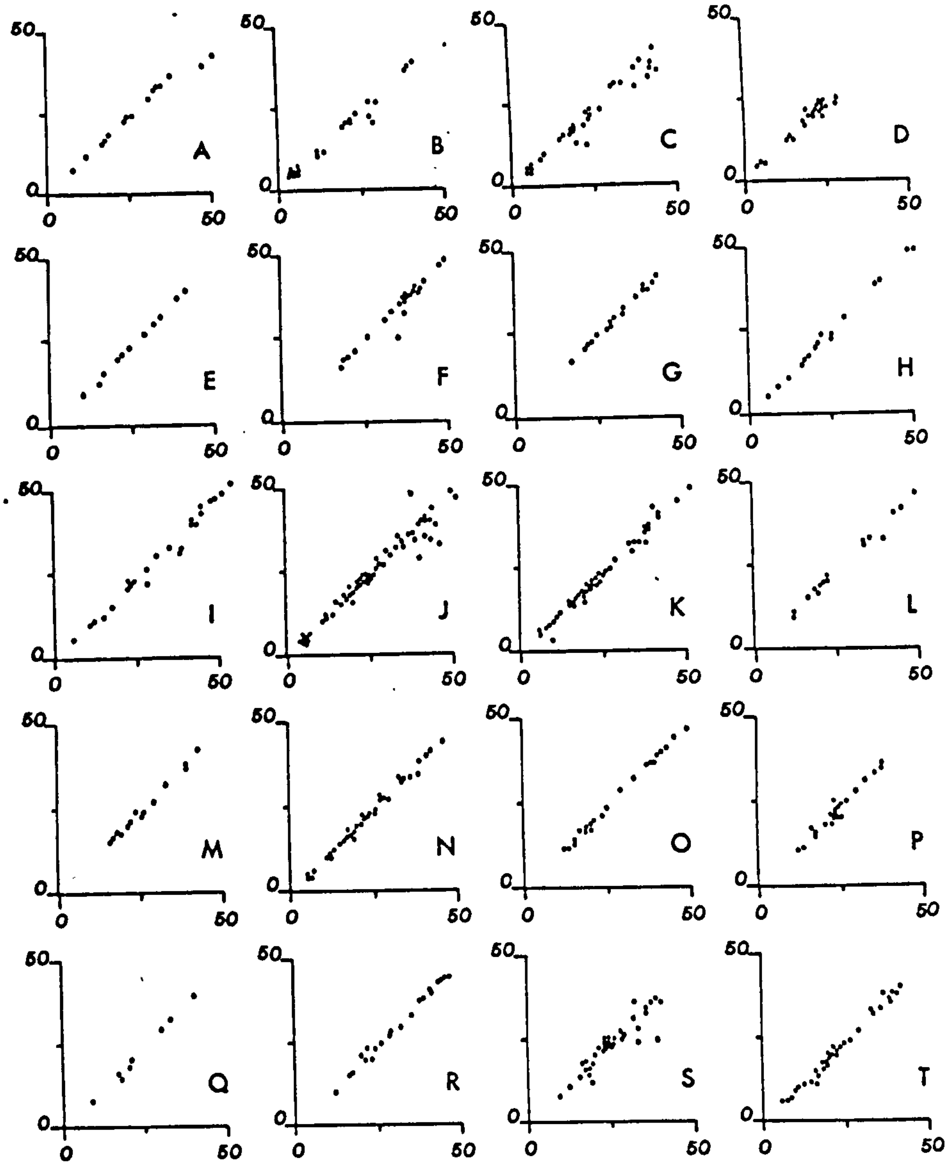
(1) Aston Munslow (SO 513867), (2) Corfton (SO 496854), (3) Ludlow (SO 512741), (4) Priors Frome (SO 576390), (5) Rushall (SO 640348).

pits which have been recorded on Palaeozoic crinoids (see Brett, 1978, for a review), but is distinguished from them by its smaller size (cf. Brett, 1978, p.222).

Thelodontites corftonensis gen. et sp. nov.

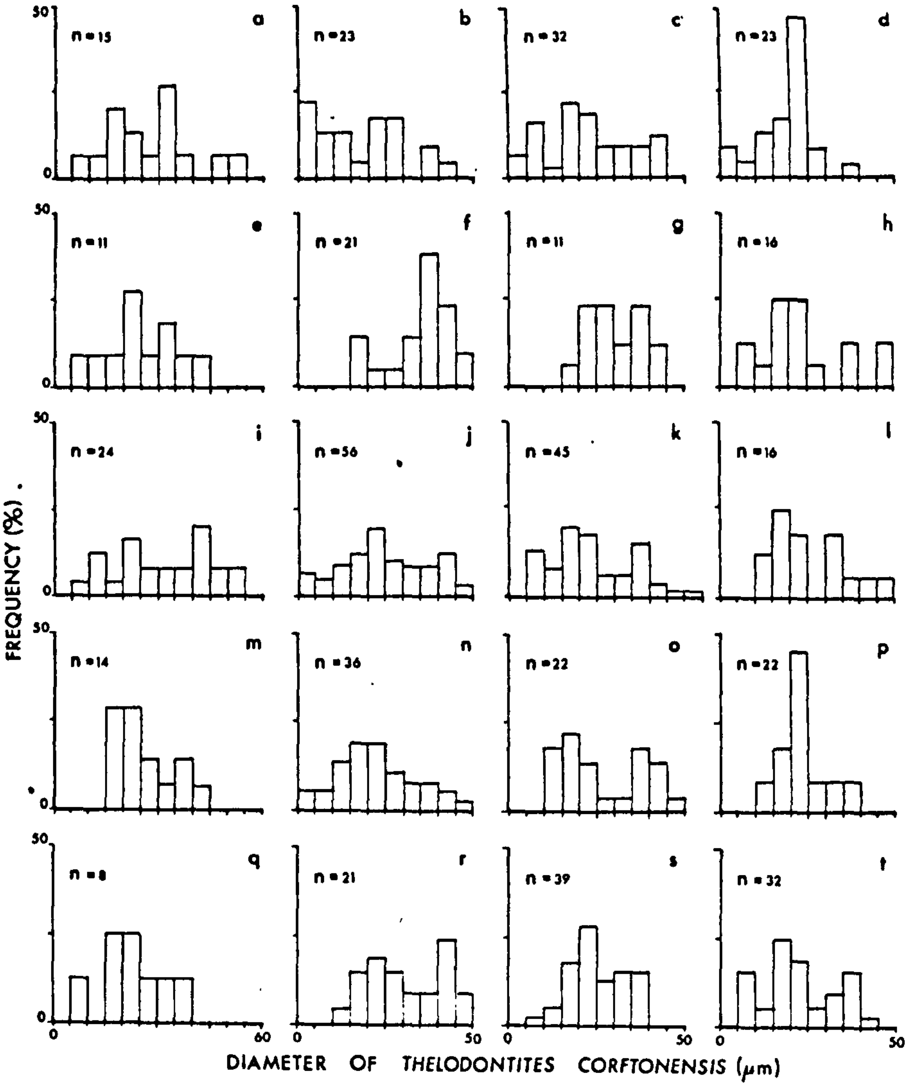
Algal solution pit	Antia and Whitaker, 1979 Fig. 1a, k; 2a
Algal form A	Antia 1979a, Pl. 17f, Pl. 18c, Pl. 19d, e

Derivation of name.	After the village of Corfton
Holotype	On a fragment of '*Onchus*' *tenuistriata* from the Ludlow Bone Bed at Corfton (British National Grid Reference SO 497853) LUDLOW MUSEUM No SHRM – Plate 1 Fig. C
Paratypes	Ludlow Bone Bed Corfton. Various bored thelodont scales. SHRM
Diagnosis	Cup shaped depression on a vertebrate grain between 0.004 and 0.07 mm in diameter
Remarks	The maximum length and width of *T. corftonensis* appears to be of about equal dimension at each locality studied (Text Figs. 2, and deposited figures) with a size range on an individual thelodont scale of between 5 and 60 microns (Text Fig. 2). The size frequency distributions of these borings on 90 thelodont scales are given in Text Fig. 3. The very different size modal peaks of *T. corftonensis* on different scales from the same locality (*e.g.* Aston Munslow Text fig. 3m and 3f) suggests that the species may have colonised the scales episodically and that its diameter increased during life. Consequently scales



Text Fig. 2.

Plot of maximum length against width of Thelodontites corftonensis gen. et sp. nov. on 20 scales of Thelodus parvidens Ag. from the Ludlow Bone Bed at Aston Munslow. Both length (x axis) and width (y axis) measurements were made at 90° to each other. Note that on scales containing 8 T. corftonensis borings (e.g. Fig. 2 Q) that they have a wide size distribution.
Similar graphs from the other localities have been deposited both with Glasgow University Library and with the British Library.



Text Fig. 3. Size frequency histogram of maximum length of T.corftonensi at Aston Munslow, on 20 T.parvidens scales. Similar graphs from the other localities have been deposited both with Glasgow University Library and with the British Library.

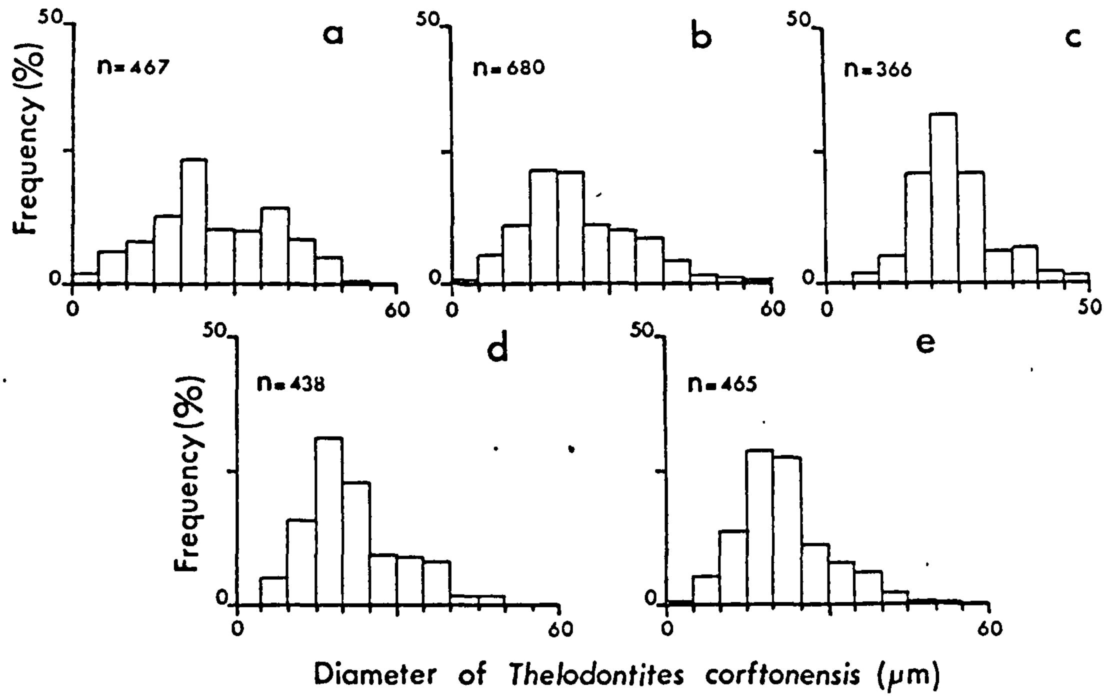
containing two or more size modal peaks (e.g. Text Fig. 3a, b, k, o, r, f) of T. corftonensis may have been colonised episodically several times.

The mean size pyramids for each locality (Text Fig. 4) may provide some clues pertaining to the natality and mortality rates prevalent in the species at different localities (cf. Clapham, 1971; Antia and Wood, 1977). Such an interpretation of these size pyramids (Text Fig. 4) is given in Table 2.

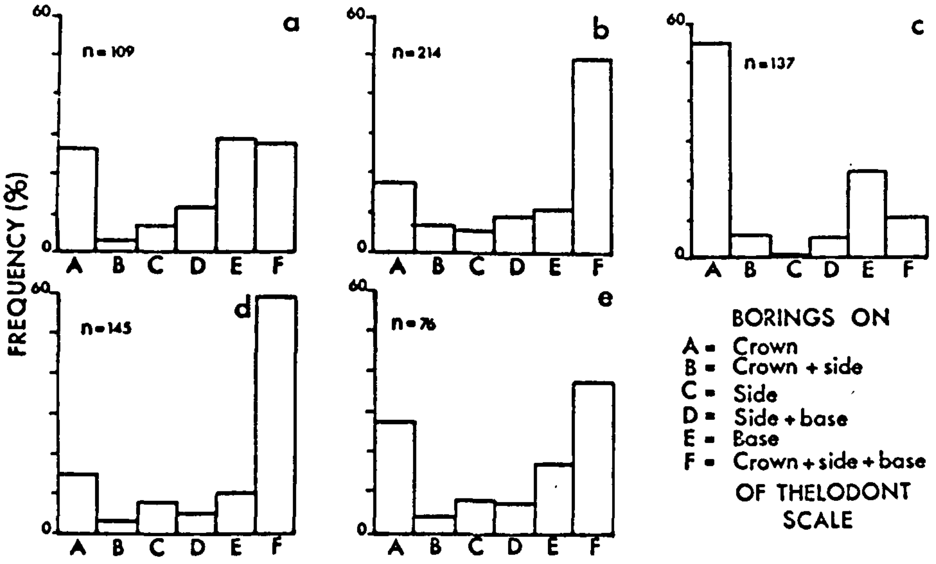
The distribution of T. corftonensis on individual thelodont scales is indicated in Text Fig. 5. As no apparent universal colonisation pattern occurs (Text Fig. 5) it is probable that the scales were colonised after the fishes' death rather than before, It is, however, interesting to note that the scales crown and base form preferred colonisation sites (Text Fig. 5). The distribution of T. corftonensis is apparently independent of the scales orientation in the bone-bed, as can be seen by a comparison of scale orientation (Text Fig. 6) and T. corftonensis distribution (Text Fig. 5). For example, at Priors Frome the thelodont scales in the bone-bed are mainly resting on their side (Text Fig. 6p), while T. corftonensis (Text Fig. 5e) occurs most commonly on the scales crowns. At Ludlow an apparent correlation between scale orientation (Text Fig. 6) and T. corftonensis colonisation (Text Fig. 5c) exists. Here it appears that T. corftonensis occurs most commonly on only scale crowns and that the scales

Table 2. An age structure table to illustrate relative natality and population structure in T. corftonensis. Interpretation based on the graphs in Text Figure 12.

Age distribution of:	Species producing very few young	Intermediate number of young	many young
1. Stable population	Aston Munslow (Text Fig. 12a)	—	—
2. Expanding population	—	—	Priors Frome Rushall (Text Fig. 12d, e)
3. Contracting population	—	—	—
4. Over-exploited population	—	Corfton Lane (Text Fig. 12b)	Ludlow (Text Fig. 12c)



Text Fig. 4. Size frequency histogram of maximum length of T.corftonensi at each locality examined, a = Aston Munslow; b = Corfton; c = Ludlow; d = Rushall; e = Priors Frome.



Text Fig. 5. Distribution of T. corftonensis borings on Thelodus parvidens scales of the various localities. a = Aston Munslow; b = Corfton; c, Ludlow; d = Rushall and e = Priors Frome.

were orientated crown up. However, at Aston Munslow, Corfton Lane and Rushall, no correlation between scale orientation and T. corftonensis distribution was noted (compare Text Fig. 5a, b, d with Text Fig. 6 A1, C2, R4). The varying orientations of thelodont scales at 32 separate bone-beds or bone-bed localities (Text Fig. 6) suggest that scale orientation may vary within a bone-bed. Since the thelodont scales were probably only temporarily static when colonised, T. corftonensis could well have colonised only the scales exposed 'upper' surface, which at the time of colonisation may have been the scales crown, side or base.

The ichnospecies have been observed by the author on thelodont scales collected about 1.2 m below the Ludlow Bone-Bed at Aston Munslow and from the Ledbury Formation at Ludlow suggesting that its range extends from the uppermost Ludlowien Series (Whitcliffe stage) into the upper Downtonian Series within the Upper Silurian.

Similar borings occur on recent intertidal carbonate fragments (Antia and Whitaker, 1979, Fig. 3c; Antia, 1979a, Plate 19, fig. 6) and on vertebrate grains from the Triassic West German Muschelkalk Grenzbonebed, and recent otoliths from the Rockall trough, they may all be assigned to the genus Thelodontites. Antia and Whitaker (1979, fig. 1h, i) recorded fungal filaments in these recent Thelodontites borings (cf. Plate 1, fig. 7) and suggested that they may have

Text Fig. 6.

Orientation of Thelodont scales in a number of Bone-Beds. L1 - 10 are the first 10 Bone Beds in the section at Ludlow. L1 = the Ludlow Bone Bed (LBB) of Antia (1977a p.145). LYE is the LBB at Lye, near Birmingham (G. R. SO 928845). D = the LBB at Deepwood near Ludlow (G. R. SO 459740). C1 = LBB at Corfton. C2 = the LBB at Corfton Sun Inn (G. R 496852). S1 = LBB at Shipton (G. R. 563918). S2 = Bone-Bed cm above LBB at Shipton. B = LBB at Brockton (G. R. SO 578939). A1 is the LBB at Aston Munslow. A2 and A3 are the first bone-beds above the Ludlow Bone-Bed at Aston Munslow (Antia, 1979a, p.145). LO1 is a bone-bed cm below the LBB at Longhope (G. R. SO 691191). LO2 is the LBB at Longhope. P = LBB at Priors Frome. O = LBB at Usk (G. R. SO 355957). R1 = LBB at Rushall (G. R. SO 640348).

R2 = LBB at Rushall (G.R. SO 640 345)

R3 = LBB at Rushall (G.R. SO 640 345)

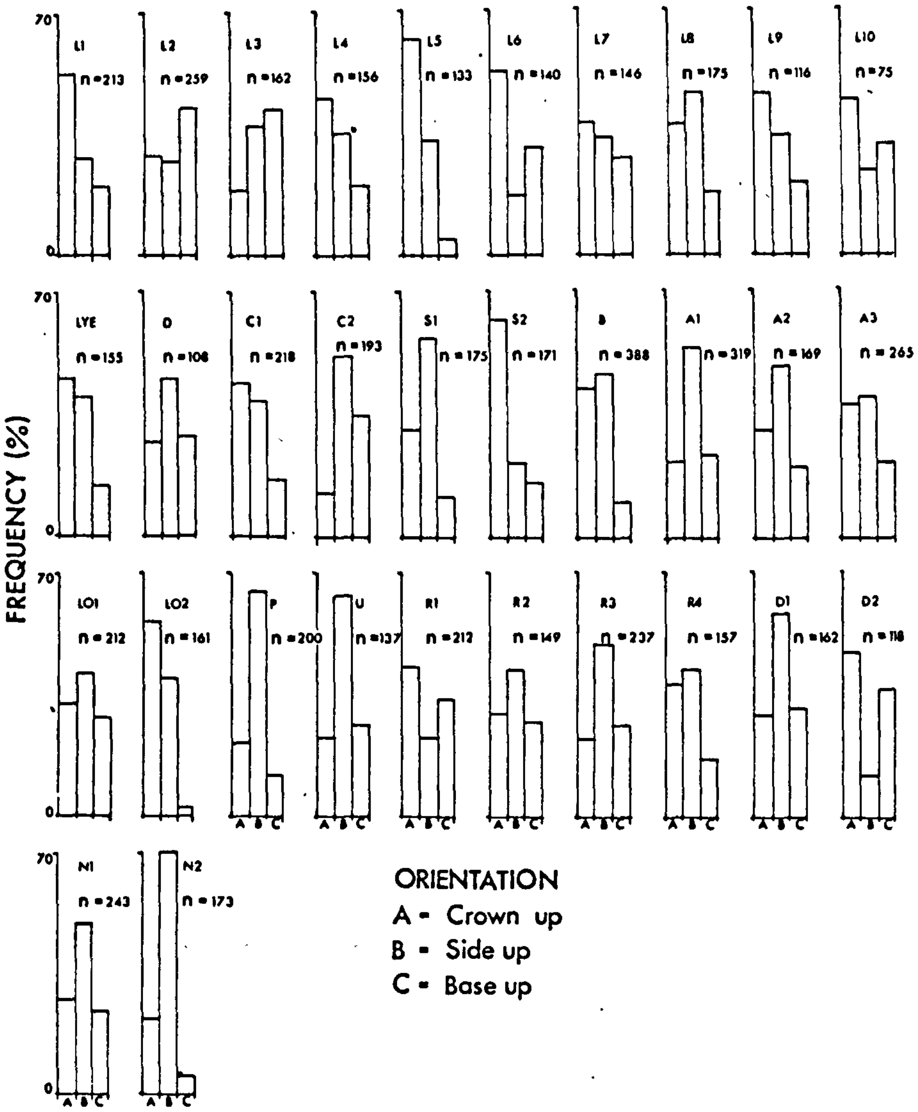
R4 = LBB at Rushall (G.R. SO 640 345)

D1 = LBB at Downton (G.R. SO 435741)

D2 = Downton Bone-Bed At Downton

N1 = Ludlow Bone-Bed at Netherton (G. R. SO 935874)

N2 = Bone-Bed 8 cm above Ludlow Bone-Bed at Netherton.


FREQUENCY (%)
70
0
L1 n=213
L2 n=259
L3 n=162
L4 n=156
L5 n=133
L6 n=140
L7 n=146
L8 n=175
L9 n=116
L10 n=75
LYE n=155
D n=108
C1 n=218
C2 n=193
S1 n=175
S2 n=171
B n=388
A1 n=319
A2 n=169
A3 n=265
LO1 n=212
LO2 n=161
P n=200
U n=137
R1 n=212
R2 n=149
R3 n=237
R4 n=157
D1 n=162
D2 n=118
N1 n=243
N2 n=173
A B C
ORIENTATION
A - Crown up
B - Side up
C - Base up

actively dissolved the clast on which they occur. However, Warne (1975, p.196) has figured some recent Thelodontites borings which he attributed to sponge borings. If Warne (1975) is correct in his interpretation, then Thelodontites could be produced by a variety of organisms

In the Ludlow Bone-Bed T. corftonensis is only present on Thelodus spp. scales and Gomphonchus spp.. Its absence from the phosphatised invertebrate shells has led Antia and Whitaker (1979, p.131) to suggest that there may have been nutritional differences between the two clast types, and that the T. corftonensis producing organism may have fed on the collagen in the vertebrate remains.

The low density occurrence of the species at Rushall and Priors Frome (Table 1) may reflect both regional and environmental variations; as it occurs in intertidal lithobonebed sediments at Ludlow and Corfton, (Antia and Whitaker, 1979; Antia, 1979a), while at Priors Frome it occurs in a clayey floatstone which may have been deposited in a subtidal environment, (cf. Antia, 1979b) and at Rushall in quartz rich sublithobonebed of uncertain environmental location.

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References

ANTIA, D. D. J. 1979a. Bone-beds: A review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering and microbiotes. Mercian Geol. vol. 7, pp.93-1~~9~~74.

ANTIA, D. D. J. 1979b. Authigenic gypsum in marine sediments - a comment. Marine Geol. vol. 32 pp.111-114.

ANTIA, D. D. J. and WHITAKER, J. H. McD. 1978. A scanning electron microscope study of the genesis of the Upper Silurian Ludlow Bone Bed. In W. B. Whalley (ed.) Scanning electron microscopy in the study of sediments. Geoabstracts, Norwich. pp.119-136.

ANTIA, D. D. J. and WOOD, B. A. 1977. Some aspects of the Palaeoecology of the E_1b zone of the Edale Shales (Namurian). In the Edale Valley Derbyshire. Mercian Geol. vol. 6, pp.179-196.

BRETT, C. E. 1978. Host-specific, pit-forming epizoans on Silurian crinoids. Lethaia, 11, 217-232.

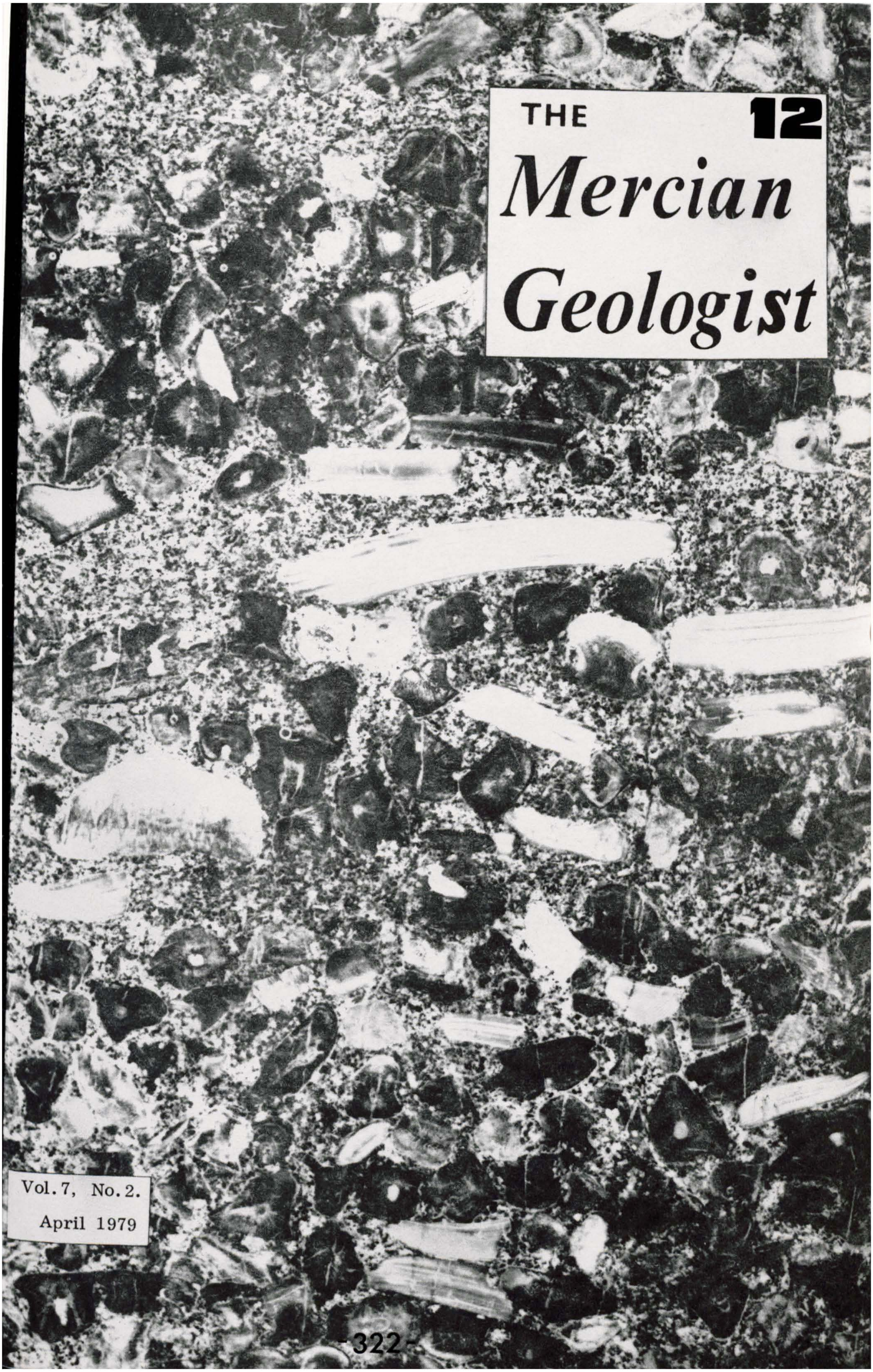
CLAPHAM, W. E. 1973. Natural Ecosystems. New York.

CLARKE, J. M. 1921. Organic dependence and disease: their origin and significance. New York State Mus. Bull. 221-222, 1-113.

HANTZSCHEL, W. 1975. Part W. Miscellanea suppliment 71. Trace fossils and problematica. In Teichert, C. Treatise on invertebrate Palaeontology. Geol. Soc. Am. Inc. Kansas. pp.W1-W269.

WARME, J. E. 1975. Borings as Trace Fossils, and the processes of Marine Bioerosion. In Frey, R. W. (ed.). The study of trace fossils. Springer Verlag Berlin pp.181-228.

WHITAKER, J. H. McD. and ANTIA, D. D. J. 1978. An S.E.M. study of the genesis of the Upper Silurian Ludlow Bone Bed. Ludlow Res. Group. Bull. No. 25, pp.63-64. Abst.



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12

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BONE-BEDS: A REVIEW OF THEIR CLASSIFICATION, OCCURRENCE, GENESIS, DIAGENESIS, GEOCHEMISTRY, PALAEOECOLOGY, WEATHERING, AND MICROBIOTAS

by

David D. J. Antia

Summary

The term *bone-bed* is redefined to include only deposits containing more than 18% phosphatic material. Such deposits are divided into three major groups (a) Lithobonebeds, (b) Biobonebeds, and (c) Pelbonebeds, on the composition of their phosphatic clasts.

The concept of bone-bed prefossilisation is critically examined and some bone-beds previously considered to be prefossilised deposits, for example the West German Muschelkalk Grenzbonebed, deemed to be primary bone-bed deposits.

A review of bone-beds from Europe and America, of Silurian to Modern age forms the main section of this paper and includes models for their formation. Vertebrate mortality and decomposition and subsequent weathering and diagenesis are all considered.

New data regarding the environments, geochemistry, sedimentology and palaeontology of the British Ludlow-Downton, German Beyrichiankalk (Upper Downton), Irish Carboniferous (Tournasian), German Triassic (Muschelkalk, Lettenkeuper), British Rhaetic, Miocene/Pleistocene, and Holocene bone-beds is included.

CONTENTS

Mercian Geol. Vol. 7, No. 2, 1979
pp.93-174, 12 text-figs, Plates 14-19.

1 - Introduction

Since 1236 bone-beds of all ages (Ordovician - Recent) have been described from rocks of many countries, but there is no single account of them. Furthermore there is no single definition of bone-beds used by all authors and no attempt has been made to compare and contrast these accumulations of bone, teeth, scales and other remains of fish, reptiles and vertebrates. This article begins with a definition of phosphorites - a group of deposits, which include bone-beds, and indicates a scheme for the classification of phosphorites and bone-beds.

The accumulation and subsequent history of modern vertebrate deposits is then outlined and followed by a review of some Silurian to Pliocene bone-beds. A comparison is made between the recent and fossil bone-beds and conclusions are drawn regarding the palaeoecology, syndepositional weathering and microbiotas of the fossil layers.

2 - Previous use of the term bone-bed

Invariably rocks termed bone-beds contain "abundant" fish scales, teeth, bones, coprolites, phosphatic concretions and nodules, phosphatic moulds and casts of shells, and phosphatic invertebrate exo-, or endo-, skeletons. Some of these deposits can contain conodonts, crustacea, calcareous shells, pebbles, quartz, heavy minerals, feldspar, clays, glauconite and calcite. Locally within a bone-bed any one clast type may dominate (See Reif, 1969; 1971).

The term bone-bed was originally applied to a recent marine deposit rich in vertebrate remains (Lyell 1834) and later to the English Rhaetic bone-bed which was described as "being composed of fragments of teeth and bones in an extraordinary manner" (Roberts, 1839, p.20). Later, Murchison (1852) termed the earlier described (Murchison, 1837, 1839) Ludlow Fish Bed, the Ludlow Bone-Bed. Page (1859, p.93) cited both the Ludlow and Rhaetic Bone-Beds as examples of bone-beds, defined as "A term applied to several thin strata or layers containing innumerable fragments of fossil bones, scales, teeth coprolites and other organic debris". This definition has been accepted by Howell (1957, p.35), while Challinor (1967,p.29) considers a bone-bed to be "a bed of rock composed of fossil bones, teeth etc., of vertebrates" (also Murawski, 1972). More recently (Reif, 1976) defined bone-beds as "sediments which are enriched in highly fractured and abraded vertebrate bones. Very often the bone fraction is well-sorted with grain sizes of fine to coarse gravel. Bone-beds appear abruptly in sections which are otherwise poor in vertebrate remains; as a rule they have high lateral persistence (up to 50,000 km^2) and a thickness of several mm up to 20 cm; often they form series of 2 to 20 layers within one section".

None of these definitious of the term bone-bed are satisfactory as they do not define precisely what a bone-bed is, i.e. how much vertebrate material is required to call a deposit a bone-bed. The current definitions have been even further confused by the interchangeable useage of the terms bone-bed and fish-bed which are regarded as synonymous by Howell (1957, p.109).

In this study it is proposed that the term bone-bed should not be applied to zones or layers of bone-bed material but only to a single layer of vertebrate rich sediment. A group of bone-beds should be called bone-bed facies (e.g. Allen, 1974a, p.126, Facies A).

Some authors (e.g. Reif, 1976) believe that a bone-bed should be traceable over a wide area (up to 50,000 km^2). However, some named bone-beds only occur with certainty in their type sections, e.g. the Temeside Bone-Bed and the Downton Bone-Bed of the Welsh Borders (Elles & Slater, 1906). It is therefore suggested that the term 'bone-bed' be applicable to deposits found either in only one locality or proved to occur over a wide area.

The term bone-bed should have no genetic connotations since different bone-beds were formed under different conditions (see Section 6) and there is general disagreement as to how some bone-beds formed.

Recent studies of four well established bone-beds-the Ludlow Bone-Bed, the British Rhaetic (Sykes, 1977) and West German Rhaetic Bone-Beds, (Reif, 1969) and that of the West German Muschelkalk (Reif, 1969) have shown (Table 1) that all these deposits contain at least 4.7% phosphatic material. This suggests that a lower limit of 4.5% phosphatic material can be used in the redefinition of the term bone-bed.

Table 1. Quartz and phosphate compositions of Bone-Beds (values gives as weight percents).

Bone-Bed	Quartz	Phosphate	Source
Ludlow Bone-Bed	0.001 - 71	5 - 85	Antia (Unpub.)
Muschelkalk Grenzbonebed	11.5 - 69	18 - 40	Reif, 1969
British Rhaetic	13.5 - 48.7	4.74 - 33.7	Sykes, 1977
German Rhaetic	18.9 - 55	6 - 35	Reif, 1969

With this percentage of phosphate, bone-beds fall within the general definition of phosphorites containing apatite as a dominant constituent (Cressman & Swanson, 1964, p.307) i.e. $P_2O_4 = 2 - 24^{+}\%$ (Swanson, 1973, p.786). Common usage of the term phosphorite includes vertebrate rich deposits, phosphatic shell and phosphatic nodular or peletal deposits, though a survey of the literature indicates a trend to restrict phosphorite to the latter type of deposit, except for the purpose of commercial exploitation. Since all three kinds of deposits merge into each other this study will define the parameters of the phosphatic deposits outlined.

2.1 Phosphatic deposits

Definition - "A phosphatic deposit is a rock or sediment containing more than 4.5% by weight of apatite". These deposits may be broadly classified with respect to apatite abundance on a three point graph (text-fig. 1a), and further subdivided on the basis of their dominant phosphatic clast (text-fig. 1b):

1. Phosphatic concretions, nodules, pellets and coprolites - Phosphorites
2. Phosphatic invertebrate shells - Phosphatic shell beds
3. Vertebrate bones, teeth and scales - Vertebrate beds

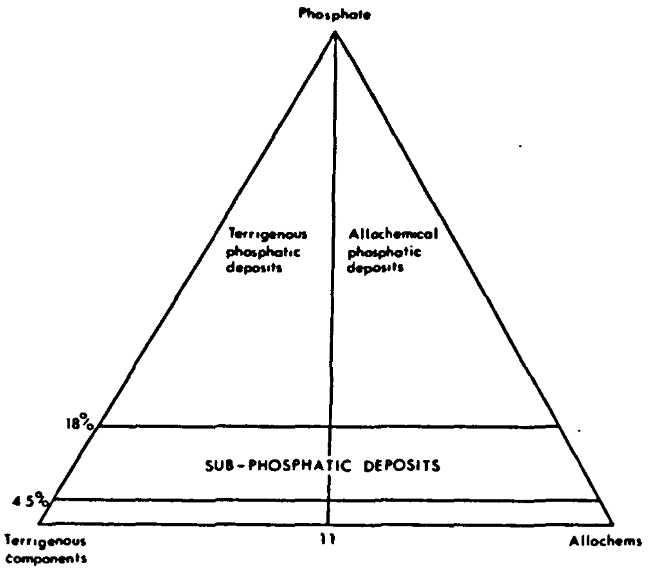
2.1.1. Phosphorites

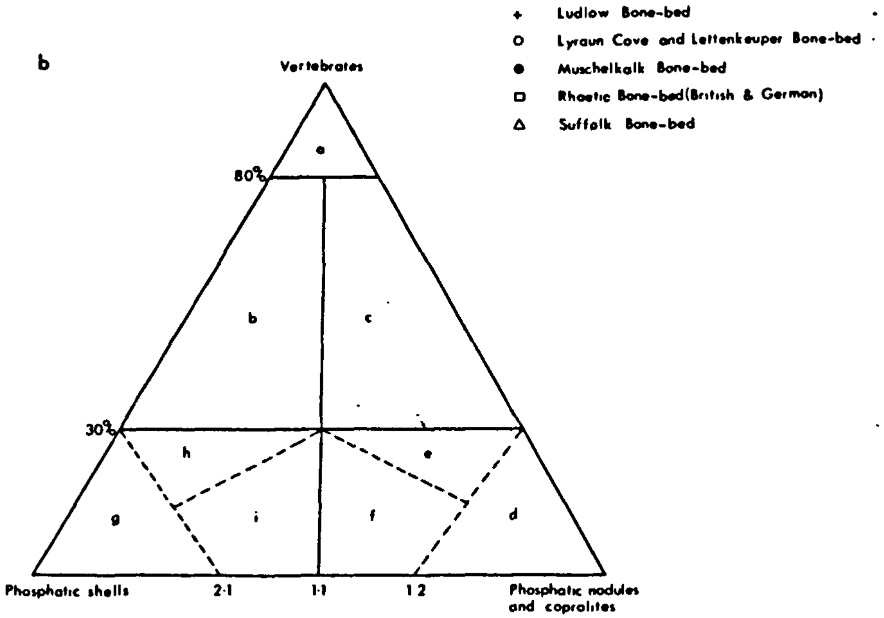
Definition - "A phosphorite is a phosphatic deposit in which the phosphatic component contains less than 30% vertebrate material; and a ratio of phosphatic pebble to phosphatic invertebrate shell, greater than 1:1 i.e. $1:1 \rightarrow \infty:1$".

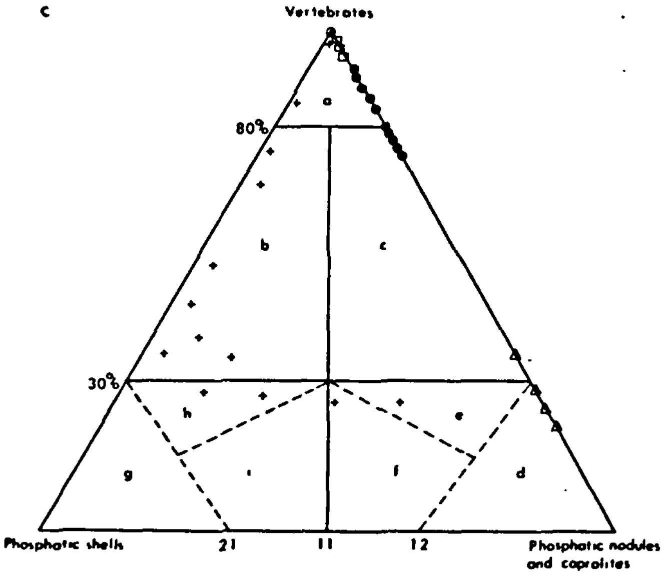
Classification - Such deposits may be subdivided on the basis of their invertebrate and vertebrate compositions (text-fig. 1b), and/or, on their pebble components. Phosphorite deposits containing less than 19.5% P_2O_5 are commonly termed sub-phosphorites (Swanson, 1970).

Example - The phosphorites of the Permian Phosphoria Formation of the central U.S.A. (Sheldon, 1963; Cressman & Swanson, 1964).

Note: These deposits include those made entirely of faecal pellets, e.g. guano.







Text-fig.1a - Component graph for the recognition of phosphatic deposits.

Text-fig.1b - Classification of phosphatic debris deposits

a = Lithobonebeds
b = Phosphatic shell bone-bed (Biobonebed)
c = Phosphatic nodule bone-bed (Pelbonebed)
d = Phosphorite
e = Vertebrate rich phosphorite
f = Phosphatic shell rich phosphorite
g = Phosphatic shell bed
h = Vertebrate rich phosphatic shell bed
i = Phosphatic nodule enriched phosphatic shell bed

Text-fig.1c - Classification of bone-beds
Key to bone-bed classifications (a - i) given in 1b.

2.1.2. Phosphatic shell beds

Definition - "A phosphatic shell bed contains less than 30% vertebrate material and a ratio of phosphatic shells to phosphatic pebbles of greater than 1:1 i.e. 1:1 → ∞:1." Such deposits can be subdivided on the basis of their phosphatic components (text-fig. 1b).

Examples - Layers F69 and F68 of the (Permian) Franson Tongue of the Park City Formation (Central, U.S.A.) and the basal *Orbiculoidea* layer of the Mede Park Member of the Phosphoria Formation (Permian - Central U.S.A.). (McKelvey *et al.*, 1959; Branson, 1916; Yochelson, 1968).

2.1.3. Vertebrate Beds

Definition - "A vertebrate bed is a phosphatic deposit in which the phosphatic component contains $\geq$ 30% vertebrate debris".

Classification - Vertebrate Beds can be divided into two types of deposits, those made of whole articulated vertebrates, and, deposits made of disarticulated vertebrate remains. It is suggested that the former deposits be named after their dominant constituent member, i.e. Fish beds refer to rocks made up of whole articulated fishes. (pl. 14, fig. a). The term bone-bed should be applied only to the latter kind of deposit, thus a bone-bed may be defined as a single layer or lens of a vertebrate rich deposit (containing $\geq$ 4.5% phosphatic material of which $\geq$ 30% is fragmented and/or disarticulated vertebrate material).

2.2. Bone-bed classification

Two attempts to classify bone-beds have been made. The first (Reif, 1969; 1971) divided Triassic bone-beds into deposits which had been diagenetically altered (prefossilised) prior to accumulation in the bone-bed and deposits in which the vertebrate fragments had not been diagenetically altered prior to accumulation and concentration in the bone-bed. These two groups were each subdivided on the basis of their matrix into calcareous, marly, sandy-clayey and sandy bone-beds.

The second attempt (Sykes 1977) to classify bone-beds, this time of Rhaetian age, discussed the possibility of dividing them into primary and secondary deposits but came to the conclusion that all bone-beds showed some secondary characteristics. The four groups of Sykes' classification are:

1. Part primary bone-beds - recognised by the random orientation of the fossils, lack of bedding, lack of abrasion of fossils.
2. Secondary bone-beds - recognised by well developed bedded layers, wear on the clasts and aligned fossils.
3. Scatter bone-beds - recognised as mudstones containing evenly distributed, disseminated vertebrate material, but variable in geographical extent.
4. Trace bone-beds - recognised as thin, often single layers, of grains and patches of vertebrate material.

Both classifications are primarily genetic with superimposed secondary sedimentological criteria. That of Reif is inadequate, mainly because it does not consider the variability or density of phosphatic debris in a bone-bed. Sykes' classification fails because in a low energy environment with minimal current activity a secondary deposit would contain those characters attributed to a primary deposit. Conversely, in a high energy environment secondary characteristics can be superimposed upon a mainly primary deposit.

In this article a classificatory scheme is outlined which acknowledges that the vertebrate component of a bone-bed is variable as are the proportions of allochems, matrix and clasts.

An initial classification (text-fig. 1b) can be based on the bone-beds phosphatic component, dividing them into three groups: (a) Lithobonebeds, (b) Biobonebeds, (c) Pelbonebeds. Those bone-beds containing between 4.5 and 18% apatite should be described as Sub-lithobonebeds, Sub-biobonebeds and Sub-pelbonebeds.

Table 2. General bone-bed terminology.

BONE - BED			
Mud supported sediment		Grain supported sediment	
Less than 10% grains	More than 10% grains		
Floatstone	Wackestone	Grainstone	Terminology
Lyraun Cove Bone-Bed	Muschelkalk Grenzbonebed	Ludlow Bone-Bed	Examples

Bone-beds can be further subdivided on the basis of matrix and clast to produce a descriptive terminology (Table 2) and may be secondarily subdivided into:

1. Carbonate bone-beds
   - (a) Micritic bone-beds are those containing a matrix which contains more than 50% lime mud.
   - (b) Sparitic bone-beds are those containing more than 50% calcite (or dolomite) spar cement in the matrix.
2. Non-Carbonate bone-beds
   - (a) Clayey bone-beds are those in which clay forms a dominant component of the matrix.
   - (b) Carbonaceous bone-beds are those in which carbon is a dominant constituent in a clay matrix i.e.>10% volatiles.
   - (c) Limonitic (or haematitic) bone-beds are those in which limonite (or haematite) is the dominant cement.

Many bone-beds contain pebbles, quartz sand, glauconite, pyrite, calcareous shells, trace fossils, sedimentary structures, heavy minerals, etc. These features should be included in an individual bone-beds description.

Examples of the different types of bone-beds are given in text-fig. 1c.

3 - Prefossilisation

Some authors (e.g. Reif, 1971; 1974; 1976; Duffin & Gazdzicki, 1977) have suggested that many bone-beds are prefossilised deposits. The concept of prefossilisation suggests that the vertebrate material under consideration has been buried after death of the animal and diagenetically altered (phosphatised) at a low Eh and normal to alkali pH's in the sediment prior to its exhumation and concentration into a bone-bed (Reif, 1971; 1976).

Reif (1969, p. 71; 1971, p.390) suggested four ways by which prefossilised vertebrate material may be recognised.

1. Fracture patterns of bone fragments
    (a) Recent bones show a predominantly fibrous breakage surfaces.
    (b) Sub-fossilised bones never have fibrous breakage surfaces and are easily worn down during sedimentation.
    (c) Fossil bones when broken have smooth breakage surfaces.

On the basis of these observations Reif (1971) suggested that the presence of smooth breakage surfaces and rounding on the bone fragments in a bone-bed indicates that they have been reworked from an earlier sediment, after they had been fossilised, before being concentrated to form a bone-bed.

2. Size distribution of quartz and vertebrate material.

Secondly, Reif (1971) suggested that while recent bone debris is less dense than quartz, fossil bone is as dense or even denser than quartz (Table 3). Therefore, if quartz and bone fragments are found together and the maximum values of their size distributions lie at the same point, then it follows that their densities must have been approximately the same during the formation of the deposit and the bone material must be prefossilised.

3. The third criterion for prefossilisation is the presence of high polish on the grains surface.

4. The phosphatisation of bone reduces its inherent elasticity and suggested that fossil bones are less likely to be well rounded.

Table 3. Quartz, Apatite, Bone, Fossil Bone and Collophane densities. (After Dana, 1858: Rogers, 1922; 1924; Deer *et al.*, 1962)

Quartz	Recent Bone	Fossil Bone	Collophane	Apatite
2.5 - 2.8	1.9 - 2.0	2.6 - 2.94	2.6 - 2.92	3.1 - 3.35

These criteria are all very subjective and provide no real test of whether or not a fossil vertebrate fragment has been prefossilised or not, because:

1. Observed smooth fracture patterns may be a result of processing fossilised material, and since studies on fracture patterns have not been done on scales or teeth (the dominant components of many bone-beds) the value of fracture pattern studies must still be in doubt. Similarly, Schafer (1972) has noted that unaltered fish scales in recent sediments are often worn or rounded.

2. Application of the equivalence principal suggests that clasts of similar densities will have similar size distributions. However, Reif's application of the theory forgets (a) that many bone-bed sediments contain no quartz grains (even locally in the Muschelkalk Grenzbonebed, his type example of a prefossilised bone-bed), (b) vertebrate material (unaltered) present in many modern sediments possess the same size modal peaks as quartz grains in the same sediment (Schafer, 1972). This observation may result because clay infilling pores in the vertebrate material may help to increase its density, or because of the differing aerodynamic properties of rounded quartz grains and vertebrate fragments, or because of diagensis (see Section 8).

3. Grain polish is by itself a dubious criterion, since many marine carbonate grains show a high polish, due to either abrasive high energy current activity or to diagenetic mineral coatings on the exterior of the grain (Farrow, pers. com. 1978). Broken surfaces of polished *Acrodus lateralis*, a shark's tooth from the Muschelkalk Grenzbonebed, *Thelodus parvidens*, a fish scale from the Ludlow Bone-Bed, and whale bones from the Suffolk Bone-Bed, are characteristically dull; thus suggesting that the polish is an exterior property of the vertebrate material and may result from abrasive or diagenetic processes.

4. The elasticity of vertebrate material is thought to decrease with increasing prefossilisation. Yet supposedly prefossilised (Reif, 1969; 1971; 1974; 1976; pers. com. 1976; 1977) specimens of *Acrodus lateralis* from the Muschelkalk Grenzbonebed occur in a variety of abrasive states ranging from well rounded worn spheres to angular broken fragments to whole teeth. This surely suggests that the inherent elasticity (i.e. ability to round with wear) of the grains has not been markedly affected by prefossilisation.

Reif (1971) regards the vertebrate material from both the Muschelkalk Grenzbonebed and the Rhaetic Bone-Bed to be made of francolite (a fluoro-carbonate-apatite). Modern bones and teeth are made of a microcrystalline arrangement of hydroxy-apatite in collagen (Glimcher and Krane, 1968). Thus alteration of the bones and teeth has presumably occurred such that:

$$\underset{\text{hydroxy-apatite}}{Ca_5(PO_4)_3OH} + \text{collagen} \rightarrow \underset{\text{francolite}}{(Ca_3F)_2(P,C)_6(O,OH\ F)_{24}(Ca,C)_4}.$$

This reaction doubtless reflects the combined effects of initial and subsequent diagenesis on the vertebrate remains, if they have been prefossilised.

Reif (1976; pers. com. 1976; 1977) also regards the Upper Silurian Ludlow Bone-Bed as a prefossilised deposit. If this is so, then a geochemical proof may be forthcoming. The thelodont fish species (*Thelodus parvidens*), which dominates the vertebrate faunas of the Ludlow Bone-Bed and the sediments immediately above and below the bone-bed, occurs in two geochemical states.

1. In the bone-bed the thelodonts tend to be made of a fluorapatite and have a polished orange-yellowy appearance (Table 4, col.6).
2. In the sediments below the bone-bed the thelodonts tend to be made of a carbonate apatite and have a white chalky appearance (Table 4, col.4).

Though both geochemical thelodont forms occur in sediments representing aerobic conditions, Burnett (1977) has shown that aerobic sediment surfaces are found above anoxic microenvironments a few centimeters below the sediment/water interface. The thelodont scales present in low densities in the sediments below the bone-bed were possibly excavated by currents after they had been altered to a carbonate apatite in a subsurface anoxic environment prior to concentration in a bone-bed (cf. Antia & Whitaker, 1978). The alteration to fluorapatite would therefore be a result of diagenesis after bone-bed deposition.

If this prefossilisation model is correct then there could be a difference in the abrasive appearance of the scales occurring in the two sediment types, and the geochemical composition of the phosphatic clasts in the bone-bed ought not to be related to the matrix of the bone-beds.

1. Abrasive features

The thelodont scales from the two sediment types though differing in chemical composition show no difference in abrasive features. In both instances the scales vary from unworn forms to partly worn forms to very well worn and rounded forms. Many of the more rounded scales are bored. These observations suggest that scales deposited in both environments were abraded on the sediment surface.

Table 4. Dry X-ray powder diffraction (X.R.D.) analysis results for
(1) Carbonate apatite (after Smith *et al.*, 1974)
(2) A phosphatic pebble from the Ludlow Bone-Bed
(3) *'Serpulites' longissimus*, *Orbiculoidea rugata*, *Lingula* sp.
(4) Thelodont fish (*Thelodus parvidens*).
Both (3) and (4) represent samples collected from the Upper Whitcliffe sediments of Aston Munslow (Salop).
(5) Fluorapatite (after Smith *et al.*, 1974)
(6) *Thelodus parvidens*
(7) *'Serpulites' longissimus*, *Orbiculoidea rugata* and *Lingula* sp.
Both (6) and (7) were obtained from the Ludlow Bone-Bed at Aston Munslow.

1	2	3	4	5	6	7
2.78	2.78	2.79	2.79	2.80	2.79	2.80
2.68	2.68	2.69	2.69	2.70	2.70	2.70
3.46	-	3.43	3.46	2.77	2.78	2.76
2.23	2.23	2.24	2.25	3.44	3.44	3.43
1.93	1.92	1.93	1.93	2.62	2.62	2.61
1.84	1.83	1.83	1.83	1.84	1.83	1.85
3.04	3.03	3.05	3.04	1.94	1.92	1.93
2.62	2.61	2.62	2.62	-	-	-

Table 5. The chemical composition of the clasts of the phosphatic components in the Ludlow Bone-Bed (Upper Silurian).
F = fluorapatite; C = carbonate apatite;
(F) = some fluorapatite present.
Localities are located on text-fig.4, p.114.

Locality	Phosphatic component Thelodont	Invertebrate	Sediment Lime-stone	Mud-silt	Sand
Usk	C	C	-	-	+
Longhope	F	C	-	+	-
Priors Frome	F	C	-	+	-
Rushall	C	C	-	-	+
Kington	F	F	+	-	-
Downton	F	F	+	-	-
Deepwood	F	C	-	+	-
Ashely Moor	F	F	+	-	-
Ludford	F	F	+	-	-
Siefton	F	-	-	+	-
Corfton	F	F	+	-	-
Aston Munslow	F	F	+	-	-
Shipton	F	C(F)	-	+	-
Brockton	F	C	-	+	-
Netherton	F	C	-	+	-
Lye	C	C	-	-	+

2. Relationship of phosphatic clast to matrix.

In the bone-bed three types of phosphatic clasts occur, carbonate apatite pebbles (Table 4, col. 2), thelodonts and other fish remains, and phosphatic invertebrate remains (pl. 14, figs. b,c) of *'Serpulites' longissimus*, *Orbiculoidea rugata*, and *Lingula* sp. Below the bone-bed the latter two remains tend to be made of a carbonate apatite (Table 4, col. 3 and 4) while in the bone-bed they occur in both a carbonate apatite (Table 5) and a fluorapatite state (Table 4, col. 6 and 7; Table 5).

Examination of the chemical composition of the two main clast types (Table 5) suggest that the clast composition is related to the nature of the matrix of the bone-bed such that:

(a) Calcareous bone-beds only have fluorapatite (phosphatic) biological clasts.

(b) Muddy and silty bone-beds have fluorapatite fish remains and carbonate apatite phosphatic shell debris.

(c) Porous poorly cemented quartz sand bone-beds contain only carbonate apatite phosphatic clasts.

This apparent relationship between chemical composition and matrix type suggests that the chemical composition of the vertebrate and invertebrate remains may be a result of post depositional diagensis, and could indicate that the scales were not prefossilised prior to inclusion in the bone-bed.

This conclusion is borne out by the presence of borings on the fish scales and not on the invertebrate fragments in the bone-beds, where both have the same chemical composition. Since the borings are specific to the thelodonts, it must be assumed there were nutritional or chemical differences between the two clast types. If this assumption is correct then it is likely that the scales were unaltered when bored, i.e. were composed of a hydroxy apatite + collagen with an enamel-like coating on their crown (Beevers & McIntyre, 1946) or carbonate apatite + collagen (Osmond & Swain, 1959). Study of boring density and distribution on the scales suggests that the crown has fewer borings than the cusp of the thelodont denticles, thus adding support to this hypothesis. The vertebrate clasts in other bone-beds show no such relationship between clast composition and sediment (Table 6).

Table 6. Geochemical composition of bone-beds

Bone-Bed	Chemistry		Sediment		
	fluorapatite	francolite	black clay	carbonate	sand
Lyraun Cove	+	-	+	-	-
Rhaetic (British)	-	+	+	-	-
Rhaetic (German)	-	+	-	-	+
Muschelkalk	-	+	+	+	+
Lettenkeuper	-	+	+	-	-
Suffolk	+	+	-	-	+

These observations suggest that the chemical composition of the phosphatic clasts in prefossilised bone-beds are not markedly affected by diagenesis in the sediment of the bone-beds, while in primary bone-beds (i.e. bone-beds which are not produced by the reworking of older sediment) there may be a marked relationship between clast composition and sediment type.

Since marine prefossilised bone-beds exist and are actively being formed, (i.e. bone-beds containing diagenetically altered vertebrate material) see Reid (1890), Baturin (1970) Frey *et al.* (1975), the chemical processes which could lead to the prefossilisation of vertebrate material will be considered here.

1. The environments of prefossilisation, - 3.1
2. Conditions favourable to prefossilisation, - 3.2
3. A geochemical model for prefossilisation, - 3.3

Reif (1976) and Baturin (1970) have noted that prefossilisation involves the phosphatisation of bones (considered to be made of a hydroxy apatite (Glimcher & Krane, 1968) and teeth (considered to be made of either a carbonate apatite (Osmond & Swain, 1959) or a hydroxy apatite (Beevers & McIntyre, 1946)). This phosphatisation involves the replacement of collagen and existing apatites with fluorapatites thus increasing their densities without altering their internal structures (Paine 1937). Since they are replacing an amorphous structure, their densities will remain the same as that for collophane (Rogers, 1917; 1922; 1924) - see Table, 3, p.99. Collophane is a term applied to any amorphous apatite (Deer *et al.*, 1962).

3.1 The environments of prefossilisation

Vertebrate remains are unlikely to be phosphatised by direct, ocean water - vertebrate reactions (Burnett, 1974), but could be altered by pore waters in a sediment. To date, only two regions of active phosphatisation are known, the Peru-Chilean shelf and the South West African Shelf seas. In both regions phosphatisation occurs within anoxic alkali sediment pore waters (Baturin, 1970; 1971; Burnett, 1977).

Actively forming phosphatised vertebrate concentrations may result from the erosion by marine and estuarine currents of older sediments (Miocene - Pleistocene) (e.g. the vertebrate concentrates of Georgia (U.S.A.) estuaries (Frey *et al.* 1975) and the Florida shelf (Burnett & Gomberg, 1977)), or recent ($\geq$ 30,000 years) phosphatic shelf sediments (Baturin, 1969; 1970).

These limited studies have suggested that vertebrate phosphatisation may occur in the anoxic alkali pore waters of some sediments.

3.2 Conditions favourable to prefossilisation

There are four major characteristics of natural aqueous solutions which favour the prefossilisation of vertebrate remains in the pore waters of sediments.

1. High dissolved inorganic phosphate content.
2. High Ca/Mg ratio.
3. High pH.
4. Suitable nucleation sites.

Phosphates may be supplied to anoxic pore waters in sediments from the reduction of hydrous ferric oxides which bind phosphate to their surfaces under oxidising conditions (Stumm & Leckie, 1970) and the decomposition of phosphorous containing organic matter. The contribution from the decaying organic matter is the more significant (Burnett, 1974). If large quantities of vertebrate material are to be prefossilised by the pore waters of organic rich sediments, then the PO_4^{3-} content of the interstitial fluids must be continually replenished, while the material is being prefossilised.

The precipitation of apatite is inhibited by Mg^{2+} ions (Bachra *et al.*, 1965; Martens & Harriss, 1970). However, diagenetic reactions in anoxic pore waters can raise the Ca/Mg ratio to beyond that of the Ca/Mg threshold value (Broecker, 1974; Burnett, 1974) to allow apatite to precipitate. Many reactions in anoxic pore waters would have this effect, for example the replacement of Fe^{3+} by Mg^{2+} in clays (Drever, 1971).

For prefossilisation to occur a high pH is required (Krumbein & Garrels, 1952; Goldberg & Parker, 1960; Robertson, 1966; Pytkowicz & Kester, 1967), because at low pH's apatite is 'soluble'. Experiments have shown (Berner, 1969) that the decomposition of fish and molluscan organic matter is accompanied by a rise in pH, which results from the formation of NH_4^+ and other nitrogenous bases, and from the breakdown of proteins and other biochemical compounds, pH is also affected by other variables such as the release of CO_2 into the pore waters during the oxidation of organic materials.

However, an increase in pH favours $CaCO_3$ precipitation (Gulbrandsen, 1969) and as dissolved carbonate species in sea water are several orders of magnitude higher than the phosphate species, a coprecipitation of apatite and calcite would result in the apatite being completely overwhelmed by calcium carbonate. Therefore if apatite is to be precipitated with minimal calcite, the dissolved PO_4^{3-} content of the pore waters would have to be raised to the point where Ca^{2+} concentrations in the pore waters are controlled by apatite rather than carbonate equilibria.

Discussions on the availability of suitable sites for apatite growth suggest that calcite forms the best surface for apatite nucleation (Stumm & Morgan, 1970) as epitaxial overgrowths and catalyses the precipitation of apatite around specific nuclei (Stumm & Leckie, 1970). When calcite is absent from the sediment, siliceous skeletal debris, brachiopod shells, fish bones and scales, apatite and feldspar crystals appear to be favoured sites for authogenic apatite growth (Deer *et al.*, 1962; Stumm & Leckie, 1970; Burnett, 1977). Clasts already enriched in apatite are preferentially chosen for authogenic apatite growth and replacement (i.e. prefossilisation). (Konta, 1959).

See Appendix - 2, p.168, for additional note.

3.3. A geochemical model for bone-bed prefossilisation

The following is a general geochemical model which may represent the most likely combination of events which could result in the phosphatisation of vertebrate (and invertebrate) material by pore water solutions in sediment, prior to the newly phosphatised materials reworking and inclusion into a 'prefossilised' bone-bed deposit. Since both vertebrate, invertebrate and coprolitic material can be prefossilised (Reif, 1969; 1971· 1976; Duffin & Gazdzicki, 1977), the model will consider apatite precipitation.

During periods of increased sea water temperature inorganic apatite precipitation may take place within the anoxic pore waters of sediment (Burnett, 1974; 1977). Within about 15 cm of the sediment/water interface, the PO_4^{3-} ion concentrations present in these anoxic pore waters can increase to about 1000 x those of the surrounding aerobic surface waters before precipitating around a suitable nucleation site. (Brooks *et al.*, 1968; D'Anglejan, 1968; Bray *et al.*, 1975; Sholkovitz, 1973.) Phosphatisation replaces the original nucleation site preserving its internal structure and including fluorine within its crystal lattices. (Paine, 1937; Kortnig, 1968; Reif, 1969; Antia & Whitaker, 1978.)

Apatite precipitation is initiated when the pore waters are supersaturated with respect to PO_4^{3-} and undersaturated with respect to oxygen. Sustained periods of apatite precipitation require a constant supply of organic phosphorous to the pore waters, so consequently such a region must have a high biological productivity to provide a large input of organic phosphorous into the sediment. Inhibitory Mg^{2+} ions would be removed by diagenetic reactions (Bachra *et al.*, 1965; Martens & Harriss, 1970) involving both the solid and fluid phases of the sediment.

General types of reactions likely to occur in the pore waters within the sediment during early diagenesis are summarised below:

1. SO_4^{2-} + 'organic matter' $\rightarrow H_2S + HCO_3^- + HOP_4^{2-} + NH_4^+ + CH_4$
   The probable C:N:P: ratio based on that for modern plankton (Richards, 1965) is 106:16:1, and
2. $2Fe^{3+}\text{clay} + 3Mg^{2+} + 4S \rightleftharpoons 3Mg^{2+}\text{clay} + 2FeS_2$ (pyrite), and/or
3. $2CaCO_3\ M + Mg^{2+} \rightleftharpoons CaMg(CO_3)_2 + Ca^{2+}$, and/or
4. $Al_2Si_2O_5(OH)_4 + 5Mg^{2+} + 10HCO_3 + H_4SiO_4 \rightleftharpoons Mg_5Al_2Si_3O_{10}(OH)_8 + 10CO_2 + 3H_2O$, and
5. $5Ca^{2+} + 3HPO_4^{2-} + F^- \rightleftharpoons Ca_5(PO_4)_3F + 3H^+$.

The resultant authogenic prefossilised particles may be concentrated into vertebrate rich deposits by changes in sea level dynamics (Baturin, 1971). Since during periods of regression the fine grained fraction of the sediment will be eroded away to concentrate the prefossilised material, initially into a coarse grained sediment and ultimately into a bone-bed. In this sort of situation electrical neutrality in the pore waters is probably maintained by counterbalancing the changes in Ca^{2+} and Mg^{2+} concentration, NH_4^+ production, and the change in SO_4^{2-} content with a coincident rise in HCO_3^- (Sayles, *et al.*,1974). i.e.

$$\Delta\, Ca^{2+} + \Delta\, Mg^{2+} + NH_4^+ - \Delta\, SO_4^{2-} = \Delta\, HCO_3^-$$

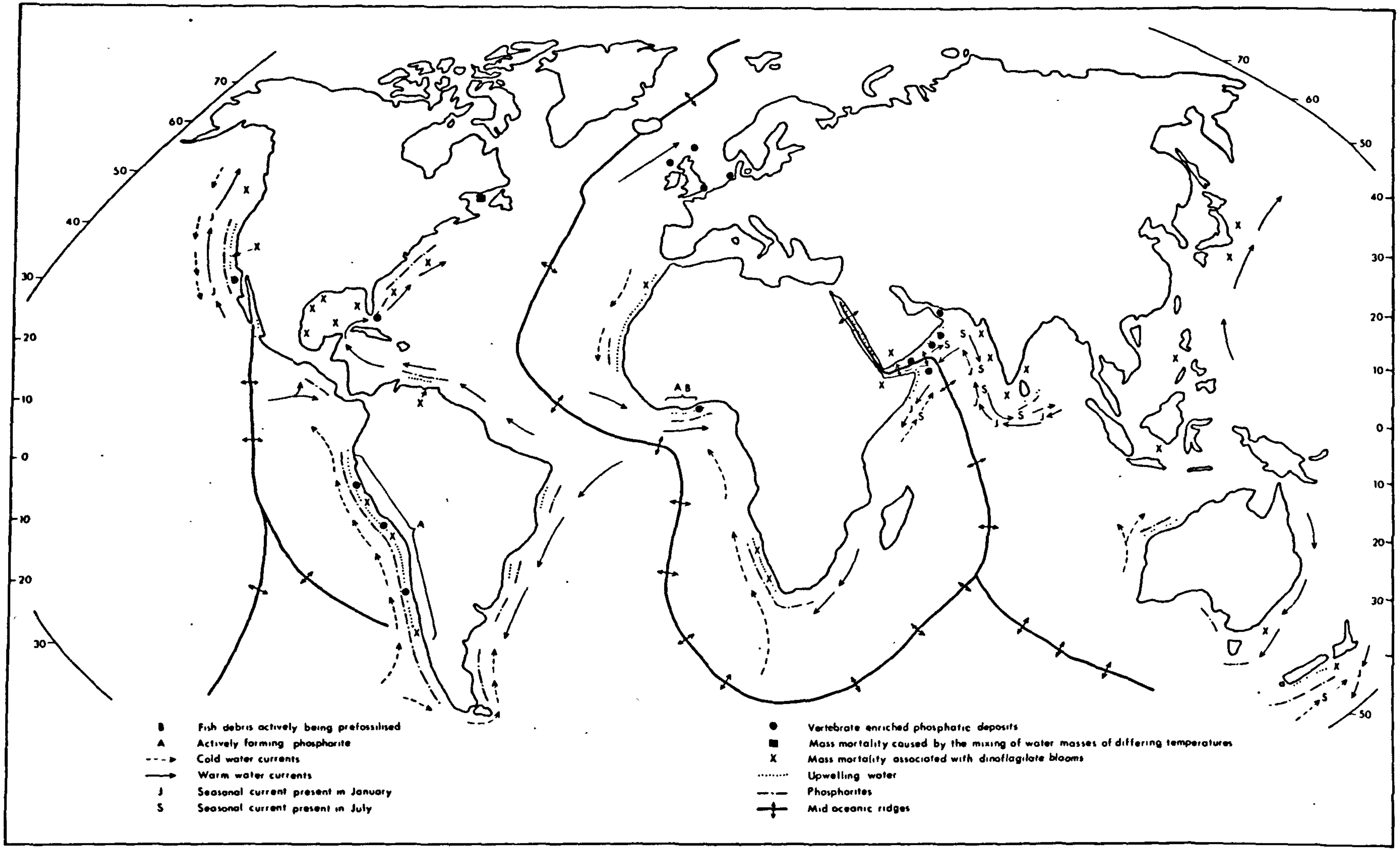
4 - On the occurrence and genesis of vertebrate rich deposits

Studied deposits rich in disarticulated vertebrate remains on the modern sea shelf commonly occur in association with coprolites, phosphatic nodules and phosphatic brachiopod shells. They almost all occur in areas of increased nutrient content of the water, and are commonly associated with regions of upwelling waters (McKelvey, 1967; also text-fig. 2). However, only two regions of vertebrate accumulation are regions of active sea bed phosphatisation today. These are off the Peru-Chile coast (Veeh *et al.*, 1973; Burnett, *et al.*, 1973; Burnett 1974: 1977; Manheim *et al.*, 1975; Burnett & Veeh, 1977) and the South West African coast (Baturin, 1969; Baturin *et al.*, 1972; Veeh *et al.*, 1974). Other phosphatic deposits found on the surface of the sea-floor (e.g. California coast, Florida coast, New Zealand Coast, South African coast, and Tasmanian coast) have been shown (Kolodny & Kaplan, 1970; Burnett & Gomberg, 1977 to be of Upper Pleistocene age.

In addition to the above phosphatic deposits unconfirmed reports exist of vertebrate sands off the U.K. notably near Rockall and Shetland. These deposits were noted by Lyell (1868: p.576, vol. 2; 3rd ed. 1834, vol. 3) as "A bed of fish bones (off Rockall).... extending for 2 miles along the bottom of the sea in 10 - 90 fathoms of water, at the eastern extremity .... of Rockall bank fish bones were met with .... Analogous formations are in progress in the submarine tracts extending from the Shetland Isles to the North of Ireland". At "(Lat.61° 51' Long. 6°30') Fish bones occur in extraordinary profusion .... this 'bone bed' .... is 3½ miles in length and 45 fathoms under water". More recent work by Dr. J.B. Wilson (pers. comm. 1977) has revealed very high concentrations of fish otoliths in the Rockall region.

4.1 Recent examples

Sediments on the S.W. African shelf and Peru - Chile shelves (text-fig. 2) consist of black muds formed at depths between 150 and 50 m. The surface waters of these regions are very rich in diatom phytoplankton, and are biologically very productive, because upwelling coastal waters bring up nutrient salts (Bakun 1978; Savidge & Foster 1978). The upwelling waters result in a massive phytoplankton production on the shelf, and consequently a large biogenic input into the underlying sediment (50 - 150 m depth). The low O_2 content of these waters allows much of the biogenic material to be input into the sediment (Baturin, 1971). This sediment becomes enriched (Baturin, 1969; 1971) in organic carbon (5-20%) and phosphorous (0.1 - 1%). In the sediments the P:C ratio varies from 1:25 to 1:60, whereas living diatoms have a ratio of 1:25 (Lisitsyn, 1969).



Text-fig.2. Map showing the distribution of oceanic currents, areas of mass mortality, regions of upwelling and vertebrate accumulation at the present time. Compiled after David (1944; 1947); Brongersama-Sanders (1956); McKelvey (1967) and the Times Atlas of the World (1974).

Both areas have alkaline reducing pore waters (Table 7) enriched in phosphorous, in which the phosphorous content of the pore waters increases with depth below the sediment/water interface (Burnett, 1977).

Table 7. Composition of pore waters in regions of phosphatisation on shelf seas

Locality	Eh	pH	Source
California	-200mv	7.2 - 7.8	D'Anglejan, 1967
West Africa	-300mv	7.2 - 8.0	Baturin, 1969; 1971
Peru/Chile	-	6 - 7	Burnett, 1974; 1971

On both the Chilean and African shelves phosphorous oversaturation of the interstitial waters leads to its precipitation in separate microzones within the sediment (i.e., where the microenvironment is most alkaline) (Baturin, 1969; 1971; Burnett, 1974; 1977). In the Peruvian shelf this microzone is situated at 15 cm below the sediment/water interface (Burnett, 1977). This precipitation induces a decrease of phosphorous concentration in the pore waters of far below 0.1 $mg.l^{-1}$ and its redistribution in the sediments results in either the formation (Baturin, 1969; 1970; 1971) of scattered soft nodules consisting of an impure gel-like calcium phosphate (5 - 10 P_2O_5) or nucleation around and/or replacement of biogenic tissue, e.g. bones, scales, teeth, shells, etc. (Konta, 1956; D'Anglejan, 1967; Baturin, 1970; 1971; Burnett, 1977).

The process surrounding the phosphatic replacement of biogenic material is poorly understood, but may relate to the much better known sequences of phosphatisation of the gel-like phosphatic nodules in the sediment, many of which contain 'densely packed' fish debris (Baturin, 1971).

Further diagenetic processes result in the lithification of the nodules, depletion in SiO_2, Al_2O_3, Fe, H_2O and C as shown in Table 8 and enrichment in P_2O_5, CaO, CO_2 and F; there is also an increase in trace elements such as uranium, gold, and vanadium (Yasgrev, 1971; Burnett, 1974). The end product of these changes is very similar to those resulting in the formation of the phosphatic nodules in the Muschelkalk Grenzbonebed (Table 8).

Table 8. The composition of stages in the phosphatisation of mud to produce a phosphatic nodule (after Baturin, 1969; 1971). Note the similarity of the composition of the hard nodule to that of a phosphatic nodule (?coprolite) from the Muschelkalk Grenzbonebed (Reif 1971).

Stage	P_2O_5	CaO	CO_2	F	SiO_2	Al_2O_3	Fe_2O_3	MgO	Organic C
1. Diatomaceous mud	0.62	3.0	2.43	Tr.	50	-	1.0	-	5.35
2. Phosphatised D. mud	5.10	6.9	1.17	0.3	49.18	2.0	1.24	2.5	3.4
3. Soft nodules	23.85	35.9	5.30	2.45	14.80	0.45	0.80	1.7	1.8
4. Friable nodules	27.70	42.27	5.34	2.70	4.87	0.38	1.00	1.3	1.0
5. Hard nodules	32.74	46.42	6.33	3.02	0.15	0.04	0.20	1.7	0.9
6. Nodule Muschelkalk Grenzbonebed	31.50	50.1	4.81	-	0.42	-	1.44	0.5	-

Chemical analyses of bone and fossil bone show that during diagensis vertebrate fragments become enriched in P_2O_5, CaO, CO_2 and F (Rogers, 1924; Baturin, 1970; Reif, 1971) and the trace elements gold, titanium, vanadium and uranium (Yasgrev & Nikitin, 1970; Yasgrev, 1971). The net similarity in the enrichment of phosphatic nodules and bone noted here suggests that similar chemical reactions take place concurrently during diagensis in the two types of material (Baturin, 1970).

These recent deposits contain about 7% phosphate material (Baturin, 1971), reworking of these deposits caused by changes in sea level dynamics could produce remanee ('prefossilised') deposits containing more than 20% phosphatic material, such as those on the Peru - Chile shelves (Burnett, 1974).

Many actively forming vertebrate and phosphate rich deposits are formed by the reworking of older sediments. Such deposits can be concentrated on either an aerobic (Burnett Gomberg, 1977) or anaerobic benthos (Frey *et al.*, 1975). Examples of the former include the Florida phosphorites, produced by the active erosion of Pliocene limestones, and those of California which may still be actively forming, but are most likely derived from slightly earlier sediments. On the Trinidad shelf these deposits are found strewn over the surface of a hard ground (Kolewijn, 1958). Another example of the latter kind of deposit are the vertebrate assemblages of the Georgia Estuaries (Western U.S.A.) produced by the active erosion of vertebrate rich Miocene and Pleistocene beds.

Vertebrate accumulations of diagenetically unaltered fish material have been recorded in the Arabian Sea, Red Sea and Persian Gulf (Stubbings, 1939), (text-fig. 2), and off the Californian coast (David, 1944; 1947). Fish bones have been recorded from the Black Sea (Andrussow, 1893; Murray, 1900; Archangnelski, 1927), and in association with coprolites near the mouth of the River Congo. High densities of the boney plates of teliost fish have been recorded (Schafer, 1966; 1972) on the swash marks on the intertidal mudflats of the Island of Mellum (West Germany). Here the fish debris has the same modal size distributions as the associated shell debris. These sediments contain up to 250 vertebra to a m^2 area of sediment. On the West German East Frisian Islands and the Island of Sylt (text-fig. 2) large fish fragments are found (Schafer, 1972) associated with coarse shell debris. On the mudflats, beaches which are exposed to a powerful swash contain vertebrate fragments which are markedly size sorted (Schafer, 1972). Similarly intertidal mudflat deposits situated on the Elbe & Wesser River mouths are enriched in worn and polished boney sturgeon plates. An extensive review of the occurrence of articulated fish on the benthos is given by Brongersama-Sanders (1949; 1957).

4.2. Models for the formation of marine bone-beds

Over the years a number of ideas relating to the formation of deposits of vertebrate remains have been found. These theories can be divided into two major groups.

1. Primary deposits - produced by the primary concentration of disarticulated vertebrate material.
2. Secondary deposits - produced by reworking and concentration from older sediments.

4.2.1. Primary deposits

Two major groups of theories regarding the genesis of primary deposits exist. The first considers the deposit to have formed over a long period of time as a condensation deposit. The second considers the vertebrate material to have been deposited, disarticulated and concentrated shortly after a catastrophe to produce a bone-bed resulting from an initial mass mortality deposit.

4.2.1.1 Condensation deposits

These are deposits formed over a long period of time by the withholding of sediment from an area, or when fish were the dominant faunas of the seas (Orton, 1878; p.628). The concentration of the deposits could also be the result of the reworking of excrementations matter representing the hard indigestable parts of fishes, which have served as food for larger kinds. Thus the fragmentary and worn appearance of the vertebrate debris could be attributable to the crushing maceration and partial digestion which they have suffered. Such deposits may form in a nook or bay where large and small fish congregate (Newbery, 1889; p.30). Fourthly, acidic anoxic bottom conditions could dissolve calcareous invertebrate material, leaving a deposit rich in phosphatic animal tissue.

4.2.1.2 Mass mortality deposits

These deposits are formed over short periods of time by the mass mortality of vertebrate organisms and may result from:

1. An Act of God

   The best documented example of this kind of mass mortality is given in the Old Testament of the Bible (Exodus, ch. 6: v. 17-21). "... I am the Lord: behold ... the water that is in the Nile ... shall be turned to blood and the fish in the Nile shall die ... All the water that was in the Nile turned to blood and the fish in the Nile died".. (R.S.V. Trans. 1973).

2. Cold waves

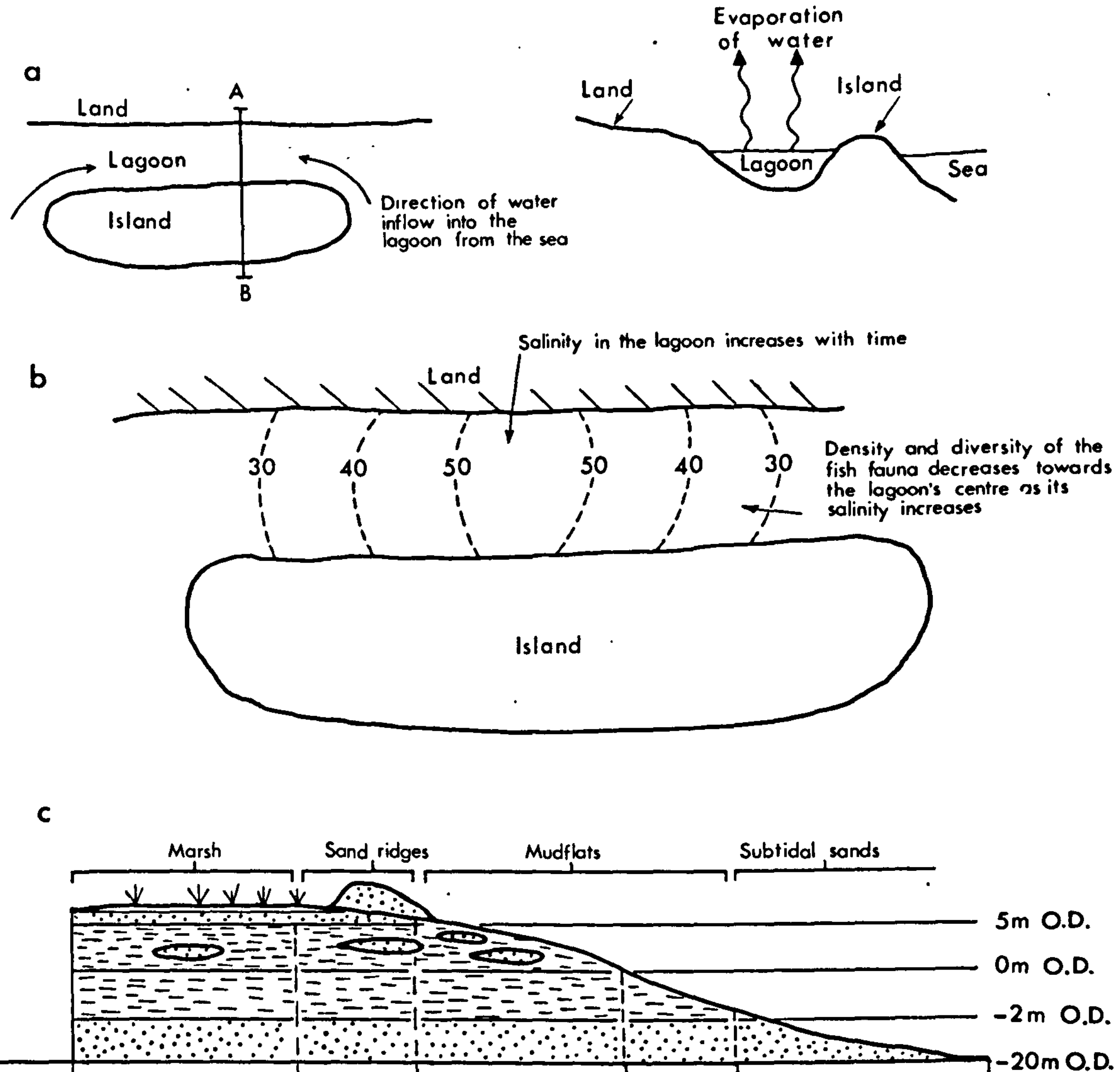
   In shallow waters, hard cold, sudden temperature drops can cause mass mortalities among fishes (Storey & Gudger, 1936; Gunter 1945, 1947). Such mass mortalities have been documented along the U.S. Gulf coast. Here a cold spell kills fishes every few years. Similar effects have been recorded (Storey, 1937; Gunter, 1947) along the west Florida coast and the Texas coast. These cold waves are less severe on the invertebrates, though they too are killed in the colder water (Gunter, 1941; Davis, 1963). The fish killed either sink to the bottom or are swept ashore (Gunter, 1947). In the Gulf Coast these deposits tend to be cyclic occurring every 6 - 14 years. The vertebrate fauna takes some three years to recover from one of these freezes (Gunter, 1945).

3. Oversalinity

   The salinities of restricted bays and coastal lagoons along the Texas coast increases drastically during dry years causing mass mortalities among fish (Gunter, 1947). These lagoons may cover some 1,400 km^2 and are separated from the sea by an island (text-fig. 3). In normal years the salinity of the lagoons gradually increases till the lagoon is barren of fish. Periodic hurricanes bring in a new influx of lower salinity salt water (normal marine) and allow the barren lagoon to be colonised by a new abundant fish fauna (Hildebrand, 1969).

4. Warm waves

   Some regions contain an abundant fish fauna living in a nutrient rich cold current of water near the cold currents junction with a warm current. Changes in the relative position of this junction can cause mass mortalities within the fish fauna. Examples of this kind of mass mortality have been recorded (Murphy, 1926; Mears, 1943) along the Peruvian coast, at the junction of the southward warm equatorial current and the cold northward coastal current (text-fig.2).



Sediment	Mudstone	Silts and sandstone	Interbedded silts muds and sands	Fissile shales	Sandstone with phosphatic nodules
Structure	Dessication structures and calcareous nodules		Symmetric ripples = 10 - 15 cm		
Biogenic Structures	Rootlets				Bioturbation
Fossils	Plants		Rare brachiopods	Brachiopods and crinoids	Brachiopods, fish plates, crinoids, bone fragments

Text-fig. 3. A Gulf Coast lagoon (a) showing water flow direction;
(b) the resulting salinity concentration contours; note that salinity increases as a result of an osmotic process;
(c) distribution of environments through the Catsgill cylothem.

5. Plankton blooms

Plankton blooms of dinoflagelates which produce toxic wastes may result in mass mortalities of fish, sometimes killing in excess of a milliard fish. These planktons often colour the sea water to give the so called red water effect. (Brongersama - Sanders, 1949; 1956).

6. Storms - water mass effect

Mortality may be caused by the mixing of adjacent 'hot' and 'cold' water masses during storms to produce layers of fish many decimetres thick on the substrate over a wide area (Verril, 1882; Huntsman, 1917; Neville, 1967).

7. Storms - stranding effect

During storms the vast shoals of fish which congregate in coastal tidal waters near the Elbe and Weser Estuaries are often injured by being thrown on to stones and sandbars or are stranded, others are cut off in narrow creeks and thrown on to the tidal flats. (Mohr, 1952)

8. Breakdown of the food chain

Mass mortalities may result from a breakdown in the food chain due to nutrient shortages, etc. (Heldt *et. al.*,1947).

9. Earthquakes

Earthquakes may severely disorientate life in coastal waters causing some species to commit mass suicide (Forbes, 1858) or die (Brongersama - Sanders, 1956).

10. Vulcanicity

Volcanic eruptions can cause mass mortalities in the sea, either by killing off the plankton (Jenkins, 1970) or by killing the fish (Brongersama - Sanders, 1956).

11. Geochemical changes in environment

Changes in the geochemical nature of the environment are known to produce mass mortalities of fish (Brongersama - Sanders, 1956) e.g. decrease in the oxygen content of the water; increase in the amount of cyanide in the water, etc.

4.2.2. Secondary deposits

Before a vertebrate deposit can be termed a bone-bed its constituent vertebrates have to be disarticulated and swept around by currents, etc. The term 'Secondary Deposit' is used here to refer to a primary vertebrate deposit which has been buried, diagenetically altered, excavated, fragmented and then further concentrated to form a bone-bed.

Since secondary bone-beds are formed by the reworking of older vertebrate deposits, by tidal, oceanic or fluvial currents, little ecological information can be derived from these deposits in intertidal, fluvial or marine environments.

5 - The decomposition of marine vertebrates

(after Schafer, 1972)

Three major groups of vertebrates are represented in bone-beds throughout time; they are fish (Ordovician - Recent), reptiles (Triassic - Cretaceous) and mammals (Jurassic - Recent). The dominant components are fish with lesser proportions of reptiles and/or mammals (mainly mantae and ceteans). In order to more fully comprehend the formation of a primary bone-bed deposit it is necessary to have some understanding of the history of the vertebrates in the interval between their death and accumulation in a vertebrate sand or bone-bed, i.e. their decomposition.

Unfortunately little is known about the geological aspects of vertebrate decomposition. Virtually nothing is known about the decomposition of marine reptiles or mammals though their processes of decomposition may be similar.

1. Decomposition of whales - physical and mechanical effects:
   - (a) Death of the whale
   - (b) Animal sinks to sea-floor
   - (c) Floated off the sea-floor (not necessarily to the surface) by decomposition gases
   - (d) Carcass may drift for weeks
   - (e) Skin ruptures and the now loosely held skeletal parts fall to the ground from the floating carcass and may be spread over a very wide area
   - (f) If the whale dies in a restricted or partly enclosed basin less than 400 x 600 km in size, then it generally reaches a beach before it disintegrates. In this instance constant battering onto the shore and refloating aids the break up of the animal.

2. Decomposition of fishes - physical and mechanical effects:
   - (a) Death of fish
   - (b) Animal sinks to the sea-floor with its back directed downwards
   - (c) Within 12 hours of death decomposition gases accumulate in the abdomen
   - (d) 3-4 days after death the decomposition gases float the fish ventral side up off the sediment
   - (e) 4-6 days after death the skin ruptures and the carcasses sink to the bottom and disintegrate rapidly
   - (f) 15-20 days after death only the skeleton (inc. scales) is left and may be broken up and rolled by currents and waves

Vertebrate remains are absent from many sediments even though the surface waters of these regions abound in fish, e.g. the west coast of Scotland. This absence may be explained if vertebrate remains provide an important food source for detritivores and scavengers, or if they are removed from the region by high current activity into deeper waters. At present no data exists to support the latter hypothesis. It is, however, known that echinoids and carniverous invertebrates are fond of fish bones and rapidly consume them (Johansen, 1929; Wasmund, 1935; p.50).

These latter observations suggest that it is unlikely that vertebrate deposits would accumulate today on an aerobic substrate with a low sedimentation rate swept by weak currents. It is more likely that they will accumulate in areas of high sedimentation rates and high energy (e.g. a tidally swept area), areas of abnormal conditions (e.g. high salinity as in a Texas type lagoon) or areas possessing an anoxic substrate (e.g. areas below the oxygen minimum depth), because they are less likely to support vertebrate bone detritivores or because they are removed into a less favourable environment, for detritivores. However, prior to the diversification and increase in abundance of echinoids in the late Triassic and Early Jurassic bone-beds were relatively common sediment types. Their gradual disappearance from aerobic environments during the Mesozoic may be linked to the rise in abundance of these efficient omniverous detritivores.

6 - Bone-beds through time

Bone-beds are not a phenomena restricted to Holocene sediments, they are found in a variety of environments and facies throughout geological time. The purpose of this section is to consider the environmental location of many of these bone-beds to see if any patterns of bone-bed genesis can be determined.

6.1 British Upper Silurian Bone-Beds

In the Palaeozoic the first bone-beds are found as thin loosely consolidated quartz rich vertebrate sands in the Ordovician (Behre and Johnson, 1933), but they do not become abundant until the Silurian. In the British Silurian the first bone-beds are recorded in the Leintwardine Beds (Middle Ludlow) as shelly layers containing phosphatic nodules (Cherns, 1977). The overlying Whitcliffe Beds (Upper Ludlow) contain a variety of bone-beds (Squirrel, 1959; Cave & White, 1971; 1978) culminating in the Ludlow Bone-Bed at the base of the overlying Downtonian Series of sediments (Upper Silurian). The Downtonian contains a large number of bone-beds, many of which are currently unrecorded in the literature.

6.1.1 Upper Ludlow Bone-Beds

Vertebrate deposits in the Upper Ludlow (Whitcliffe Beds) occur in two major facies (termed here Facies A and Facies B) and form discontinuous bone-beds traceable over distances of less than 1 km.

1. Facies A consists of an interbedded sequence of quartz silts, locally enriched in muscovite mica, but with few shells. Alternating silt units (5 - 10 cm thick) have flat erosive bases. The internal structure of inphase current ripple lamination or parallel lamination has been largely destroyed by bioturbation. The facies contains shell bands 1 - 15 mm thick which have an erosive lower contact and are made of ~~commutated~~ comminuted shell fragments. They frequently contain ostracod carapaces and occasionally a high density of fish scales associated with euhedral biotite crystals. The shell or bone-bed layers acted as an impassable substrate for burrowing organisms in the sediments overlying the deposit.

   The absence of lenticular or flaser bedding suggests that these marine sediments were not formed as subtidal tidal deposits. The sharp erosive contacts between silt layers and the high intensity of bioturbation destroying in some instances the internal lamination of the deposit suggest that sedimentation was episodic on an aerobic benthos, and that the sedimentation might be related to the effects of storm activities (Watkins & Berry, 1977) bringing in fresh sediments onto a shallow (≥ - 50 m O.D.) sea-floor.

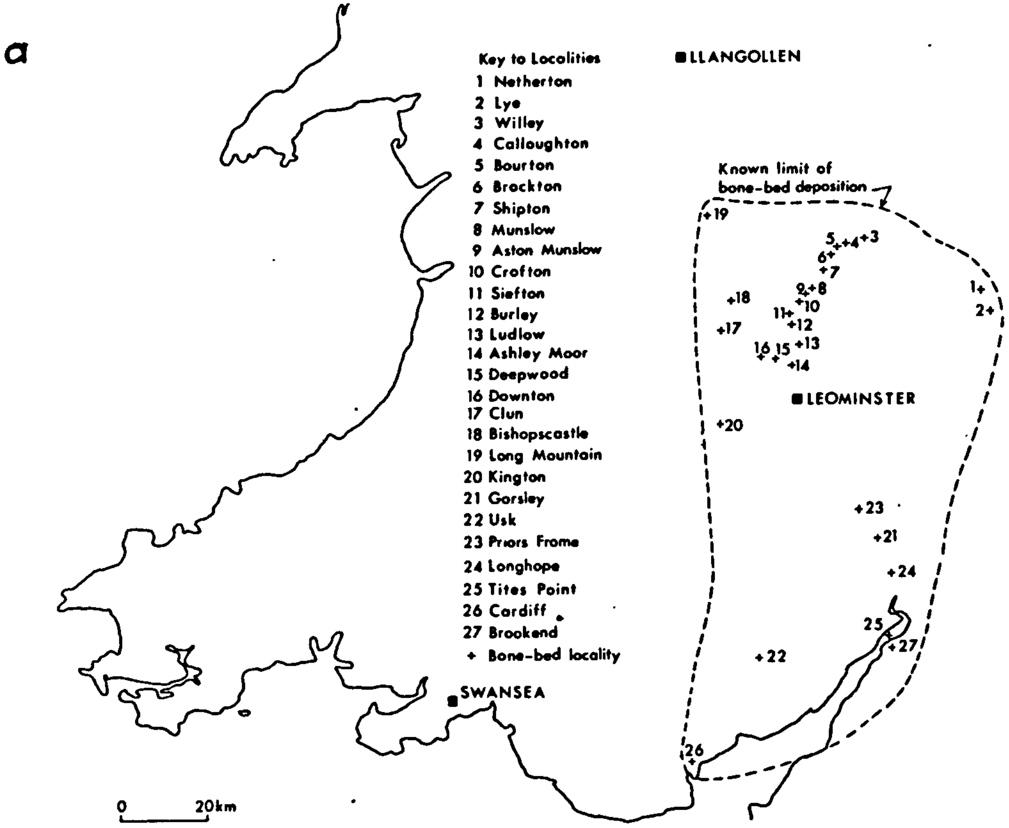
   The presence of biotite in the bone-beds may be a result of diagenetic reactions, though the sequence above and below the deposits contains no biotite. It is more likely that the biotite is derived from bentonites, which are biotite rich, and that a bentonite ashfall could have been responsible for the death of the fish in the bone-bed.

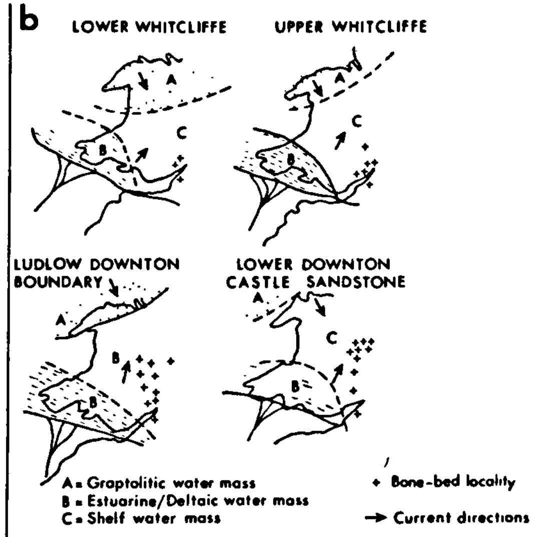
Text-fig.4a. Map of Wales and the Borderlands showing the localities containing deposits assigned to the Ludlow Bone-Bed.

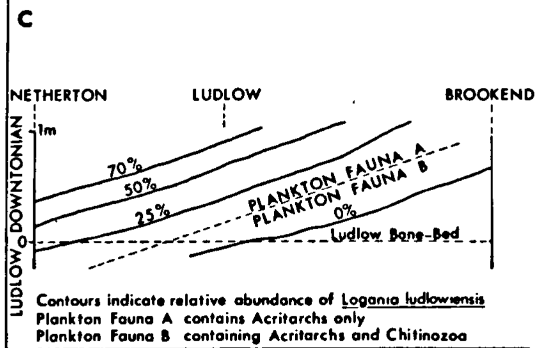
Text-fig.4b. Location of bone-beds, Plankton masses and Palaeogeography in the Upper Silurian (adapted from Watkins & Berry, 1977).

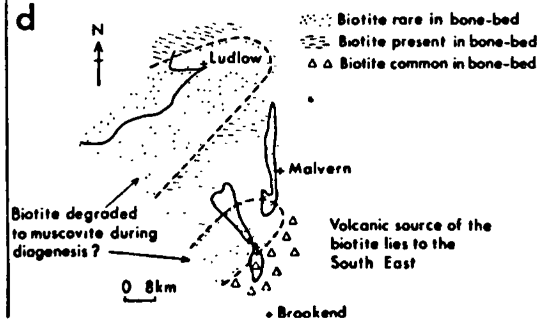
Text-fig.4c. Thelodont Species and Plankton distributions in the Upper Silurian.

Text-fig.4d. Distribution of Biotite in the Ludlow Bone-Bed
(Modified after Tucker, 1960).









2. Facies B consits of an interbedded sequence of lenticular bedded silts and clayey silts. Individual units range in thickness from 0.5 to 8 cm. The clayey silts commonly contain *Chondrites*. The silts may be made of quartz (0.005 - 0.15 mm grain size), shell debris (0.2 - 3.0 mm grain size) and, rarely, fish scales (0.06 - 0.95 mm grain size). These latter deposits occasionally form thin bone-beds (1 - 6 mm thick) and may have formed in a subtidal (-30 - 0 m O.D.) shelf region of oscillating tidal currents with an aerobic benthos.

6.1.2. Downtonian Bone-Beds

In the Downtonian, bone-beds are a fairly common sediment type and are present in a variety of facies, including some named bone-beds.

1. The Ludlow Bone-Bed is a stratigraphically important horizon which was once considered to mark the Silurian/Devonian boundary but now marks the basal layer of the Downton series (Upper Silurian), Holland *et at.*, (1963). The Bone-Bed has been recorded over a wide area (text-fig. 4a) and may be described as either a bone-bed facies (Allen, 1974a) containing a number of bone-beds within a short vertical sequence of strata (ca. 25 cm) or as the basal vertebrate sand layer marking the junction of the Whitcliffian and Downtonian faunas. This is the sense in which the term is used here.

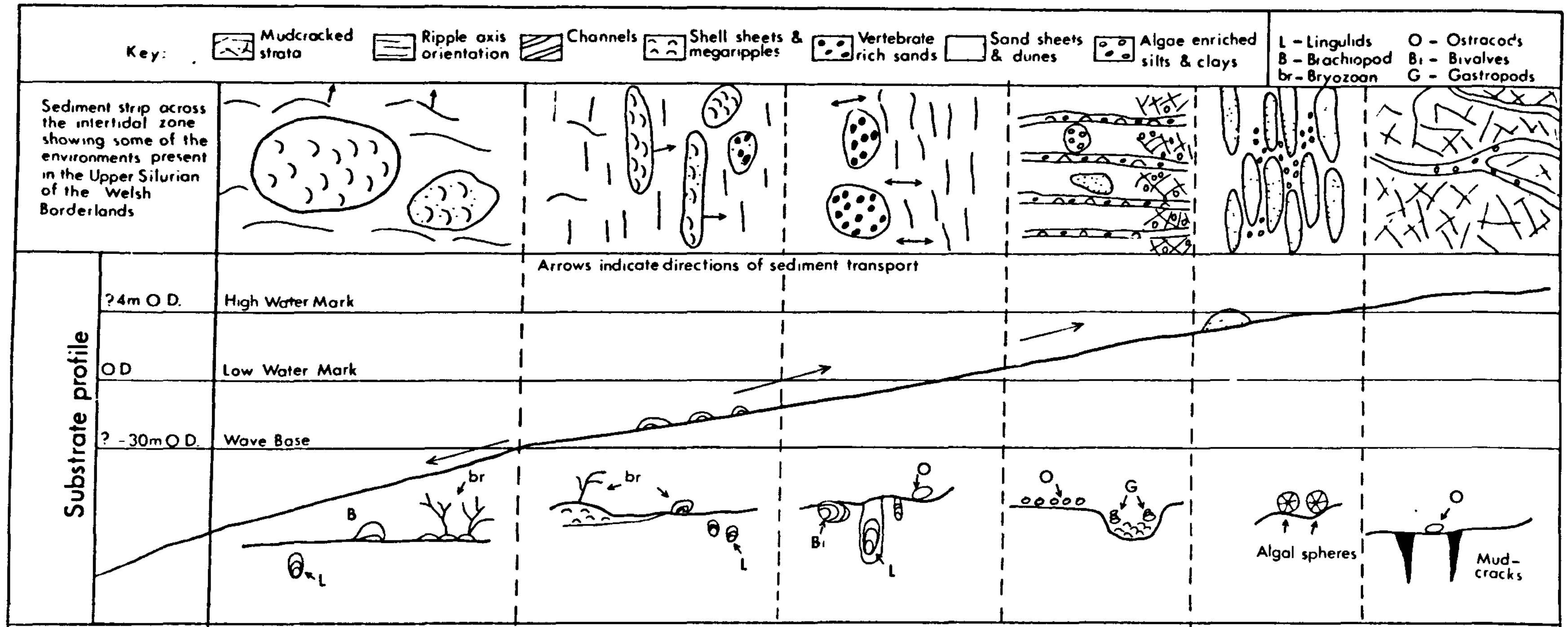
   The Bone-Bed may be described as a lenticular bedded sand (1 - 130 mm thick) composed of thelodont fish scales (0.06 - 1.2 mm grain size), phosphatic shell fragments (0.15 - 30.0 mm grain size), phosphatic nodules (0.35 - 25.3 mm grain size), and rare quartz grains (0.04 - 3.5 mm), see cover and pl. 14, figs. b,c. Thelodont scales, which may or may not be worn, form the dominant part of the bone-bed (pl.14, figs. d,e,f).

   Examination of the rare quartz grains show a variety of grain types, varying from quartz shards (pl. 14, fig. k), rounded grains showing evidence of eolean abrasion (pl. 14, fig. g), euhedral crystals (pl. 14, fig. h) some of which contain worn edges (pl. 14, fig. i) and high energy intertidal crescent shaped abrasion chips (pl. 14, fig. j).

   The features present on the quartz grains suggest that the Ludlow Bone-Bed is an intertidal deposit (cf. Krinsley & Doornkamp, 1973). This interpretation is supported by the fauna and lenticular bedded nature of the deposit, suggesting deposition in a region of tidal flow (cf. Reineck & Singh, 1975; Allen, 1974a; Antia & Whitaker, 1978).

2. Facies C - In the sediments immediately overlying the Ludlow Bone-Bed a number of other bone-beds are present. These occur in an interbedded sequence of intertidal (Allen, 1974a) lenticular and flaser bedded silts as either discontinuous rippled sand sheets ($\leq$ 5 mm thick) forming an integral part of a lenticular bedded strata, (e.g. the Downton Bone-Bed of Elles and Slater, 1906), laminae within rippled silts, or as thin vertebrate sand sheets (0.1 cm thick). Burrows within the facies are commonly infilled with vertebrate sand. The bone-beds contain thelodont fish scales and phosphatic shell fragments.

3. Facies D - At Ludlow about 1 m above the Ludlow Bone-Bed is a mudcracked channeled series of flaser bedded silts and clays. The channels are infilled with abundant thelodont fish scales associated with ostracod and molluscan shell debris forming bone-beds (1 - 3 cm thick) infilling runnel like channels. The sediments of this facies bear some morphological similarities to the modern mudmound facies found high in the intertidal zone (Greensmith & Tucker, 1967).



Environment	Muds, silts and shell sheets	Tidally influenced, shell gravels and muds	Mudcracks	Runneled muds mudcracked at top of zone	Chenier or Dune sands	Marsh sediments
Bone-beds	FACIES A	FACIES B	Ludlow Bone-Bed and FACIES C	FACIES D		TEMESIDE Bone-Beds
Sedimentary structures	Shell sheets, silt wedges, current ripples	Shell sheets and mega-ripples Current rippled and lenticular bedded muds and silt	Lenticular bedded silts and muds	Mudcracks, runnels	Trough cross bedding	Mudcracked channels calcite glaebules
Biogenic structures	*Chondrites* burrows	*Chondrites* burrows	U-shaped burrows	U-shaped burrows		
Ecology	Endo~~Epi~~fauna = Lingulid brachiopods & bivalves	Lingulid brachiopods and bivalves	Lingulid brachiopods and bivalves			
	Epifauna = Articulate brachiopods and ostracods	Articulate brachiopods and ostracods	Endobyssate bivalves and ostracods	Ostracods Algae small gastropods	Algae *Pachytheca*	Ostracods
	Encrusting fauna = Bryozoans	Bryozoans				

Text-fig.5. The environments of Upper Silurian (Whitcliffe/Downtonian) bone-bed deposition.

4. The Temeside Bone-Bed (Elles & Slater, 1906) is a channel infill deposit which cuts into a series fine-grained red clays (grain size ≤ 0.03 mm) which are extensively mudcracked and contain calcite glaebules, indicating that the deposit is cutting into supratidal sediments (Allen, 1974b). The bone-bed contains abundant plant fragments, fish scales and pellets, fish spines and rare angular quartz grains (pl. 14, fig. 6). Fish remains include those of thelodonts (*Thelodus parvidens*, *Logania ludlowiensis*, *T. trilobatus*), acanthodians (*Gomphoncus murchisoni*, *G. tennustriata*), and the cyphaspid, *Hemicyclaspis murchisoni*. The lowest Gedinnian conodont, *Ozarkodina remscheidensis*, has been recorded from a bone-bed infilling a scour hollow 60 cm below the Temeside Bone-Bed at Ludlow (GR S0522742).

6.1.3 The ecological significance and faunas of the bone-beds

As discussed earlier (p.100-102) the British Upper Silurian bone-beds may be primary deposits and therefore reflect the composition of the fish schools in the overlying waters (David, 1944). The deposits are located in a number of environments both subtidally and intertidally (text-fig. 5) and may represent mass mortality deposits in which the fish have been broken up after death. They do not mark stratigraphical faunal breaks, though some do represent a facies change (e.g. the Ludlow Bone-Bed). In this latter instance much of the fauna found immediately above the Bone-Bed has been recorded elsewhere from horizons below bone-bed (e.g. Hoppe, 1931; Atkins, pers. com. 1978).

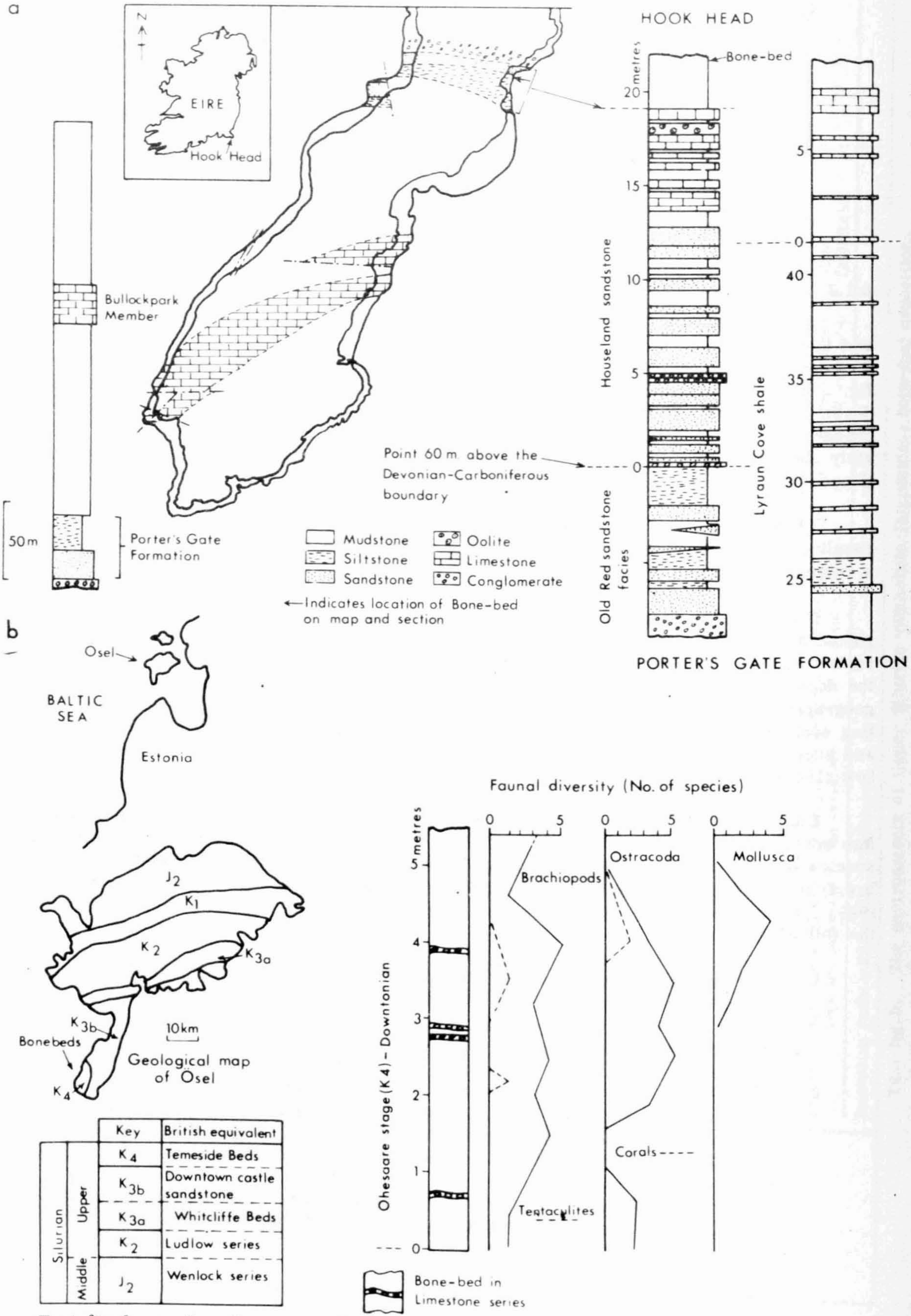
If the bone-beds do represent mass mortality deposits then they may have formed as a result of volcanic activity, since many of the deposits contain euhedral biotite (text-fig. 4d), a common constituent of local bentonites.

If this catastrophic interpretation of mortality is correct then study of the bone-beds should allow an ecological model for the Ludlow fish fauna to be considered. As many sections contain multiple bone-beds, changes in the composition of the fish faunas will be reflected in the deposits. The location of the Upper Silurian bone-beds, and plankton masses and a palaeogeography are given in text-fig. 4b. This figure illustrates the effect of the northward migrating southern estuarine/deltaic environment on the distribution of bone-beds and water masses and suggest that the schools of fish were confined to a relatively narrow northward migrating belt (100 km wide) on the shelf sea.

Examination of the faunal composition of these resulting deposits allows variations in fish school composition with distance and time to be studied. Study of the two dominant fish species present in the bone-beds (*Logania ludlowiensis* and *Thelodus parvidens* (pl. 14, figs. b,e,f) in relation to the plankton composition of the waters (data from Richardson & Lister, 1969; Swanson & Dorning, 1977; Dorning, oral com. 1977; White, oral com. 1978) allows the following observations to be made (text-fig. 4c).

1. Throughout the Upper Ludlow (Turner, 1973; pers. com. 1977) *Thelodus parvidens* forms the dominant fish remains in the sediments and bone-beds, suggesting that it was the dominant species of fish present in the overlying waters.

2. The change in relative abundance of *Logania ludlowiensis* making it the dominant species in the bone-beds is apparently related to a change in the composition of the plankton faunas (text-fig. 4c). A possible interpretation of this change could suggest that the fish schools dominated by *T. parvidens* were plankton feeders, while the schools dominated by *L. ludlowiensis* may have also utilised another food source (e.g. benthic algae). Thus increased nutritional pressure on *T. parvidens* due to a decrease in the diversity of its food supply, coinciding with a southward migration of part of the *L. ludowiensis* population (Turner, 1973) feeding on ?plankton and ?algae may have allowed it to compete successfully with *T. parvidens* for dominance in the local fish schools.



		Key	British equivalent
Silurian	Upper	K_4	Temeside Beds
		K_{3b}	Downtown castle sandstone
		K_{3a}	Whitcliffe Beds
		K_2	Ludlow series
	Middle	J_2	Wenlock series

Text-fig. 6 a. Location map and section showing the position of the Lyraun Cove Bone-Bed.
b. Map of the Island of Osel (Estonia) showing the bone-bed outcrop.
Stratigraphy after Kaljo & Sarv (1966).

After the mass mortality of fish (however caused), decomposition and disaggregation, the fish scales were transported into a number of environments.

1. The environment of death

   No articulated thelodont fish have been recorded from the Whitcliffe or Downtonian sediments though some whole cyathaspid headshields were recorded above the Ludlow Bone-Bed at Tites Point (Tites Point collection I.G.S. Lond.).

   If the fish died in a littoral or sublittoral environment not influenced by strong or oscillating currents, complete fish skeletons would be expected. The *Cyathaspis* headshield noted here occurs in littoral sediments and the fish was by nature a "mudgrubber" (David, 1956) and thus more likely to be preserved in its entirety.

   Thus the fish probably died in a region affected by subtidal current and were broken up by them. The disarticulated scales were then rolled around on the sediment surface and some colonised by algae (see Section 10). The scales may then have been transported from their environment of death both seaward and landward (text-fig. 5), before being concentrated in a bone-bed.

2. The ecology of the bone-beds

   Many bone-beds contain or are associated with *in-situ* faunas. The bone-bed facies A and B contain no such faunas though the sediments above and below contain an endemic fauna of brachiopods, bivalves and bryozoans. The Ludlow Bone-Bed contains a fauna of burrowing bivalves and the bone-bed facies C and D occur is sediments containing an autochthonous necrocenosis of ostracods, bivalves and gastropods. The Temeside Bone-Bed occurs in sediments containing a carapace fauna of rare ostracods. Since only the Ludlow Bone-Bed contains evidence of an in place fauna it is probable that the vertebrate sands did not form a good ecological habitat. The ecological habitats of the bone-bed environments are illustrated in text-fig. 5.

6.2 The Upper Silurian Bone-Beds of Osel

Deposits termed bone-beds have been recorded (Hoppe, 1931; Gross, 1967; 1971) on the Estonian Island of Saaremaa (Osel) in the Downtonian Ohesaare (K4) Stage (text-fig. 6). The bone-beds may be described as thin layers (5 - 23 cm thick) of either crystalline limestones with fish debris (K4c) or as sandy crystalline limestones rich in fish debris (K4a). Although the dominant vertebrate remains are thelodont scales a total of 27 vertebrate species belonging to the Thelodonti, Acanthodei, Actinopterygii, Heterostraci and Arthrodira have been recorded (Mark-Kurik, 1969). The bone-beds may be correlated with those of the Temeside shales of the British Upper Silurian sequence (cf. Cocks *et al.* 1972; Turner, 1973). They occur in a sequence of thin interbedded marls, clays and limestones (Hoppe, 1931). Locally some of the limestones are bioturbated, others dominated by a shelly fauna (text-fig. 6). The faunas across the bone-beds are dominated by crinoid ossicles, ostracods and brachiopods. The presence of the brachiopods *Salopina* sp., *Protochonetes ludloviensis*, *Microsphaeridiorhynchus nucula* suggest that the bone-bed sediments were formed in a shallow marine environment (cf. Calef & Hancock (1974; on the *Salopina* community), Lawson (1975; on the *Salopina-Protochonetes* association), and Boucot (1975; on Benthic assemblage 2)) above wave base. This conclusion is supported by other general sedimentology, palaeontology and ecostratigraphy studies from Estonia at this stratigraphic level, (Gailite 1972; Kaljo & Jurgenson, 1977; Kaljo oral com. 1978).

6.3 Bone-beds of the Beyrichienkalk erratics

Within north German glacial drift are a large number of glacial erratics from a marine Upper Silurian formation termed the Beyrichienkalk.

A large percentage of these erratics contain vertebrate remains (Romer, 1955) which have been described by Gross (1947) and some contain bone-beds (Brotzen, 1933). Samples of a Beyrichien bone-bed were obtained by the present author from Dr. Jahnke of Göttingen University. This material obtained from Loc. 22 Heiligenhafer, Geschiebe, N. Germany (Göttingen, Geology and Palaeontology Institute locality number) may be described as a vertebrate coccinia within an ostracod limestone.

The limestone sediment in which the bone-bed occurs may be described as a sparite containing orthocones, nuculoid bivalves, small bellerophon-like gastropods, small rhynchonellid brachiopods, or thick brachiopods and ostracods. The ostracod species observed by the author include *?Aparchites sinuatus* Hall, *Bythocypris* cf. *phillipsiana* (Jones & Hall) *Nodibeyrichia pustulosa* Hall and all occur as a carapace fauna. These ostracods suggest by comparison with those of Nova Scotia (Copeland, 1960, 1964) and those of Britain (Straw & Woodward, 1932; Shaw, 1969) that the sediments are of Upper Downtonian age.

The bone-bed itself may be described as a wackestone made of thelodont and acanthodian scales. Ostracod carapaces are common, but in most cases their interior has been replaced during diagenesis by phosphate. Similar internal phosphatic casts and moulds of small bellarophontid gastropods are common. Lingulid brachiopods (*Lingula* cf. *missindenesis* Straw) with both valves joined, are present within some small phosphatic nodules. The phosphatic elements present in the bone-bed are dominated ($\geq$ 80%) by fish remains belonging to the genera *Gonioporus*, *Katoporus*, *Thelodus*, *Logania*, *Nosteolopis* and *Gomphonchus*. These remains are poorly abraded and are dominated by poorly weathered scales. Some of the scales contain algal solution pits of the type illustrated in pl. 18, fig. e. The grain size of the phosphatic elements of the bone-bed is in the range 0.2 - 1.2 mm.

The bone-bed is regarded (Romer, 1955; Halstead & Turner, 1973) as having formed in an estuarine or near shore marine shelf environment. This interpretation is supported by the presence of a marine invertebrate fauna belonging to the near shore benthic assemblage 2 of Boucot (1975).

6.4 Devonian bone-beds

Accumulations of fragmented vertebrate debris have been recorded in the Lower Devonian Catsgill Delta facies and the Middle Devonian Limestones of Ohio, U.S.A.

6.4.1 The Catsgill Delta Facies

The Lower Devonian Catsgill Facies represents a deltaic sequence of interbedded sandstones and conglomerates in the north eastern states of the U.S.A. (Allen & Friend, 1969) which allowed the development of a prograding muddy marine shore line to the south of the delta (text-fig. 3, p.99) in Pennsylvania (Walker & Harms, 1971). Similar estuary/deltaic associations with prograding muddy shore lines are found adjoining the Thames Estuary (Greensmith & Tucker, 1967; 1975; Antia, 1977), the Mississippi Delta (Gould & McFarlan, 1959) and elsewhere (Price, 1955).

These prograding muddy shore lines may form chenier plains (Price, 1955), which are swept by a mud laden subtidal traction current. The coarse debris (sand, shells, pebbles, vertebrate debris, etc.) is concentrated into lag concentrates by storms, currents and wave activity, and migrated across the intertidal zone to accumulate as ridges of sand, shell and cobble on the junction of the tidal mudflats and the supratidal marsh.

In the Catsgill Coastal Plain environment, Walker & Harms (1971) have recorded 60 transgressions and regression of this coastline. Each transgression producing a sequence of sediments representing a variety of subtidal and intertidal environments (text-fig. 3). Similar sequences have been recorded in recent post glacial coastal plain sediments (Greensmith & Tucker, 1976).

The basal unit of each of the Catsgill transgressive sequences is a subtidal siltstone bone-bed rich in quartz, brachiopod and crinoid debris, phosphatic nodules, bone fragments and fish plates. It rests on a sharp, discordant erosive surface which is commonly bioturbated.

6.4.2 Middle Devonian bone-beds of the Central U.S.A.

Four bone-beds have been described (Wells, 1943; 1944; 1947) from the Delaware and Upper Columbus Formations of the Middle Devonian (Late Ulsterian) limestones of central Ohio (text-fig. 7h).

The bone-beds are local concentrations or zones of pelopsammic material outcropping over a wide area, which formed in a shallow shelf sea near a land area (text-fig. 7a). The phosphatic organic constituents are generally worn scales, teeth, plates and bone fragments of agnathid, arthrodiran, ptyctodontid, scanthodian, selachian and crossopterygian fishes. Other less common constituents include conodonts, arenaceous foraminifera, ostracods, scolecodonts, sponge spicules, and lycopod spore exines. Locally crinoid ossicles, corals, bryozoans, gastropods, brachiopods, and bivalves dominate the fauna. The phosphatic component of the bone-beds is made of a carbonate apatite (Westgate & Fischer, 1933).

The individual bone-beds may be described as follows:

1. The First Ohio Bone-Bed (text-fig. 7h) consists of a thin (5 - 8 cm thick) vertebrate sand rich in angular, rounded and frosted quartz grains (≤0.3 mm long) and accessory chert.
2. The Second Ohio Bone-Bed (text-fig. 7h) covers an area of several hundred square kilometres (Orton, 1878) and consists of a thin (0 - 40 cm thick) vertebrate and crinoidal diastemic sand containing limestone intraclasts, chert, and angular, rounded and frosted quartz grains (≤ 0.8 mm).
3. The Third Ohio Bone-Bed (text-fig. 7h) forms the topmost bed of the Columbus limestone (Stauffer, 1909) and is an extensive, 0 - 32 cm thick, diastemic vertebrate sand rich in coarse crinoidal debris, containing well rounded and frosted quartz grains (≤ 0.5 mm). Some of the vertebrate remains have been replaced by opal. The deposit rests on an erosive surface in the Columbus Limestone which cuts through corals and brachiopod shells and marks an important faunal change (Table 9). Locally the bone-bed infills a channelled and mudcracked underlying surface (text-fig. 7b,c,d).
4. The Fourth Ohio Bone-Bed (text-fig. 7h) is a crinoidal vertebrate sand (5 - 8 cm thick) containing phosphatic nodules and rounded frosted quartz and chert grains (≤ 1 mm).

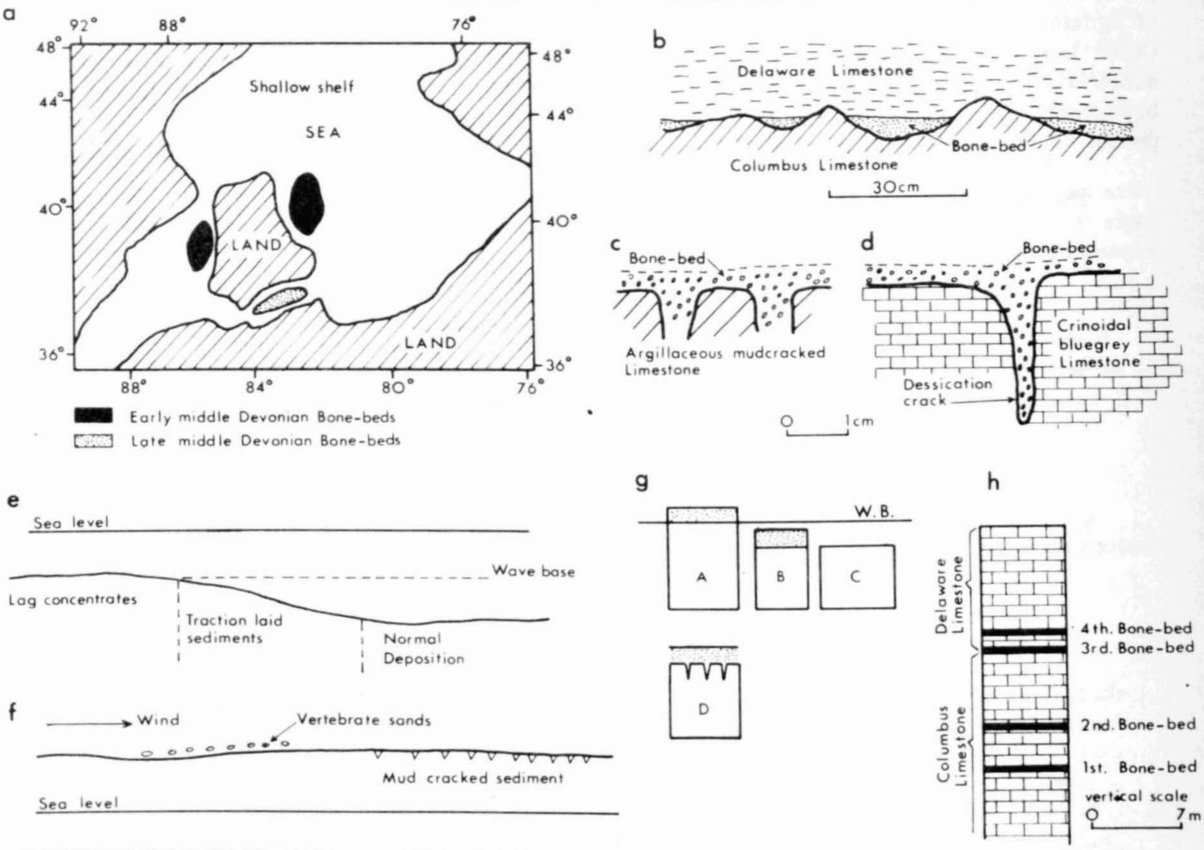
Three other bone-beds of local extent have been recorded from the Middle Devonian of Ohio, Indiana and Kentucky. The East Liberty Bone-Bed (Newberry, 1873) is a diastemic dolomitic vertebrate sand (0 - 30 cm thick) rich in pyrite, phosphatic nodules and rounded, frosted and rutilated quartz grains. Secondly, the Rocky Branch Bone-Bed (Foersets, 1906) is a calcareous vertebrate sand (5 cm thick) containing rolled frosted quartz grains and phosphatic nodules some of which are internal phosphatic moulds of gastropods, bivalves and pelmatozoans. The third one is the Kiddville Bone-Bed (Wells, 1944), a thin vertebrate sand rich is spores, inarticulate brachiopods, fragmented conodonts, phosphatic nodules, and rounded, frosted, polished and rutilated quartz grains, some of which occur as perfect euhedral overgrowths.

Table 9. Faunas across the Columbus/Delaware limestone boundary (Westgate & Fischer, 1933).

1 = *Nucleocrinus verneudi*;		6 = *Stropheodonta demissa*;	
2 = *Spirifer acuminatus*		7 = *S. perlana*;	
3 = *S. duodenarius*;		8 = *Rhipidomella vanuxemi*;	
4 = *Reticularia fimbriata*;		9 = *Delthyris consobrina*;	
5 = *Leptaena rhombiodalis*;		10 = *Martinia maia*;	

C = common; P = present; R = rare

	Species 1	2	3	4	5	6	7	8	9	10
Delaware Limestone	-	-	-	-	P	P	P	P	C	C
Bone-bed	-	-	-	R	C	C	C	C	C	C
Top of Columbus Limestone	C	C	C	C	-	-	-	-	-	-
Columbus Limestone	P	P	P	P	P	P	P	P	-	-



Text-fig.7. Middle Devonian Bone-beds

(a) Palaeogeography

(b-d) Sections through the third bone-bed

(e-g) Environments of bone-bed deposition

A = bone-beds formed as lag concentrates W.B. = Wave Base

B = bone-beds concentrated by traction currents

C = normal deposition (no bone-beds formed)

D = bone-beds formed as lag concentrates in the intertidal zone.

(h) The stratigraphic location of the bone-beds

Data for fig. obtained from Westgate & Fischer (1934), and Wells (1944).

A variety of models have been proposed to account for the origin and distribution of the Ohio Bone-Beds. The early models suggested that they formed as a condensation deposit, a mass mortality deposit or from the reworking of coprolites and they are summarised by Wells (1944).

Wells (1944) following examination of the bone-beds decided that:

1. The vertebrates were fragmented after death and transported.
2. All the bone-beds have a uniform mode or origin.
3. They are associated with diastems resulting from fluctuations with respect to wave base on the bottom of a very shallow sea.
4. In some places they represent lag concentrates, in others rapid subaqueous accumulations of coarser material transported from areas of lag concentration with a bipassing of finer particles (text-fig. 7e, 7g).

Subsequent (post 1947) detailed biostratigraphic work utilising a foraminifera zonal scheme (Conkin & Conkin, 1975) has shown that the sections described by Wells (1944) contain a total of 16 bone-beds (Conkin, 1969; Conkin *et al.*, 1972; 1973) and that the bone-beds are associated with paracontinuities. These are disconformities which exhibit a slight though clearly discernable channelling and a small but significant faunal discontinuity. Conkin & Conkin (1975) note that the rocks which overlie paracontinuities in the Delaware and Columbus Limestones often contain a basal detrital unit, such as a bone-bed.

However, since these more recent accounts of the Ohio, Devonian bone-beds supply no appreciable new sedimentological, petrographic and environmental information relating to these bone-beds, the interpretation of Wells (1944; 1947), outlined here, remains the best available account of their formation and petrology.

6.5. A Tournaisian (L. Carboniferous) bone-bed from Hook Head, Co. Wexford, Eire

Although the geology, palaeoenvironments and palaeontology of the Hook Head peninsula (text-fig. 6, p.118) have been extensively described (Smyth, 1930; Sleeman *et al.*, 1974; Sleeman, 1977), little is known about the nature of the phosphatic nodules and fish debris of the Lyraun Cove Member of the Tournaisian Porters Gate Formation.

The fish debris is disseminated throughout the Lyraun Cove Member but is concentrated in a thin dark grey shelly fine-grained siltstone containing about 15% shell, 25% fish debris, and 5 - 10% pyrite; termed here the Lyraun Cove Bone-Bed (text-fig. 6).

The shelly debris of the bone-bed consists of crinoid ossicles, smooth ostracods and small brachiopods (? *Spirifer tornacensis* de Kon). The fish debris comprises worn and fragmented blue grey fish scales (≥ 99%), rare teeth (≤ 1%) and conodonts (Johnston pers. com. 1978). The pyrite forms small (0.1 - 0.4 mm) nodules of framboidal pyrite or as internal moulds of ostracods and gastropods. Some fish scales have acted as a nuclei for pyrite growth in the concretions and are partially engulfed. The pyrite has a diagenetic origin. Both the fish and shell debris occur within the same size range 0.1 - 1 mm (modal range (0.3 - 0.5 mm).

The early Hook Head Tournaisian sediments represent a marine transgression and show a gradual transition from a fluviatile to a marine environment. The sediments pass up from a fining-up sequence of conglomerates, sandstones and siltstones in the Old Red Sandstone facies represented by the Old Town Bay Formation (text-fig. 6), into a series of flaserbedded sandstones containing bipolar cross stratification and trace fossils. This latter sediment type is represented by the Houseland Member of the Porters Gate Formation and is thought to have been deposited in a variety of intertidal and shallow subtidal marine environments (Sleeman *et al.*, 1974; Sleeman, 1977).

The Houseland Member is overlain by the Lyraun Cove Member, which comprises a sequence of grey sand lensed mudstones and bioturbated siltstones containing ossilation ripples (text-fig.6). Phosphatic nodules and fish remains are common throughout the sequence. The Member is considered to represent a low energy shallow marine environment rarely influenced by tidal currents and storms (Sleeman, 1977). The overlying Hookhead Formation represents a shallow water open shelf tidally influenced marine environment (Sleeman *et al.*, 1974). Thus the Lyraun Cove Bone-Bed accumulated in a low energy marine environment. This environmental interpretation is not supported by the well sorted and fragmented nature of the beds clasts, but these may have been swept into the environment as a well sorted lag concentrate.

The presence of pyrite and phosphate nodules in the Member suggest that sediment pore waters were both sulphurous and anoxic (Eh -200 to -300; pH 6 - 7; Berner, 1970; Baturin, 1971), when the nodules formed, and may suggest that the Lyraun Cove Bone-Bed is a transported deposit of shell and fish debris, possibly transported during a storm, from a tidally influenced environment to this environment presenting ?foetid bottom conditions.

6.6. The German Middle/Upper Triassic Bone-Beds

Bone-beds have been recorded (Wagner, 1913; Aust, 1969; Reif, 1969; 1971; 1974; 1976; Bachmann & Gwinner, 1971; Gwinner & Hinkelbein, 1976, etc.) from the Upper Muschelkalk (mo3) and Lower Lettenkeuper (kul) of south west Germany, within a standard stratigraphic profile across the Muschelkalk/Keuper boundary which may be presented as follows, from base to top (after Reif, 1974):

1. Obere Terebratelbank (mo3) - A blue grey limestone (40 - 50 cm thick) containing convolute bedding, stylolites, and rare bone-beds.

2. Frankische Grenzschichten (mo3) - A blue grey glauconitic shelly limestone locally interbedded with ostracod rich clays (the *Bairdia* Ton) and occasional conglomeratic layers (0 - 100 cm thick).

3. The Grenzbonebed (mo3) - Rippled bone-bed (4 - 20 cm thick) rich in fish debris and coprolites, often with a rich trace fossil fauna on its upper surface.

4. The Untervitriolschiefer (kul) - Grey laminated clays 40 - 80 cm thick) occasionally rippled locally containing layers rich in ostracod debris.

5. Wagner's Plattenhorizon (kul) - A grey siltstone rich in bone debris (8 - 15 cm thick) locally flaser bedded.

6. The Oberevitriolschiefer (kul) - Grey laminated clays (40 - 60 cm thick) occasionally rippled, locally flaser bedded towards the upper part of the unit.

7. The Blaubank (kul) - A blue grey limestone (20 - 40 cm thick) with local patches of diagenetically dissolved calcite or gypsum crystals (Porenkalk (Reif, 1974) and shell debris. Bone-beds are commonly developed at the units base. Stylolites are common.

8. The Dolomitsche Mergelschiefer (kul) - A sequence of alternating blue grey dolomitic limestones, silts, clays and grits with occasional layers of fish and coprolite debris (60 - 100 cm thick).

9. The Untere Dolomite (kul) - Blue grey dolomite locally rippled, with some sandy layers (40 - 80 cm thick).

10. The Estherien-Schichten (kul) - Black shales with interbedded cross-bedded sandstones rich in plant debris (2 - 10 m thick).

11. The Upper Lettenkeuper (kul) - Black shales with interbedded dolomites, bone-beds and algal stromatolites (5 - 15 m thick).

The most important of the bone-beds is the Grenzbonebed which forms the uppermost layer of the Frankische Grenzschichten. Within the Frankische Grenschichten are a number of thin (1 - 3 cm thick) discontinuous bone-beds traceable only a few metres, but owing to their relative position in the quarry faces, usually 30 - 70 m above the ground, they have proved difficult to study in depth. However, like the Grenzbonebed they may represent "condensation" or omission deposits (Reif, 1971) and may provide evidence of a slow down in the deposition rate of the Muschelkalk Limestone towards its top.

The thick bone-bed forming the top of the Muschelkalk Limestone (the Grenzbonebed) marks both a facies and a faunal change (Table 10) and may represent a change in the axis of the Muschelkalk Basin (Reif pers. com. 1977).

6.6.1. The Grenzbonebed

The Grenzbonebed (pl.15, fig.h) has been extensively described by Reif (1969; 1971; 1974; 1976) and Aust (1969). It is a thin deposit (0.5 - 30 cm thick) of rippled or parallel laminated carbonate clay or sand enriched in vertebrate debris and phosphatic nodules, including coprolites. The ripples tend to be symmetric low wavelength (7 - 15 cm) subtidal current ripples.

Within the bone-bed four facies are present - conglomeratic, sandy, clayey, and carbonate; their general distribution pattern is indicated in text-fig. 8, and their description follows:

1. The conglomeratic facies

   A deposit 5 - 20 cm thick composed of platy subrounded to angular pebbles (0.5 - 20 cm across), sometimes imbricated, in a vertebrate rich matrix. The pebbles are comprised of micrite, shelly bioclastic micrite and reworked vertebrate rich micrite, and are often bored.

2. The sandy facies

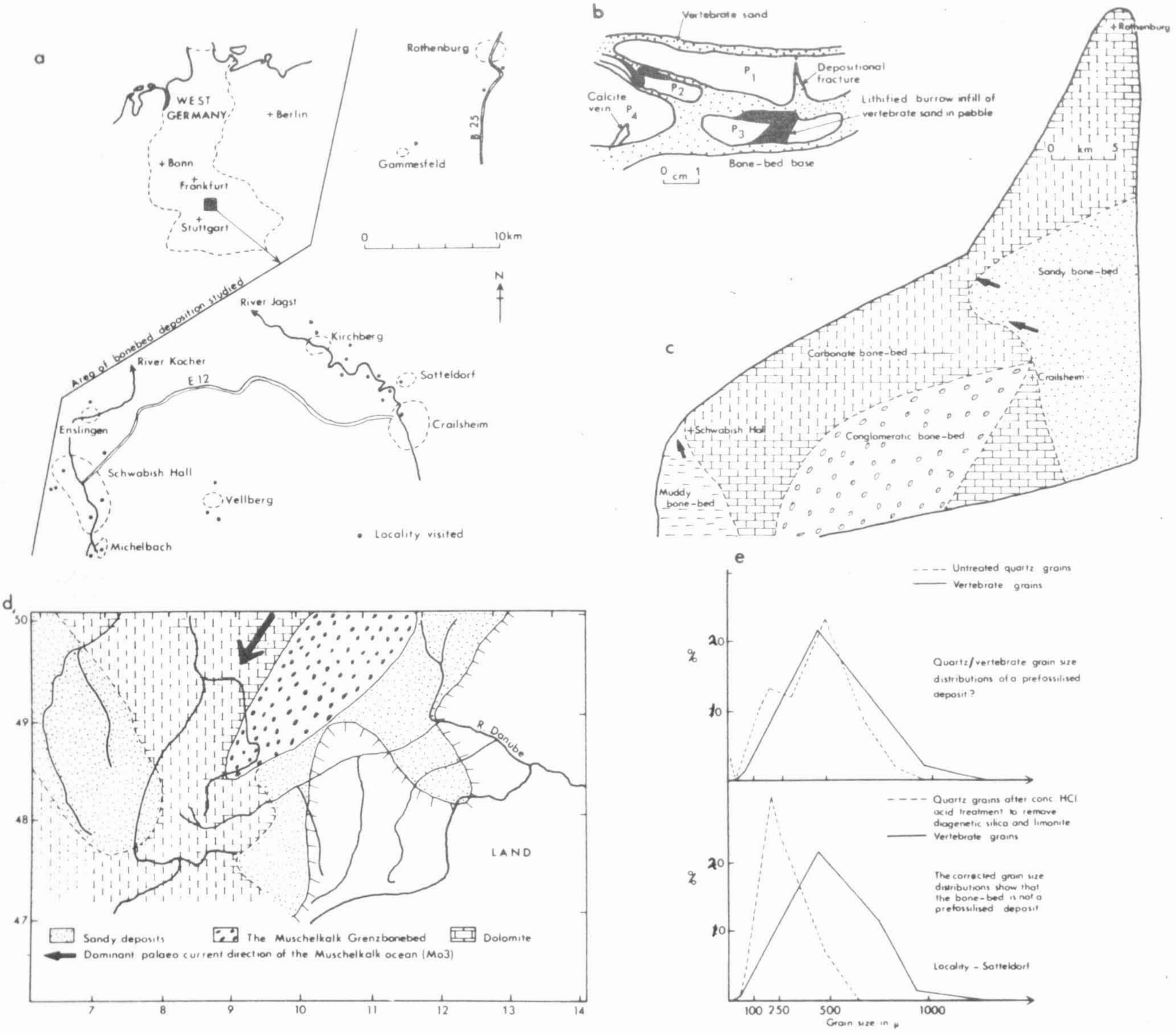
   A quartz sand deposit enriched in vertebrate remains. Both the quartz and vertebrate clasts may occur as well rounded high spherocity grains. The quartz grains are often coated by limonite (pl.15, fig.g) and by diagenetic silica (pl.15, figs. d,e).

3. The clay facies

   Thin deposits (less than 8 cm thick) of grey clay enriched in fish scales, normally parallel laminated, though ripple laminated clays have been recorded within the facies.

4. The carbonate facies

   Poorly bedded micrite deposits rich in vertebrate debris. S.E.M. studies of the sediments of this facies show that locally the vertebrate clasts may be rounded (pl.15, figs. j,l) though many of the clasts are angular (pl.15, figs. c,f) or unabraded (pl.15, figs. g,h). Many of the clast surfaces are chipped and uneven as a result of abrasive processes (pl.15, fig.i). The matrix of the limestone is rich in both calcite (pl.15, fig.c) and dolomite crystals (pl.15, fig.b) and rare clays. Some of the vertebrate clasts in the bone-bed are bored (pl.15, fig.k), possessing a boring diameter between 0.004 and 0.010, mm. Their general morphology is very different to the algal dissolution pits recorded on vertebrate clasts in the Ludlow Bone-Bed by Antia & Whitaker (1978) (pl.18, fig.c; pl.19, figs. d,e). They may, however, represent algal borings similar to those described by Bathurst (1975).



Text-fig.8. a Location map of sections through the Muschelkalk Grenzbonebed examined.
b Tracing of pl. 14, fig. n, explaining the features present.
c Facies distributions in the Muschelkalk Grenzbonebed.
d Palaeogeography of the Muschelkalk Grenzbonebed.
e Grain size distributions in the Muschelkalk Grenzbonebed.

Table 10. Ranked faunal distributions across the Muschelkalk/Keuper boundary (Mo3/Ku1) in South West Germany based on unpublished researches of the author. The individual stratigraphic units (1 - 11) are described in the text.

Species	Stratigraphic Unit										
	1	2	3	4	5	6	7	8	9	10	11
Brachiopoda											
Coenothyris vulgaris (Sch.)	1	1	1	-	-	-	-	-	-	-	-
Lingula tenuissima Bronn	-	-	2	1	1	1	1	1	2	2	3
Gastropoda											
Loxonema obsoletum Zieten	-	8	-	-	-	-	-	-	-	-	-
Omphaloptycha pyramidata (Ko.)	-	9	-	-	-	-	-	-	-	-	-
Cephalopoda											
Ceratites semipartitus Mont.	5	12	-	-	-	-	-	-	-	-	-
Bivalia											
Anoplophora lettica Quen.	-	-	-	-	2	-	2	-	-	-	2
A. brevis Schaur	-	-	-	-	-	-	4	2	1	-	-
Enantiostreon difforme (Sch.)	3	3	4	-	-	-	-	-	-	-	-
Gervilleia costata Sch.	-	4	-	-	-	-	-	-	-	-	-
Hoernesia socialis Sch.	2	2	3	-	-	-	-	-	-	-	-
Myophoria intermedia Schaur	4	10	-	-	-	-	-	-	-	-	-
M. goldfussi Alb.	-	-	-	3	3	2	3	3	3	-	4
Mytilus eduliformis Sch.	-	5	-	-	-	-	-	-	-	-	-
Pecten discites Sch.	-	7	-	-	-	-	-	-	-	-	-
Echinodermata											
Encrinus liliiformis Sch.	6	11	-	-	-	-	-	-	-	-	-
Estherids											
Isuara minuata Goldf.	-	5	-	2	-	-	-	-	-	1	1

Table 11. A component analysis of the Muschelkalk Grenzbonebed

Vertebrate Component	Locality									
	1	2	3	4	5	6	7	8	9	10
Pointed teeth	3.4	2.6	34.5	3.1	1.4	6.5	3.0	4.1	-	1.4
Concavo-convex teeth	-	-	4.2	1.0	-	0.3	-	-	-	-
Flat teeth	64.0	53.2	38.8	60.3	29.2	58.6	57.5	34.2	65.2	71.6
Fish scales	12.8	37.7	22.4	16.4	59.7	24.6	36.4	37.0	13.4	16.4
Phosphatic nodules	18.6	6.5	-	9.1	8.3	9.8	3.0	24.7	21.4	10.4
Fish spines	1.2	-	-	-	-	-	-	-	-	-
Vertebra	-	-	-	-	1.4	-	-	-	-	-

Key to localities:

Locality 1 - Rothenburg ob der Tauber. 1:50,000 Map No. L6726. GR 867699.
2 - Gammesfeld. Map No. L6726. GR 803674.
3 - Satteldorf. 1:35,000 Map of Kirchberg. Reference 10° 2.6' 49° 10.9'
4 - Burlesmagen. Map as for 3. Reference 10° 1.9' 49° 10.9'.
5 - Hornberg. Map as for 3. Reference 9° 59.5' 49° 13.4'.
6 - Eselsteige. Map as for 3. Reference 10° 0.8' 49° 9.8'.
7 - Schwabish Hall. 1:50,000 Map L6924. GR 524415.
8 - Klinenacker. Map No. L6924. GR 524415.
9 - Hessental. Map No. L6924. GR 555407.
10 - Enslingen. Map No. L6924. GR 549478.

The relative abundances of the major groupings of vertebrate remains may alter over a short area, and locally one fraction may dominate the fauna (Table 11).

6.6.2. The time period represented by the Grenzbonebed

Study of the conglomeratic fractions of the bone-bed suggest that it represents a long depositional period. Since some of the lithified limestone pebbles (derived as intraclasts from the Muschelkalk Limestone Grenzbonebed junction) contain a lithfied burrow infill of bone-bed which predates the formation of the pebbles (pl.14, fig.n; text-fig.8). Thus indicating the following processes may have occurred:

1. Semilithification of the limestone.
2. Burrowing into the semilithified sediment.
3. Burying of the burrows with a vertebrate sand.
4. Lithification of the limestone and burrow infills with a calcite clay cement.
5. Scouring and fragmentation of the substrate.
6. Transport of these fragments and inclusion in a vertebrate sand.
7. Burial and lithification of the fragments in the vertebrate sand.

The time period involved for this lithification of the limestone sediment may be a few hundred or thousand years (Bathurst, 1975).

The absence of burrows in the bone-bed suggests that the sediment was too unstable to accommodate an ichnofauna or that the substrate was too foetid/nutrient poor to support an ichnofauna or that the bone-bed was buried very soon after its deposition. The presence of trace fossils on the upper surface of the bone-bed suggests that the last interpretation may be correct.

The phosphatic elements of the bone-bed have been derived from limnofluviatile, terrestial and marine environments (Reif, 1971). They may occur as perfectly preserved vertebrate teeth, bones, etc., or as well rounded high spherocity highly abraded fragments (pl.15, fig. i). This suggests that some of the vertebrate remains have been transported over a large area and that the bone-bed is a multicomponent deposit.

These observations suggest that the bone-bed represents a period of sediment omission, during which the substrate was gradually becoming lithified, and was swept and temporarily buried by actively moving vertebrate sands.

6.6.3. The source of the phosphatic debris in the Grenzbonebed

Reif (1969; 1971) considers much of the vertebrate material in the Grenzbonebed to be prefossilised and suggests that it has been derived from eroded sediments and concentrated on a lithified substrate as a lag deposit. However, much of the fauna in the Grenzbonebed is not present in the underlying sediments (Schmidt, 1928) and represents faunas from a variety of environments (terrestial, limnofluvial and marine). The vertebrate remains are commonly worn and abraded with grain size distributions which differ from that of the associated quartz grains (text-fig. 8). Quartz grains are rare or absent in some of the deposits, suggesting perhaps that the bone-bed is not a prefossilised deposit.

It is therefore suggested that the bone-bed formed as a lag concentrate of vertebrate material, derived from a variety of habitats, elongated in the direction of the dominant palaeocurrents (text-fig. 8) on the surface of a lithified or semilithified carbonate mud.

6.6.4. The Lettenkeuper bone-beds

Within the Lettenkeuper (Upper Triassic) of West Germany (Crailsheim - Rothenburg, text-fig. 8) a number of bone-beds have been recorded (Reif, 1969; 1974) within the Keuper regression sequence. These will be considered from the base (1.) of the sequence as follows:

1. Vitriolschiefer Bone-Beds

   The Vitriolschiefer is a dark clay rich in vertebrate material. In its middle section it contains a deposit (≤ 15 cm thick) termed the Plattenhorizon, which contains 3 - 5 thin bone-beds varying in thickness from 0.1 to 1 cm. The Plattenhorizon is a rippled clayey silt layer resting with an erosive base on the underlying shales. The bone-beds contain little pyrite or glauconite (Reif, 1969) and are frequently associated with lingulid and bivalve shells and shell fragments. They contain a rich fauna of perfect and worn fish fragments with some rolled phosphatic nodules (?coprolites). Vertebrate fragments are in the size range 0.2 to 44 mm.

2. Blaubank Bone-Beds

   Within the Blaubank thin bone-beds (≤ 1 cm thick) are present (rarely more than one bone-bed at a given section). Their matrix varies from that of a shelly dolomite to a dolomite sand and contains fragments of vertebrate material (varying from perfect to trite fragments and specimens), 0.1 to 40 mm in length.

3. Dolomitischen Mergelschiefern

   Bone-beds are rare within the Dolomitischen Mergelschiefern. They occur as thin layers (≤ 4 mm thick) of largely unworn vertebrate fragments (bones, teeth and scales), 0.5 - 6 cm long, in a sandy matrix.

4. Unteren Dolomiten

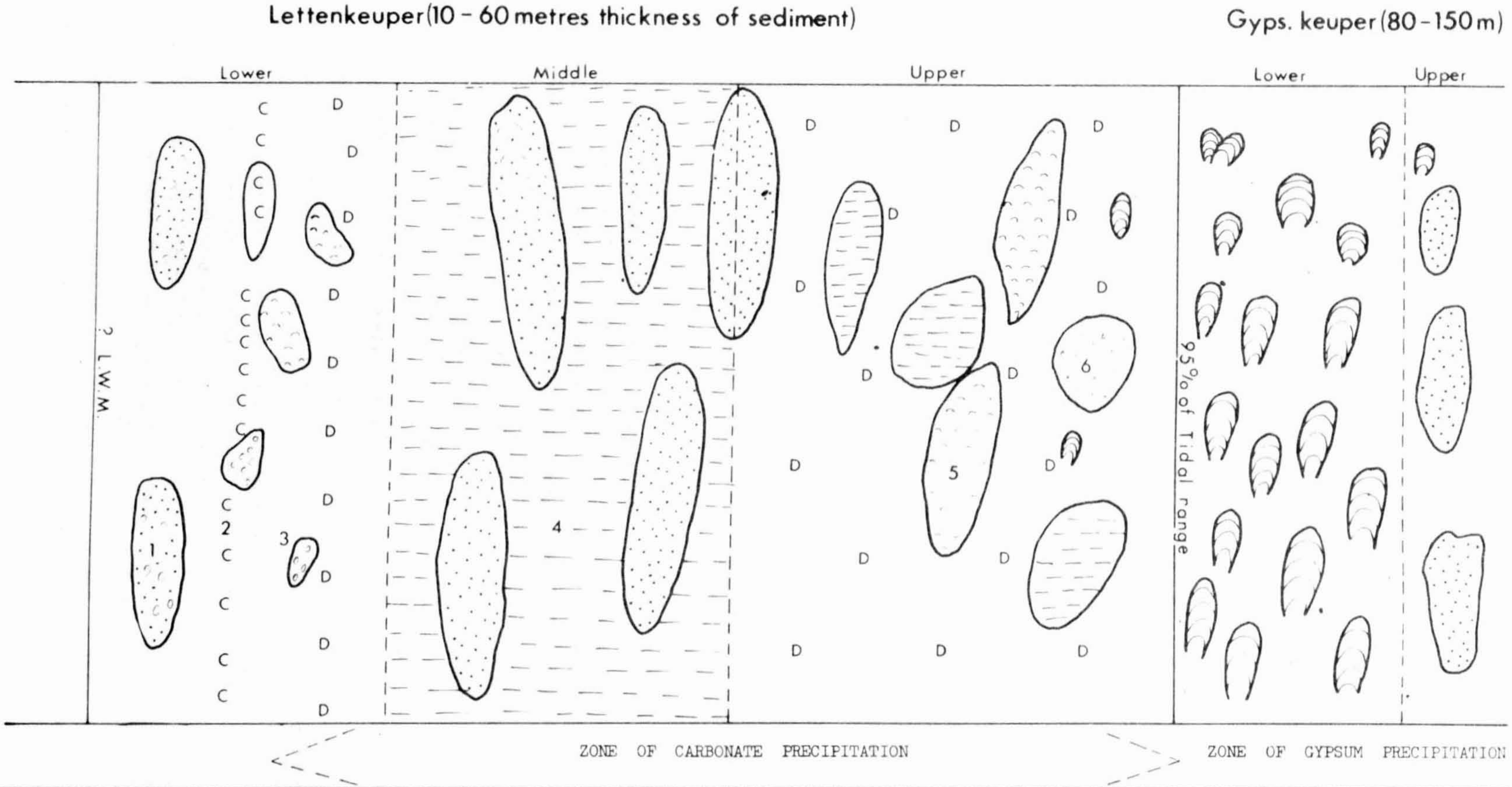
   Bone-beds are very rare in the Unteren Dolomiten but when present consist of a rippled vertebrate quartz sand (≤ 1 cm thick) with a dolomitic matrix. The vertebrate fragments are in the size range 0.4 to 8 mm and are poorly abraded, consisting largely of teeth and scales.

5. The Estherien-Schichten

   Within the Estherien-Schichten bone-beds are very rare, though occasionally thin vertebrate lags are found underlying the sandstone layers. These lags consist of coprolites, unworn vertebra, teeth and scales, in the size range 0.6 to 38 mm and are rarely more than one layer thick (1 - 40 mm thick).

6. The Upper Lettenkeuper

   At Michelbach (text-fig. 8) a vertebrate rich carbonaceous black clay (30 cm thick, containing 29% vertebrate remains) occurs in a sequence associated with some gypsiferous and dolomitic algal stromatolites, dolomites and thin shell layers. The horizon is rich in broken fish scales (*Gyrolepis quenstedti* Dames), 0.4 to 3 mm across, and sharks jaw bones (pl.16, fig.g) of *Acrodus lateralis* Ag..



Structure	Parallel Ripple Lamination + Lenticular Bedded Horizons	Trough Cross Bedding and Parallel Lamination	Rare Algal Stromatolites, Parallel & Rippled Lamination	Algal Stromatolites
Environment	Foetid Mudflats with vertebrate sand sheets and rare shell sheets	Foetid Mudflats containing Migrating Perched Sand Bodies and shell sheets (?high intertidal)	High Mudflat zone with shell sheets, dolomitic muds and foetid black muds (?supratidal)	Supratidal

Text-fig. 9. An environmental model for bone-beds in the Lettenkeuper. C = Carbonate precipitation. D = Dolomite precipitation.
1 = Vitriolschiefer Bone-beds, 2 = Blaubank, 3 = Dolomitischen Mergelschiefern and Unteren Dolomiten,
4 = Estherien - Schichten, 5 = Shell sheets in the Upper Lettenkeuper, 6 = Muddy Bone-beds in the Upper Lettenkeuper e.g. Michelbach Bone-Bed.

6.6.5. Environmental model for the Lettenkeuper bone-beds

Examination of the lower part of the Upper Triassic sequence of West Germany (i.e. the Lettenkeuper) shows a regression sequence passing up from the black shales of the Vitriolschiefer into a dolomitic sequence (The Blaubank to Unteren Dolomiten), containing primary carbonate or gypsum crystals (Reif, 1974). The overlying black shales contain thin shell and sand layers and trough cross-bedded sand wedges (1 - 2 m thick), rich in plant fragments (The Estherien-Schichten). These black shales and sandstones are overlain by a sequence of dolomitic marls containing rare stromatolites, black shales and shell beds, the Upper Lettenkeuper. In turn these sediments are overlain by a thick sequence of gypsiferous algal stromatolites in red and green clays, the GipsKeuper. The Lettenkeuper is interpreted as a regression sub-to supratidal sequence in text-fig. 9, deposited in a region of low terregenous sediment input.

Examination of the shell deposits in the Lettenkeuper show them to represent either a liptocenosis or taphocenosis occurring as shell sheets (0.2 - 5 cm thick). The invertebrate composition of these shell sheets and the Lettenkeuper sediments is outlined in Table 10, p.126 Examination of the shell orientations show that 80 - 100% of the shells are orientated concave down. The size distributions of the shells show that shell deposits low in the intertidal zone (e.g. in the Vitriolschiefer) are markedly transported (cf. Antia & Wood, 1977; Alexandrowicz, 1978) while those in the Upper Lettenkeuper are not; thus suggesting that the amount of shell transport decreases up the intertidal zone! Examination of the bone-beds also shows a similar pattern with the percentage of unworn vertebrate remains increasing up the intertidal zone.

6.7. Rhaetic bone-beds

Rhaetic bone-bed deposits have been recorded in Germany, Switzerland, France, Luxemberg, Britain and Poland (Duffin & Gazdzicki, 1977). In West Germany a bone-bed marks the Rhaetic/ Liassic boundary whilst in Britain bone-beds are found in the lower parts of the Rhaetic. Bone-beds from these two countries are perhaps the best known of the Rhaetic bone-beds and were formed on the margin of the Rhaetic sea (text-fig. 10a).

6.7.1. West German Rhaetic Bone-bed

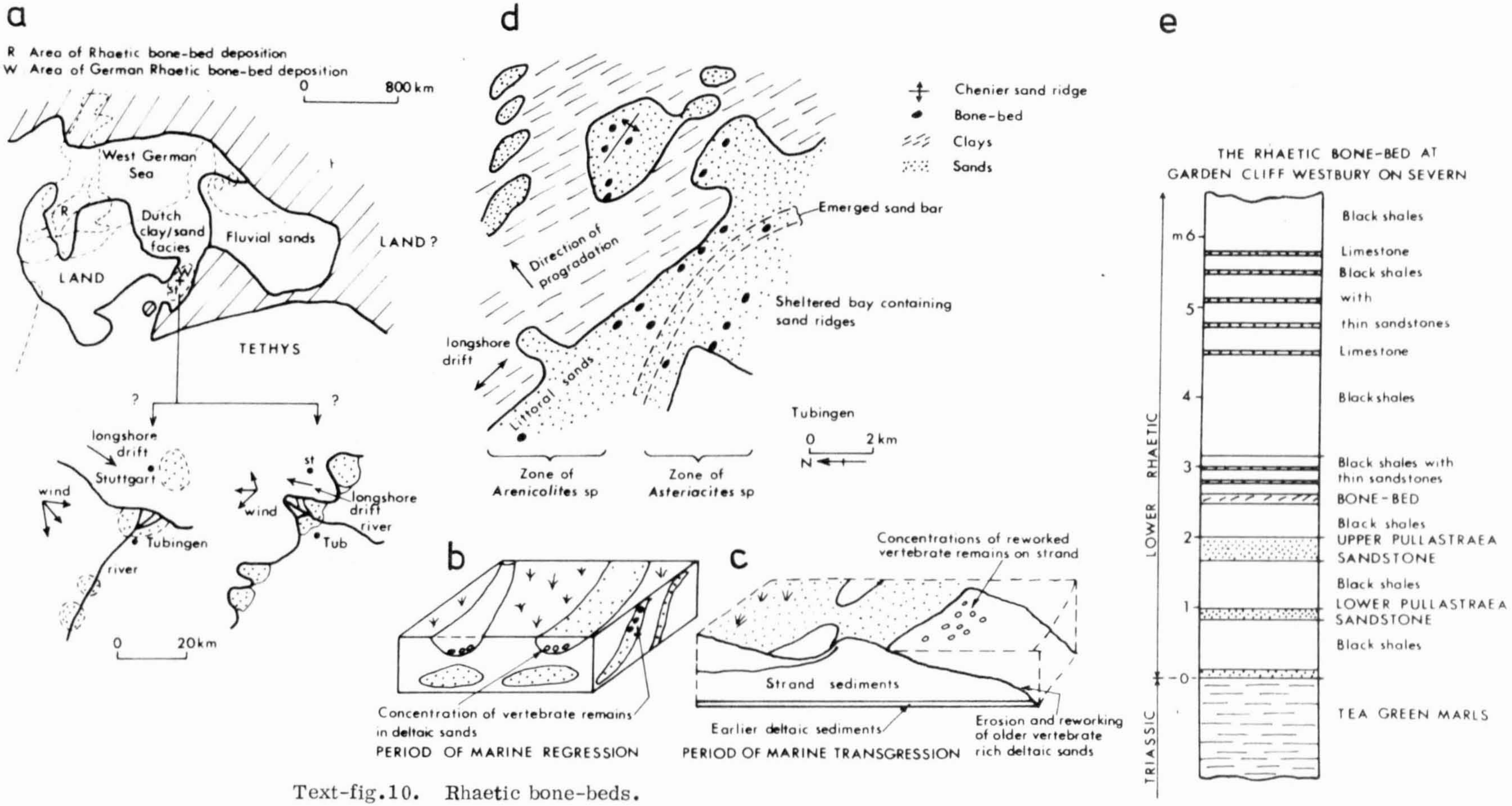
In West Germany the bone-bed (text-fig. 10a) has been extensively described both from a palaeontological (Endlich, 1870; Schmidt, 1928; Huene, 1933; Reif, 1977) and sedimentological (Aepler, 1974) stance. Vertebrate fragments are found in association with a molluscan fauna of *Rhaetavicula contorta* (Geyer & Gwinner, 1968; Aepler, 1974).

The vertebrate remains commonly have a size range 0.125 - 0.25 mm, though fragments in excess of 2 cm in length are known and include worn and unworn remains of the sharks *Hybodus* and *Acrodus*, the dipnoid fish *Ceratodus*, the ganoid fish *Saurichthys* and the reptiles *Triglyphus* and *Microlestes*. (Schmidt, 1928; Geyer & Gwinner, 1968).

During his study of the sedimentology of Rhaetic bone-beds Aepler (1974) observed three different environmental settings for bone-bed deposition, viz:

1. Lagoonal placer deposits,
2. In deltaic deposits during periods of regression,
3. In intertidal chenier plain type sediments deposited during periods of transgression,

and suggested the following model to account for the deposition of the German bone-beds. Aepler (1974) envisaged an initial deltaic model (text-fig. 10b) of sediment deposition in which primary vertebrate deposits were included in lagoonal sediments deposited in small lagoons between channels in a prograding Rhaetic delta during period of stable or falling sea level. Channel switching caused by transported sediment choking the river channels may have preceded the reworking of vertebrate remains in the lagoonal sediments causing them to be redeposited within a sequence of deltaic sands (text-fig. 10b). Subsequent rises in sea level led to a marine transgression. The net outcome of this transgression was a reworking of vertebrate



Text-fig.10. Rhaetic bone-beds.

a = Palaeogeography of the Rhaetic oceans.
b = Regression Delta bone-beds.
c = Transgression Delta bone-beds.
d = Facies distributions in the German Rhaetic intertidal zone.
e = Section through the British Rhaetic Bone-bed.

material in the deltaic sands (text-fig. 10c) and its migration and concentration on a chenier-like coastal plain (text-fig. 10d), containing chenier sand dunes up to 1 m high and 2 to 8 km long. The vertebrate concentrates occur in the sandy facies of the coastal plain and form both uni- and bi-modal deposits with a mean size skewness distribution indicative of a littoral beach or dune sand environment. Two trace fossil faunas have been recorded which appear to be depth stratified (text-fig. 10d). The fauna occurring in the higher part of the intertidal zone is of *Arenicolites*, a U-shaped burrow resembling those produced by *Corophium* in the model intertidal zone. Like *Corophium* its modern ?equivalent, *Arenicolites* occurs on small muddy banks within the zone some 5 - 20 cm high. The lower part of the Rhaetic intertidal or high subtidal zone contains *Asteriacites* (ophorioid nesting traces).

6.7.2. British Rhaetic Bone-Beds

British Rhaetic bone-beds have been recorded in Somerset, Gwent, Glamorganshire, Dorset, Leicestershire, Nottinghamshire, Yorkshire and Northern Ireland (Sykes, 1977; Arkell, 1933). In Scotland vertebrate remains do occur (Tyrrell, 1928), but not in sufficient quantities to constitute a bone-bed. The Rhaetic bone-beds have been the subject of many reviews (e.g. Wickes, 1904; Sykes, 1977; Hamilton, 1977) and are most abundant in the Lower Rhaetic. (Sully and Westbury Beds - Table 12).

Table 12. The divisions of the British Upper Triassic.
(after Kent 1968, Taylor 1968)

	Ostracod Zone	Lithological Unit	Thickness
Upper Rhaetic	*Hungarella moorei*	Watchet Beds	0 - 2.3 m
		Langport Beds	0 - 8 m
		Cotham Beds	0 - 8 m
Lower Rhaetic	*H. bristolensis*	Westbury Beds	0.3 - 15 m
	H. martini		
	Rhombocythere penarthensis	Sully Beds	0 - 4.2 m
'Keuper'		Tea Green Marls	3 - 30 m
		Red marls(undiff)	10 - 170 m

They are contained within a sequence of interbedded black shales, sandstones and limestones (text-fig. 10e). Much of the vertebrate fauna present in the bone-beds and associated strata has been illustrated by Schmidt (1928) and Duffin (1978).

Many theories have been proposed to account for the origin of these bone-beds ranging from a sudden massacre of vertebrates, to a temporary abundance of vertebrate life, to a condensation deposit. Likewise many different environmental models for the Lower Rhaetic have been proposed. These range from deposition in an anoxic subtidal environment (Kendall & Wroot, 1924) through to deposition on an intertidal mudflat (Short, 1904; McKerrow, 1978). The Keuper - Rhaetic - Liassic sediments of Britain are commonly considered to represent a marine transgression, which started in the ?late Keuper (Arkell, 1933).

Prior to this marine transgression, central and southern Britain formed a very extensive sabkha environment (Nickless *et al.*,.1976; Jeans, 1978) which deposited the Keuper Marls and resulted in the formation of evaporite deposits. This period of stable water level and sabkha formation was succeeded by a gradual relative increase in sea level, which led to a marine transgression over the sabka plain from south to north, such that an ostracod zone of the standard Rhaetian sequence is missing from the Nottinghamshire Rhaetic rocks (Anderson, 1964). The absence of this zone does not imply a faunal break at the junction of the Tea Green Marls and the Rhaetic, but rather a later arrival of the transgressive marine sediments in this area.

Commonly the 'start' of the marine transgression is marked by a 2 - 3 cm thick layer of vertebrate rich marl (Richardson, 1911), which is succeeded by 3 - 4 m of unfossiliferous marlstones and may have been deposited in a supratidal environment. The succeeding sediment is a bone-bed containing pebbles of the underlying marl and remains of the fish *Hybodus*, *Acrodus*, *Gyrolepsis* and *Ledidotus* and the mollusc *Rhaetavicula contorta*, and may represent a transported deposit formed low in the intertidal zone. The overlying sediments consist initially of interbedded sandstones and shales containing shell beds of *R. contorta* and *Pleurophorous* in association with ?darwinulid ostracods (Richardson, 1911; Anderson, 1964) which may represent an oligohaline to mesohaline intertidal environment (Morkhoven, 1963). The sands and shales are succeeded by black shales containing interbedded, lenticular bedded and flaser bedded shelly limestones, bioturbated sandstones and bone-beds, including *the* Rhaetic Bone-Bed.

Faunal diversity increases up the sediment sequence, and the fauna includes a number of mesohaline to fully marine ostracods (Anderson, 1964; Morkhoven, 1963), numerous trace fossils (pl.16, fig.c; pl.19, fig.h), the coral *Heterastraea* (Richardson, 1905), the molluscs *Protocardia rhaetica*, *R. contorta*, *Chlamys valoniensis*, *Cardium cloacinum*, and the starfish *Ophiolepis damesii* (Harrison, 1876). In Arran the ?Westbury Beds contain the estherid *Isuara minuata* (Newton, 1901). This latter species occurs, in association with plant debris in the Bristol district (Sollas, 1901) and, in great abundance in the Cotham Beds (Arkell, 1933), which are considered to represent an intertidal deposit (Mckerrow, 1978).

The bone-beds vary in thickness from 0.1 to 15 cm, are locally flaser bedded and consist of dark muddy quartz sands locally enriched in vertebrate fragments (pl.16, figs. f,g,h), coprolites (containing shell gragments, crustacean and vertebrate remains, and quartz grains), and phosphatic nodules.

The vertebrate remains vary from perfect to highly abraded teeth, scales and bones belonging to reptiles, elasmobranch, ganoid and dipnoid fish. The reptile remains present include vertebra of the archosaurian *Rysosteus*, and teeth and bones referable to *Ichthyosaurus* and *Plesiosaurus* (cf. Arkell, 1933; Duffin, 1978). The fish remains include the teeth and fin spines of the hybodont sharks *Hybodus*, *Acrodus* and *Nemacanthus*; the earliest euselachian sharks *Pseudodalatias barnstonensis* (Sykes), (Sykes, 1971, 1974; Reif, 1978); the ganoid fish (primitive boney fish) *Bigeria* and *Gyrolepis* and dental plates of the dipnoid lungfish *Ceratodus*.

It has been suggested (Wickes, 1908; Kendall & Wroot, 1924; Neville, 1967) that the rounded vein quartz pebbles present in the bone-beds could be stomach stones (gastroliths) which were swallowed by marine reptiles to aid digestion (Wieland, 1907).

Many hypotheses have been advanced to account for the bone-beds. These include (1) mass mortality due to the effects of increased salinity as the 'marine' animals entered the hypersaline Keuper lakes (Jukes-Browne, 1892), (2) formation as a storm deposit (Short, 1904; Neville, 1967), (3) concentration due to a reduced rate of sediment deposition (Richardson, 1901; Kendall & Wroot, 1924; Arkell, 1933), (4) concentration due to wave action (Donovan, 1955; Hamilton, 1977), (5) lag concentration resulting from the reworking of vertebrate poor sediments (Duffin & Gazdzicki, 1977) and (6) a mass mortality caused by reduced salinity resulting from an influx of fresh water (Kent, 1968).

The bone-beds are often local in extent (Arkell, 1933) and are highly variable in composition, for example, Short (1904) notes that at Redland (ST 585753) *Acrodus minimus* is the dominant vertebrate, while at Chipping Sodbury and Penarth (ST 186697) *Saurichthys* and *Sphaerodus minimus* are the dominant forms respectively. This variability coupled with the knowledge that in 1867 a violent storm in the Bay of Fundy drove fish into shallow water and onto the shore, so that fish were piled to a depth in excess of 30 cm on the coast, led Short (1904, p.182) and later Neville (1967) to suggest that bone-beds result from storm deposition in shallow coastal waters. The presence of numerous local islands in the Rhaetic sea (Richardson, 1901; Arkell, 1933) some of whose coastlines are closely associated with bone-bed localities (Richardson, 1901; Sykes, 1977) gives credence to this model. The presence in the bone-beds of mudballs (Short, 1904) and bone-bed material infilling sun cracks (Woodward, 1888) appears to confirm a coastal or mudflat depositional site for some of the bone-beds, (Greensmith & Tucker, 1973).

Hamilton (1977) came to the conclusion that the bone-beds are formed as strand line deposits, which have been winnowed and abraded by wave action and shore line currents, and that some of the vertebrate material may have been derived through a reworking of the Keuper sediments. However, it is possible that some of the bone-beds represent subtidal deposits (Duffin, pers. com. 1978).

If Kents (1968) environmental model for the Westbury Beds is accepted here, then the Westbury Beds represented a broad shallow estuarine environment containing small islands, and considerable local variation in temperature, salinity and oxygenation, in which circulation was impeded by widespread growth of aquatic weed. Such an environment is inherently unstable. Fluctuations in any of the physical or chemical variables in the environment (e.g. oxygenation, temperature, salinity, etc) caused by any number of external or internal processes (e.g. a storm, a plankton bloom, etc) could have resulted in a fish mortality and ultimately concentration of the fish remains into a vertebrate sand (bone-bed) of local extent in both subtidal and intertidal environments (Wells, 1944).

6.8. Middle Jurassic bone-beds on the Scottish Island of Eigg (text-fig. 11)

The presence of a bone-bed on the Island of Eigg in the Middle Jurassic *Mytilus* shales of the Great Estuarine Series was first noted by Miller (1858; p. 75 & 219). Later work by Barrow & Tait (in Harker, 1908), Hudson (1962; 1963a, b; 1964; 1966) and Hudson & Harris (in press) has described their faunas and established the bone-beds stratigraphical position.

Hudson (1966) records 3 vertebrate rich (bone-bed) horizons (labelled 1 - 3) which he considers to have been deposited in a coastal lagoon.

Bone-bed 1 (Hugh Millers Reptile Bed)

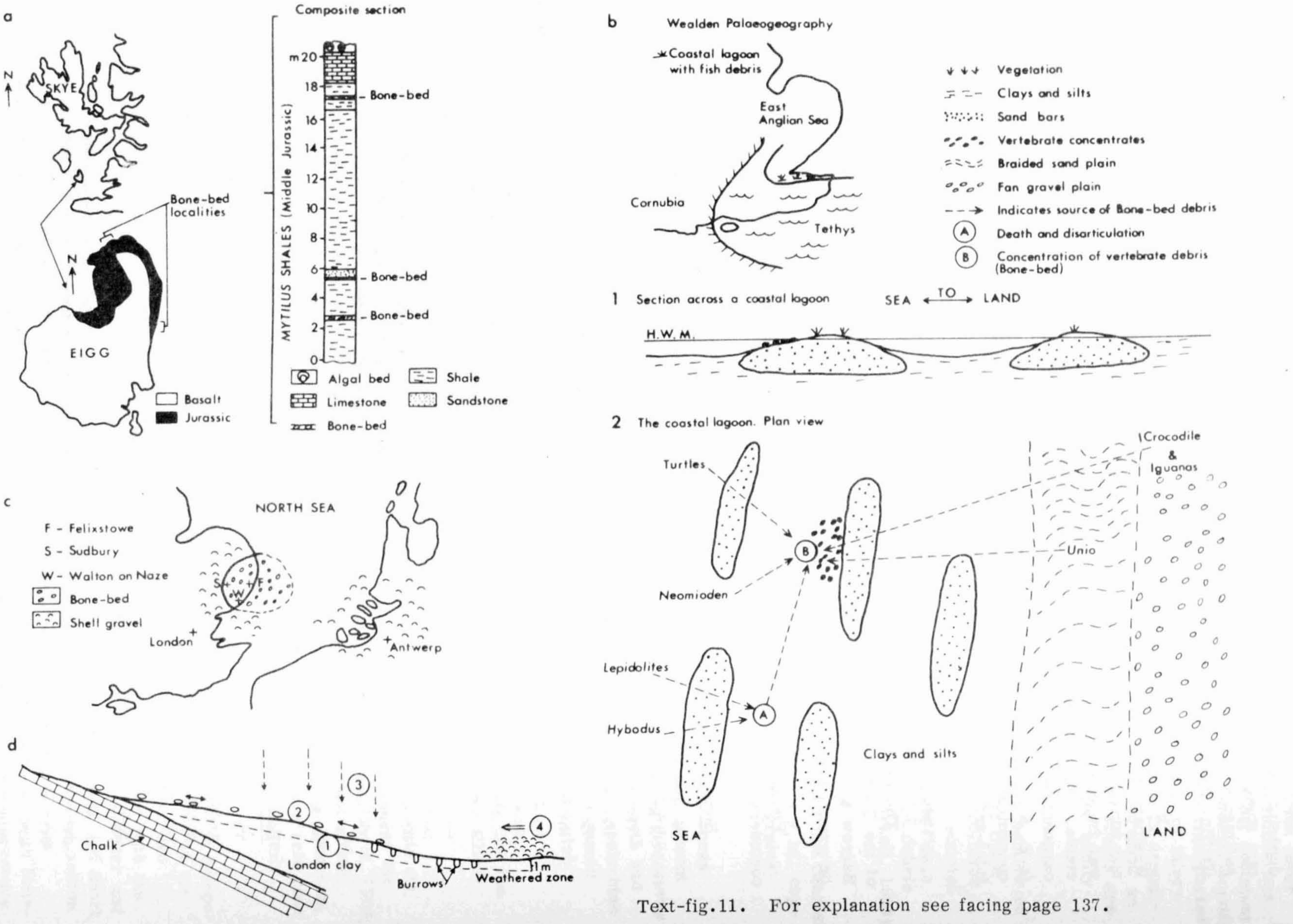
A vertebrate rich dark grey shelly limestone, 15 cm thick, extending for at least 3 km laterally. The vertebrate component is black in colour (?fluorapatite or ?francolite) comprising phosphatic fish teeth, scales and fin spines, and reptilean bones. The dominant fish include the sharks *Hybodus*, *Acrodus* and the holostean *Lepidotus*. The reptile remains include disarticulated specimens of plesiosaurs, turtles, tortoises, crocodiles and pterodactyls. The bones and fish remains are fragmented (Hudson, 1966; p. 276). Secondary pyrite is common throughout the deposit and has replaced some of the shells (e.g. ostracods). The invertebrate shell component of the bone-beds contains abundant small gastropods (*Globularia hebridica*, *Cylindrobullina inermis* and *Tornus praecursor*) and bivalves (*Unio andersoni* and *Mytilus strathairdensis*). Hudson (1963a, b) regards the gastropods as euryhaline species; *Mytilus strathairdensis* is considered (Hudson, 1963a, b) to have lived in brackish marine water (salinity between 16.5 and 9 pp. thousand) and *Unio andersoni* is considered (Hudson, 1963a, b; Tan & Hudson, 1974) to have lived in freshwater (salinity 0.5 - 3 pp. thousand). If this conclusion is correct then postmortum intermixing of brackish and freshwater species must have taken place during the processes forming the bone-bed.

Bone-bed 2 (The Complex Bed)

The lowest parts of the Complex Bed (text-fig. 11) consist of well rounded quartz grains associated with abundant rounded partly pyritised fragments of fish phosphate associated with *Mytilus strathairdensis* and may have been deposited in brackish marine waters (Hudson, 1966).

Bone-bed 3 (The Fish Bed)

A *Mytilus* shell limestone (5 cm thick), containing abundant black phosphatic fish debris (about 10% by volume). This debris consists of fish otoliths and the teeth, spines and scales of the sharks *Hybodus* and *Acrodus*. Most of the sharks teeth are worn and the abundance of *Mytilus* may suggest that the bone-bed was formed subtidaly in brackish marine conditions.



Text-fig.11. For explanation see facing page 137.

6.9. The Wealden Bone-beds (Cretaceous)

Within the Wealden Beds of Britain a number of bone-bed horizons have been recorded (Allen, 1949; 1975). These bone-beds may be described as buff sands, poorly sorted, containing commutated scales, teeth and bones (1 - 45 mm in length) of *Lepidotus* and *Hybodus*; the bones and teeth of reptiles (crocodiles, turtles and iguanas) and teeth of small mammals. They are associated with detritial quartz, glauconite, the casts/moulds of the molluscs *Viviparus*, *Neomiodon* and *Unio*; and abundant ostracod carapaces of *Theriosyrioecum fittoni* (Mantell) (Allen, 1949; 1975; Anderson, 1964).

Originally these deposits were considered to be the product of floods shifting over a subareal deltaic plain, containing scattered evershifting lagoons (Kirkaldy, 1939) and were regarded as freshwater - brackish water estuarine deposits by Allen (1949). However, analysis of the clasts show that the deposits contain multienvironmental components:

1. *Hybodus* is generally considered to be a marine shark (Duffin, pers. com. 1977).
2. *Lepidotus* is found in sediments containing freshwater and marine shells (Allen *et al.*, 1973) and may be a euryhaline form.
3. The reptiles noted could all be found in a littoral or deltaic environment, and the mammals noted were presumably terrestrial.
4. The glauconite is considered to be a derived component from eroded Jurassic strata. The individual glauconite grains represent abraded foraminiferal moulds (Allen *et al.*, 1964).
5. The molluscs noted belong to the following salinity environments:
    (1) *Unio* - fresh water environments (Hudson, pers. com. 1975)
    (2) *Viviparus* - fresh brackish water environments (Allen & Keith, 1964)
    (3) *Neomioden* - marine water environments (Allen *et al.*, 1973)
6. *Theriosynoecum* is a fresh - brackish water ostracod genus (Morkhoven, 1963).

The bone-beds occur as sand lenticles or scour/channel fill deposits on sands in a cyclothemic type sequence:

1. Clay rich in rootlets
2. Bone-beds
3. Cross-bedded sands
4. Ostracod rich dark shales, at base.

This cyclothemic pattern was initially described in terms of an estuarine/deltaic environment (Allen, 1949; 1954), but fits equally well the coastal lagoonal model recently proposed for the Wealden (Allen 1975), text-fig. 11. Using this model the sources of the bone-bed components can be identified and suggest that postmortum faunal mixing due to current and/or wave activity occurred in the Wealden lagoons.

The initial cause of death of the fishes is indeterminable at present though in modern coastal lagoons episodic mass mortalities of fish take place for a variety of reasons every 6 - 14 years (Gunther, 1947).

Elsewhere in the Wealden and on the Isle of Wight, thin layers (0.5 - 3 mm) of fish debris (vertebrae, bones, and scales) are associated with a rich ostracod fauna (observed in conjunction with B.A. Wood).

Text-fig.11. a. The Geology of the Island of Eigg (After Hudson, 1966). b. An environmental model of bone-bed deposition in the Wealden Beds (Modified after Allen, 1975). c. Location map of the Suffolk Bone-Bed. d. Depositional model for the Suffolk Bone-Bed. 1 = The Miocene/Pliocene North Sea sea-floor of London Clay was weathered and eroded by the sea, excavating phosphatic nodules and vertebrate remains within the deposit. 2 = These were then rolled around on the sea-floor to form a remains deposit of both worn and unworn derived fossils. 3 = Contributions to the content of the bone-bed were made from the overlying waters. 4 = The bone-bed was then buried by migrating shell sheets composed of commutated shell fragments.

6.10. The Suffolk Bone-Bed (Lower Pleistocene)

The Suffolk Bone-Bed occurs at the base of the British (East Anglian) Pleistocene Crag deposits (Chatwin, 1937) and may have been the first British deposit in which vertebrate remains were noted (Ralphe, circa. 1236). The bone-bed was mined for phosphate in the nineteenth century, yielding 3,000 to 12,000 tons annually (Reid, 1890). It may be described as a thin (15 to 30 cm thick) coarse-grained quartz sand (grain size 1.5 to 3 mm), containing well rounded sandstone pebbles (Miocene age; 5 - 26 cm in diameter), flint pebbles, bored phosphatised pebbles of London Clay, phosphatised arthropods (e.g. crabs), black phosphatised sharks teeth, rolled bone fragments, fish dental plates, mineralised and porous bone fragments. Most of the phosphatic pebbles are in the size range 1 to 23 cm. A variety of the phosphatic clasts are illustrated in pl.16, figs. h-p.

Examination of the Suffolk Bone-Bed in the Sudbury district, Walton-on-the-Naze and at Felixstowe (text-fig. 11) allow the following generalisation to be made:

1. The bone-bed rests on an uneven erosional surface which cuts across the London Clay, Reading and Thanet Beds, and the Chalk. This erosional surface on the London Clay undulates and contains small shallow scour channels (up to 1 m in width). The surface is underlain by a 1 m thick weathered zone, and is extensively bored (densities varying between 30 and 300 borings per square metre have been observed at Walton-on-the-Naze). The overlying one-bed consists of a coarse quartz sand with some commutated shell debris, infilling the borings and forming a nodule rich vertebrate sand. The phosphatic clasts are well sorted and tend to be concentrated in hollows on the London Clay surface such that one hollow may contain an abundance of cetean fragments and another phosphatic nodules.

2. The phosphatic clasts in the bone-bed are mainly phosphatised nodules of London Clay, 2 - 12 cm long, usually rounded and bored; cetean bones, 1 - 26 cm long, often mineralised and bored; ear and rib bones are almost always mineralised broken rounded and polished; vertebrae were only recorded as unmineralised light porous bone; sharks teeth, 0.5 - 15 cm long, usually black in colour, varying in preservation from perfect to worn and broken teeth, the first parts to be removed by abrasion being the roots; fish remains (0.5 - 4 cm long) as chiefly worn and rounded dental plates; mammal remains (0.5 - 17 cm long) as worn and rounded teeth and bones; and phosphatised arthropods (replaced crabs, etc).

3. The shell gravels overlying the bone-bed commonly contain articulated, slightly gaping, derived valves of *Glycimeris glycimeris* (pl.18, figs.i-j). The size distributions of these valves suggest that they may represent an indigenous fauna in the shell gravels (Appendix - 1, p.167) which was buried alive during the last major reworking of the shell gravel by currents, etc. (cf. Thomas, 1975). If *G. glycimeris* hasn't changed its life habits since the Pliocene then it is probable that the bone-beds were buried by actively moving, aerobic current swept subtidal shell deposits formed in a shallow shelf sea, between -15 and -75 m O.D. cf. Tebble (1966); Thomas (1975).

4. The bone-bed is overlain by the Pliocene Coralline Crag in the Aldebury/Orford district (Boswell, 1928) and the Pleistocene Red Crag at Walton-on-the-Naze and elsewhere (Reid, 1890; Harmer, 1900; Boswell, 1928; 1929). Thus suggesting that the top of the bone-bed is diachronous.

6.10.1. Depositional model for the Suffolk Bone-Bed (text-fig. 11c, p.136)

The Bone-bed contains a variety of phosphatic clasts derived from a variety of sources. Some of the material has been derived from the London Clay (e.g. the phosphatic nodules, phosphatised arthropods, some sharks teeth and bone), while the remainder has been derived either from now eroded Miocene/Pliocene deposits or has been concentrated in the bone-bed from a contemperaneous fauna. An interpretation of the bone-beds depositional history may be presented as follows:

1. The Miocene/Pliocene sea floor had a base of London Clay which was weathered to a depth of 1 m below the sediment water interface. This clay deposit was extensively attacked by biogenic activity and scouring currents, to produce an extensively scoured and bored surface to the sea floor. Phosphatic clasts derived from the London Clay were concentrated into a well sorted lag deposit on the surface of this sea floor (text-fig. 11). Many of the clasts show signs of marked abrasion. The phosphatic nodules show evidence of 'Pholad' borings (pl.16, fig.k) and along with the cetean rib bones small ($\leq$ 1 cm) circular depressions (pl.16, fig.i) which may represent barnacle or limpet 'borings'. Thus the bone-bed contained a rich indigenous fauna, only known from its trace fossils, which colonised a variety of hardground substrates represented by the London Clay, the phosphatic nodules and the vertebrate fragments.

2. Contributions of cetean bones, sharks teeth, phosphatic nodules and fish remains were made to the accumulating bone-bed from the surrounding waters abd the eroded sediments above the London Clay (text-fig.11).

3. This bone-bed or vertebrate sand was eventually buried by migrating shell sheets (text-fig. 11).

Throughout the Red Crag vertebrate remains (rolled sharks teeth, rolled bone and fish dental plates) can be found usually as well rounded black sand grains (1 - 4 mm) and more rarely as readily identifyable remains. Occasionally thin (1 - 2 cm thick) bone-beds are present and contain about 20% quartz sand, 50 - 60% shell, and 20 - 30% vertebrate remains. At Brightwell (GR TM251431, near Ipswich) the bone-bed's vertebrate component is in the size range 0.3 - 4.0 cm and consists of 60% rolled and worn black bone fragments, 30% rolled and worn blue grey and black sharks teeth and 10% rolled and worn fish dental plates. These bone-beds represent lag concentrations on shell gravel surfaces and contain both indigenous and London Clay derived vertebrate remains.

6.11. The Rockall Bone-Bed (Recent)

The continental slope sediments around Rockall contain a historically important bone-bed (Lyell, 1834, vol. 3). However, it still remains unsampled in modern times.

Recently, June/July 1978, Dr. G.E. Farrow and colleagues have sampled the continental slope sediments around Rockall. Although they did not record Lyell's bone-bed, they did record a very high concentration (? < 5%) of fish otoliths in the sediment (Farrow, oral com., 1978; Pye, oral com., 1978).

Samples of the sediment and otoliths given to the author for examination, by Dr. Farrow, from 57° 9.2'N 14° 57.6' sampled at a depth of 387 m may be described as follows:

1. The sediment is a carbonate sand (mean grain size 300μ), rich in foraminifera which dominate the sediment (≃ 65%) and occur as whole shells and fragments. Bivalve shell fragments are common (≃ 10%). Lithic fragments, quartz grains and sponge spicules are present (≃ 25%) and the former vary from elongate subangular large (1 mm long) grains to compact high spherocity well rounded grains (300 μ long). The remainder of the sediment is made of a mixture of otoliths, shells and small pebbles.

2. Large shells and shell fragments are present (≥ 1 cm). The bivalve shell material recorded mainly belonged to the bivalve genus *Artica*. All the bivalve shells were disarticulated (about half were fragmented) and on all specimens the external ornament was starting to flake off. Most of the remaining shell debris belonged to calcareous tube worms. Some of these fragments were colonised by fenestrate bryozoans. Many of the shell fragments contain ?fungal and ?algal micro-borings.

3. Within the sediment are a number of pebbles. These fall into two groups - lithic rock fragments (5 - 20 mm in length) and lithified rounded carbonate pebbles (2 - 6 cm) with the same composition as the surrounding sediment (i.e. that of a foraminiferal quartz sand).

   The lithic rock fragments are sometimes colonised by calcareous tube worms, while the more friable carbonate pebbles may be extensively bored. Boring diameters vary from ≤1 to 5 mm.

4. The fish otoliths present in the sample examined vary in colour from a dull pink to white to cream to cream-grey. They vary in length from 6 mm to 14 mm with a mean length of 9.1 mm. 30% of the otoliths are chipped. They show no evidence of abrasive rounding, though some chip marks are present. The weathering features of the otoliths may be described as follows: (A detailed account of clast weathering in bone-beds is given in section 7)

Five stages of weathering were observed on the otoliths and these stages can be related to those recorded by Behrensmeyer (1978) and summarised in section 7. The proportions of otoliths in each weathering stage, at a number of points in the Rockall Trough, sampled by Dr G.E. Farrow and co-workers, are given in Table 13.

The weathering stages observed form a continuum ranging from unweathered to highly weathered, implying that material is being continually added to the deposit at a very slow rate and that individual otoliths may have lain on the sediment surface for more than 15 years and possibly for several hundred.

Table 13. Weathering stages present on Otoliths from the seabed near Rockall. Key to the weathering stages is given in Table 14, p.142.

Locality	Depth	Sample Size	Weathering Stage					
			0	1	2	3	4	5
57° 9.2'N 14° 57.6'W	387 m	21	0	31	69	0	0	0
57° 36.9'N 14° 0.2'W	175 m	1	100	0	0	0	0	0
57° 28.0'N 13° 07.2'W	270 m	11	9	18	54	18	0	0
57° 3.3'N 15° 0.5'W	250 m	21	9	19	62	5	5	0
57° 34.9'N 14° 30.8'W	220 m	40	13	23	50	10	5	0
57° 37.7'N 13° 37.3'W	180 m	28	18	21	36	14	11	0
57° 19.5'N 14° 51.6'W	260 m	11	18	27	27	27	0	0

The unweathered otoliths range from unbored to highly bored material, containing gastropod radula marks which often expose a very complex network of fungal borings present just below the otolith's surface (pl.17, fig.6). Some of these otoliths show a mosaic pattern of cracks under the light microscope (weathering stage 1). Most of these cracks are not visible under the Scanning Electron Microscope. However, some of them appear to form the initial sites of concentric outer layer peeling (pl.17, fig.a, weathering stage 2). This peeling becomes very marked on some of the more weathered otoliths (pl.17, figs. d, e) and eventually patchyly exposes the inner structure of the otolith (pl.17, fig.c, weathering stage 3). Continued weathering further degenerates the otoliths exposing just the internal structure and often forming deep cracks (weathering stage 4).

Thus it could be inferred from the data presented here that the Rockall Bone-Bed described by Lyell (1834) may present a similar set of weathering, abrasion and microbiotal features and represent a condensation deposit.

6.12. Bone-bed genesis - a conclusion

Bone-beds have been recorded in a variety of subtidal and intertidal environments and tend to form as lag concentrates. They may result from the reworking of older, vertebrate poor, sediments to produce a secondary bone-bed or form from a primary concentration of drifting vertebrate material on the seafloor. However, examination of the bone-beds through time suggests that no single model of bone-bed genesis will suffice and that for most of the deposits insufficient data exists for a valid environmental model of bone-bed genesis to be made.

7 - Bone weathering

Vertebrate remains, including bones, decompose on and in the sediment. This decomposition, which forms a normal part of nutrient recycling within the oceans, also determines whether or not a bone will survive to become fossilised. The fossilisation of bone is therefore dependant on the intensity and rate of the various destructive processes and the chance for permanent burial prior to total destruction. In this context the term bone embraces teeth and scales.

At the present time little is known about how these processes affect bones or how they may consequently bias the vertebrate fossil record in bone-beds. As a result most authors (e.g. Wells, 1944; Reif, 1969, 1971, 1976; Aepler, 1974; Allen, 1974a; Sykes, 1977; Antia & Whitaker, 1978) have ignored suggestions (e.g. Behrensmeyer, 1978) that some grain size biasing in vertebrate assemblages could be due to weathering. Instead they regard wave and current activity as the primary cause of grain size biasing in bone-beds.

Following recent advancements in the study of the bone weathering, Behrensmeyer (1978, p.151) has outlined a time related six stage scale of bone weathering, and the features characterising each weathering stage are listed in Table 14, p. 142. The establishment of a time related scale of bone weathering has important implications for future bone-bed research because it enables:

1. an estimate of the time interval between the death of the fish and the permanent burial of the bone-bed to be made;
2. it enables the amount of grain size biasing in a bone-bed caused by weathering to be assessed;
3. it may help to determine whether or not a given bone-bed developed as a 'direct' result of a mass mortality.

For the purposes of this study a preliminary examination of bone-bed weathering has been made by the author, to assess the practical value of weathering as a tool for the interpretation of bone-beds.

Table 14. Weathering stages observable in a variety of bone-beds.
Weathering stages 0 - 5 are explained as follows (after Behrensmeyer, 1978):

0 Vertebrate material shows no sign of cracking or flaking due to weathering.

1 Cracks parallel to the fibre structure appear. In some bones a mosaic cracking of surfaces may develop.

2 Outermost thin concentric layers of cyamine show flaking, usually with cracks in the initial stages.

3 The internal fibrous structure starts to appear patchily over the 'bone' surface.

4 The fibrous structure of the 'bone' is clearly visible. Weathering has penetrated the inner cavities, cracks are open and have splintered or rounded edges.

5 Vertebrate material falls apart, in situ, is fragile, and easily broken by moving.

		Weathering Stages					
		0	1	2	3	4	5
1.	Upper Whitcliffe Bone-Beds (Ludlow Series, Upper Silurian, U.K.)						
	Thelodus spp. (scales)	+	+	-	-	-	-
	Logania sp. (scales)	+	+	-	-	-	-
	?*Gomphonchus* sp. (spine fragments)	-	+	+	-	-	-
2.	Ludlow Bone-Bed (Downton Series, Upper Silurian, U.K.)						
	Thelodus spp.	+	+	+	-	-	-
	Logania spp.	+	+	-	-	-	-
	?*Gomphonchus* sp. (fragments)	-	+	+	+	-	-
	Gomphonchus sp. (scales)	+	+	-	-	-	-
	Gomphonchus sp. (fin spine)	-	-	+	+	+	-
	Nosteolopis sp. (scale)	+	+	-	-	-	-
	Cythaspis sp. (headshield)	-	-	-	+	+	+
3.	Lower Downton Castle Sandstone Bone-Beds (Downton Series, Upper Silurian, U.K.)						
	Thelodus spp. (scales)	+	+	+	-	-	-
	Logania sp. (scales)	+	+	-	-	-	-
	Gomphonchus sp. (fragments)	-	+	+	+	-	-
	Gomphonchus sp. (fin spine)	-	-	+	+	+	-
	Sclerodus sp. (headshield)	-	-	-	-	+	+
	Cythaspis sp. (headshield)	-	-	-	+	+	+
	Climatius sp. (fin spine)	-	-	+	+	+	-
4.	Temeside Bone-Bed (Downton Series, Upper Silurian, U.K.)						
	Thelodus sp. (scales)	-	-	+	+	-	-
	Logania sp. (scales)	-	+	+	-	-	-
	Climatius sp. (fin spine)	-	-	-	+	+	+
	Gomphonchus sp. (fin spine)	-	-	-	+	+	-
	Gomphonchus sp. (fragments)	-	-	-	+	+	-
	Cythaspis sp. (fragments)	-	-	-	+	+	-
5.	Muschelkalk Grenzbonebed (Middle Triassic, West Germany)						
	Acrodus spp. (teeth)	-	+	+	-	-	-
	Hybodus sp. (teeth)	-	+	+	-	-	-
	Gyrolepis sp. (scales)	-	-	+	+	-	-
	Colobodus sp. (scales)	-	+	+	+	-	-
	Saurichthys sp. (teeth)	-	+	+	-	-	-
	Reptilian bones	-	-	-	+	+	-
	Acrodus sp. (fin spine)	-	-	+	+	-	-
6.	Lettenkeuper Bone-Beds (Upper Triassic, West Germany)						
	Acrodus spp. (teeth)	-	+	+	-	-	-
	Acrodus sp. (jaw bone)	-	-	-	+	+	-
	Gyrolepis sp. (scales)	-	-	+	+	-	-
	Reptilian bones	-	-	-	+	+	-
7.	Rhaetic bone-beds (British and West German)						
	Acrodus sp. (teeth)	-	+	+	+	-	-
	Hybodus sp. (teeth)	-	+	+	-	-	-
	Rysosteus	-	-	+	+	-	-
	Reptilian bones	-	-	+	+	+	-
8.	Suffolk Bone-Bed (Miocene/Pliocene, U.K.)						
	Sharks teeth var.	-	+	+	+	-	-
	Cetean bones	-	-	-	+	+	-
9.	Crag bone-beds (Lower Pleistocene, U.K.)						
	Sharks teeth var.	-	+	+	+	-	-
	Fish dental plates var.	-	+	+	-	-	-
	Cetean bones	-	-	-	+	+	-

7.1. Weathering versus abrasion

Bone weathering produces a distinctive set of external features which can be grouped in a number of stages (Table 14). These stages differ from those produced by abrasion in the following respects:

abrasion can produce small chip marks on the grain surface (pl.14, fig.i; 16, fig.f),
and/or, remove large chunks off the ends of bone surface (pl.14, fig.o; 16, fig.g),
and/or, round individual grain surfaces (pl.15, fig.l; 16, fig.d).

Weathering features are always superimposed on the grain, thus a highly rounded and abraded bone fragment need only show (pl.15, fig. j) features associated with weathering stage 1 (cracks parallel to the fibre structure), while a less abraded scale (pl.14, fig.o) can show features associated with weathering stage 2 (outermost thin layers of cyamine start to peel off). Similar weathering stage 2 features are also present on highly abraded bone fragments (pl.16, fig.d). Weathering can also aid abrasive processes. Another example, (pl.16, fig.b) illustrates a tooth which, having reached weathering stage 1, split along a crack parallel to its fibre structure during an abrasion phase in its depositional history. Thus weathering and abrasion both produce distinctive features which may be superimposed on each other.

7.2. Assessing differential weathering

Differing bone types can weather at slightly different rates (Behrensmeyer, 1978, p.153). Similarly differential weathering can occur on a single bone. In the latter case the bones are usually more weathered on the lower than the upper surfaces (Behrensmeyer, 1978, p.154). As a result of the weathering process, vertebrate material could be preferentially destroyed and removed from the deposit it was accumulating in, by weathering, thus biasing the grain size distributions of the deposit. Individual grains could be partially destroyed after accumulation in the bone-bed, before the bone-beds burial, thereby altering the grain size distribution of the deposit. In the Suffolk Bone-Bed sharks teeth, which have had their pulp destroyed by weathering, are present (pl.16, fig.j).

If different types of vertebrate material weather at different rates, an examination of bone-bed cumulates should support this hypothesis. Nine bone-beds were examined with this point in mind and the weathering stages of the various vertebrate components are noted in Table 14.

The results show that in each bone-bed teeth and scales are comparatively unweathered, while fin spines, headshields and endoskeletal bones were markedly weathered. Thus suggesting that either the scales and teeth were more recent additions to the vertebrate faunas or that different vertebrate material weathered at different rates. Since it is unreasonable to suggest that the scales and teeth are more recent additions to the faunas (Reif, 1969; 1971), it is probable that the different types of vertebrate material weathered at different rates. The cyamine outer coatings of the teeth and scales may have helped to shield them from rapid weathering and disintegration, while the less well protected and more fibrous fin spines and bones may have weathered more rapidly.

In all the bone-beds examined (Table 14) it was the least weathered fraction which dominated the fauna. However, since this fraction (usually teeth and scales) represents the smallest grain size elements of the fauna, it may result from a mixture of both current activity, concentrating the finer particles into a unimodal assemblage, and weathering removing some of the less resistant (and sometimes larger) clasts.

The data presented here (Table 14) seems to support Behrensmeyer's (1978) hypothesis that bone weathering can result in or could casue grain size biases in vertebrate assemblages. The palaeoecological implications of such an observation are that prior to compositional reconstructionsof marine vertebrate faunas from a fossil assemblage, the extent of faunal depletion due to weathering has to be assessed. Further, a unimodal vertebrate condensation deposit forming in a region of slack current activity could owe its unimodality to weathering rather than sedimentological processes. Thirdly, in some marine vertebrate deposits (e.g. the Ludlow Bone-Bed, the Muschelkalk Grenzbonebed and the Rhaetic Bone-Bed) algal and fungal borings are commonest on the least weathered components of the deposit (Antia & Whitaker, 1978; Duffin, pers. com., 1978) perhaps indicating a substrate preference for poorly weathered material which is likely to be on the sea bed for a long period of time.

7.3. Weathering rates

A scale (Table 14) of bone weathering rates has been outlined by Behrensmeyer (1978, p.157). However, in the previous section it was noted that different bone types weather at different rates. Thus for Behrensmeyer's (1978) scale of weathering rates to have any palaeoecological or sedimentological significance a scheme of correction factors has to be developed. To obtain a correction factor value it was assumed that fin spines and bone weather at the same rate in the sea, as those in terrestrial lake bed and soil environments (Table 15).

The dominant weathering peak of these bones was then tabulated against the dominant weathering peak of the teeth and scales (Table 15). From this tabulated data the possible residence time on the sediment surface represented by each weathering stage present on the teeth and scales was determined (Table 15). This theoretical relationship between weathering stage and time may bear little similarity to the real time intervals represented by the weathering scales, but can be used to indicate a relative time sequence of events in the fossil record.

7.4. On the significance of weathering stages and rates

An analysis of the relative abundances of each of the various weathering stages on fish scales in a number of bone-beds should give an estimate of the minimum residence time of the scales on the substrate surface. This would then help to determine if the bone-beds formed as the result of a single mortality, a number of mortalities, a condensed sequence, or from the reworking of vertebrate poor sediments.

In each bone-bed listed in Table 16, 150 - 400 thelodont scales were examined for weathering features using a scanning electron microscope and the results recorded in Table 14. The scales were extracted using 30% acetic acid solution from their matrix, then washed in 30% hydrogen peroxide solution. In a test sample taken from the Ludlow Bone-Bed at Ludlow it was shown (Table 16) that there is no significant differences in the weathering features observed on the acid treated scales and on untreated scales present in the sediment.

Most of the results listed in Table 16 show a low incidence of weathering stage 1. The relatively high abundance of weathering stage 0 (up to 94%) may suggest that most of the scales had a low residence time on the substrate (≤ 6 years) but the presence of weathered scales in low abundances in stage 1 and 2 suggests that some scales may have been drifting on the substrate surface for more than 6 years.

The presence of abundance peaks in weathering stage 0 and 2 (e.g. Rushall) suggests two major 'short' periods of scale addition to the substrate separated by at least 6 years and may be longer than 15 years (i.e. not a steady inflow of vertebrate material). If the scale assemblages do result from mass mortalities, than 6 - 15 years may indicate the minimum time interval between any two mass mortalities (cf. 7 years recorded between recurring recent mass mortalities by Gunter, 1947).

In almost all the intertidal and shelf bone-beds (i.e. those of the Whitcliffe Beds, Ludlow Bone-Bed, Downton Castle Sandstone) the least weathered scales dominate the faunas, suggesting a fairly rapid (≤ 6 years) burial. However, it is interesting to note (Table 16) that the scales in higher intertidal sediments (Ludlow, Downton Castle Sandstone, Bone-beds 11 and 12) are dominated by weathering stage 2, indicating a longer preburial residence period on the substrate. A similar situation is observable in the supratidal bone-beds of the Temeside Beds (Table 16).

7.5. Bone weathering - conclusions

Since work on bone weathering and its application is in its infancy, readers are advised to regard the ideas and statements in this section as hypotheses which need testing through additional research on recent and fossil bones. However, the points which should be emphasised are that bone weathering can reveal information regarding the differential weathering and destruction of clasts, and important data concerning the relative residence times of the vertebrate material on the substrate and the genesis of the deposit.

Table 15. Weathering stages related to the number of years since the death of the animal
Column 1 and 2 based on Behrensmeyer (1978)

Possible range in years since death of the fin spines and bones	Weathering stage present on the fin spines & bones	Weathering stage present on scales and teeth corresponding to equivalent stage on fin spines, etc.	Weathering stage present on scales and teeth	Possible range in years since death of the teeth and scales
0 - 1	0	0	0	0 - 6
0 - 3	1	0	1	4 - 15⁺
2 - 6	2	0/1	2	6⁺ - 15⁺
4 - 15⁺	3	0/1/2/3	3	6⁺ - 15⁺
6 - 15⁺	4	1/2/3	4	
6 - 15⁺	5	1/2/3	5	

Table 16. Percentages of Thelodont scales in each weathering stage.

		Weathering Stage (%)				Locality
		0	1	2	3	
Ludlow Bone-Bed (L.B.B.)		85	10	5	-	Ludlow
		87	9	4	-	Ludlow (untreated)
		64	26	10	-	Aston Munslow
		62	24	14	-	Shipton
		73	16	11	-	Brockton
		82	11	7	-	Corfton
		69	6	25	-	Corfton Lane
		92	4	4	-	Deepwood
		94	4	2	-	Ashley Moor
		44	7	49	-	Rushall
		78	10	12	-	Longhope
		62	6	32	-	Priors Frome
		86	8	6	-	Lye
		19	6	75	-	Usk
		89	8	3	-	Downton
Downton Castle Sandstone Bone-Bed	1. 1 cm above L.B.B.	58	6	36	-	Ludlow
	2. 3.3 cm " "	76	3	21	-	Ludlow
	3. 4.9 cm " "	85	1	14	-	Ludlow
	4. 7.1 cm " "	81	4	15	-	Ludlow
	5. 8.9 cm " "	80	2	18	-	Ludlow
	6. 9.1 cm " "	87	5	8	-	Ludlow
	7. 9.7 cm " "	92	4	4	-	Ludlow
	8. 10.1 cm " "	93	6	1	-	Ludlow
	9. 24.2 cm " "	86	5	9	-	Ludlow
	10. 53.7 cm " "	84	4	12	-	Ludlow
	11. 110.2 cm " "	24	5	71	-	Ludlow
	12. 124.9 cm " "	30	4	65	1	Ludlow
Bone-bed	1. 1.2 cm " "	84	6	10	-	Aston Munslow
	2. 3.6 cm " "	82	9	9	-	Aston Munslow
	3. 5.9 cm " "	86	7	7	-	Aston Munslow
Temeside Shales	(1) 60 cm below T.B.B.	3	4	86	7	Ludlow
	(2) Temeside Bone-Bed (T.B.B.)	-	5	93	2	Ludlow
	(3) 25-60 cm above T.B.B.	4	4	82	10	Ludlow
Upper Whitcliffe Beds (Upper Ludlow)						
		79	11	10	-	Longhope
		96	1	3	-	Ludlow
		38	18	46	-	Aston Munslow

8 – Diagenesis of bone-beds

In the analysis of bone-bed sediments it is important to consider the diagenesis of the sediment, since many grains change shape, size and composition during diagenesis.

8.1. Diagenetic clasts

Biogenic clay or mud pellets produced by the ingestion and excretion of mud by organisms may be transported as detritial particles (Pryor, 1975) and included in bone-bed sediments. These pellets are commonly altered either at the sediment water interface to glauconite (Wilson & Pittman, 1977) or in the sediment pore waters to collophane (Burnett, 1977; Weaver & Beck, 1977). The pellets are ovoid in outline and may contain an internal structure of concentric rings. They have a low grain and bulk density and will be coarser-grained than the associated quartz, fish debris and rock fragments in the sediment. Examples of deposits containing the two types of pellets are a glauconitic bone-bed at the top of the Downton Castle Sandstone in the Brookend bore hole (Cave & White, 1978), and some phosphatic pebble horizons in bone-beds in the Lower Downton Castle Sandstone. In the latter instance the phosphate, collophane, has replaced (Antia & Whitaker, 1978) the authigenic clay structure of the pellet (pl.18, fig.a). Two stages, at least, of diagenesis of the pellet are indicated, by the formation of a honeycomb clay structure in the pellet (before inclusion in the bone-bed?) and by replacement of the honeycomb structure by phosphate (carbonate apatite), possibly after inclusion in the bone-bed.

These diagenetic phosphatic pellets can be distinguished from small phosphorite nodules by an S.E.M. examination of their internal structure. Since phosphorite nodules are formed of a crystalline sheet arrangement of apatite (Baturin & Dubinchuk, 1974), they can be distinguished from coprolites on their gross morphology and internal structure.

Pyrite framboids (pl.18, fig.b) and nodules present in the Ludlow, Lyraun Cove and Rhaetic Bone-Beds are also of an authigenic nature since the nodules are unstable outside an anoxic sulphorous environment (Berner, 1970). Studies on the formation of such clasts suggest that they form in anoxic sulphurous pore waters during early sediment diagenesis at two or more centimetres depth below the sediment water interface and sometimes take years to grow (Berner, 1970; Elverhi, 1977).

Bone-bed residues occasionally contain equidimensional grains (up to 3 mm long) formed of fibrous layers of clays (pl.18, fig.g) approx. 8 - 40 μ in length. These grains formed as authigenic clay linings or infillings of pores in the sediment (Wilson & Pittman, 1977).

8.2. Diagenetic grain coatings

Grains within a stabilised bone-bed sediment (e.g. the Ludlow Bone-Bed) may become coated with layers of authigenic clays or cryptocrystalline silica (Antia & Whitaker, 1978). The clay coatings, which may assume a crystalline, platy or honeycomb structure (pl.18, figs. c,d,e) are absent from grain contacts and coat all grains regardless of composition (Hayes, 1970). In later diagenesis idiomorphic quartz overgrowths may attach to the quartz nuclei (pl.18, fig.h) and cover the clay coatings prior to carbonate sedimentation (pl.18, fig.l).

8.3. Diagenetic alteration of grain shape and texture

Diagenetic reactions can alter a quartz grain's shape and texture by either clay or silica plastering (Antia & Whitaker, 1978) such that grain surfaces become smooth or secondarily complex. Silica plastering is a form of grain growth in which the grain is coated by a thin sheet-like layer of silica. Silica plastering on a grain's surface (pl.15, figs. d,e; 18, fig.h) can alter its net shape. Examples of bone-beds containing diagenetically enlarged quartz grains are the Rhaetic and Muschelkalk Bone-Beds (text-fig. 8; pl.15, figs. d,e; 18, fig.f).

Thus examination of the diagenetic history of a bone-bed can explain the presence of glauconitic, phosphatic, pyrite and clay clasts and give an indication of the depositional geochemical environments of the pore waters. Study of the effect of diagenesis on individual grains can aid studies on the genesis of bone-beds (Antia & Whitaker, 1977; 1978) and markedly affect skewness kurtosis and modal values of grain size distributions (Wilson & Pittman, 1977; also text-fig. 8e). Failure to consider the diagenetic history of the sediment can lead to unnecessary complex and erroneous environmental models for bone-bed genesis.

9 – The ecological importance of primary bone-beds

Bone-beds comprised largely of fish debris and formed by the disarticulation and concentration of fish remains which died in a catastrophic event are considered here to represent primary deposits. Such mortalities may occur in a given area at rates varying between 1×10^4 to 1.4×10^4 per million years (Gunter, 1947) and each catastrophe may kill more than a milliard (10^9) fish (Brongersama-Sanders, 1956). In all instances these massive fish deaths, however caused, will 'accurately' reflect the composition of the fish schools in mortalities reaching the benthos (David, 1944) and this composition is reflected in the disarticulated scale faunas resulting from a mortality (David, 1944).

At the present time individual schools of fish vary in size from 0.5×10^1 to 5×10^9 individuals; occupy regions varying in length from 0.1×10^1 to 1×10^6 m, and occur in densities ranging from 0.1 to 30 individuals per m^3. Individual schools may be monospecific or polyspecific, though schools of many species tend to have an unstable composition and readily disband into monospecific groups (Truskanov & Shcherbino, 1963; Radakov, 1973).

Hence a study of bone-bed distribution and composition in an area containing many bone-beds could yield information regarding the composition of schools over an area and the variation of school composition with time.

Similarly, examination of scale lengths and growth lines can give useful full information regarding the natality, mortality and survivorship of a species, in addition to information regarding the effect of predation on the species (Antia & Wood, 1977). Study of these changes can yield information regarding increased or decreased predator pressure on a species, over a period of time. For example, Nikolskii (1969, p. 192) has shown that as the predation rates on a fish species increase, the mean scale size of the fish species decrease.

10 – The microbiotas of bone-beds

All sand grains form potential microbial environments and may support a rich biota of bacteria, algae, diatoms, hydroids, fungi, ciliates and other organisms. Of these forms only diatoms and calcareous algae contain preservable skeletons (pl.19, fig.a). Endolithic algae leave recognisable traces in the form of dissolution pits (pl.19, figs.b,e) and borings (pl.19, figs. f-h). Most other forms (e.g. fungi and bacteria) are only likely to be preserved if they are replaced during very early sediment diagenesis by silica or apatite (Antia & Whitaker, 1978).

Two important forms present in modern microbiotas, the diatoms and calcareous algae, are considered to have appeared in the middle to late Mesozoic and are therefore unlikely to be represented in early Mesozoic or Palaeozoic microbiotas.

At the present time different grain types will contain differing microbiotas and ecological successions (Sieburth, 1975). Commonly the biotas are patchily distributed over a grain's surface (Meadows & Anderson, 1966; 1968). Thus:-

1. a piece of wood will show an algal, bacterial, hydroid succession
2. a plastic bottle will show a diatom, bacterial, hydroid succession
3. an oolith will show an algae, bacteria, fungi succession (Bathurst, 1975)
4. carbonate grains from a high energy environment show an algal, diatom, bacteria, succession
5. quartz grains show a diatom, algae, bacteria, ciliate succession. If the grain is from a low energy environment it may be completely covered by its biota. If it is from a high energy environment then the biota is confined to hollows on the grain's surface. If it is from a very high energy environment then only bacteria are present on the grain's surface.

6. vertebrate grains will show a rod-shaped bacteria, algae succession. Both forms use the grain as a source of nutrition (Sieburth, 1975).

In most of these microbiotas the primary colonists produce a nutrient fish film on the surface of the grains which can support bacteria on an originally non-nutrient surface.

In the fossil record, evidence from borings has established the presence of a microbiota on many carbonate grains (Bathurst, 1975) and filaments (?fungal) have been recorded on quartz grains in association with bored vertebrate grains in the British Silurian (Antia & Whitaker, 1978).

An S.E.M. examination of vertebrate quartz and shell grains from the subtidal and intertidal environments represented by the West German Muschelkalk Grenzbonebed (pp.124-128) and the British Upper Silurian Bone-beds (pp.115-119) allowed the following observations and conclusions to be made about the patterns of microbial succession.

10.1. Muschelkalk Grenzbonebed (subtidal deposit formed below wave base)

No evidence of a microbial fauna was noted on the scales or quartz grains (7 specimens examined). However, endolithic algal borings were recorded on the surface of one tooth (pl. 15, fig.k). Possible algal borings have also been recorded in teeth (Duffin, 1977; pers.com.) and shell fragments (pl.19, figs.f-h) from the Rhaetic Bone-Bed. (Bone-bed 15 Blue Anchor Bay - Richardson, 1911).

10.2. Upper Silurian bone-beds

Two types of Upper Silurian bone-beds occur, subtidal and intertidal, both contain different non-vertebrate clast types and thus a potentially different microbial fauna.

1. Subtidal bone-beds formed above wave base consist of thin shell/vertebrate debris sheets containing a fine grained (5 - 50μ) quartz sand component and a diagenetic carbonate matrix. Study of 1000 - 2000 shell fragments from such deposits revealed 3 fragments all of *Lingula* sp. which had been bored by ?endolithic algae. Examination of the Thelodont scales showed that 10 - 15% of them contained algal dissolution pits and of these about 20% contained endolithic algal borings. This suggests that algae formed the dominant "preservable" elements of the fauna of the microbiota.

2. In the low intertidal zone (e.g. the Ludlow Bone-Bed) both the vertebrate and quartz grains contain evidence of microbial colonisation (Antia & Whitaker, 1977; 1978). The quartz grains may contain silicified ?fungal filaments (pl.18, fig.k) with a distinctive branching pattern. Small silica granules patchily distributed on the surfaces of some of the quartz grains could be interpreted as silicified coccoid bacteria and some of the silicifilament mats present may represent filamentous bacteria. Development of quartz overgrowths on the quartz grains (including their epibiota) is considered to have taken place within a few years of the sediments burial in the substrata, possibly within 20 cm of the sediment water interface.

   Since the filaments cover all surfaces on the grain (i.e. are not confined to cracks and hollows on the grain) it is likely that they represent a colonisation stage within the substratum, which is post sediment stabilisation, within say, 20 cm of the sediment water interface (Meadows & Anderson, 1968).

   An S.E.M. examination of 54 quartz grains revealed 48 containing fungal filaments. Of these latter grains 2 contained "coccoid bacteria" and one "filamentous bacteria". The bacterial colonies are restricted to localised areas, forming colonies of several hundred individuals.

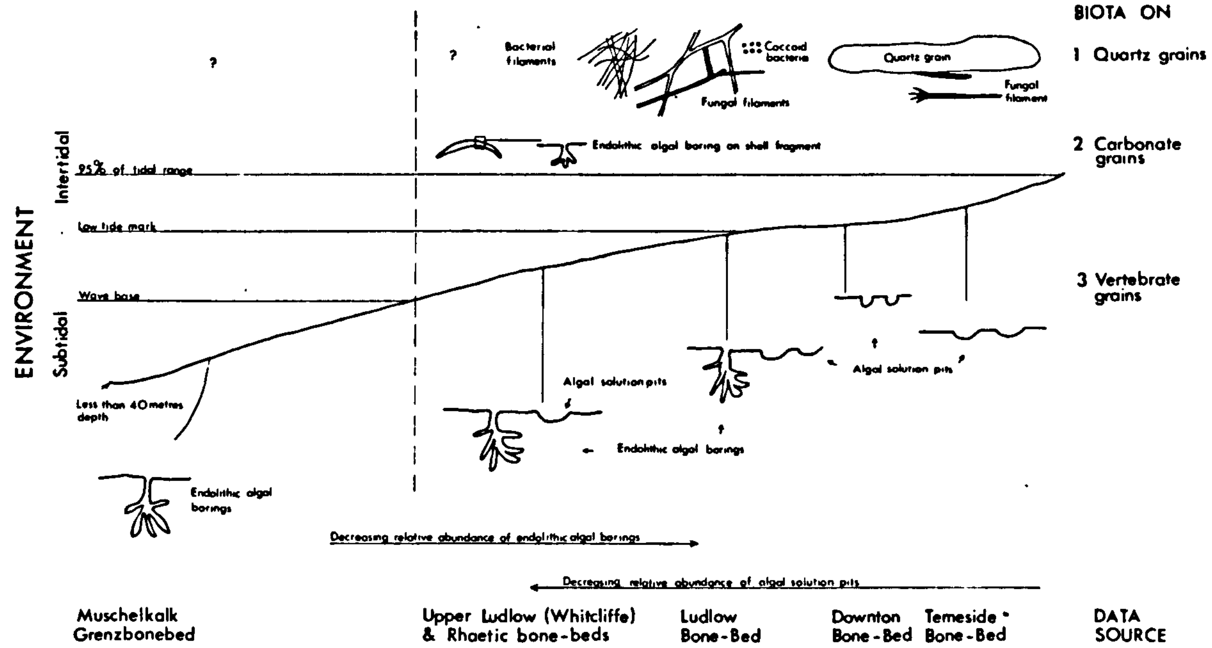
The fungal filaments are found over the entire surface of the grains and probably (in view of their widespread distribution) represent the first stages in the subsurface colonisation of these grains in an anoxic alkali environment. Later succession stages allowed colonisation by coccoid bacteria and bacterial filaments.

The invertebrate fragments show no evidence of microbes though presumably they once contained them, though the phosphatic nodules do contain phosphatised filaments of ?fungal origin (pl.19, fig.k).

The vertebrate fragments contain evidence of algae on their surfaces, both in the form of algal dissolution pits (pl.19, figs. d,e) and algal borings. These latter borings have a larger diameter and are less regularly distributed than histological pores revealed by abrasion.

5 - 40% of the thelodont scales contain algal dissolution pits (termed here Algal Form A) and of these less than 10% contain endolithic algal borings. Thus suggesting that an initial colonisation of the grains by Algal Form A was followed by a subsequent colonisation by endolithic algae, (Algal Form B).

3. Vertebrate and quartz grains from the high intertidal/supratidal zone (e.g. The Temeside Bone-Bed) were examined under the S.E.M. for a remnant microbial fauna. Of 280 thelodont scales examined only one contained evidence of a microbiota in the form of algal dissolution pits and one quartz grain contained two silicified ?fungal filaments (pl.19, figs. i-l) differing in style from those recorded in the Ludlow Bone-Bed.



Text-fig. 12. A general environmental synthesis of microbial biotas in the Lower Palaeozoic and Early Mesozoic bone-beds.

10.3 General microbial synthesis (text-fig.12)

In this section a new and speculative field of bone-bed analysis has been examined and the conclusions drawn regarding the distribution and diversity of (Lower Palaeozoic and early Mesozoic) microbial biotas within the subtidal and intertidal environments may be applicable to bone-beds other than those investigated. It is expected that diatoms and calcareous algae will form an important part of the microbiota of late Mesozoic and Cainozoic bone-beds and may in part replace some of the non-calcareous algal forms.

The main microbial points to arise out of this study were the comparative distribution of algal dissolution pits and algal borings on vertebrate grains. The former are located in tidally influenced environments with the latter preferring subtidal marine environments. Occasionally, early silicification on the surface of grains has preserved fungal and bacterial elements of the microbiota. Such elements appear to increase in diversity and abundance along a supra littoral to subtidal transect, though this may be a reflection of their preservation potential.

Further study of microbiotas in both recent and fossil sediments should lead to a greater understanding of the early geochemical and diagenetic conditions prevalent in the subsurface (0 - 20 cm depth) environments presented by fossil vertebrate sands (bone-beds).

Since Swinchatt (1969) has shown that sediments containing endolithic algal borings are most likely to be formed at depths of less than 40 m, and that abundant borings indicate formation at less than 18 m depth, it is unlikely that bone-beds formed in waters deeper than 40 m will contain algal borings on static grains.

11 — Discussion and Conclusions

This paper has sought to first produce a criterion for an improved bone-bed classification utilising both modern sedimentological terminology and the variation in the phosphatic composition of the bone-beds.

This classification, though descriptive, is important since it gives an insight into the sedimentology and diagenesis of the bone-beds. For example, the phosphatic nodules present in the bone-beds described here originate from a number of different sources:

1. Faecal droppings forming coprolites. An example of a bone-bed in which most of the phosphatic pebbles originate as faecal droppings is the U.K. Rhaetic Bone-Beds (Duffin, oral com. 1978; Mayall, oral com. 1978).

2. Phosphate nucleation and replacement of clays around suitable sites (e.g. phosphatic shells and crinoid stems). This type of nodule originated in an anoxic subsurface environment in the pore waters of a loosely consolidated sediment. Their presence may indicate that the bone-bed includes material which has been derived from the reworking of sediment containing phosphate nodules formed during early diagenesis. A good example of this type of deposit is the Ludlow Bone-Bed at Longhope (text-fig. 5). Many of these nodules contain *Trypanites* borings indicating post formational exposure.

3. Phosphate nodules are present as broken abraded internal moulds and casts of gastropods, bivalves and brachiopods. These nodules frequently contain phosphate pseudomorphing after clays (Antia & Whitaker, 1978). An example of a bone-bed containing this type of phosphatic nodule is the Ludlow Bone-Bed (Antia & Whitaker, 1978).

4. Some bone-beds (e.g. the Beyrichienkalk Bone-Beds) contain phosphate centres to the shells and carapaces of ostracods and gastropods. These nodules form during post depositional diagenesis.

5. In some bone-beds (e.g. the Upper Ludlow Bone-beds of the Brookend borehole, Cave & White (1978), bored mud pebbles are present which contain a surface rim of phosphate. This rim also lines the sides of borings into the pebbles. This phosphatisation occurred during bone-bed diagenesis. The phosphate was probably derived from partial solution of fish debris in the bone-bed.

The genetic distinction of the phosphatic nodules in bone-beds into predepositional diagenetic nodules, coprolites and postdepositional diagenetic nodules is important because it allows elimination of clasts from the original vertebrate sand cumulate. Similarly a removal of the diagenetic coatings on individual grains will enable a 'true' grain size and shape analysis of bone-beds to be made.

It is envisaged that future bone-bed sedimentological work will concentrate on scanning electron microscope analysis of abrasive features on bone-bed sediments and grain size and shape analysis.

The former analytical method has received some attention (Antia & Whitaker, 1977, 1978; Whitaker & Antia, 1978). The latter has been used by Reif (1969; 1971) to prove and dispute (Antia, this paper text-fig. 8) prefossilisation of the Muschelkalk Grenzbonebed. Weight, density, shape, rollability (a property of particles which utilises size, shape and density) and grain settling times are important properties which can influence the dynamic behaviour of sand grains during the transport and deposition of a bone-bed. Common sense dictates the belief that rounder and more spherical grains should be better transported in bottom traction (cf. MacCarthy, 1933). However, recent studies suggest that this belief may be erroneous (Winkelmolen, 1971) and that a comparative analysis of grain size and rollability could help to determine how a bone-bed formed and the source of its various components. (Passega, 1964; 1977; Winkelmolen, 1971; 1978; Veenstra and Winkelmolen, 1976).

The preliminary investigations outlined here suggest that a study on the syndepositional weathering of vertebrate clasts can reveal valuable information regarding, the relative weathering rates of different clast types, the relative residence time on the sediment surface of individual clast types and the genesis of the bone-bed.

The investigation of the distribution of bone-beds throughout the geological record suggests that bone-beds may mark major unconformities (e.g. Suffolk Bone-Bed) or para continuities (Devonian Ohio Bone-Beds). They may occur as discontinuous conformable deposits within a sediment sequence (e.g. British Upper Silurian Bone-beds). Thirdly, they commonly develop in estuarine environments and occasionally form in association with phosphorites on the continental shelf in regions of nutrient upwelling.

Although this study has reviewed the formation of some bone-bed deposits it is *not* comprehensive - other bone-beds exist but remain poorly described at the present time. Examples of these poorly described bone-beds are the Permian bone-beds of the U.S.A. (Parrish 1978), the deltaic Middle Jurassic bone-beds of Thailand (Ridd, oral com. 1978), the numerous otolith beds of the Cainozoic (Malz, 1978a, b), the Lower Devonian bone-beds of Spitzbergen (Goujet and Blieck, 1977) and those of the Lower Muschelkalk of Poland (Liszkowski, 1973).

Although bone-bed research is in its infancy, despite its early start, pre-1236, a number of conclusions regarding the findings and direction of bone-bed researches can be made:

1. Research indicates that no single mode of bone-bed formation will suffice.
2. Detailed examinations of bone weathering, bone-bed sedimentology and diagenesis can reveal important genetic and ecological information.
3. Future bone-bed research should concentrate on the sedimentology and faunas across individual bone-beds instead of treating them in isolation. In doing so they will re-appraise the various models of bone-bed genesis and the techniques for determining the genesis of individual deposits.

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13 - References

AEPLER, R.	1974. Der Rhätsandstein von Tübingen - ein Kondensiertes Delta. *N. Jb. Geol. Paläont. Abh.*, vol.142, pp.113-162.
ALEXANDROWICZ, S.W.	1978. A Quantitative study on the origin *Dreissena polymorpha* shell accumulations in Szczecin Bay, Baltic Sea. *Bull. Acad. Pol. Sci.*, vol.25, pp.75-82.
ALLEN, J.R.L.	1974a. Sedimentology of the Old Red Sandstone (Siluro-Devonian) in the Clee Hills Area, Shropshire, England. *Sedimentary Geology*, vol.12, pp.73-167.
ALLEN, J.R.L.	1974b. Studies in fluviatile sedimentation: implications of pedogenic carbonate units, Lower Old Red Sandstone, Anglo-Welsh outcrop. *Geol. Jl.*, vol.9, pp.181-208.
ALLEN, J.R.L. & FRIEND, P.E.	1968. Deposition of the Catsgill facies; Appalachian Region with notes on some other Old Red Sandstone Basins. *Spec. Pap. Geol. Soc. Amer.*, vol.106, pp.21-74.
ALLEN, P.	1949. Notes on Wealden Bonebeds. *Proc. Geol. Ass.*, vol. 60, pp.275-283.
ALLEN, P.	1954. Geology and Geography of the London - North Sea Uplands in Wealden times. *Geol. Mag.*, vol.91, pp.498-508.
ALLEN, P.	1975. Wealden on the Weald - a new Model. *Proc. Geol. Ass.*, vol.86, pp.389-437.
ALLEN, P. & KEITH, M.L.	1964. Carbon isotope ratios and palaeosalinities of Purbeck - Wealden carbonates. *Nature*, vol.208, pp.1278-1280.
ALLEN, P., DODSON, M.H. & REX, D.C.	1964. Potassium - Argon dates and the origin of Wealden glauconites. *Nature*, vol.202, pp.585-586.
ALLEN, P., KEITH, M.L., TAN, F.C. & DEINES, P.	1973. Isotopic ratios and Wealden environments. *Palaeontology*, vol.16, pp.209-221.
ANDERSON, P.W.	1964. Rhaetic Ostracoda. *Bull. Geol. Surv. G.B.*, No. 21, pp.133-174.
ANDRUSSOW, N.	1893. Einige Resultate der Tiefseeuntersuchungen im Schwarzem Meere. *Mitt. Geogr. Ges. Wien.*, vol.36, pp.373-393.

ANTIA, D.D.J. 1977. A comparison of diversity and trophic nuclei of live and dead Molluscan faunas from the Essex Chenier Plain, England. *Paleobiology*, vol.3, pp.404-414.

ANTIA, D.D.J. & WHITAKER, J.H. McD. 1978. A scanning electron microscope study of the genesis of the Upper Silurian Ludlow Bone Bed. In Whalley, W.B. (Ed.) *Scanning electron microscopy in the study of sediments*, pp.119-136. Geoabstracts Ltd., Norwich, England.

ANTIA, D.D.J. & WOOD, B.A. 1977. Some aspects of the Palaeoecology of the E_1b zone of the Edale Shales (Namurian) in the Edale Valley, Derbyshire. *Mercian Geol.*, vol.6, pp.179-196.

ARCHANGUELSKI, A.D. 1927. On the Black Sea sediments and their importance for the study of sedimentary rocks. *Bull. Soc. Nat. Moscou*, n.s., vol.35, sect. geol., vol.5, pp.199-289.

ARKELL, W.J. 1933. *The Jurassic system in Great Britain.* Clarendon Press, Oxford, 681p.

AUST, H. 1969. Lithologie, Geochemie and Paläoutologie des. Grenzbereichs Muschelkalk-Keuper in Franken. *Abh Naturwiss. Ver. Würzberg*, vol.10, pp.3-155 Würzberg.

BACHMANN, G.H. & GWINNER, M.P. 1971. Nordwurttemberg. *Sammlung Geologischer Führer*, No.54.

BACHRA, B.N., TRAVTZ, O.R. & SIMON, S.L. 1965. Precipitation of Calcium carbonates and phosphates - III; the effect of magnesium and fluoride ions on the spontaneous precipitation of calcium carbonates and phosphates. *Arch. Oral. Biol.*, vol. 10, pp.731-738.

BAKUN, A. 1978. Guinea current upwelling. *Nature*, vol.271, pp.147-150.

BATHURST, R.G.C. 1975. *Carbonate sediments and their diagenesis.* Elsievier, 2nd Ed., 658p.

BATURIN, G.N. 1969. Authigenic Phosphate concretions in recent sediments of the South West African Shelf. *Doklady Earth Sci.* Sections, vol.189, pp.227-230.

BATURIN, G.N. 1970. Recent authigenic phosphorite formation on the South West African Shelf. *Inst. Geol. Sci., U.K.*, Rept. No. 70/13, pp.87-97.

BATURIN, G.N. 1971. Stages of phosphorite formation on the seafloor. *Nat. Phys. Sci.*, vol.232, pp.61-62.

BATURIN, G.N. & DUBINCHUK, V.T. 1974. Electron Microscope study of Oceanic phosphate rocks. *Doklady Earth Sci.* Sections, vol.218, pp.237-240.

BATURIN, G.N., MERKULOVA, K.I. & CHALOV, P.I. 1972. Radiometric evidence for the recent formation of phosphatic nodules in marine shelf sediments. *Marine Geology*, vol.13, pp.37-41.

BEEVERS, C.A. & McINTYRE, D.B. 1946. The atomic structure of fluorapatite and its relation to that of teeth and bone material. *Min. Mag.*, vol.27, pp.254-257.

BEHRE, C.J. & JOHNSON, J.H.	1933. Ordovician and Devonian fish horizons in Colorado. *Am. Jl. Sci.* 5th ser., vol.25, pp.477-486.
BEHRENSMEYER, A.K.	1978. Taphonomic and ecological information from bone weathering. *Paleobiology*, vol.4, pp.150-162.
BERNER, R.A.	1969. Chemical changes affecting dissolved calcium during the bacterial decomposition of fish and clams in seawater. *Marine Geology*, vol.7, pp.253-274.
BERNER, R.A.	1970. Sedimentary pyrite formation. *Am. Jl. Sci.*, vol.268, pp.1-23.
BOSWELL, P.G.H.	1928. The geology of the country around Woodbridge, Felixstowe and Orford. *Mem. Geol. Surv. Eng. & Wales.* Sheets 208 and 225, H.M.S.O. London, 80p.
BOSWELL, P.G.H.	1929. The geology of the country around Sudbury (Suffolk). *Mem. Geol. Surv. Eng. and Wales.* Sheet 206, H.M.S.O. London, 91p.
BOUCOT, A.	1975. *Evolution and extinction rate controls.* Elsievier. 427p.
BRANSON, E.B.	1916. The lower Embar of Wyoming and its fauna. *Jl. Geol.*, vol. 25, pp. 639-664.
BRAY, J.T., BRICKER, O.P., & TROUP, B.N.	1973. Phosphate in the interstitial waters on anoxic sediments; oxidation effects during sampling procedure. *Science*, vol.180, pp.1362-1364.
BROECKER, W.S.	1974. Interstitial water studies, Leg. 15 - introduction and summary. In Heezen, B.E., MacGregor, I.G. *et al. Initial reports of the deep sea drilling project*, vol.15. pp.1069-1073; vol.20, pp.751-756.
BRONGERSMA-SANDERS, M.	1957. Mass mortality in the sea. In Hedgepath, J.W. (ed) Treatise on marine ecology and palaeoecology, vol.1, Ecol., *Mem. Geol. Soc. Amer.*, 67.
BRONGERSMA-SANDERS, M.	1949. On the occurrence of fish remains in fossil and recent marine deposits. *Bijdragen Tot Die Dierkinde.* vol.28, pp.65-76.
BROOKS, R.A., PRESLEY, B.J. & KAPLAN, I.R.	1968. Trace elements in the interstitial waters of marine sediments. *Geochim Cosmochim. Acta.*, vol.32, pp.397-414.
BROTZEN, F.	1933. Erster Nachweis von Unterdevon im Ostseegebiete durch Konglomeratgeschiebe mit Fischreste *Zeitschr. f. Geschiebeforschung*, vol.9, pp.55-63.
BURNETT, W.C.	1974. *Phosphorite deposits from the seafloor off Peru and Chile.* Radiochemical and geochemical observations concerning their origin. University of Hawaii. Ph.D. thesis. 164p.
BURNETT, W.C.	1977. Geochemistry and origin of phosphorite deposits from off Peru and Chile. *Bull. Geol. Soc. Am.*, vol.88, pp.813-823.

BURNETT, W.C. & VEEH, H.H. 1977. Uranium - series disequilibrium studies in phosphorite nodules from the west coast of South America. *Geochim. Cosmochim. Acta.*, vol.41, pp.755-764.

BURNETT, W.C., VEEH, H.H. & SOUTAR, A. 1973. Geochemistry and radiometric ages of sea floor phosphorites from the continental margin of Peru and Chile. *Abstr. Geol. Soc. Am.*, with programme, vol.5, pp.18-19.

BURNETT, W.C. & GOMBERG, D.N. 1977. Uranium oxidation and probable subaerial weathering of phosphatised limestone from the Pourtales Terrace. *Sedimentology*, vol.24, pp.291-302.

CALEF, C.E. & HANCOCK, N.J. 1974. Wenlock and Ludlow marine communities in Wales and the Welsh Borderlands. *Palaeontology*, vol.17, pp.779-810.

CAVE, R. & WHITE, D.E. 1971. The exposures of Ludlow rocks and associated beds at Tites Point and near Newnham, Gloucestershire. *Geol. Jl.*, vol.7, pp.239-254.

CAVE, R. & WHITE, D.E. 1978. Stratigraphy of the Brookend (Vine Farm) Borehole. *Ludlow Research Group Bull.*, No.25, pp.44-45.

CHALLINOR, J. 1967. *A dictionary of Geology* 3rd ed., University of Wales Press Cardiff, 298p.

CHATWIN, C.P. 1937. East Anglia and Adjoining Areas: *British regional Geology Series.* H.M.S.O. London, 91p.

CHERNS, L. 1977. *The palaeoecology of the Lower Leintwardine of the Welsh borderlands and Wales.* Ph.D. Thesis. Glasgow University.

COCKS, L.R.M., HOLLAND, C.R., RICKARDS, R.B. & STRACHAN, I. 1971. A correlation of Silurian rocks in the British Isles. *Geol. Soc. London, Spec. Rep.* No.1, pp.103-136.

CONKIN, J.E. 1969. Bone Beds in the Middle Devonian Delaware Formation of central Ohio. *Abstr. Geol. Soc. Am.*, North central meeting p.7.

CONKIN, J.E. & CONKIN, B.M. 1975. Middle Devonian Bone Beds and the Columbus-Delaware (Onondagan-Hamiltonian) contact in central Ohio. *Bull. Am. Pal.*, vol.67, pp.99-122.

CONKIN, J.E., CONKIN, B.M. & LIPCHINSKY, Z.L. 1973. Middle Devonian (Hamiltonian) Stratigraphy and Bone Beds on the east side of the Cincinnati Arch in Kentucky: Part 1. - Clark, Madison and Casey counties. *Univ. Louisville Studies in Palaeontology and Stratigraphy*, No. 2, 44p.

CONKIN, J.E., CONKIN, B.M. & LOWRIE, D.J. 1972. Middle Devonian Bone Beds in Ontario. *Abstr. Geol. Soc. Am.* North-central section, Dekalb, Ill., 314p.

COPELAND, M.J. 1960. Ostracoda from the Upper Silurian Stonehouse Formation, Arisaig, Nova Scotia, Canada. *Palaeontology*, vol.3, pp.93-103.

COPELAND, M.J. 1964. Stratigraphic distribution of Upper Silurian Ostracoda, Stonehouse Formation, Nova Scotia. *Bull. Geol. Surv. Canad.*, vol.117, pp.1-13.

CRESSMAN, E.R. & SWANSON, R.W. 1964. The stratigraphy and Petrology of the Permian Rocks of South Western Montana. *U.S. Geol. Surv. Prof. Paper* 313-C, pp.275-569.

DANA, J.D. 1858. *A system of Minerology*, 4th ed., Appleton, London, 534p.

D'ANGLEJAN, B.F. 1967. Origin of marine phosphorites off Baja California. *Marine Geol.*, vol.5, pp.15-44.

D'ANGLEJAN, B.F. 1968. Phosphate diagenesis of carbonate sediments as a mode of in situ formation of marine phosphorites: Observations in a core from the eastern Pacific. *Canadian Jl. Earth Sci.*, vol.5, pp.81-87.

DAPPLES, E.C. 1967. Diagenesis in sandstones. In Larsen, G. & Chilingar, G.V. (ed.). *Diagenesis in sediments*, pp.91-125.

DAVID, L.R.I. 1944. Use of fish scales in Micropalaeontology. *Carneg. Inst. Washington Publ.* 551, pp.25-43.

DAVID, L.R.I. 1947. Significance of fish remains in recent deposits off the coast of Southern California. *Bull. Am. Assoc. Petrol. Geol.*, vol.31, pp.367-370.

DAVID, L.R.I. 1956. Fishes (other than Agnatha). *Mem. Geol. Soc. Am.*, No.67, pp.999-1010.

DAVIS, D.S. 1963. Some effects of the severe winter 1962/1963 on the Blackwater Estuary. *Central Electricity Research Laboratories Lab. Note* No. RD/L/N/85/63, 7p.

DEER, W.A., HOWIE, R.A. & ZUSSMAN, J. 1962. *Rock Forming Minerals*, vol.5, *Non silicates.* London.

DONOVAN, D.T. 1955. *Mesozoic.* In MacInnes, C.M. & Whittard, W.F. (eds) *Bristol and its adjoining countries.* Brit. Assoc. Adv. Sci. pp.23-28.

DROVER, J.I. 1971. Magnesium - iron replacement clay minerals in anoxic marine sediments. *Science*, 172, pp.1334-1336.

DUFFIN, C.J. 1978. Collections and collectors of note. 4. The Bath Geological Collections. f, The importance of certain vertebrate fossils collected by Charles Moore: An attempt at scientific perspective. *Geol. Curators Group News letter*, vol.2, pp.59-67.

DUFFIN, C.J. & GAZDZICKI, A. 1977. Rhaetian fish remains from the Tatra Mountains. *Acta Geologica Polonica.*, vol.27, pp.333-348.

ELLES, G.L. & SLATER, I.L. 1906. The Highest Silurian rocks of the Ludlow District. *Jl. geol. Soc. Lond.*, vol.62, pp.195-220.

ELVERHI, A. 1977. Origin of framboidal pyrite in clayey Holocene sediments and in Jurassic black shale in the North Western part of the Barents Sea. *Sedimentology*, vol.24, pp.591-595.

ENDLICH, F.M. 1870. *Das Bone-Bed Wurttembergs.* Dissertation. Tübingen University. 28p.

FREY, W.R., VOORHIES, M.R., & HOWARD, J.D. 1975. Estuaries of the Georgia Coast U.S.A. Sedimentology and Biology VIII. Fossil and Recent skeletal remains in Georgia estuaries. *Senckenbergania marit.*, vol.7, pp.257-295.

FOERSTE, A.F. 1906. The Silurian, Devonian and Irvine formations of east-central Kentucky. *Kentucky Geol. Surv. Bull.*, vol.7, pp.1-369.

FORBES, C. 1858. On a quantity of Crabs thrown up on a beach in Payta Bay. *Jl. geol. Soc. Lond.*, vol.14, p.294.

GAILITE, L. 1972. Environmentally controlled assemblages of Downtonian Ostracodes in the East Baltic Area. Eesti Teaduste Akadeemia Toimetised. 21 *Koide Keema Geoloogia* part 4, pp.351-357 (in Russian).

GEYER, O.F. & GWINNER, M.P. 1968. *Einfuhrung in die Geologie von Baden - Wurttemburg.* 2. Auflage. Schweizerbart'sche Verlag. Stuttgart. 228p.

GLIMCHER, M.J. & KRANE, S.M. 1968. The organisation and structure of bone and the mechanism of calcification, pp.69-251. In Gould, B.S. (ed.) *Treatise on collagen*, vol.2, *Biology of Collagen* Part B. Academic Press, London.

GOLDBERG, E.D. & PARKER, R.H. 1960. Phosphatised wood from the Pacific Sea Floor. *Bull. Geol. Soc. Am.*, vol.71, pp.631-632.

GOULD, H.R. & McFARLAN Jr., E. 1959. Geological history of the Chenier Plain, South Western Louisiana. *Trans. Gulf. Coast. Ass. Geol. Soc.*, vol.9, pp.261-270.

GOUJET, D. & BLIECK, A. 1977. La faune de vertebres de l'horizon "Vogti" (Groupe de Red Bay, Spitsberg). Comparison avec les autres faunes ichthyologiques du Devonien inferieur europeen. *C.R. Acad. Sc. Paris* Series D, vol.116, pp.1513-1515.

GREENSMITH, J.T. & TUCKER, E.V. 1967. Morphology and evolution of inshore shell ridges and mudmounds on modern intertidal flats, near Bradwell, Essex. *Proc. Geol. Ass.*, vol.77, pp.329-346.

GREENSMITH J.T. & TUCKER, E.V. 1973. Peat balls in late-Holocene sediments of Essex, England. *Jl. Sed. Pet.*, vol.43, pp.894-897.

GREENSMITH, J.T. & TUCKER, E.V. 1975. Dynamic structures in the Holocene Chenier Plain setting of Essex, England. In Hails, J. & Carr, A. (eds.) *Nearshore sediment dynamics and sedimentation*, pp.251-272.

GREENSMITH, J.T. & TUCKER, E.V. 1976. Major Flandrian transgressive cycles, sedimentation and palaeogeography in the coastal zone of Essex, England. *Geol. Mijnbouw*, vol.55, pp.131-141.

GROSS, W. 1947. Die Agnathen und Acanthodier des obersilurischen Beyrichienkalks. *Palaeontographica*, vol.96A, pp.91-158.

GROSS, W. 1967. Uber Thelodontier - Schuppen. *Palaeontographica*, vol. 127A, pp.1-67.

GROSS, W. 1971. Downtonische and Dittonische Acanthodier - reste des Ostseegebietes. *Palaeontographica*, vol.136A, pp.1-82.

GULBRANDSEN, R.A. 1969. Physical and chemical factors in the formation of marine apatite. *Econ. Geol.*, vol.64, pp.365-382.

GUNTER, G. 1941. Death of fishes due to cold on the Texas coast, January 1940. *Ecology*, vol.22, pp.203-208.

GUNTER, G. 1945. Some characteristics of ocean waters and the Laguna Madre. *Texas Game and Fish.* vol.3, pp.21-22.

GUNTER, G. 1947. Catastrophism in the sea and its palaeontological significance, with special reference to the Gulf of Mexico. *Am. Jl. Sci.*, vol.245, pp.669-676.

GWINNER, M.P. & HINKELBEIN, K. 1976. Stuttgart and Umgebung. *Sammlung Geologischer Führer*, No.54.

HALSTEAD, L.B. & TURNER, S. 1973. Silurian and Devonian Ostracoderms. In Hallam, A. (ed.) *Atlas of Palaeobiogeography*, Elsevier, London, pp.67-79.

HAMILTON, D. 1977. *Aust Cliff.* In Savage, R.J.G. (ed) *Geological escursions in the Bristol District.* University of Bristol Press. pp.110-118.

HARKER, A. 1908. The geology of the small isles of Inverness-shire. *Mem. Geol. Surv. Scot.*, 210pp.

HARMER, F.W. 1900. The Pliocene Deposits of the East of England - Part II: The Crag of Essex (Waltonian) and its relationship to that of Suffolk and Norfolk. *Jl. geol. Soc. Lond.*, vol.56, pp.705-744.

HARRISON, W.J. 1876. On the Occurrence of the Rhaetic Beds in Leicestershire. *Jl. geol. Soc. Lond.*, vol.32, pp.212-218.

HAYES, J.B. 1970. Polytypism of Chlorite in sedimentary rocks. *Clays and Minerals.* vol.18, pp.285-306.

HELDT, H., RIVIERE, A. & BELLAIR, P. 1947. Origines possibles des bonebeds. *C.R. Hebd. Acad. Sci.*, vol.225, pp.882-883.

HILDEBRAND, H.H. 1969. *Laguna Madre, Tamaulipas; observations on its hydrography and fisheries.* In *Lagunas Costeras*, Un Simposio. Mem. Simp. Intern. Lagunas Costeras. UNAM-UNESCO. Nov. 28-30 1967. Mexico. D.F. pp.679-686.

HOLLAND, C.H., LAWSON, J.D. & WALMSLEY, V.G. 1963. The Silurian rocks of the Ludlow District, Shropshire. *Bull. Brit. Mus. (Nat. Hist.).* vol.8, pp.93-172.

HOPPE, K. - H. 1931. Die Coelolepiden und Acanthodier des Obersilurs der Insel Osel. *Palaeontographica*, vol.76, pp.35-94.

HOWELL, J.V. 1957. Glossary of Geology and related Sciences. *NAS-NRC publication* 501, Washington, 325p.

HUDSON, J.D. 1962. The stratigraphy of the Great Estuarine Series (Middle Jurassic) of the Inner Hebrides. *Trans. Edinb. Geol. Soc.*, vol.19, pp.139-165.

HUDSON, J.D. 1963a. The recognition of salinity controlled Mollusc assemblages in the Great Estuarine Series (Middle Jurassic) of the Inner Hebrides. *Palaeontology*, vol.6, pp.318-326.

HUDSON, J.D. 1963b. The ecology and stratigraphical distribution of the invertebrate fauna of the Great Estuarine Series. *Palaeontology*, vol.6, pp.327-348.

HUDSON, J.D. 1964. The petrology of the sandstones of the Great Estuarine Series and the Jurassic Palaeogeography of Scotland. *Proc. Geol. Ass.*, vol.75, pp.499-528.

HUDSON, J.D. 1966. Hugh Miller's Reptile Bed and the *Mytilus* Shales, Middle Jurassic, Isle of Eigg, Scotland. *Scott. Jl. Geol.*, vol.2, pp.265-281.

HUDSON, J.D. & HARRIS, J.P. 1977. Sedimentology of the Great Estuarine Group (Middle Jurassic) of North West Scotland. Leicester Univ., Geol. Dept., Pub. No. 515. Ass. des Sedimentologists Francais (in press).

v. HUENE, E. 1933. Zur Kenntnis des Württembergischen Rhatbonebeds, mit Zahnfunden neuer Sauger und saugerahnlicher Reptilien. *Jh. Ver. vaterl. Naturkde. Wurttemberg*, vol.89, pp.65-128.

HUNTSMAN, G.A. 1917. *Canadian Fisherman Magazine.* May Issue.

JEANS, C.V. 1978. The origin of the Triassic clay assemblages of Europe with special reference to the Keuper marl and Rhaetic of parts of England. *Phil. Trans. R. Soc.* Series A, vol. 289, pp.549-639.

JENKINS, W.A.M. 1970. Chitinozoa. *Geoscience and Man.*, vol. 1, pp.1-21.

JOHANSEN, A.C. 1929. Mortality among porpoises, fish and the larger crustaceans in the waters around Denmark in severe winters. *Rept. Da. Biol. Stat.*, vol.35, pp.63-97.

JUKES-BROWNE, A.J. 1892. *The Building of the British Isles.* London, Geo. Bell & Sons, 465p.

KALJO, D. & SARV, L. 1966. On the correlation of the Baltic Upper Silurian. *Esti NSV TA Toimetised*, vol.2, pp.277-287, Tallinn (In Russian).

KALJO, D. & JURGENSON, E. 1977. *Sedimentary facies of the East Baltic Silurian.* In Kaljo, D. (ed.) *Facies and Fauna of the Baltic Silurian.* pp.122-148 (In Russian).Acad.Sciences Estonian S.S.R.Inst.

KENDALL, P.F. & WROOT, H.E. 1924. *Geology of Yorkshire. An illustration of the evolution of Northern England.* Hollinek Bros., Vienna, 995p.

KENT, P.E. 1968. In Sylvester-Bradley, P.C. & Ford, T.D. *The geology of the East Midlands.* Leicester University Press, Leicester.

KIRKALDY, J.F. 1939. The History of the Lower Cretaceous period in England. *Proc. Geol. Ass.*, vol.50, pp.379-417.

KOLDEWIJN, B.W. 1958. Sediments of the Paria - Trinidad Shelf. *Rept. Orinoco Shelf Expedition*, vol.3, 109p.

KOLODNY, Y. & KAPLAN, I.R. 1970. Uranium isotopes in seafloor phosphorites. *Geochim. Cosmochim. Acta.*, vol.34, pp.3-24.

KONTA, J. 1956. Regularly orientated growth of two phosphates in the scales of Permian Fishes (Palaeoniscidae). *Casopis pro mineralogii a geologii.*, vol.1, 15p. (M.A. 13 - 192).

KORITNIG, S. 1963. Zur Geochemie des Fluors in den Sedimenten. *Forschr. Geol. Rheinld. u. Westf.*, vol.10, pp.231-238.

KRINSLEY, D.H. & DOORNKAMP, J.C. 1973. *Atlas of quartz sand surface textures.* Cambridge University Press, Cambridge, 91p.

KRUMBEIN, W.C. & GARRELS, R.M. 1952. Origin and classification of chemical sediments in terms of pH and oxidation reduction potentials. *Jl. Geology*, vol.60, pp.1-33.

LAWSON, J.D. 1975. Ludlow benthonic assemblages. *Palaeontology*, vol.18, pp.509-525.

LISITSYN, A.P. 1969. *Recent sedimentation in the Bering Sea.* Isdatel-'stvo Nauka. Moscow (1966 Russian edition). I.P.S.T., 1969.

LISZKOWSKI, J. 1973. A bone bed from the "Wellen-Beds" of the Lower Muschelkalk (Lowermost Anisian) at Wolica near Kielce (Holy Cross Mts.). *Przegl. Geol.*, vol.12, pp.644-648.

LYELL, C. 1868. *Principles of Geology.* (also 1834 edition, vol.3.) London.

MacCARTHY, G.R. 1933. The rounding of beach sands. *Am. Jl. Sci.*, 5th series, vol.25, pp.205-224

McKERROW, W.S. (ed.) 1978. *The ecology of fossils.* London.

MALZ, H. 1978a. Massengrab fossiler Ohrsteine. *Umschau* 78, vol.1, pp.27-28.

MALZ, H. 1978b. Aquitane Otolithen - Horizonte im Untergrund von Frankfurt am Main. *Senckenbergiana Lethaia*, vol.58, pp.451-470.

MANHEIM, F., ROWE, G.T. & JIPA, D. 1975. Marine phosphorite formation off Peru. *Jl. Sed.. Pet.*, vol.45, pp.243-251.

MARK - KURIK, E. 1969. Distribution of vertebrates in the Silurian of Estonia. *Lethaia*, vol.2, pp.145-152.

MARTENS, C.S. & HARRISES, R.C. 1970. Inhibition of apatite precipitation in the marine environment by magnesium ions. *Geochim. Cosmochim. Acta.*, vol.34, pp.621-625.

McCONNELL, D. 1958. The apatite-like mineral of sediments. *Econ. Geol.*, vol.53, pp.110-111.

McKELVEY, V.E. 1967. Phosphate deposits. *U.S. Geol. Surv. Bull.*, No.1252-D, pp.1-21.

McKELVEY, V.E., WILLIAMS, J.S., SHELDON, R.P., CRESSMAN, E.R., CHENEY M. & SWANSON, R.W. 1959. The Phosphoria, Park City and Skedhorn Formations in the Western Phosphate Field. *U.S. Geol. Surv. Prof. Paper*, No.313-A, pp.1-47.

MEADOWS, P.S. & ANDERSON, J.G. 1966. Micro-organisms attached to marine and freshwater sand grains. *Nature*, vol.212, pp.1059-1060.

MEADOWS, P.S. & ANDERSON, J.G. 1968. Micro-organisms attached to marine sand grains. *Jl. Mar. Biol. Ass. U.K.*, vol.48, pp.161-175.

MEARS, E.G. 1943. The Callao painter. *Sci. Month.*, vol.57, pp.331-336.

MILLER, H. 1858. *The cruise of the Betsey.* Edinburgh.

MOHR, E. 1952. Der Stör. *Neue Brehmbücharei. Akad. Verlagsges.* G. & P. Leipzig.

MORKHÓVEN, F.P.C.M. Van. 1963. *Post Palaeozoic ostracoda.* Elsievier. London. 2 vols.

MURAWSKI, H. 1972. *Geologisches Wörterbuch.* Ferdinand Enke Verlag. Stuttgart. 260p.

MURCHISON, R.I. 1837. On the fishes of the Ludlow Rocks on Upper Ludlow beds of the Silurian System. *Rep. Brit. Ass.* for 1837 Transactions of the sections, 91p.

MURCHISON, R.I. 1839. *The Silurian System.* London.

MURCHISON, R.I. 1852. On some of the remains of the Bonebed of the Upper Ludlow rock. *Jl. geol. Soc. Lond.*, vol.9, pp.16-17.

MURPHY, R.C. 1926. Oceanic and climatic phenomina along the West coast of South America during 1925. *Geogr. Rev.*, vol.16, pp.26-54.

MURRAY, J. 1900. On the deposits of the Black Sea. *Scott. Geogr. Mag.*, vol.16, pp.673-702.

NEVILLE, R.S.W. 1967. The Rhaetic (Part 1 of the Bonebed). *Jl. Univ. Sheffield Geol. Soc.*, vol.5, pp.33-37.

NEWBERRY, J.S. 1873. Ohio Devonian System. *Ohio Geol. Sur.*, vol.1, pp.140-167.

NEWBERRY, J.S. 1899. The Paleozic fishes of North America. *U.S. Geol. Surv. Mon.*, vol.16, pp.1-340.

NEWTON, E.T. 1901. On a remarkable volcanic vent of Tertiary age in the Island of Arran, enclosing Mesozoic fossiliferous rocks - Part II: Palaeontological notes. *Jl. geol. Soc. Lond.*, vol.57, pp.229-241.

NICKLESS, E.F.P., BOOTH, S.J. & MOSLEY, P.N. 1976. The celestite resources of the area North-East of Bristol. *Inst. Geol. Sci. Mineral Ass.*, *Rept.* 25, 84p.

NIKOLSKII, G.V. 1969. *Theory of fish population dynamics as the biological background for rational exploitation and management of fishery resources.* Oliver & Boyd, Edinburgh. 323p.

ORTON, E. 1878. The geology of Franklin County. *Geol. Surv. Ohio.*, vol.3. Geology and Palaeontology, pt. 1. Geology, ch. 84, pp.596-646.

OSMOND, J.K. & SWAIN, H.J. 1959. Unit - cell dimensions of recent and fossil tooth apatites. *Abstr. Geol. Soc. Am.*, vol.70, p.1653.

PAGE, D. 1859. *Handbook of geological terms and geology.* Blackwood, London, 416p.

PAINE, G. 1937. Fossilisation of Bone. *Am. Jl. Sci.*, vol.34, pp.148-157.

PARRISH, W.C. 1978. Paleoenvironmental analysis of a Lower Permian Bonebed and adjacent sediments, Wichita County, Texas. *Palaeogeogr. Palaeoclimat. Palaeoecol.*, vol.24, pp.209-237.

PASSEGA, R. 1964. Grain size representation by CM patterns as a geological tool. *Jl. Sed. Pet.*, vol.34, pp.830-897.

PASSEGA, R. 1977. Significance of CM diagrams of sediments deposited by suspension. *Sedimentology*, vol.24, pp.723-733.

PRICE, W.A. 1955. The environment and formation of the Chenier Plain. *Quaternaria*, vol.2, pp.75-86.

PRYOR, W.A. 1975. Biogenic sedimentation and alteration of argillaceous sediments in shallow marine environments. *Bull. Geol. Soc. Am.*, vol.86, pp.1244-1254.

PYTHOWICZ, R.M. & KESTER, D.R. 1967. Relative calcium phosphate saturation in two regions of the North Pacific Ocean. *Limnol. Oceanog.*, No.12, pp.714-718.

RADAKOV, D.U. 1973. *Schooling in the schooling of fish.* Wiley & Sons, London.

RALPHE, MONK OF COGGESHALL ?1236. In Camden, W. 1586. *Britannia sive florentissimorvm regnorvm, Angliae, Scotiae, Hiberniae, et insvlarvm adiacentium ex intima antiquitate chorographica discripto.* London.

REID, C. 1890. The Pliocene deposits of Britain. *Mem. Geol. Surv.* U.K. H.M.S.O., London. 326p.

REIF, W.-E. 1969. *Bonebeds an der Muschelkalk - Keuper - Grenze in Ostwürttemberg.* Dip. Arbeit. Tübingen University. 123p.

REIF, W.-E. 1971. Zur genese der Muschelkalk - Keuper - Grenzbonebeds. *N. Jb. Geol. Palaont.*, Abh. 139, pp.369-404.

REIF, W.-E. 1974. Profile des Muschelkalk - Keuper - Grenzbereichs im Jagsttal (Trias, Baden - Wurttemburg). *Oberrhein. Geol.* Abh 23, pp.43-54.

REIF, W.-E. 1976. Sedimentologie und Genese von Bonebeds. *Zbl. Geol. Palaont.* Teil II.H5/6, pp.252-255.

REIF, W.-E. 1977. Tooth enamaleloid as a taxonomic criterion: 1. A new euselachian shark from the Rhaetic Liassic boundary. *N. Jb. Geol. Palaont.* Mh. 9, pp.565-576.

REIF, W.-E. 1978. Tooth enameloid as a taxonomic criterion. 2. Is "*Dalatias*" *barnstonensis* Sykes 1971 (Triassic, England) a squalomorphic shark? *N. Jb. Geol. Palaeont.* Mh. 1, pp.42-58.

REINECK, H.E. & SINGH, I.B. 1975. *Depositional sedimentary environments.* Springer Verlag. New York. 439p.

RICHARDSON, L. 1901. Mesozoic geography of the Mendip Archipelago. *Proc. Cotteswold Nat. Fld. Club.* vol.14, pp.59-69.

RICHARDSON, L. 1905. The Rhaetic and contiguous deposits of Glamorganshire. *Jl. geol. Soc. Lond.*, vol.61, pp.385-425.

RICHARDSON, L. 1911. On the Rhaetic and contiguous deposits of West, Mid. and East Somerset. *Jl. geol. Soc. Lond.*, vol.67, pp.1-72.

RICHARDSON, J.B. & LISTER, T.R. 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh borderland and South Wales. *Palaeontology*, vol.12, pp.201-252.

ROMER, A.S. 1955. Fish origins - fresh or salt water? Papers in Marine Biology and Oceanography. Suppl. to vol.3, *Deep-Sea Research*, pp.261-280.

ROBERSON, C.E. 1966. Solubility implications of apatite in sea water. *U.S. Geol. Surv. Prof. Paper*, No. 550-D, pp.178-185.

ROBERTS, G. 1839. *An Etymological and Explanatory dictionary of the terms and language of geology.* Longmans, London. 183p.

ROGERS, A.F. 1917. A review of the amorphous minerals. *Jl. Geology*, vol.25, pp.515-537.

ROGERS, A.F. 1922. Collophane a much neglected mineral. *Am. Jl. Sci.*, vol.3, pp.269-279.

ROGERS, A.F. 1924. Minerology and petrography of fossil bone. *Bull. Geol. Soc. Amer.*, vol.35, pp.535-556.

SAVIDGE, G. & FOSTER, P. 1978. Phytoplankton biology of a thermal front in the Celtic Sea. *Nature*, vol.271, pp.155-156.

SAYLES, F.L., MANHEIM, F.T. & WATERMAN, L.W. 1974. Interstitial water studies on small core samples: leg. 15. *Initial reports of the deep sea drilling project*, vol.20, pp.783-804.

SCHAFER, W. 1972. *Ecology and Palaeoecology of marine environments.* Oliver & Boyd, Edinburgh. 567p.

SCHMIDT, M. 1928. *Die Lebewelt unferer Trias.* Oehringen.

SHAW, R.W.L. 1969. Beyrichiacean ostracodas from the Downtonian of Shropshire. *Geologiska Föreningens i Stockholm Förhandlinger*, vol.91, pp.52-72.

SHELDEN, R.P. 1963. Physical stratigraphy and mineral resources of Permian Rocks in western Wyomming. *U.S. Geol. Surv. Prof. Paper*, No. 313-B, pp. 49-273.

SHOLKOVITZ, E. 1973. Interstitial water geochemistry of the Santa Barbara Basin sediments. *Geochim. Cosmochim. Acta.*, 37, pp.2043-2073.

SHORT, A.R. 1904. On some Rhaetic sections in the Bristol district, with consideration on the mode of deposition of the Rhaetic Series. *Jl. geol. Soc. Lond.*, vol.60, pp.170-193.

SIEBURGH, J.M. 1975. *Microbial seascapes.* University Park Press, London.

SLEEMAN, A.G. 1977. Lower Carboniferous transgressive facies in the Porter's Gate Formation at Hook Head, Co. Wexford. *Proc. R. Irish Acad.*, Sect.B, vol.77, pp.269-284.

SLEEMAN, A.G., JOHNSTON. I.S., MAYLOR, D. & SEVASTOPULO, G.D. 1974. The stratigraphy of the Carboniferous rocks of Hook Head, Co. Wexford. *Proc. R. Irish Acad.* Sect. B, vol.74, pp.227-244.

SMITH, D.K. (ed.) 1974. Selected powder diffraction data for minerals - Search Manual. Publication. M - 1 - 23. Joint committee on Powder diffraction standards, Pennsylvania.

SMYTH, L.B. 1930. The Carboniferous rocks of Hook Head County Wexford. *Proc. R. Irish Acad.* Sect. B, vol.39, pp.523-566.

SOLLAS, I.B.J. 1901. Fossils in the Oxford University Museum, V: On the structure and affinities of the Rhaetic Plant *Naiadita*. *Jl. geol. Soc. Lond.*, vol.57, pp.307-312.

SQUIRRELL, H.C. 1958. New occurrences of fish remains in the Silurian of the Welsh Borderland. *Geol. Mag.*, vol.95, pp.328-332.

STAUFFER, C.R. 1909. The Middle Devonian of Ohio. *Ohio Geol. Surv. 4th ser. Bull.* vol.10, 240p.

STOREY, M. 1937. The relation between normal range and mortality of fish due to cold at Sanibel Island. *Ecology*, vol.19, pp.10-26.

STOREY, M. & GUDGER, E.W. 1936. Mortality of fishes due to cold at Sanibel Island, Florida. *Ecology*, vol.17, pp.640-648.

STRAW, S.H. & WOODWARD, A.S. 1932. The fauna of the Palaeozoic rocks of the Little Missenden Boring. *Sum. Pr. Geol. Surv. G.B.*, pp.112-142, London.

STUBBINGS, H.G. 1939. The marine deposits of the Arabian sea. An investigation in their distribution and biology. *Sci. Rept. John Murray Exp.* 1933-34, vol.3, pp.31-158.

STUMM, W. & LECKIE, J.O. 1970. *Phosphate exchange with sediments, its role in the productivity of surface waters. Advances in Water Pollution Research.* 2. Perm. Press, New York.

STUMM, W. & MORGAN, J.J. 1970. *Aquatic Chemistry. An introduction emphasising chemical equilibria in natural waters.* Wiley, New York.

SWANSON, R.W. 1973. Geology and Phosphate deposits of the Permian Rocks in Central Western Montana. *U.S. Geol. Surv. Prof. Paper*, No. 313-F, pp.779-833.

SWANSON, V. & DORNING, J.K. 1977. Acritarchs and Chitinozoa from the Whitcliffian (Silurian) Dinas Bran Beds of Llangollen, Clwyd, North Wales. *Jl. Univ. Sheffield Geol. Soc.*, vol.7, pp.71-78.

SWINCHATT, J.P. 1969. Algal borings: possible depth indicator in carbonate rocks and sediments. *Bull. Geol. Soc. Am.*, vol.80, pp.1391-1396.

SYKES, J.H. 1971. A new Dalatiid Fish from the Rhaetic Bone Bed at Barnstone, Nottinghamshire. *Mercian Geol.*, vol.4, pp.13-22.

SYKES, J.H. 1974. Teeth of *Dalatias barnstonensis* in the British Rhaetic. *Mercian Geol.* vol.5, pp.39-48.

SYKES, J.H. 1977. British Rhaetian Bone-beds. *Mercian Geol.*, vol.6, pp.197-240.

TAN, F.C. & HUDSON, J.D. 1974. Isotopic studies on the palaeoecology and diagenesis of the Great Estuarine Series (Jurassic) of Scotland. *Scott. Jl. Geol.*, vol.10, pp.91-128.

TAYLOR, F.M. 1968. *Permian and Triassic Formations.* In Sylvester-Bradley, P.C. and T.D. Ford (eds) *The Geology of the East Midlands.* Leicester University Press, Leicester, pp.149-173.

TEBBLE, N. 1966. *British bivalve seashells.* Brit. Mus. (Nat. Hist.) Lond., 212p.

THOMAS, R.D.K. 1975. Functional morphology, ecology and evolutionary conservatism in the Glycymerididae (Bivalvia). *Palaeontology*, vol.18, pp.217-254.

TRUSKANOV, M.D. & SHCHERBINO, M.N. 1962. Taking Atlanto-Scandinavian herring as an example for determining the size of dense aggregations of fish. *Trudy PINRO* No.14.

TUCKER, E.V. 1960. Ludlovian biotite bearing bands. *Geol. Mag.*, vol.97, pp.245-249.

TURNER, S. 1973. Siluro-Devonian Thelodonts from the Welsh Borderlands. *Jl. geol. Soc. Lond.*, vol.129, pp.557-584.

TYRRELL, G.Y. 1928. The geology of Arran. *Mem. geol. Surv. U.K.*, pp.1-292.

VERRILL, A.E. 1882. Evidence for the great destruction of life last winter. *Amer. Jl. Sci.*, vol.24, 366p.

VEEH, H.H., BURNETT, W.C. & SOUTAR, A. 1973. Contemporary phosphorite in the continental margin of Peru. *Science*, vol.181, pp.845-847.

VEENSTRA, H.J. & WINKELMOLEN, A.M. 1976. Size, shape and density sorting around two barrier islands along the north coast of Holland. *Geol. Mijnbouw*, vol.55, pp.87-104.

WAGNER, G. 1913. Beitrag zur stratigraphie u. Bildungsgeschichte des oberen Hauptmuschelkalkes u. d. unt. Lettenkohle in Franken. *Geol. u. Palaont. Abhandle*, N.F. 12.

WALKER, R.G. & HARMS, J.C. 1971. The 'Catsgill delta' a prograding muddy shoreline in Central Pennsylvania. *Jl. Geol.*, vol.79, pp.381-399.

WASMUND, E. 1935. Die Bildung von anabituminosem Leichenwachs unter Wasser. In Erdolmuttersubstanz. *Schr. Geb. Brennstoff-Geol.*, vol.10, pp.1-70.

WATKINS, R. & BERRY, W.B.N. 1977. Ecology of a late Silurian fauna of graptolites and associated organisms. *Lethaia*, vol.10, pp.267-286.

WEAVER, C.E. & BECK, K.C. 1977. Miocene of the S.E. United States: a model for chemical sedimentation in a peri-marine environment. *Sediment. Geol.*, vol.17, pp.1-234.

WELLS, J.W. 1943. Fish remains from the Middle Devonian bonebeds of the Cincinnati Arch Region. *Abst. Bull. Geol. Soc. Am.*, vol. 54, p.1834

WELLS, J.W. 1944. Middle Devonian bonebeds of Ohio. *Bull. Geol. Soc. Am.*, vol.55, pp.273-302.

WELLS, J.W. 1947. Provisional palaeoecological analysis of Devonian rocks of the Columbus region. *Ohio Jl. Sci.*, vol.47, pp.119-126.

WESTGATE, L.G. & FISCHER R.P. 1933. Bonebeds and Crinoidal sands of the Delaware limestone of Central Ohio. *Bull. Geol. Soc. Am.*, vol.44, pp.1161-1172.

WICKES, W.H. 1904. Rhaetic bone beds. *Proc. Bristol Nat. Soc.*, vol.2, pp.213-225.

WICKES, W.H. 1908. Pebble swallowing animals. *Proc. Bristol Nat. Soc.*, vol.5, pp.23-31.

WIELAND, G.R. 1907. Gastroliths. *Science*, vol.25, pp.66-67.

WILSON, M.D. & PITTMAN, E.D. 1977. Authigenic clays in sandstones. Recognition and influence on reservoir properties and palaeoenvironmental analysis. *Jl. Sed. Pet.*, vol.47, pp.3-31.

WINKELMOLEN, A.M. 1971. Rollability, a functional shape property of sand grains. *Jl. Sed. Pet.*, vol.41, pp.703-714.

WINKELMOLEN, A.M. 1978. Size, shape and density sorting of beach material along the Holderness coast, Yorkshire. *Proc. York. Geol. Soc.*, vol.42, pp.109-141.

WOODWARD, H.B. 1888. Notes on the Rhaetic Beds and Lias of Glamorganshire. *Proc. Geol. Ass.*, vol.10, pp.529-538.

YASYREV, A.P. 1971. Concretionary phosphorite of the Russian Platform - an intermediate gold collect in Placer Formation. *Doklady Earth Sci. sections*, vol.199, pp.206-208.

YASYREV, A.P. & NIKITIN, N.M. 1970. Trace elements in bone phosphate. *Doklady Earth Sci. sections*, vol.194, pp.187-189.

YOCHELSON, E.L. 1968. Biostratigraphy of the Phosphoria, Park City and Shedhorn Fromations. *U. S. Geol. Surv. Prof. Paper*, No. 313-D, pp.571-660.

14 - Appendix - 1 (See p.138)

A life table for some closed articulated valves of *Glycimeris glycimeris* from the Red Crag at Walton on the Naze, Essex.

Key to the columns of the Table

1 - Age interval given in number of growth rings
2 - Sample size
3 - Proportion dying in the age interval
4 - Number living at age x assuming an initial population of 10,000
5 - Number dying in interval
6 - Number of timespans lived in the interval
7 - Total number of timespans lived beyond age x
8 - Observed expectation of life at age x
9 - Proportion of survivors over the age interval

1	2	3	4	5	6	7	8	9
0	57	10000	0.3800	3800	8100	16803	1.68	0.62
1	48	6200	0.5161	3200	4600	8703	1.40	0.48
2	22	3000	0.4889	1467	2267	4103	1.37	0.51
3	13	1533	0.5652	866	1100	1836	1.20	0.44
4	5	667	0.5000	333	501	736	1.10	0.50
5	4	334	0.8000	267	201	235	0.70	0.20
6	1	67	1.0000	67	-	-	-	-
7	-	-	-	-	-	-	-	-

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Appendix - 2

Since this paper went to the proof stage (Dec. 1978), a paper on the prefossilisation of fish spines has appeared (Maisey, 1978), which reveals an alternative method for the identification of prefossilised fish material, to that outlined by Reif (1969; 1971) and critically examined in Section 3, p.98, of this paper.

Maisey (1978) observed that fin spines of *Sphenacanthus* (Selachii) and *Gyracanthus* (Acanthodii) occurring in a sediment matrix of fine carbonaceous clays and micas from the Staffordshire Coal Measures (Carboniferous) commonly have the lower part of their spine lumen infilled with clays and the upper part infilled with diagenetic feldspar (albite rich plagioclase). This feldspar also infilled the pore spaces of the spine oseodentine and coated the spines exterior, but only where pieces of the spines outer wall had been broken away prior to feldspar crystallisation. The clay grains resting against the feldspar on the outer surface of the spine have not been altered and post date the feldspar crystallisation (Maisey, 1978). This latter observation led Maisey to suggest that the spines had been prefossilised prior to inclusion in the sediment, in which they were found.

However, these observations do not prove that the fin spines are prefossilised material, because both clays and feldspars are commonly produced by diagenesis within the same sediment (Waugh, 1978). Thus it could be suggested that the observations made by Maisey (1978) indicate that the precipitation of clays post-date the precipitation of feldspar within the sediment during diagenesis, after burial of the unaltered fin spine. Further indications that the fin spines were not prefossilised prior to burial in the sediment are given by the presence of diagenetic calcite, quartz, siderite and pyrite locally infilling cavities in the spines and locally replacing the apatite of the spine (Maisey, 1977; 1978). All these minerals can occur together in a sediment as products of complex diagenesis (Blanche & Whitaker, 1978).

If the fin spines observed by Maisey (1978) were fossilised prior to their inclusion in the sediment in which they were found then one of the following two observations should have been made.

1. If the vertebrate material is prefossilised then the feldspar crystallites should contain abrasion features on their external surfaces.
2. Similarly the spines could be regarded as prefossilised if it could be shown that the feldspar would not have grown in the diagenetic micro-environments presented by the sediment containing the spine through time.

Maisey (1978) observed that some of his fin spines were broken at their tips revealing the diagenetic feldspar, indicating that they may have been prefossilised, but does not say whether the breaks were of syndepositional origin or a result of laboratory processing. Similarly he does not indicate whether or not abrasion features are present on any of the feldspars on the exterior of the spines. Consequently because neither criterion outlined here were fulfilled, it remains a distinct possibility that the fin spines examined by Maisey (1978) were not prefossilised. However, the two points listed above should prove a useful test to aid determination of prefossilisation in vertebrate grains which contain diagenetic precipitates on their external surface.

Additional references

BLANCHE, J.B. & WHITAKER, J.H.McD.	1978. Diagenesis of part of the Brent Sand Formation (Middle Jurassic) of the northern North Sea Basin. *Jl. Geol. Soc. Lond.*, vol.135, pp.73-82.
MAISEY, J.G.	1977. Structural notes on a Cladoselachian dorsal spine. *N. Jb. Geol. Palaont. Mh.* (1). pp.47-55.
MAISEY, J.G.	1978. Preservation and prefossilisation of fossil fin spines. *N. Jb. Geol. Palaont. Mh.* (10) pp. 595-599.
WAUGH, B.	1978. Authigenic K-feldspar in British Permo-Triassic Sandstones. *Jl. Geol. Soc. Lond.*, vol.135, pp.51-56.

Explanation for Plate 14

(a) Oligocene fish from a lacustrine fish bed - note complete preservation of the bones and compare with the random orientation of scales in a bone-bed (pl.14, fig.d) (x 1).

(b) Bedding plane surface of the Ludlow Bone-Bed - Ludlow. Note the presence of black orientated '*Serpulites*' sp. fragments (x ½).

(c) Detail of the Ludlow Bone-Bed (x 2) showing the larger phosphatic clasts of the bone-bed. 1 = '*Serpulites*' sp. fragments; 2 = *Orbiculoidea rugata* fragment; 3 = Acanthodian fish plate (?*Gomphonchus* sp.).

(d) Detail of the Ludlow Bone-Bed showing the smaller phosphatic clasts. Note the randomly orientated *Thelodus parvidens* scales in a fine grained quartz silt matrix (x 30).

(e) A *Thelodus parvidens* Ag. scale from the Ludlow Bone-Bed (x 60).

(f) A *Logania ludlowiensis* Gross. scale from the Ludlow Bone-Bed (x 60).

(g) Quartz grain from the Ludlow Bone-Bed showing a concave fracture and rounded form indicative of eolian abrasion (x 60).

(h) Diagenetic euhedral quartz overgrowth from the Ludlow Bone-Bed (x 60).

(i) Diagenetic euhedral overgrowth from the Ludlow Bone-Bed showing preburial abrasion features, e.g. rounded edges (x 50).

(j) Crescentic abrasion pit on a crystal face on an abraded quartz overgrowth from the Ludlow Bone-Bed (x 1000).

(k) Angular quartz shard (x 30) from the Ludlow Bone-Bed; derived originally from a benthonite ?(cf. Marsh, R.C., 1976, PhD. Thesis Leicester Univ.).

(l) Angular quartz grain from the Temeside Bone-Bed (x 45).

(m) *Saurichthys apicalis* Ag. from the Muschelkalk Grenzbonebed. This species forms a dominant constituent of the pointed tooth fauna of the bone-bed (x 24) - a stereopair.

(n) A polished section through the conglomeratic fraction of the Muschelkalk Grenzbonebed. Note the presence of limestone pebbles, some of which contain vertebrate sand infilled burrows (arrowed). A more detailed explanation of the section is given in the text (page 128) and in text-fig. 8.

(o) An abraded fish scale from the Muschelkalk Grenzbonebed (*Gyrolepis* sp.). Such semi-complete scales are common throughout the bone-bed (cf. pl.15, fig.h) (x 12).

Explanation for Plate 15

(a) Detail (x 900) of the matrix of the Muschelkalk Grenzbonebed showing late diagenetic calcite crystals infilling a vug in the bone-bed's sediment.

(b) Detail (x 950) of the Muschelkalk Grenzbonebed showing the 'early' diagenetic dolomite crystals which form much of the bone-bed's sediment.

(c) Detail (x 925) of the Muschelkalk Grenzbonebed showing a fish fragment (centre), mica plates and diagenetic carbonate crystals.

(d) A quartz grain from the Muschelkalk Grenzbonebed with its diagenetic limonite coating removed. Note the semieuhedral faces of the grain indicate an earlier phase of silica precipitation during diagenesis (x 54). Arrow indicates area detailed in fig. e.

(e) Diagenetic silica plastering on the surface of quartz grain (fig. e) (x 153).

(f) Broken flat tooth of *Acrodus lateralis* Ag. in a diagenetic dolomite matriz in the Muschelkalk Grenzbonebed (x 150).

(g) Stereopair of a limonite encrusted (?originally pyrite) quartz grain from the Muschelkalk Grenzbonebed (x 45).

(h) Bedding plane surface of the Muschelkalk Grenzbonebed (x 1) showing a high density of vertebrate debris including *Gyrolepis* sp. fragments (arrowed).

(i) Detail of an abraded and solution pitted surface of an *Acrodus* tooth in the Muschelkalk Grenzbonebed (x 306).

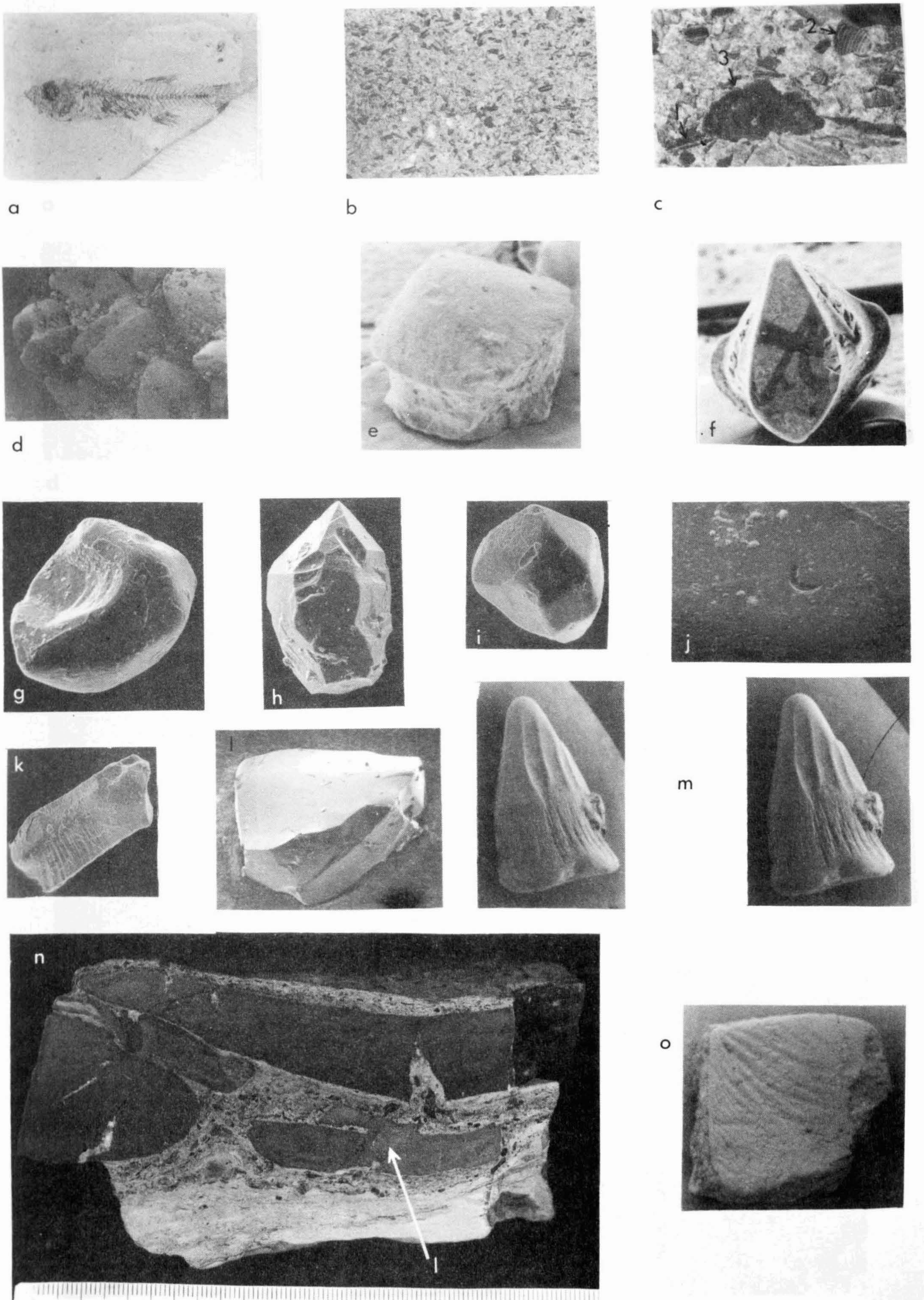
(j) Stereopair of an abrasion rounded vertebrate fragment from the Muschelkalk Grenzbonebed. Note its high sphericity. (x 60).

(k) Endolithic algal borings on a *Saurichthys* tooth from the Muschelkalk Grenzbonebed (x 920).

(l) Stereopair of an *Acrodus* tooth fragment showing a preburial break (arrowed) which has acted as a nucleous for the diagenetic growth of apatite. Rhaetic Bone-Bed. Blue Anchor locality (see Sykes, 1977, for details). (x 60).

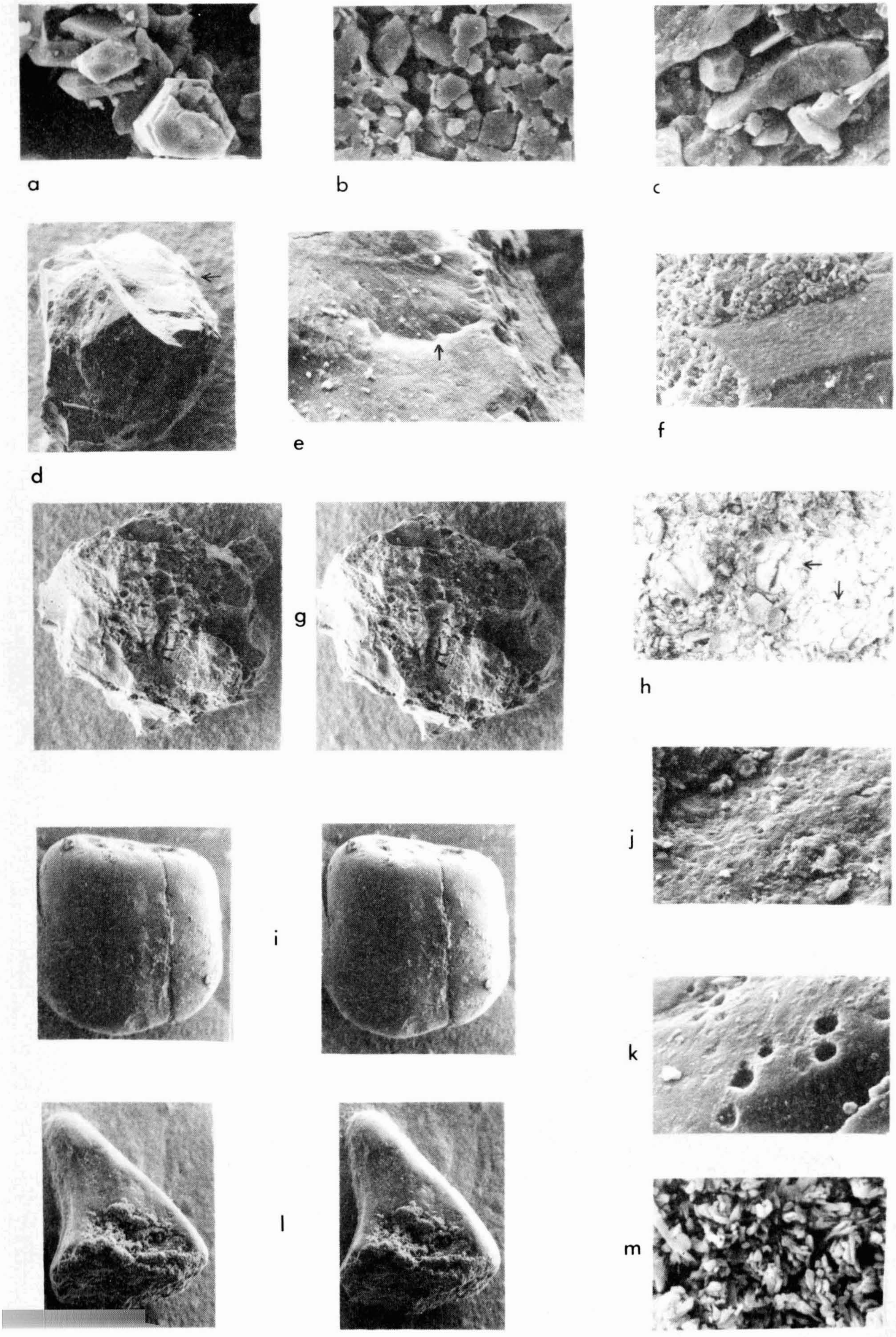
(m) Detail of the diagenetic apatite overgrowths (x 1000).

Plate 14



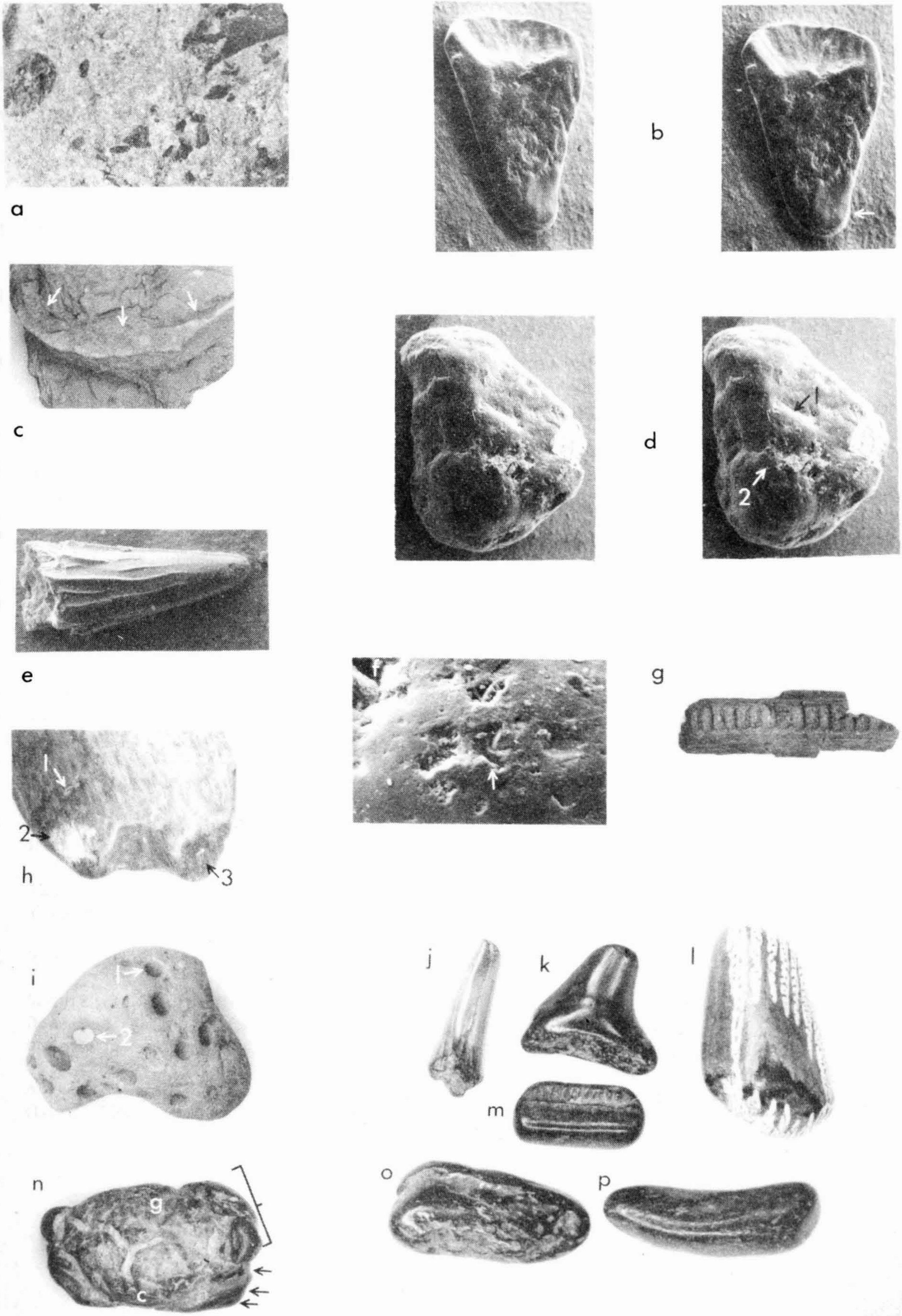
Antia, on bone-beds. For explanation see p.169.

Plate 15



on bone-beds. For explanation see p.170.

Plate 16



Antia, on bone-beds. For explanation see p.171.

Explanation for Plate 16

(a) The Rhaetic Bone-Bed - Bedding plane surface. Westbury on Severn. (x 1).

(b) ?*Saurichthys* sp. tooth showing a syndepositional uneven fracture along its length, dividing it into two equal halves. This fracture surface has been modified during diagenesis to give in places (arrowed) a smooth fracture surface - stereopair. (x 21). Rhaetic Bone-Bed. Blue Anchor locality.

(c) A crustacean burrow from the Pullastra Sandstone underlying the Rhaetic Bone-Bed - Westbury on Severn. (x $\frac{1}{4}$).

(d) An abraded vertebrate fragment showing abrasion pits (1) and algal borings (2) from the Rhaetic Bone-Bed. Blue Anchor. - stereopair. (x 30).

(e) ?*Saurichthys* tooth from the Rhaetic Bone-Bed. Note its apparent lack of abrasive features compared to b and d and pl. 14, fig. m. These four vertebrate fragments illustrate the extreme variation in the abrasive features present in any one bone-bed. (x 28).

(f) Detail (x 225) of the abraded surface of a rounded vertebrate fragment showing abrasive chip markings (arrowed) from the Rhaetic Bone-Bed. Blue Anchor.

(g) A jawbone fragment of *Acrodus lateralis* from the Michelbach Bone-Bed, Michelbach, W. Germany. Upper Lettenkeuper. (x $\frac{1}{2}$).

(h) Mineralised (phosphate enriched) cetean bone from the Suffolk Bone-Bed ? barnacle borings (1); regions of poor mineralisation (2); and abrasion rounded fracture surfaces (3) - Walton on the Naze. (x $\frac{1}{2}$).

(i) Pebble of London Clay from the Suffolk Bone-Bed showing pholad borings (1), some of which were infilled with clay prior to their burial in the bone-bed (2). - Walton on the Naze. (x $\frac{1}{2}$).

(j) Unmineralised sharks tooth from the Suffolk Bone-Bed - Walton on the Naze. (x 2).

(k) Mineralised sharks tooth derived from the London Clay (Lower Eocene) and found in the Suffolk Bone-Bed (Pliocene/Pleistocene) - Walton on the Naze. (x 2).

(l) Mineralised abraded mammalian tooth from the Suffolk Bone-Bed. Bawdsey cliff, Felixstowe. (x 2).

(m) Mineralised fish dental plate - Suffolk Bone-Bed, Walton on the Naze. (x 2).

(n) Mineralised (phosphatised) crab derived from the London Clay and found in the Suffolk Bone-Bed, Walton on the Naze; g = gastric region; c = cardiac region; arrows indicate the walking legs; brackets indicate the claw (chela + carpus). (x $\frac{1}{2}$).

(o/p) Abraded mineralised mammalian bone fragments from a thin bone-bed in the Red Crag (Lower Pleistocene) at Brightwell, Suffolk. (x 2).

Explanation for Plate 17

(a) Otolith - detail of surface showing ?fungal borings and the initial stages in the development of weathering stage 2 (i.e. concentric outer layer peeling). (x 450).

(b) Otolith - detail of surface showing ?fungal borings aligned parallel to the otoliths outer surface, which have been partly exposed by a gastropod boring. The ridges and grooves observable in this figure result from a scraping of the otoliths surface by a gastropod radula. This particular otolith contained no weathering features, and illustrates the high density of microbial borings present on many of the unweathered (weathering stage 0) otoliths from the Rockall Trough. (x 800).

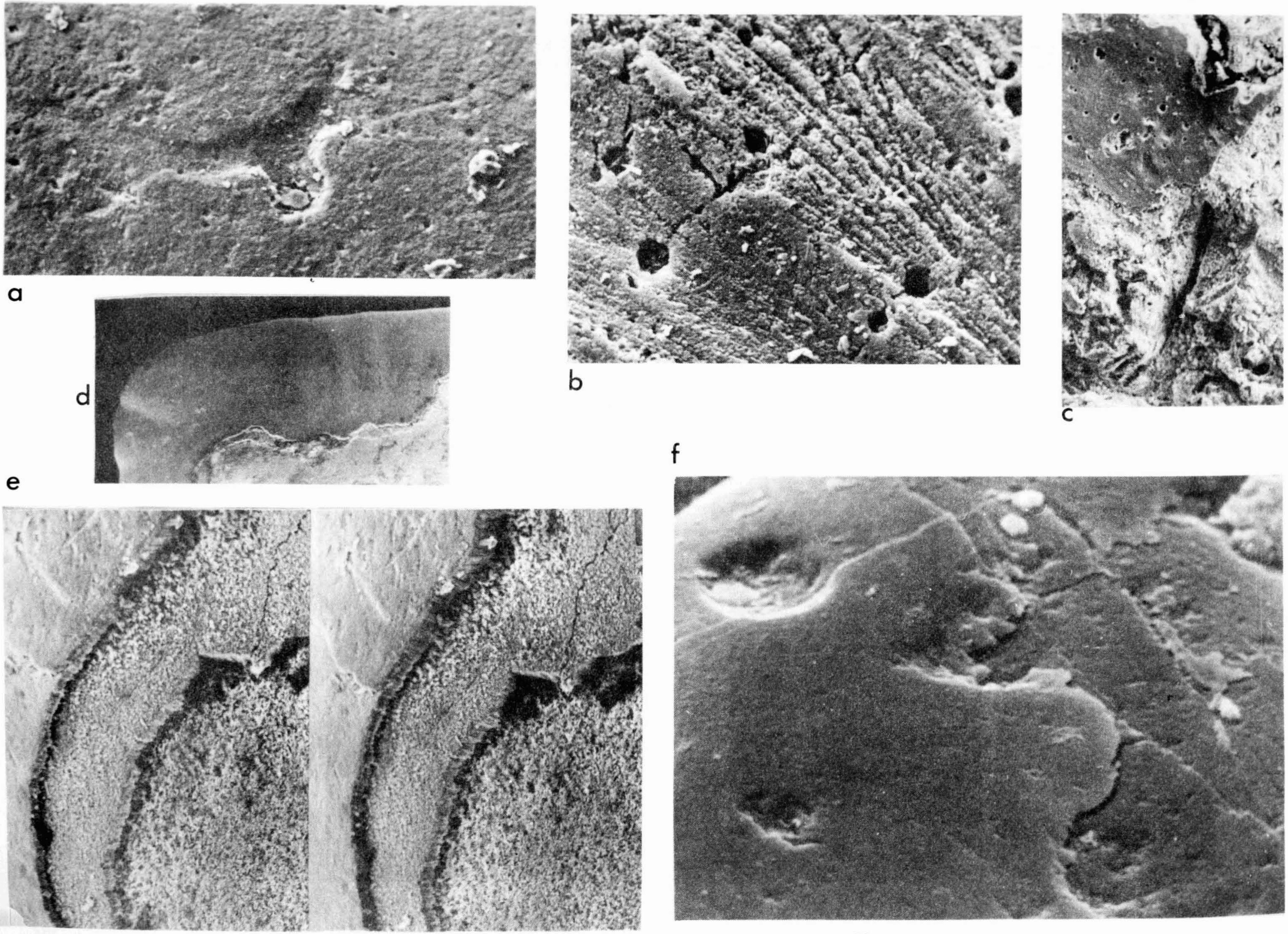
(c) Otolith - detail of the surface of a weathered otolith (weathering stage 3) showing the reminants of the resistant outer layer surrounded by the less resistant inner fiberous layer. This latter layer contains a deep crack with rounded margins, of a type which is common on the most highly weathered vertebrate remains (weathering stages 4 and 5). (x 50).

(d) Otolith - Low magnification (x 10) view of the outer surface of an otolith showing a well developed peeling of the outermost concentric layers. i.e. typical weathering stage 2 features.

(e) Stereopair showing well developed concentric layer peeling on the surface of an otolith. (x 300).

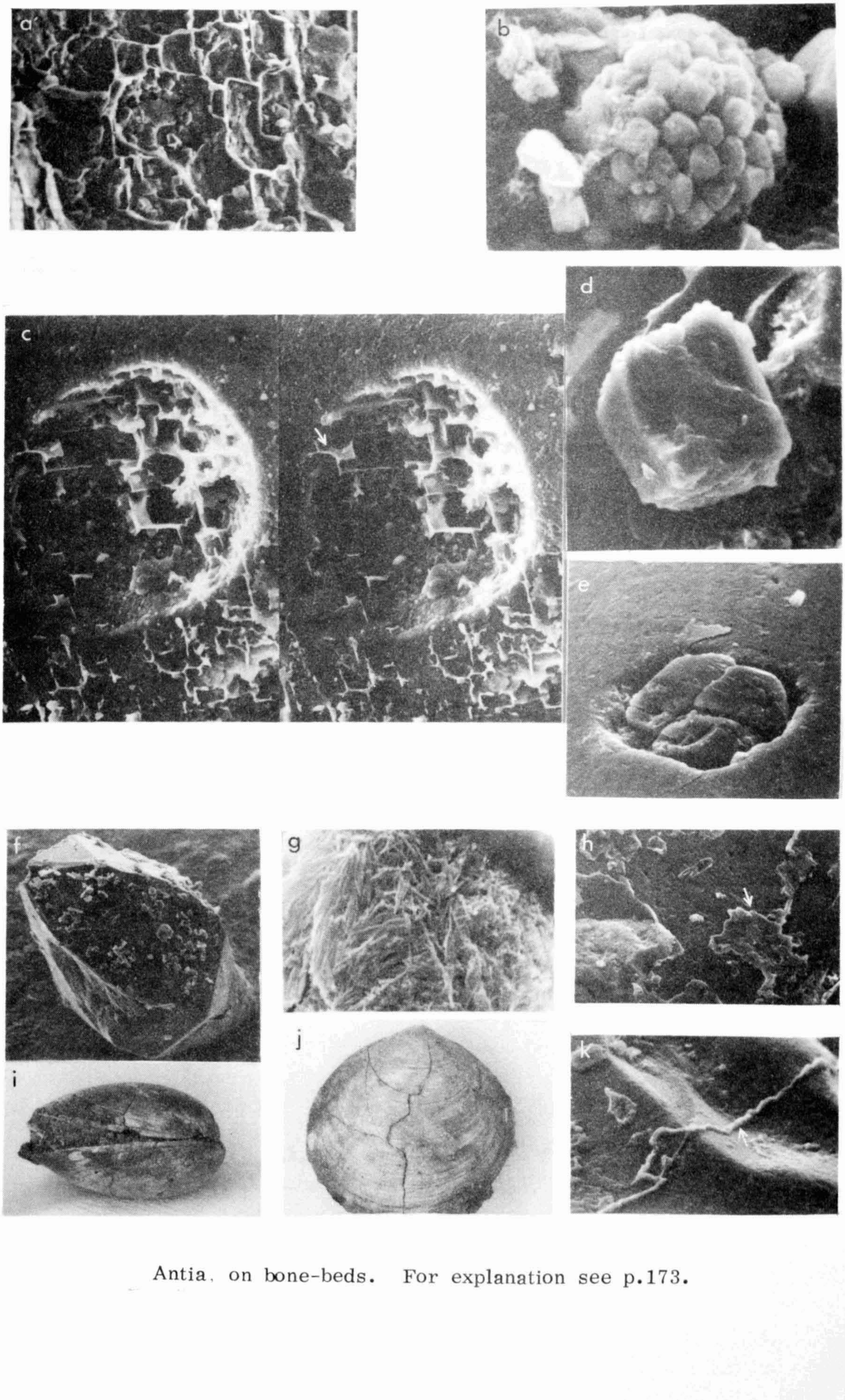
(f) The outer surface of a thelodont scale (*Thelodus parvidens*, showing algal dissolution pit (see also Section 10), concentric peeling of the outermost layers (weathering stage 2 features), abrasion chip marks, and cracks (reminant weathering stage 1 features ?) from the Ludlow Bone-Bed at Corfton (x 750).

Plate 17. Weathering and microbial features on otoliths and thelodonts. This plate has been placed for sideways viewing.



Antia, on bone-beds. For explanation see p.172.

Plate 18



Antia, on bone-beds. For explanation see p.173.

Explanation for Plate 18

(a) Apatite pseudomorphing after clays in a phosphatic nodule from the Ludlow Bone-Bed. (x 1000).

(b) Pyrite framboid from the Ludlow Bone-Bed (x 3000).

Chlorite
(c) ~~Kaolinit~~e infilling an algal solution pit on the surface of a thelodont scale. Note the honeycomb nature of the clay structure - stereopair. From the Ludlow Bone-Bed. (x 2500). *

Carbonate
(d) ~~Kaolin~~ite crystal from the matrix of the Ludlow Bone-Bed. (x 900). *

Carbonate
(e) ~~Kaolinit~~e crystals completely infilling an algal solution pit on a thelodont scales surface. (x 800). *

(f) Quartz grain from the Rhaetic Bone-Bed - Blue Anchor locality. Note the euhedral diagenetic crystal faces on the grain. (x 80).

(g) A fibrous clay from a clay pebble in the Ludlow Bone-Bed. (x 2500).

(h) Silica plastering on the surface of a quartz grain in the Rhaetic Bone-Bed, Blue Anchor locality. (x 600).

(i) Articulated *Glycimeris glycimeris* shell from the Red Crag at Walton on the Naze. (x $\frac{3}{4}$).

(j) Articulated *Glycimeris glycimeris* shell. (x $\frac{3}{4}$).

(k) Silicified filament on the surface of a quartz grain in the Ludlow Bone-Bed. (x 650).

* Wrong photograph inserted in the plates. Not noticed till after publication

Explanation for Plate 19

(a) Microbial flora of diatoms on a modern carbonate grain. (x 1000).

(b) Algal solution pits (x 200) on a modern carbonate grain - Sales Point, Bradwell, Essex (see Antia, 1977, for locality details).

(c) An algal bored carbonate grain from the Rhaetic Bone-Bed. Blue Anchor. (x 23).

(d) Algal solution pits on a thelodont fish scale (*Thelodus parvidens*) from the Ludlow Bone-Bed. (x 25).

(e) Detail (x 500) of the solution pits. Note their similarity to those illustrated in b.

(f) Detail (x 225) of algal borings on a carbonate grain from the Rhaetic Bone-Bed, Blue Anchor.

(g) Detail of ? fungal borings on a carbonate grain from the Rhaetic Bone-Bed, Blue Anchor. (x 450).

(h) Detail (x 263) of a large algal boring on a carbonate grain from the Rhaetic Bone-Bed, Blue Anchor.

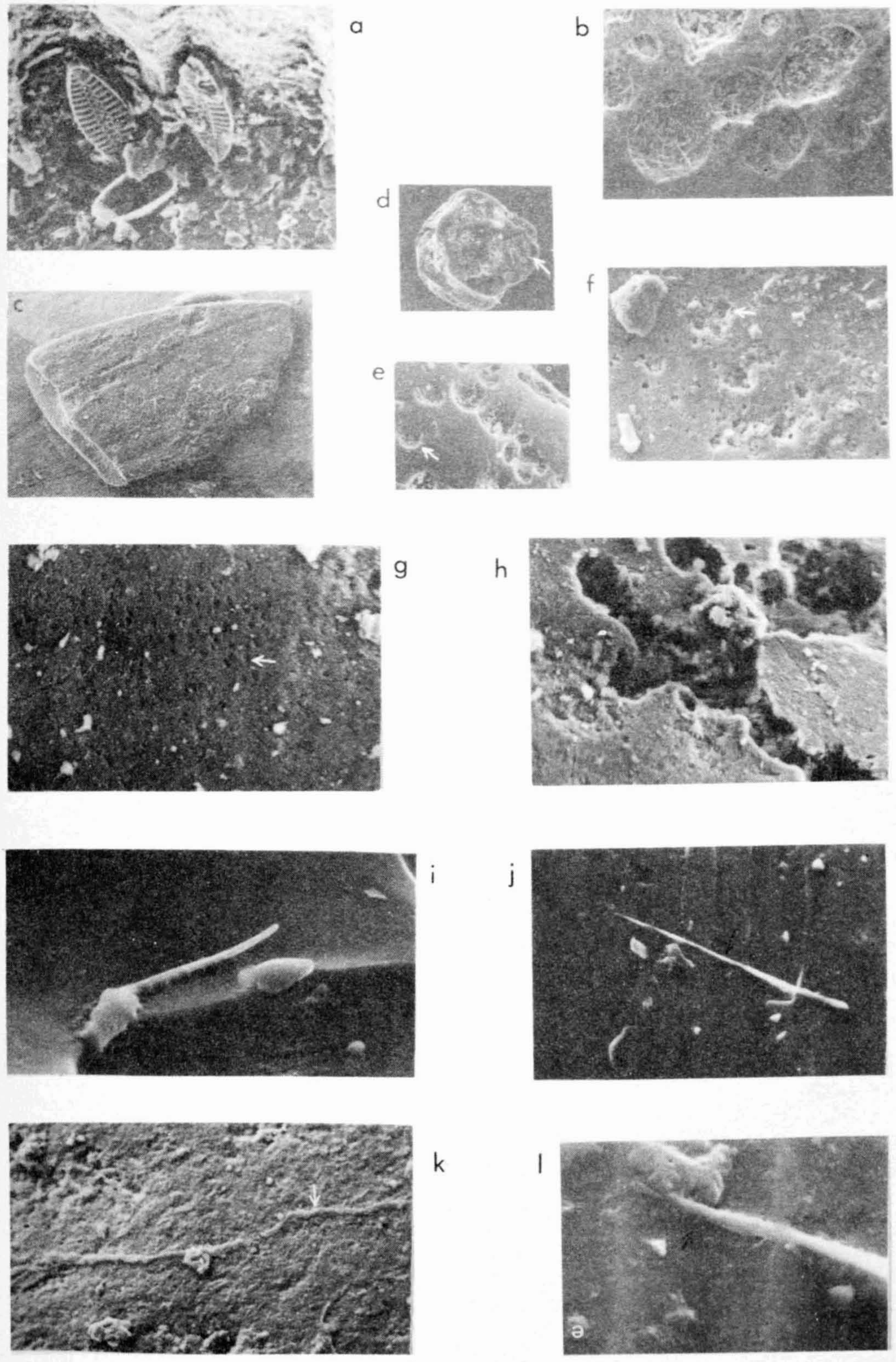
(i) Silicified fungal filament (side view) on a quartz grain from the Temeside Bone-Bed, Ludlow. (x 1000).

(j) Another silicified fungal filament (same species) on a quartz grain from the Temeside Bone-Bed, Ludlow - viewed from above. (x 250).

(k) Phosphatised fungal filament on a phosphorite nodule - Ludlow Bone-Bed, Ludlow. (x 1200).

(l) Detail of the holdfast of the silicified fungal filament illustrated in j from the Temeside Bone-Bed. (x 2500).

Plate 19



Antia, on bone-beds. For explanation see p.174.

CONTENTS

Reprint from:
Mercian Geologist, Vol.7, No.2, April 1979,
pp.93-174, 15 text-figs., plates 14 - 19.

A LIFE TABLE ANALYSIS OF THE LOWER PLEISTOCENE, WALTONIAN RED CRAG BIVALVE SPECIES GLYCIMERIS GLYCIMERIS (LINN.)

by

David D.J. Antia

Summary

The size distributions of disarticulated valves of the bivalve species Glycimeris glycimeris (Linn.) were examined and taken to indicate that marked sedimentological size sorting of shells had occurred within the Waltonian Red Crag at Walton on the Naze, Essex. The age distributions of the articulated G. glycimeris shells, found out of life orientation, enabled a life table analysis to be made of the species, and conclusions to be drawn about natality and mortality rates within the species.

Introduction

The Waltonian Red Crag of Walton on the Naze consists of a series of interbedded cross bedded shell sand wedges/megaripples and silt sheets, containing localised areas of bioturbation. Most of the bivalve shells in the shell sands are disarticulated, fragmented and abraded. However, some glycimerids have been found (Antia, 1979) with closed articulated valves in layer 7 - see Kendall, 1931, for a key to the position of the layers referred to here in the cliff section at Walton on the Naze.

The presence of closed articulated glycimerid valves in a shell gravel indicates that minimal postmortem sedimentological transport of the dead animals has occurred (Thomas, 1975). This view is contrary to those outlined by Antia & Wood (1977) who showed that the glycimerids obtained from layer 11 have skewed size distribution (Fig. 1a) which they interpreted as being representative of a highly transported sedimentological deposit.

In order to test the validity of these view points, ten cubic metres of sediment from layer 7 were sieved through a 1 mm mesh and all the whole (unfragmented) glycimerid valves removed and their lengths measured. In the instance of whole closed articulated valves only the number of annual growth rings were recorded.

Results and discussion

The size distributions of the disarticulated bivalve shells in layers 7 and 9 (Fig. 1a, b) suggest that marked size sorting of the shells has occurred and that a life table interpretation of the data would be invalid. However, the age distributions (Fig. 1c) of the closed articulated glycimerid valves (none of which were found in life orientation) are indicative of a minimally sorted population (i.e. a near life assemblage), and possibly confirm Thomas's opinion (Thomas, 1975, p.223) that the presence of glycimerid shells with their valves articulated and closed, but not in life position, in a

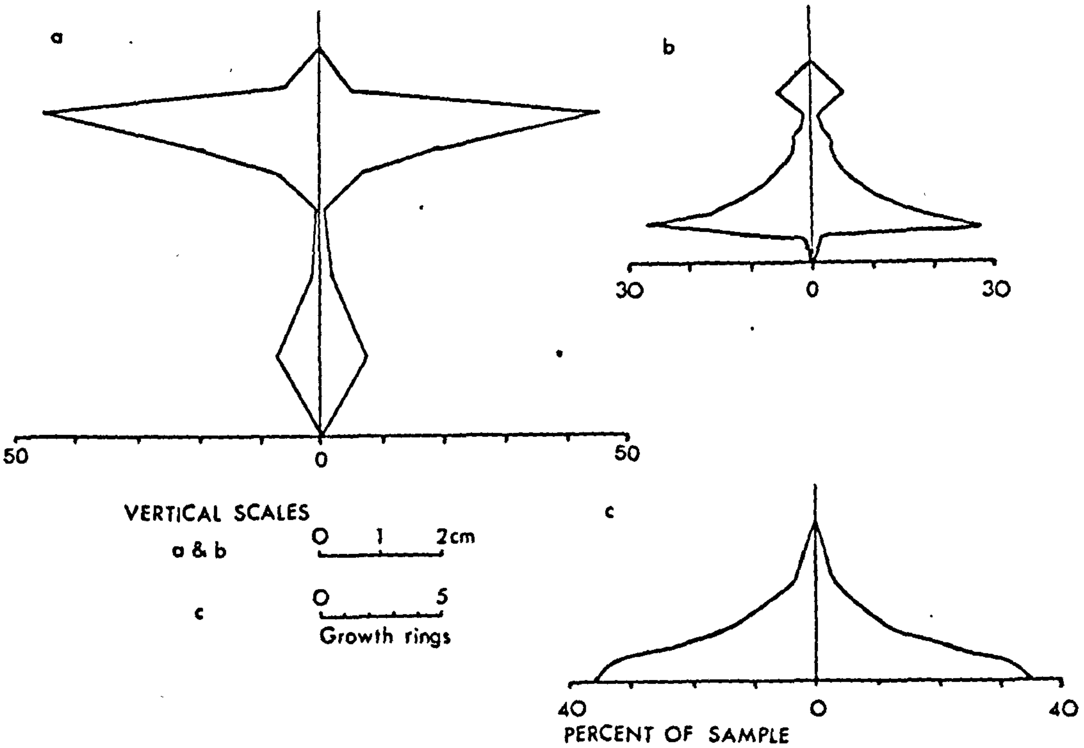


Figure 1 (a) Size distributions of disarticulated *Glycimeris glycimeris* valves from layer 11; (b) Size distributions of disarticulated *Glycimeris glycimeris* valves from layer 7; (c) Age distribution of articulated *Glycimeris glycimeris* shells from layer 7.

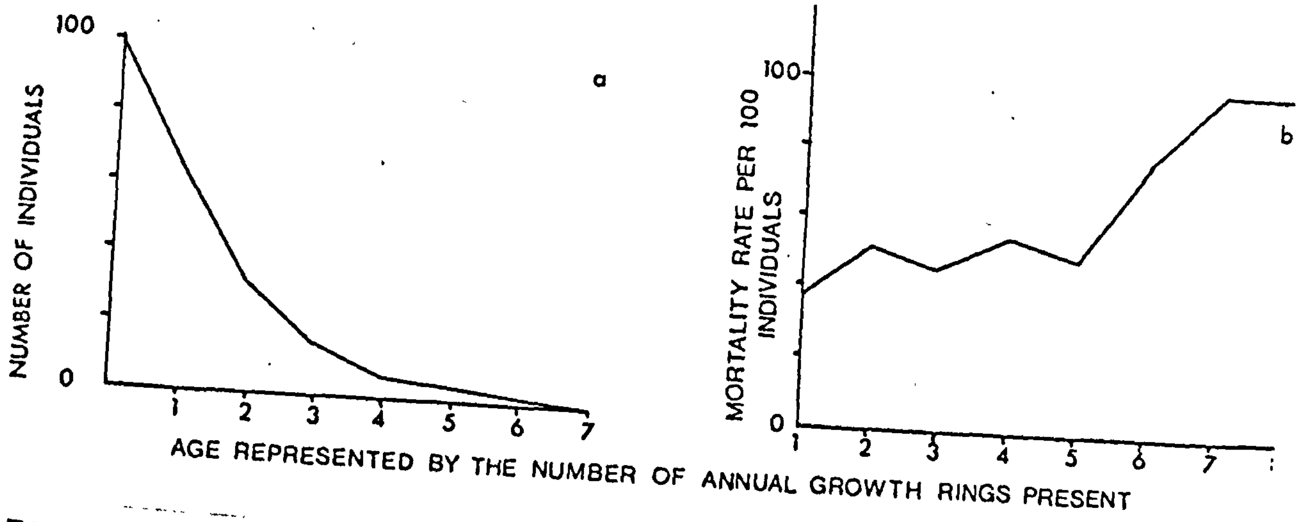


Figure 2 (a) Survivorship graph and (b) Mortality rate graph for the articulated *Glycimeris glycimeris* shells in layer 7.

shell gravel/sand indicates that the shells were buried alive. If this assumption regarding the cause of death is accepted, then a life table can be compiled.

The principles of life table analyses outlined by Deevy (1950), Sellmer (1967), Pielou (1969), Reyment (1971), Krebs (1973), Valentine (1973) and Antia & Wood (1977) suggest that meaningful conclusions can be drawn from minimally sorted populations regarding the natality and mortality rates, population structure and maturation of a species.

If this is so then an examination of the age pyramids (Fig. 1c), survivorship curve (Fig. 2a) and the mortality rate graph (Fig. 2b), drawn from the data presented in the life table (Table 1), could suggest that the Crag species <u>Glycimeris glycimeris</u> (Linn.)

(1) produced many young and possessed the age distribution of an expanding population (see Fig. 1c; cf. Clapham, 1972, p.94),

(2) in which mortality was concentrated on young individuals; the probability of death decreased with age (see Fig, 2a; cf. Deevy, 1950),

(3) the species reached sexual maturation by the second age interval and physiological breakdown due to aging was most marked between the fifth and seventh age interval (see Fig. 2b; cf. Sellmer, 1967; Valentine, 1973; Antia & Wood, 1977).

Since <u>Glycimeris glycimeris</u> was not found in life orientation (and a life table analysis suggests that valid interpretations can be made about the population) it seems likely that the animals were washed out of their shallow burrows and subsequently buried during the last major reworking of the shell gravel in which they are now entombed. This interpretation of death fits in well with current knowledge concerning the life habits of the glycimerididae (Thomas, 1970, 1975) and implies a subtidal origin for layer 7 as a clean shell gravel, swept by strong currents, occurring at a depth of between -16 and -100 m O.D.; see Boillot (1965), Holme (1966), Cabioch (1969), Thomas (1970, 1975) and Tebble (1966).

Conclusions

This study has indicated that disarticulated valves of G. glycimeris within the Waltonian Red Crag show a marked degree of sedimentological size sorting; and suggest that closed articulated valves of G. glycimeris, found out of life orientation, may have been buried prior to death and are thus representative of the original life population as a near life assemblage.

Table 1. A life table for the closed articulated valves of <u>Glycimeris glycimeris</u> from layer 7.

Key to the columns of the table.

1 - Age interval given in number of growth rings

2 - Sample size

3 - Proportion dying in the age interval

4 - Number living at age x assuming an initial population of 10000

5 - Number dying in interval

6 - Number of timespans lived in the interval

7 - Total number of timespans lived beyond age x

8 - Observed expectation of life at age x

9 - Proportion of survivors over the age interval

1	2	3	4	5	6	7	8	9
0	57	10000	0.3800	3800	8100	16803	1.68	0.62
1	48	6200	0.5161	3200	4600	8703	1.40	0.48
2	22	3000	0.4889	1467	2267	4103	1.37	0.51
3	13	1533	0.5652	866	1100	1836	1.20	0.44
4	5	667	0.5000	333	501	736	1.10	0.50
5	4	334	0.8000	267	201	235	0.70	0.20
6	1	67	1.0000	67	-	-	-	-
7	-	-	-	-	-	-	-	-

References

ANTIA, D.D.J. and WOOD, B.A. 1977. Some aspects of the palaeoecology of the E_1b Zone of the Edale Shales (Namurian) in the Edale Valley, Derbyshire. Mercian Geol., Vol. 6, pp. 179-196.

ANTIA, D.D.J. 1979. Bone-Beds: A review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering and microbiotas. Mercian Geol., Vol. 7, pp. 93-174.

BAILLOT, G. 1964. Geologie de la Manche occidentale. Annales de L'institut Oceanographique, Vol. 42, pp. 1-220.

CABIOCH, L. 1968. Contribution a la connaissance des pleuplements benthiques de la Manche occidentale. Cah. Biol. Mar., Vol. 9(5) suppl., pp. 493-720.

CLAPHAM, W.B. 1972. Natural Ecosystems. 248 pp. Macmillan, London.

DEEVEY, E.S. 1950. The probability of death. Sci. Amer., Vol. 182, pp. 58-60.

HOLME, N.A. 1966. The bottom fauna of the English Channel. Part 2. J. Mar. Biol. Ass. U.K., Vol. 46, pp. 401-493.

KENDALL, P.F. 1931. The Red Crag of Walton on the Naze. Geol. Mag., Vol. 68, pp. 405-420.

KREBS, C.J. 1973. Ecology. 694pp. Harper & Row, London.

PIELOU, E.C. 1969. An introduction to mathematical ecology. Wiley, London. 286pp.

REYMENT, R.A. 1971. An introduction to quantitative palaeoecology. 226pp. Elsevier, London.

SELLMER, G.P. 1967. Functional morphology and the ecological life history of the gem clam, Gemma gemma (Eulamellibranchia: Veneridae). Malacologia, Vol. 5, pp. 137-223.

TEBBLE, N. 1966. British Bivalve Seashells, Brit. Mus. (Nat. Hist.) Lond., 212p.

THOMAS, R.D.K. 1970. Functional morphology, ecology and evolution in the genus Glycimeris (Bivalvia). Unpub. Ph.D. thesis, Harvard Univ. 397pp.

THOMAS, R.D.K. 1975. Functional morphology, ecology and evolutionary conservatism in the glycimerididae (Bivalvia). Palaeontology, Vol. 18, pp. 217-254.

VALENTINE, J.W. 1973. Evolutionary palaeoecology of the marine biosphere. 511pp. Prentice-Hall, New Jersey.

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13

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SCANNING ELECTRON MICROSCOPY IN THE STUDY OF SEDIMENTS

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A SCANNING ELECTRON MICROSCOPE STUDY OF THE GENESIS OF THE UPPER SILURIAN LUDLOW BONE BED

* D. D. J. Antia & ** J. H. McD. Whitaker

ABSTRACT

The Ludlow Bone Bed horizon (Basal Downtonian) consists of a rippled thelodont sand formed low in the intertidal zone as a lag concentrate. SEM examination of the clasts reveals an abundance of thelodont scales, acanthodian and brachiopod fragments with accessory phosphorite and quartz. About 20% of the thelodonts are markedly abraded and these often contain borings comparable to recent intertidal algal borings. Many quartz grains bear authigenic, euhedral, bipyramidal overgrowths formed within the sediments. These overgrowths show varying degrees of abrasion, indicating that there was local reworking of the original subtidal sediment and concentration of the abraded quartz euhedra, fish debris, phosphatic shell fragments and internal moulds and casts to form the bone beds. Grain edges may be plastered with cryptocrystalline silica and fungal filaments on the grains surfaces may be silicified, before final sediment stabilisation.

Both worn and unworn euhedra may show a second generation of diagenetic overgrowths after sediment stabilisation and burial.

INTRODUCTION

The Ludlow Bone Bed forms an historically important geological horizon (Griffiths 1973), once considered to represent the Silurian/Devonian boundary (Stamp 1923). At present it marks the junctions of the Ludlow and Downtown (Pridoli) series (Upper Silurian) and the junctions of the Whitcliff and Temeside stages (Holland *et al* 1963; Allen 1974).

Although the Ludlow Bone Bed is described as two distinct layers (Elles & Slater 1906) found within the marked roadside cleft at Ludlow, detailed work by one of us (DDJA, unpublished) has revealed the presence of 8 separate bone beds and shown the cleft to be diachronous. Within its main outcrop the bone bed may be described at Aston Munslow, Corfton, Deepwood, Brockton, Ludford, Netherton, Orleton,

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Shipton and Willey, as a thin (0.1 - 13 cm thick) rippled discontinuous unimodal sand (mean grain size approx. 0.25 mm) with a gingerbread appearance, comprised largely of thelodont scales (up to 1000 scales per cm^2 bedding plane surface area) and acanthodian fragments; with secondary phosphatic brachiopod fragments, small phosphatic concretions, pachythecids, eurypterids, ceratiocarids, conodonts and quartz grains. Nonphosphatised brachipods (chiefly *Protochonetes ludloviensis, Howellella elegans, Craniops implicata, Salopina lunata, Lingula sp. nov., and Microsphaeridiorhynchia nucula,* ostracods (chiefly *Nodibeyrichia verrucosa, Frostiella groenvalliana*, Londinia arisaigenesis* Cytherellina siliqua, Kummerowia* sp., Jefina* sp., Cavellina sp., Poniklacella sp., and Thilipsura* sp*), bivalves (chiefly *Modiolopsis complanata*, Pteronitella retroflexa, and Fuchsella amygdalina),* gastropods (chiefly *Loxonema gregaria*, L. obsoleta, Umbospira (Platyschisma) helicites* Platyschisma williamsi*, and Cymbularia carinata*),* and cephalopods (chiefly *Leurocycloceras whitcliffense)* accumulate as ripple hollow infill above and below the bone bed layers. Asterized species are only found above the basal bone bed horizon. In places (Brockton SO 578938, Shipton 563917, and Ludford 512742) the bone bed can clearly be seen to form an integral part of flaser-bedded strata, thus implying an intertidal origin for the bone bed as suggested by Allen (1974), and implied by Antia (1977), instead of a subtidal origin as a shallow marine shelf sediment (Hain 1969; Reif 1976; personal communication 1976) or a storm generated sheet (Watkins, in press).

Studies have concentrated on the thelodonts (DDJA using gold coated (75 nm thickness for sediment, 50 nm thickness for clasts) specimens on a Cambridge 600 SEM) and quartz grains (JHMcDW using aluminium coated (25 nm thickness) specimens on an ISI 60 SEM), although other clasts have been examined.

The quartz grains, thelodonts, phosphatic nodules and acanthodian debris examined were extracted (by DDJA) by acid treatment, using the techniques outlined by Turner (1973) from Ludford Lane (SO 512742) and Aston Munslow (SO 512865). Sediment samples consisted of untreated rock chips.

NON-CALCAREOUS CLASTS FROM THE BONE BED

The basal thelodont layer at Ludford consists largely of thelodonts (ca. 90%). Within the bone bed facies (Facies A - Allen 1974), for example (1) the bone bed horizon 6 at Ludford (512742) is dominated by phosphatized *Gomphonchus* spp. spine fragments; (2) *Thelodus parvidens* forms the dominant clast in the lower bone beds, but is replaced in the higher bone beds by *Logania ludlowiensis* as the dominant clast, (3) the bone bed contains varying amounts of debris acanthodian and phosphorite eg. 50% at Deepwood (Holland *et al* 1963); and Corfton lane (SO 497852), Ludford Lane 20% Aston Munslow (SO 512865), 1% Corfton - Sun Inn (SO 496851), (4) the density of quartz grains is also variable (expressed as number per gram of sediment)

(a) 12 at Ludford, (b) 0 at Deepwood), (c) 0.4 at Aston Munslow.

(1) Thelodonts

Two specimens dominate the thelodont fauna (1) *Thelodus parvidens* (70 - 95%) and *Logania ludlowiensis* (5 - 30%). They occur chiefly as unabraded scales (Figs 1, a-e and 3d) though some scales show attrition marks, borings and some degree of abrasion (Figs 1f, g, k and 3a). The borings appear to be similar to recent intertidal algal borings found in carbonate clasts at Sales Point, Bradwell, Essex (See Antia 1977 for location) (Figs 1h, i; 3c). Many of the clasts are imbricated and randomly orientated.

(2) Acanthodian fragments

These occur as broken, worn, often recrystallised fragments of ~~*Scolithus*~~ Sclerodus *pustiliferous* and other fishes (Fig 2, m-o).

(3) Conodont fragments

An extensive low diversity conodont fauna has been recorded from the Ludlow bone bed (Aldridge 1975). However, this study has only recorded worn fragments of *Ozarkodina confluens* and *Distomoda dubius* from the bone bed at Aston Munslow (identified by Alridge 1977, personal communication).

(4) Brachiopod fragments

Occur as worn fragments of *Orbiculoidea rugata* Fig 1m, n) (no other forms have been recorded) as about 1% of the bone bed by volume at Aston Munslow.

(5) Phosphorite deposits

Phosphorite nodules occur as the internal moulds and casts of *Loxonema gregaria, Cymbularia carinata* and *Orthoceras* sp. (Fig 1o, p). Some contain algal borings (Fig 1s) and consist of replaced authigenic clays containing angular quartz grains (Fig 1t) while others are comprised of faecal pellets (Fig 1q, r).

(6) Eurypterid fragments

Eurypterid debris forms a minor part of the deposits and is made up largely of *Pterygotus* spp. (Fig 1u).

(7) Quartz grains

Quartz grains form a minor component of the bone beds, and range from euhedral bipyramidal (ca. 15%) to spherical rounded grains (ca. 5%) (Fig 2a-d). The euhedral grains occur as hexagonal bipyramidal forms either with sharp or worn edges (Figs 2e-h) often with later diagenetic overgrowths (Fig 2i-1). Many of the subrounded grains show euhedral faces (Figs 2b, i, u and 3e). The grains may be pitted or polished (Fig 3e) and are often covered by siliceous filaments (Figs 2u and 3e, f). These filaments are of late stage origin since they transgress across pitted and fractured surfaces (Fig 2q-r). They often display triple junctions, with junction angles approximating to 120° (Fig 1t, w) and may possibly represent silicified fungal hyphae cf. Edwards & Perkins (1974). Some of the quartz

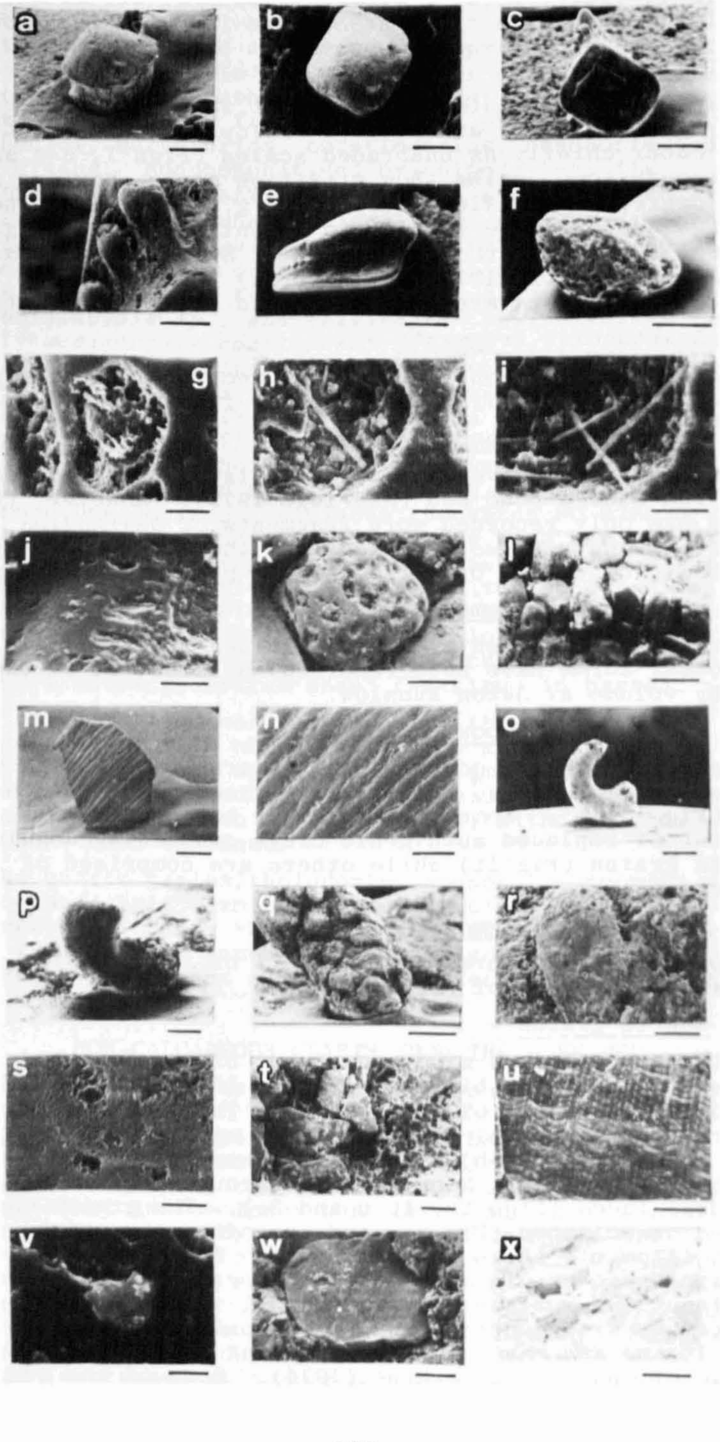
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Figure 1 Number in parenthesis = Scale Bar length. Unabraded thelodont scales. (a) *Thelodus parvidens* (100 µ), (b) *Thelodus parvidens* - dorsal view (100 µm), (c) *Logania ludlowiensis* - upper body scale (100 µm), (d) *Logania ludlowiensis* - lower body scale (20 µm), (e) detail of latter (100 µm). Worn thelodonts (f) Rounded worn bored thelodont (*T. parvidens* - note boring density on the spongy cusp of the denticle the crown of this denticle (not shown) has almost no borings (200 µm), (g) Detail of a boring with a raised cusp in its centre indicating uneven dissolution of the thelodont during its formation (20 µm), (h & i) Recent algal dissolution pits in a carbonate grain from the low intertidal (rippled mud facies) of Sales Point, Bradwell, Essex - note the presence of algal filaments - see also Plate 3c (15 µm), (j) Attrition marks on a *Logania ludlowiensis* denticle (10 µm), (k) Well rounded, worn, bored, thelodont (*T. parvidens*) in sediment - note close packed nature of the clasts and that the thelodont has been worn after as well as before it was bored (100 µm), (l) Bedding plane surface of the bone bed - note imbricated nature of the clasts (200 µm), (m) Shell fragment of *Orbiculoidea rugata* (200 µm), (n) Detail of the ornamented surface (20 µm), (o) Internal case of ?*Cymbularia carinata* (200 µm), (p) Internal cast of ?*Loxonema gregaria* (200 µm), (q) Internal cast of ?*Orthoceras semipartitum* made largely of faecal pellets (200 µm), (r) Detail of faecel pellets (40 µm), (s) ?Algal borings on the surface of *L. gregaria cast* (10 µm), (t) Internal structure of an internal cast of *L. gregaria* - note quartz grains (2) and replaced clays (1) (20 µm), (u) Surface of a *Pterygotus* sp. fragment (50 µm), (v) Kaolinite grain on the surface of a bored thelodont (20 µm), (w) Worn mica grain (20 µm), (x) Diagenetic quartz in Upper Whitcliffe sediment (20 µm).

grains contain small pits with raised rims (Figs 2u and 3e, j,k). These are probably pressure solution cavities formed at the junction of two grains of different chemical compositions. Some of the quartz shards (Fig 3f) may be derived from bentonites. On some of the quartz grains 'spherulite' and doughnut-like structures are present (Fig 2x, y).

Thus the quartzes show the following diagenetic and depositonal phases/forms:

a) Original unaltered (probably β) quartzes occurring as well-rounded grains and angular shards (Figs 2a and 3f)

b) Secondary euhedral (α) quartzes formed as overgrowths nucleated around the initial quartz (Fig 2d, 1). These overgrowths were probably formed in a clay rich

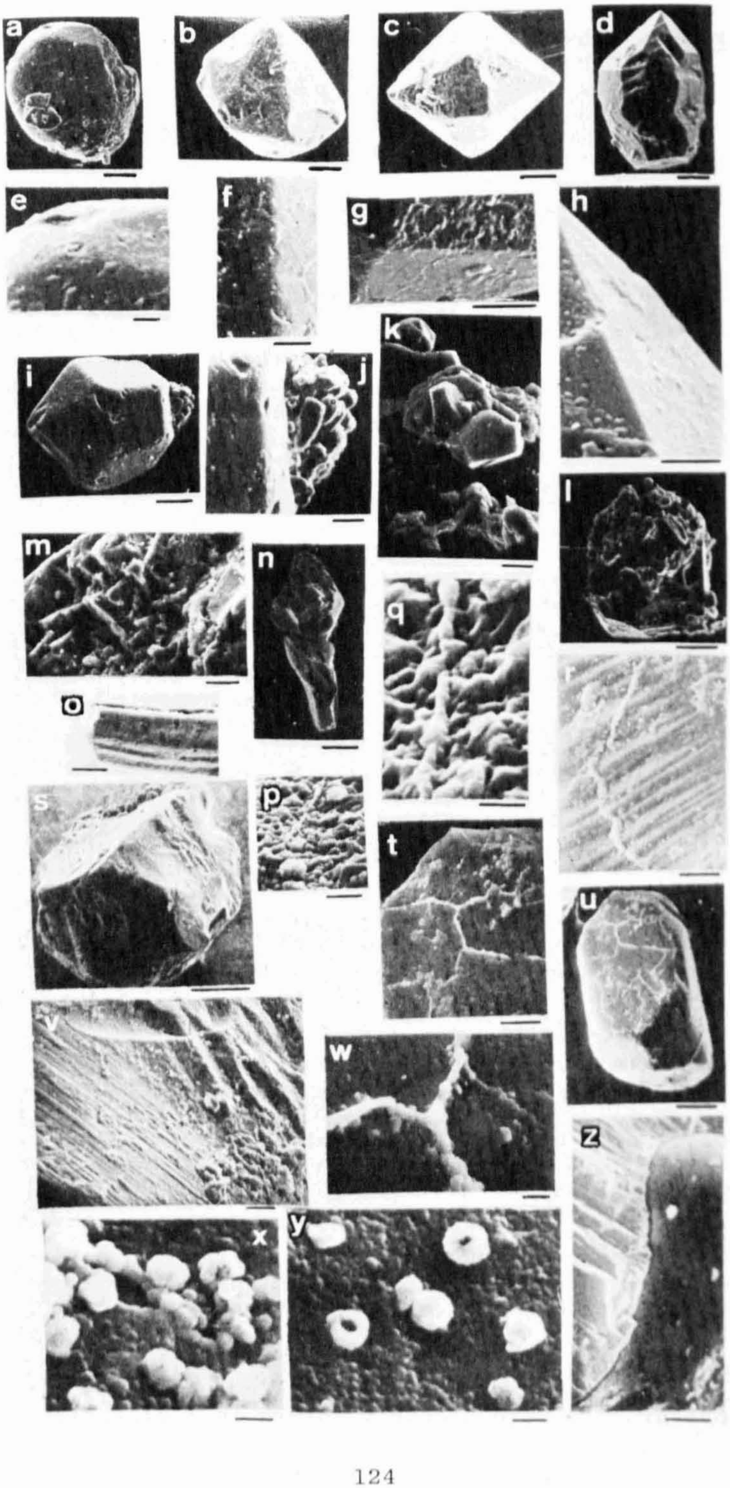
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Figure 2 Number in parenthesis = Scale Bar length. Quartz grains. (a) Well rounded quartz grain (100 µm), (b) Worn quartz grain with some euhedral faces (100 µm), (c) Euhedral bipyramid (100 µm), (d) Euhedral quartz grain with unworn edges (100 µm), (e.h) Rounded to sharp grain edges for grains (a-d) (20 µm), (i) Rounded euhedral quartz grain with secondary unworn euhedral overgrowths (100 µm), (j) Detail of overgrowths (50 µm), (k) Detail of euhedral overgrowths on an unworn quartz grain (20 µm) (l) the unworn grain (100 µm), (m) Detail of recrystalised surface of an acanthodian fragment (20 µm), (n) The acanthodian fragment showing post prefossilisation wear and post sediment stabilisation recrystalisation (100 µm), (o) Part of an *Onchus muchisoni* spine (Acanthodian) (100 µm), (p) Siliceous ?fungal filament on the pitted surface of quartz grain (20 µm), (q) Detail of the filament (4 µm), (r) Detail of a filament on the fractured surface of a quartz grain (Plate 3f) (20 µm), (s) A feldspar grain (25 µm), (t) Detail of filaments on the surface of a quartz grain (25 µm), (u) The worn euhedral quartz grain covered in filaments (50 µm), (v) Detail of the cleavage on the feldspar grain (s) (10 µm), (w) Detail of a filament triple junction (2 µm), (x) Quartz spherulites and rosettes on the surface of a quartz grain (2 µm), (y) Quartz 'doughnuts' on the surface of a quartz grain (2 µm), (z) Thelodont denticle (t) in calcite cement (c) (30 µm).

carbonate sediment, since Al-Sheikly (personal communication 1977) has shown that the lower the clay content of a carbonate sediment the larger the hexagonal prism faces of the (diagenetic) bipyramidal euhedral overgrowths.

c) Exhumed rolled quartzes - varying degrees of abrasion; (Figs 2a-c, i, u and 3e)

d) Stabilisation of the grain in the sediment was followed by subsequent fungal overgrowths. Later movement of silica from the porewaters replaced the fungal walls (Figs 2p-r, t, u, w) and provided thin silica sheet overgrowths on some grains (Fig.3l) to give a polished appearance.

e). Late phase diagenetic precipitation of secondary quartz overgrowths on the primary overgrowths (Fig 2i-l).

The Ludlow bone bed is not unique in containing euhedral quartz overgrowths since they have also been recorded in the Rhaetic Bone Bed (Sylvester-Bradley & Ford 1968), and the Kiddville bone bed of Kentucky (Foersete 1906; Wells 1944, p 285).

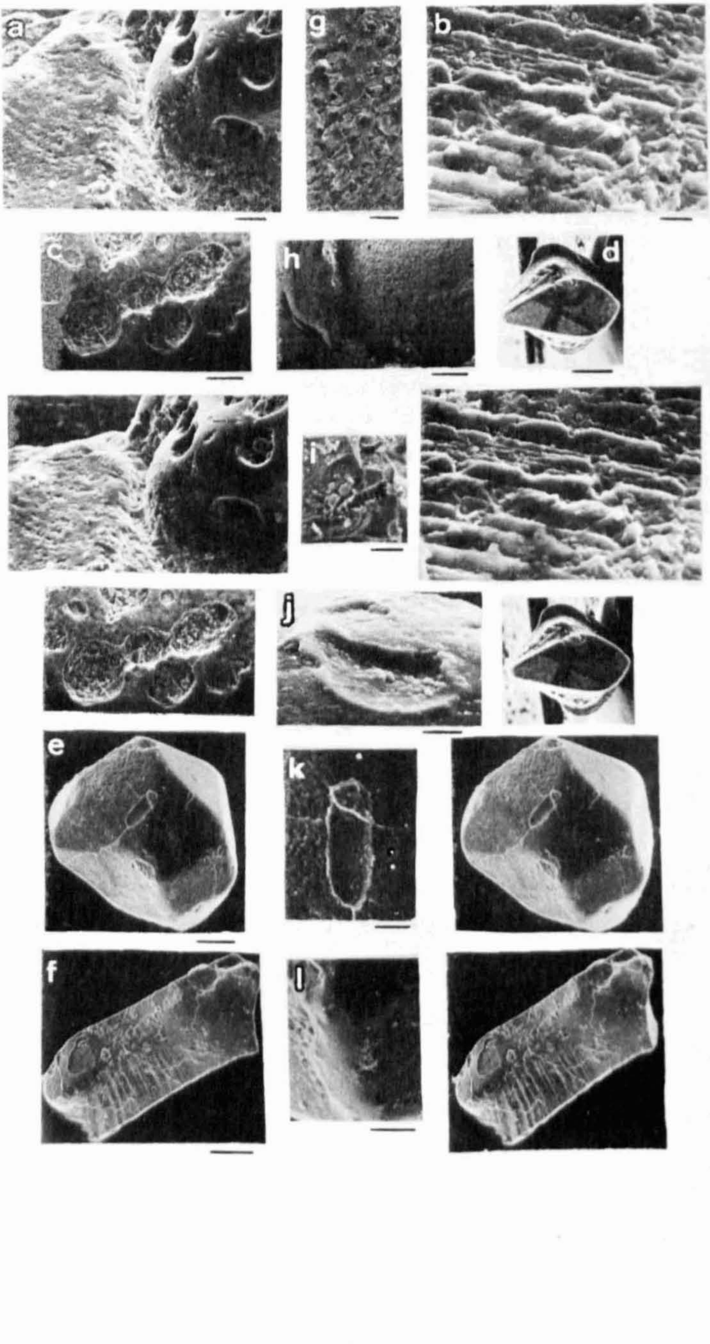
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Figure 3 NB. The individual picture of stereopairs on this page have been interposed to save space. Number in parenthesis = Scale Bar length. (a) Junction of a rounded bored thelodont (*P. parvidens*) with a worn quartz grain. Note-pitting on the quartz grain and the clay rim around the thelodont - stereopair (40 µm), (b) Well cleaved calcite cement - stereopair (10 µm), (c) Algal dissolution hollows (borings) on a recent carbonate grain from Sales Point, England - note morphological similarity to the thelodont borings - stereopair (50 µm), (d) *Logania ludlowiensis* scale - variant - note almost unworn condition of the scale - stereopair (100 µm), (e) Quartz euhedra showing worn edges, quartz plastering (1), pressure solution pits and filaments - stereopair (100 µm), (f) Quartz shard cut by filaments (Detail Plate 2r) - stereopair (200 m), (g-i) *Pachytheca sphaerica* - a round spherical algae (up to 6 mm in diameter) comprised of an inner layer of tubes radiating from a centre (the external surface expression of the tube illustrated in (g) (20 µm). The internal mass of tubes is covered by a thin outer layer (h (100 µm) shows the junction of the two layers) which contains small tubes with an annular structure, (i) (10 µm) Pressure solution pits bordered with a clay rim are shown in j and k (50 µm/ 40 µm), (k) A quartz plastered edge is shown in l (50 µm).

Feldspar grains derived from ?bentonites occur rarely (1 grain recorded) in the Ludlow Bone Bed at Ludford Lane (Figs 2s, v).

(9) Sediment

Below the bone bed diagenetic calcite and quartz comprise much of the sediment (Fig 1x). In the bone bed carbonate (Figs 2z and 3b) and kaolinite grains (Figs 1v) dominate the matrix with accessory muscovite grains (Fig 1w).

DISCUSSION

The Ludlow Bone Bed is an unusual, but by no means unique, accumulation of fish debris (cf. Reif 1976). It was formed as a littoral lag concentrate on or about the low watermark in a chenier environment (Antia 1977 - in preparation). Although a discussion of the environmental location of the bone bed is not the purpose of this paper, the source of the fish debris deserves some mention. Many theories for the origin of this debris have been proposed and are summarised by Griffiths (1973). In general theories range from the suggestion of mass mortality to condensation. In contrast to these theories we would like to propose the following schematic model for the clast source and intertidal formation of the Ludlow Bone Bed with the schematic environments illustrated in Fig 4.

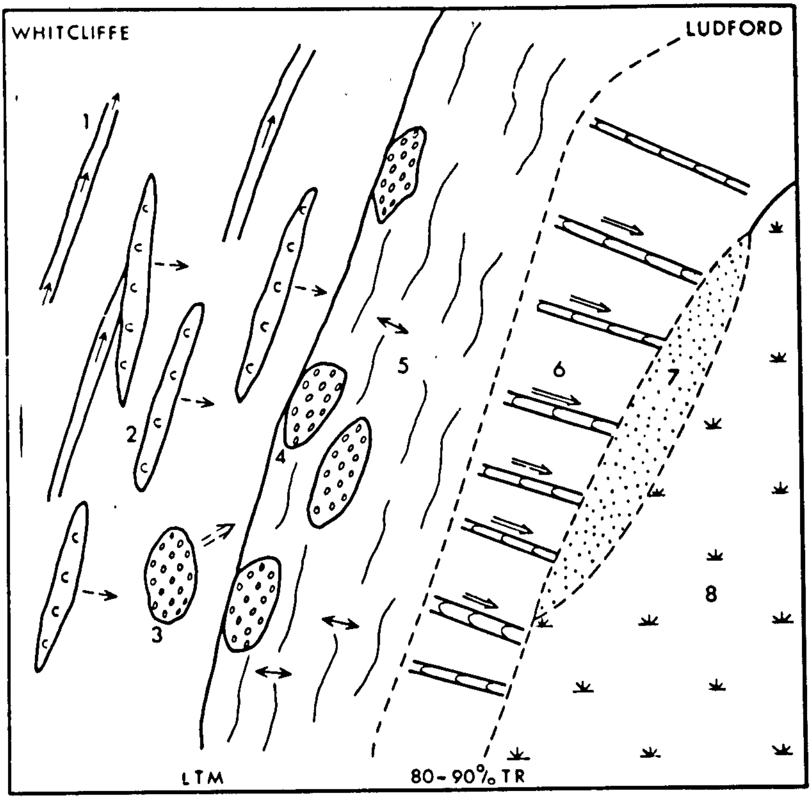

Figure 4 Detailed schematic environmental model (approx. 1 km wide) based on the type Whitcliffe and Ludlow/Downtonian boundary sections at Whitcliffe (507742) and Ludford Lane (512742) for the environments present during the Late Whitcliffe - Early Downtonian in the Ludlow Region. Arrows indicate directions of sediment movement. L.T.M. = Low Water Mark. T.R. = Tidal Range.
1) Subtidal shallow channels (<1m wide x <30 cm deep) with some concentrated shell debris at base (507742).
2) Migrating subtidal shell mega ripples (amplitude approx 4 - 15 cm wavelength 3 - 10 m) made of worn brachiopod shells *Protochonetes* sp. *Microphaeridiorhynchus* sp. and *Salopina* sp.) containing an extant fauna of podocopid ostracoda and bryozoans (507742). Some of these mega ripples have cut across and infilled the subtidal channels (506743).
3) Small subtidal patches (often rippled) of Thelodont-rich clays or shelly silts formed by a winnowing effect by the currents on the excavated material from the channels (512865).

Figure 4 (Contd)

4) Intertidal bone bed (Thelodont sand) often forming an integral part of flaser-bedded strata and commonly overlying rippled shell patches and *Chondrites* rich muds.

5) Intertidal rippled mudflats (markedly flaser bedded) often containing small thelodont sand patches infilling burrows or forming part of flaser-bedded strata. The *in situ* fauna on these mudflats included endobyssate colonies of *Modiolopsis* sp. and shallow burrowing brachipods *(Lingula minima)*.

6) Mud mounted topography (512742, 512865), intertidal, formed by the temporary re-excavation of the lower rippled mudflats (5). Individual channels can be traced in excess of 10 m (512742). The extant fauna of these channels included *Umbospira* sp. and *Frostiella* sp.

7) Perched trough cross bedded sand sheets (?chenier sands) which sometimes bury the underlying channels of the mud-mounted topography (512742). They contain no extant fauna - and may be supratidal in nature.

8) ?High intertidal - supratidal marsh sediments consisting of fine grained parallel laminated silts, rich in plant debris/fragments, the algae *Pachytheca* Fig 3g-i) and rare disarticulated ostracods (512742).

1) Subtidal setting - carbonate-clay-silt substrate with a burrowing soft bodied fauna and calcareous epifauna.

(a) Fish die (with normal natality and mortality rates operative) and lie on substrate surface. Either normal decomposition of the soft parts occurs phosphatising the dermal scales on the fish (Burnett 1974) or anaerobic burial of the fish occurs with subsequent phosphatisation (Burnett 1974).

(b) Since complete thelodont fishes have not been recorded in the Whitcliffe near Ludlow, even though their scales are abundant (>0-50 per m^2), it is unlikely that the scales were disarticulated prior to burial. In modern Peruvian subtidal sediments both phosphate and silica precipitate out at about 15 cm depth in the substrate (Burnett 1974). It is also possible that similar chemical processes were operative in the subtidal Whitcliffe sediments. If they were, then it is envisaged that the euhedral quartz overgrowths formed at this stage in addition to unphosphatised scales becoming phosphatised and phosphatic concretions forming internally in gastropod and cephalophod shells.

(c) Local chanelling and bioturbation within the Whitcliffe may have excavated the quartz grains and phosphatic debris, prior to their washing onshore by local currents and wave action. Both channels and bioturbation are common in the Whitcliffe eg. Aston Munslow (511876 & 512865),

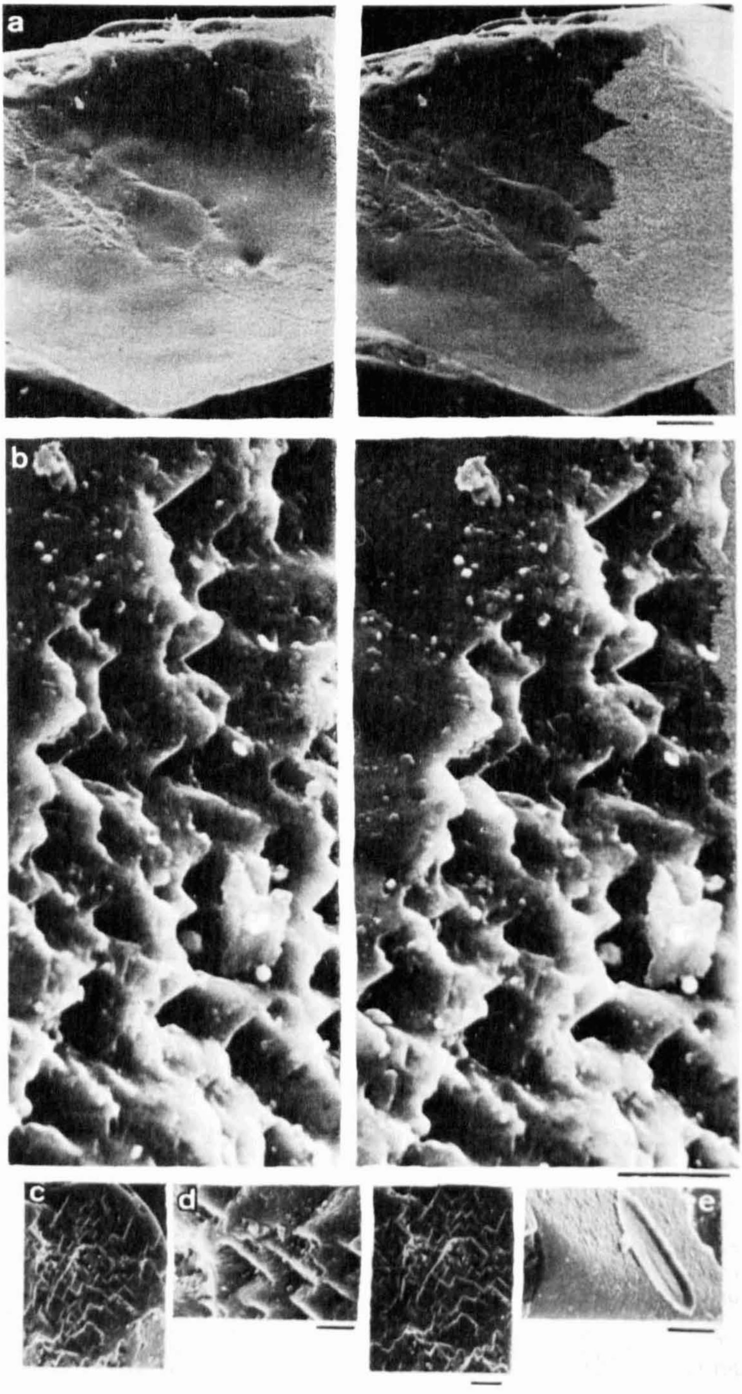
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Figure 5 a) Rounded quartz grain from the Ludlow Bone Bed Ludford Lane, showing a cryptocrystalline silica plastering which covers both the edges and surfaces of the grain and post dates the development of the tabular plates on the grain. Scale Bar = 75 µm

b) Tabular plates on a quartz grain surfaces (L.BB. Ludford Lane). Note 1) the two preferred orientations of plate edge formation, 2) that the plates form parallel to the crystal surfaces, 3) some of the plate edges are fractured possibly indicating abrasive effects on the plate. Scale Bar = 3 µm.

c) Large well-formed tabular plates on a quartz grain surface (L.BB., Corfton Lane) form parallel to the crystal surface. Scale Bar = 40 µm (Stereopair)

d) Detail of plates figures in Fig 5c. Scale Bar = 10 µm

e) Rounded edge of a quartz grain (L.BB., Corfton Lane) note the distribution of the tabular 'micro' plates. Scale Bar = 10 µm

Bourton (595964), Brockton (577939), Callaughton (617975), Hillpike (438760), Ludford (512742), Ludlow (504745 & 491743), Medley (477833), Munslow (522875) and Mortimer Forest (495719 & 496727).

2) Littoral environments - Flaser-bedded muds and silts forming rippled mudflats containing a high density low diversity fauna of ostracods, modiolopsids, lingulids and umbospirids.

(a) Bone bed debris concentrated and swept into pockets by tide and current. The white phosphatic debris (thelodont scales) was colonized by boring algae (the black phosphatic debris (*Gomphonchus* sp. and Brachiopod shells) was not bored, probably because they contained no collagen (Reif 1977, personal communication) when the thelodonts were colonized. A high energy origin for the bone bed is indicated since coprolites (an essential attribute of a low energy bone bed (Reif 1977, personal communication) are rare or absent. Supposed coprolites from the Ludlow bone bed in the Aepler collection (Tübingen University), when viewed in thin section can be shown to be carbonised limonite mudpellets rich in angular quartz grains and articulate brachiopod shell fragments.

(b) Period of silt/mud deposition - caused by increased sediment load in the estuary? - possibly seasonal in origin.

(c) Repetition of process to produce next bone bed layer, or continuation of mudflat facies depending on stage in the regression cycle.

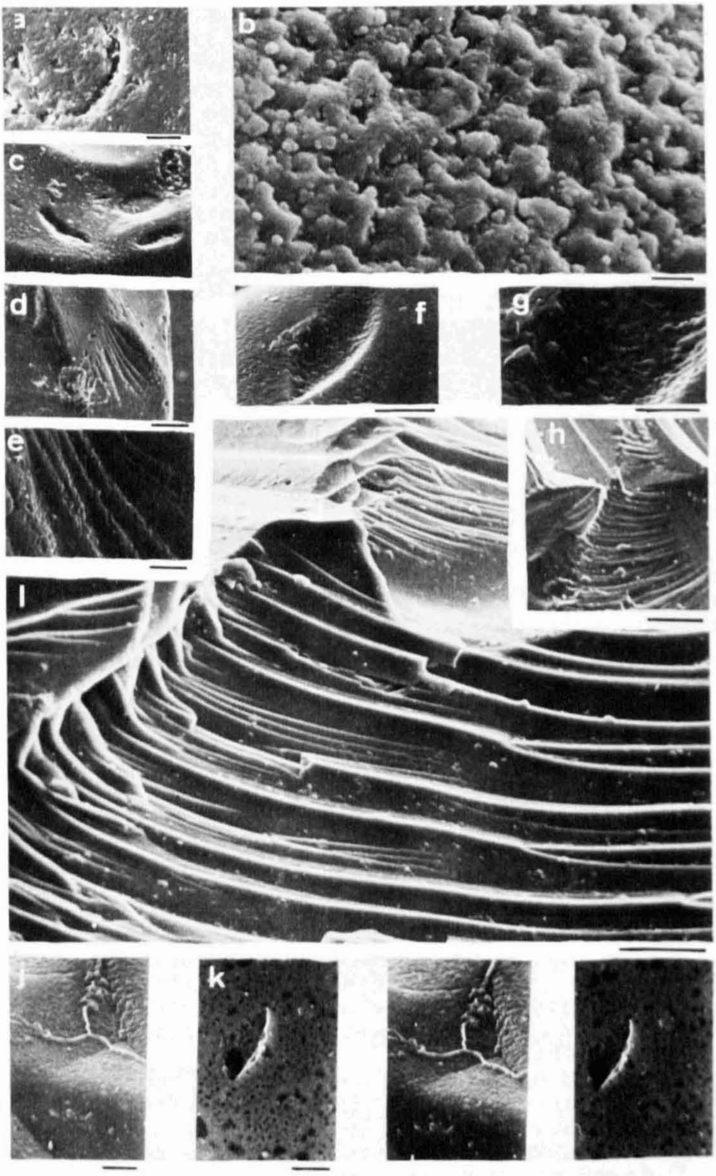
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Figure 6 a) Crescentic chip mark (L.BB. Corfton Lane). Scale Bar = 40 µm
b) Tabular plates (L.BB. Aston Munslow - grain illustrated Fig 3e) which have been modified percolating pore waters and contain quartz spherulites. Scale Bar = 2 µm
c) Crescentic chip marks (L.BB. Corfton Lane). Scale Bar = 40 µm
d) Surface of a quartz grain showing a fracture (L.BB. Corfton Lane). Scale Bar = 40 µm
e) Detail of fracture; note the tabular microplates on the fracture surface. Scale Bar = 10µm
f) Crescentic chip mark (L.BB. Corfton Lane) Scale Bar = 40 µm
g) Detail of chip mark (Fig 6f) showing microplates in the chip. Scale 1 cm = 20 µm
h) Fracture in a quartz grain produced by mechanical crushing (L.BB. Ludford Lane). Scale Bar = 100 µm
i) Detail of the fracture. Scale Bar = 10 µm
j) Detail of a quartz grain surface showing the relationship of the quartz plates to grain rounding. (L.BB. Corfton Lane). Note the filament with a triple junction. Scale Bar = 10 µm (Stereopair)
k) Chip mark on a smooth crystal surface (L.BB. Corfton Lane). Scale Bar = 10 µm. (Stereopair)

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REFERENCES

Aldridge, R.J., 1975, The stratigraphic distribution of conodonts in the British Silurian. *Journal of the Geological Society of London*, 131, 607-618

Upper Silurian Ludlow Bone Bed

Allen, J.R.L., 1974, Sedimentology of the Old Red Sandstone (Siluro-Devonian) in the Clee Hills area, Shropshire, England. *Sedimentary Geology,* 12, 73-167

Antia, D.D.J., 1977, A comparison of diversity and trophic nuclei of live and dead molluscan faunas from the Essex Chenier Plain, England. *Paleobiology,* 3, 404-414

Burnett, W.C., 1974, *Phosphate deposits from the sea floor off Peru and Chile: radio-chemical and geochemical investigations concerning their origin.* PhD thesis, Hawaii Institute of Geophysics, Honolulu, Hawaii, 164 pp

Edwards, B.D. & Perkins, R.D., 1974, Distribution of microborings within continental margin sediments of the South Eastern United States. *Journal of Sedimentary Petrology,* 44, 1122-1135

Elles, G.L. & Slater, I.L., 1906, The highest Silurian rocks of the Ludlow district. *Quarterly Journal of the Geological Society of London,* 62, 195-220

Foersete, A.F., 1906, The Silurian, Devonian and Irvine formations of East-Central Kentucky. *Kansas Geological Survey Bulletin,* 7, 369 pp

Griffiths, A.L., 1973, *Aspects of nineteenth-century stratigraphy in the Welsh Borderlands, with particular reference to rocks at the Silurian-Devonian boundary.* MSc. thesis, London University External

Hains, B.A., 1969, *The geology of the Craven Arms area.* Institute of Geological Sciences, London, 70 pp

Holland, C.H., Lawson, J.D. & Walmsley, W.G., 1963, The Silurian rocks of the Ludlow District, Shropshire. *Bulletin British Museum (Natural History),* 8, 93-172

Reif, W.-E., 1976, Sedimentologie und Genese von Bonebeds In: Seilacher, A (ed), *Palaökologie. Konstruktionen, Sedimentologie, Diagenese und Vergesellschaftung von Fossilien.* (Bericht 1970 - 1975 des Sonderforschungs-berichers 53, Tübingen). *Zentralblatt. Geologie und Paläontologie.* Teil II, (H.5/6), 252-255, Stuttgart

Stamp, L.D., 1923, The base of the Devonian with special reference to the Welsh borderland. *Geological Magazine,* 6), 276-336, 367-372, 385-410

Sylvester-Bradley, P.C. & Ford, T.D., 1968, *Geology of the East Midlands.* Leicester University Press

Turner, S., 1973, Siluro-Devonian thelodonts from the Welsh Borderlands. *Journal of the Geological Society of London,* 129, 557-584

Watkins, R., Benthic community organization in the Ludlow series of the Welsh Borderland. *Bulletin British Museum (Natural History) Geology. In press.*

Wells, J.W., 1944, Middle Devonian bone beds of Ohio. *Bulletin of Geological Society of America,* 55, 273-302

QUESTIONS

Q: P. Bull, Swansea University
How can you tell that some of the rounding of the euhedral crystal edges is not due to a cryptocrystalline silica plastering?

Q: D. H. Krinsley, Arizona State University
One can determine if the edges of quartz grains have been abraded by recognising plates on these edges. Plasting of silica should cover edges and surfaces.

A: D. D. J. Antia
Although Dr. Krinsley's statement answers Dr. Bull's question, it would perhaps be best to clarify the answer with a series of illustrated examples and comments:

On the recognition of abrasive rounding versus rounding by cryptocrystalline silica plastering in quartz grains.

If a quartz grain edge is rounded because it has been plastered by cryptocrystalline silica then its surface will appear to be very smooth (Fig 31, Fig 5a) much smoother than on an unplastered crystal (grain) edge (Fig 2e-h, Fig 5e). Plastering by cryptocrystalline silica may be confined to only the edges of the grain (Fig 3e, 1) or cover both grain edges and surfaces (Fig 5a). In the bone bed plastering occurs as a post depositional, early diagenetic stage, post dating the formation of tabular plates on the grains (Fig 5a).

However, if a grain has suffered abrasive rounding then three features will usually be present on the grains surfaces.

1) Tabular plates over the grains surface
2) Crescentic abrasive chip marks
3) Rounded (but not smooth) edges and fracture marks

Tabular plates on quartz grains in the Ludlow Bone Bed are orientated parallel to the crystal (grain) surfaces (Fig 5b, c, d) and are of varying sizes ranging from 3 - 40 µm in length (Fig 5b, c, d).

Crescentic chip marks occur on the quartz grains (Fig 6a, c, f, g, k) on either smooth crystal faces (Fig 6k) or on 'smooth' surfaces covered by small tabular plates (<5 µm) - Fig 6a, c, f, g, Many of these chip marks also contain a lining of tabular plates (Fig 6f, g) perhaps indicating that the grains had been abraded post chipping?

The grain edges of abrasively rounded grains tend to be smooth surfaces, made irregular, by the presence of tabular plates on their edges (Fig 5e, Fig 6j). Similar features are noticed on fractured quartz grains (Fig 6d, e) where the development of plates has given the fracture edges a rounded appearance (Fig 6e). This rounded appearance contrasts sharply with the angularity of fresh fractures produced by the mechanical crushing of samples (Fig 6h, 1).

Since plates are not present on grains which have only suffered mechanical abrasion (Fig 6h, i) it seems likely that their origin may be related to syndepositional differential dissolution of the quartz grain surfaces, and/or early post depositional dissolution in the porewaters predating the deposition of cryptocrystalline silica on the grains (Fig 5a). Similar interpretations of the tabular plates on quartz grains have been made by Weaver & Beck (1977, *Sedimentary Geology*, 17, pp 1-234; cf. pp 161-162)

However, some of the tabular plates on grains plastered with cryptocrystalline silica show evidence for solution rounding of the plates (Fig 6b). These plates may have acted as crystalline growth nuclei for the many quartz rosettes present on their surfaces (Fig 6b).

It is therefore suggested that the tabular plates arise as a result of syndepositional chemical solution processes which may modify pre-existing mechanical abrasion features such as chip marks and fractures. The presence of plates on a quartz grain aids the abrasive mechanical weathering processes, since it may require less energy to remove a small 'cleavage like' plate from a grain than to chip or fracture it. Such tabular plates, once formed may be modified by pore solutions after sediment stabilisation, and act as nuclei for later diagenetic crystal growths.

PHOSPHATE PEBBLES: A KEY TO THE RECOGNITION OF A SUBMARINE DISCONTINUITY AT THE LUDLOVIAN-DOWNTONIAN BOUNDARY (UPPER SILURIAN) IN THE WELSH BORDERLANDS

D. D. J. ANTIA

Abstract

A thin phosphorite rich bone-bed (The Ludlow Bone-Bed) in the Lower Downtonian (Upper Silurian) of the Welsh Borderlands appears to mark a submarine discontinuity of considerable regional extent. This bed, characterised by fish scales, phosphatic pebbles and steinkerns, occurs in outcrop for about 100 km, over an area of 5,000 sq. km, and has been found to mark the junction between two major biotopes. Although no erosion surface is associated with the bed, an erosion event is indicated by the presence of reworked diagenetic structures within it.

Prior to erosion, phosphorite (carbonate apatite) concretions formed as a diagenetic cement in buried near-surface soft muds. These sediments were subjected to erosion resulting in exhumation and subsequent concentration into a lag deposit.

Introduction

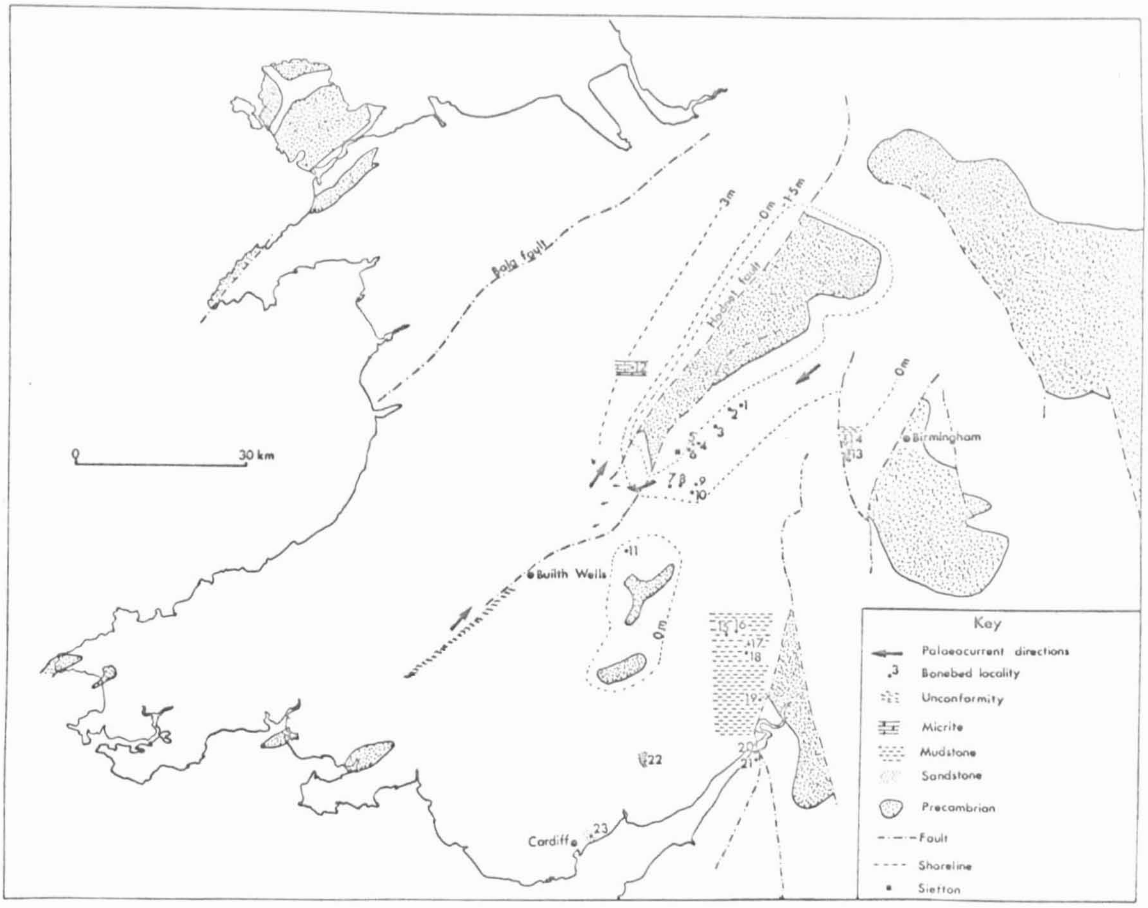
Most previous workers (e.g. Palmer & Fürsich, 1974; Fürsich, 1979), interpreting features associated with submarine discontinuities, have tended to deal with erosional events marked by clear-cut erosion surfaces. Such surfaces are distinct and take a variety of forms including corrosion crusts, hard grounds and breaks marked by mineral crusts. However, other studies (e.g. Lutze, 1967; Voigt, 1968; Kennedy & Klinger, 1972; Baird & Fürsich, 1975; Baird, 1976, 1978; Cherns, 1977; Kennedy et al., 1977; Brown & Farrow, 1978) have shown that some submarine discontinuities lack a clear-cut erosion surface and frequently contain phosphate or carbonate nodules on their surfaces. Such deposits are called hiatus concretions (Voigt, 1968). Hiatus concretions are commonly found as either concretions which were finally buried in sediments differing greatly from those in which they were formed (e.g. The Florida and West African phosphorites -- Baturin, 1970; Birch, 1971b; Burnett & Gomberg, 1977) or as concretions which were buried in sediments similar or identical to those in which they were formed (e.g. the British Lower Leintwardine Beds concretions -- Cherns, 1977). Such concretions usually record colonisation by boring and burrowing during early soft and firm ground stages (Fürsich, 1979). Some may contain evidence for several phases of concretion growth (e.g. Dietz et al., 1942; Kennedy & Garrison, 1975; Cherns, 1977). Once formed, a hiatus concretion deposit may rest on the sediment surface for a few years or a few millions of years (Kolodny & Kaplan, 1970; Burnett, 1974; Burnett & Gomberg, 1977).

This paper will describe structures associated with a regional discontinuity that lacks a clear cut erosion surface. The stratum in question is a thin bone-bed, which grades laterally into a phosphorite and has been termed the Ludlow Bone-Bed. It marks an abrupt regional change in faunal sequence (Elles & Slater, 1906; Holland et al., 1963) and sedimentary facies (e.g. Lawson, 1953, 1954; Walmsley, 1959; Squirrell & Tucker, 1960; Phipps & Reeve, 1964; Greig et al., 1969; Cave & White, 1972, 1978; Allen, 1974; Antia, 1979a). In most localities no erosion surface is visible and this bone-bed can easily be mistaken for part of a continuous sedimentary sequence. However, it is suggested here that this bone-bed marks the position of a true discontinuity whose formation is related to a change in the chemical composition of the Silurian sea.

Geological Setting

Exposures of The Ludlow Bone-Bed, although intermittent, have been observed in past years over an area of about 5,000 sq. km (Fig. 1) extending from Birmingham and Much Wenlock in the North, through Ludlow, to Usk, May Hill, Cardiff and Tites Point in the South (see Phillips, 1842; Murchison, 1859; Stamp, 1924; Lawson, 1954; Walmsley, 1959; Cave & White, 1972; White &

Fig.1



Map showing location of bone-bed outcrops mentioned in the text, palaeocurrents after Bailey & Rees (1973) and regions of Precambrian rock on the sea floor after Wills (1976, 1977). Localities are - 1, Willey (SO 673991); 2, Brockton (SO 578939); 3, Shipton (SO 563918) 4, Aston Munslow (SO 512865); 5, Corfton (SO 497853); 6, Corfton Sun Inn (SO 496852), 7, Downton (SO 435741); 8, Deepwood (SO 459740); 9, Ludlow (SO 512742); 10, Ashley Moor (SO 471673); 11, Kington (see Banks, 1856); 12, Long Mountain (SJ 331307); 13, Lye (SO 928845); 14, Netherton (SO 935874); 15, Priors Frome (SO 577391); 16, Perton (SO 644330); 17, Gorsley (SO 677257); 18, Rushall (SO 640348); 19, Longhope (SO 691191); 20, Tites Point (SO 688046) 21, Brookend Borehole (SO 687023); 22, Usk (SO 355957); 23 Rhymney (see Strahan & Cantrill 1912, p8).

Coppack, 1978; Antia & Whitaker, 1979). The postulated discontinuity occurs at the contact of the Upper Whitcliffe Beds (top Ludlovian) and the overlying Downton Castle Formation (basal Downtonian). This contact marks the base of the Ludlow Bone-Bed (Holland et al., 1963; Allen, 1974; Antia, 1979a).

The uppermost Upper Whitcliffe Beds are characterised by shelly calcareous lenticular bedded siltstones (Antia, 1979a) and the overlying Downton Castle Formation by limonitised lenticular bedded, channelled and mudcracked sandstones and siltstones (Allen, 1974; Antia, 1979a). These two units are distinguished on the marked faunal and sedimentological changes that occur at their junction (Elles & Slater, 1906; Holland et al., 1963; Allen, 1974), which are indicated in Tables 1 to 5 and Figs. 2 and 3.

The Ludlow Bone-Bed is marked by a thin (1 to 150 mm thick) black clay, silty shale, micrite, sparite or quartz sand, which is rich in fish scales, phosphatic nodules and fossil shells. Despite its thinness, the bed is remarkably persistent when traced laterally. Although some recent studies have suggested that the Ludlow Bone-Bed in the Ludlow district might not mark a disconformity (e.g. Antia, 1979a; Antia & Whitaker, 1979), other studies (e.g. Stamp, 1924; Allen & Dineley, 1976) suggest that the magnitude of the hiatus marked by the bone-bed may increase towards the south.

Local Palaeogeographic setting

The Ludlow Bone-Bed is found in four different sedimentary facies or environmental situations in the Welsh Borderlands.

1. In calcareous siltstones representing a shallow marine environment containing a Downtonian fauna and thin bone-beds, e.g. Loc. 12, Fig. 1, Wallop Hall, Longmountain, G.R. S.J. 331 307 (Palmer, 1971, p.150).
2. As lithobonebeds marking the junction between intertidal and subtidal facies, e.g. Localities 1-10, Fig. 1, (cf. Elles & Slater, 1906; Robertson, 1927; Allen, 1974; Antia & Whitaker, 1979; Antia, 1979a etc.)
3. As pelbonebeds and phosphorites in black clays probably deposited in a subtidal environment, e.g. Loc. 14-21, Fig. 1 (cf. Phillips, 1848;

Gardiner, 1927; Lawson, 1954, 1955; Squirrell & Tucker, 1960; Cave & White, 1971, 1978; Antia, 1979b).

4. As quartz-rich bone-beds probably deposited in a subtidal environment, e.g. Loc. 13, 22, 23, Fig. 1 (cf. Sellas, 1879; King & Lewis, 1912; Walmsley, 1958; Antia, 1979b).

It has been suggested (e.g. Tucker, 1960; Bailey & Rees, 1973; Wills, 1975, 1977) by the close of the Silurian that locally the Precambrian basement was exposed to the surface. These basement regions, indicated on Fig. 1, may have represented subtidal positive regions or regions of land during the uppermost Silurian (cf. Bailey & Rees, 1973).

It is interesting to note that Siefton (near Corfton see Fig. 1) was an area of intertidal sedimentation at the end of the Whitcliffian (Antia, 1979c), while at the same time Ludlow was a region of subtidal sedimentation (Allen, 1962, 1974). The later arrival of the intertidal facies at Ludlow (cf. Antia & Whitaker, 1979) may indicate that the Precambrian basement in the Church Stretton region which is bounded to the north by the Hodnet fault and to the south by the Church Stretton fault zone may have formed part of an emerging positive area during the late Whitcliffian and may even have formed a land region by the uppermost Whitcliffian. The relative position of the shore line (depicted by the intertidal subtidal boundary) of this land mass is indicated in Fig. 1 at three different times around the Ludlow - Downton series boundary (1) 1.5 metres below the boundary (data after Antia, 1979c), (2) at the boundary (after Allen, 1979; Antia & Whitaker, 1979; Antia, 1979a) and (3) 2-3 metres above the boundary (after Palmer, 1971). Each of these shorelines are based on points in Ludlovian - Downtonian transition sections around the Church Stretton Precambrian region, in which the position of the facies change from intertidal to subtidal environments is known relative to the series boundary.

Similarly, near Birmingham the effects of another rising fault-bounded Precambrian mass, termed here the Birmingham positive area, can be seen. At Lye, the junction between Whitcliffian subtidal and Downtonian intertidal sedimentary facies is marked by a quartz sand containing fish remains and an erosive base (Plate 1C). This sand facies was probably deposited as a lag concentrate in either an intertidal or a subtidal environment. Its appearance at Netherton (King & Lewis, 1912; Antia, 1979b) above the black phosphatic clays which were probably deposited in a subtidal environment, may herald a slightly later arrival here of shallower marine or intertidal conditions than that at Lye.

The great differences in sedimentation rates over the Welsh Borderlands (cf. Holland and Lawson, 1963) make any correlation of shore lines around differing land masses above and below the Ludlow - Downton boundary impractical.

In the Perton to Brookend region the Ludlow Bone-Bed is marked by a clay enriched in phosphatic nodules and fish debris or a phosphorite. This bone-bed facies is commonly overlain by lenticular bedded non-calcareous limonite rich siltstones and mudstones (Facies B of Allen, 1974), e.g. Perton, Rushall and Longhope, containing Frostiella groenvalliana and podocopid ostracods. However, in the Brookend borehole it is overlain by a laminated, microfaulted sandstone (Facies D, Allen, 1974). In all these sections the underlying Whitcliffian sediments were probably deposited in a subtidal environment and contain a large number of bone-beds (Squirrell, 1958; Squirrell & Tucker, 1960; Tucker, 1960; Cave and White, 1971, 1978).

Since the clayey bone-bed deposition and phosphorite formation probably occurred subtidally (cf. Baturin, 1969; Burnett, 1977; Antia, 1979a, c), and quite slowly (cf. Birch, 1979 etc.), it is possible that the period of intertidal sediment deposition at the bone-bed localities noted in this region on Fig. 1, arrived sometime after it had reached the Ludlow region. The general uplift in the region was probably initiated around the fault bounded Malvern Precambrian area. This Precambrian area may have also formed a rising positive region during the late Whitcliffian and early Downtonian.

In the Usk region deposition of a quartz-rich bone-bed was followed by the deposition of non-calcareous lenticular bedded siltstones and mudstones containing a Whitcliffian type brachiopod fauna (Walmsley, 1959). It is also interesting to note that near Llandeilo the Downtonian (Siveter, 1974; oral com. 1979) Tilestones and Cennen Beds contain a Whitcliffian type brachiopod fauna (Squirrell and White, 1978). However, in this region the Ludlow - Downton Series boundary is marked by an unconformity (cf. Potter & Price, 1965; Squirrell and White, 1978). In the basinal regions of the Knighton - Clun Forest district no exposures of this boundary or the Ludlow Bone-Bed were observed by Stamp (1918), Earp (1938, 1940) or Holland (1958).

The gradual emergence during the late Ludlovian and early Downtonian of a number of fault bounded 'land' regions in the Welsh Borderlands and Wales may be linked to both the closing of the Iapetus Ocean (cf. McKerrow & Ziegler, 1972; Phillips et al., 1976) and the closure of the East Midlands aulacogen (Evans, 1979). It is interesting to note that British Rhaetian Bone-Bed deposition is also closely associated with contemporary islands (Richardson, 1904; Wickes, 1908) and that similar relationships have been postulated for West German Rhaetic Bone-Beds (Aepler, 1974). British Jurassic Bone-Beds (Hudson, 1966) and the Wealden Bone-Beds (Allen, 1975; Antia, 1979a).

Evidence of a discontinuity event

1. Faunal evidence

The Ludlow Bone-Bed marks a sharp break between two different marine biofacies and lithofacies, over the southern half of its outcrop (Fig. 2; Tables 1 and 2). In the northern half of its outcrop a transitional fauna is present just above the bone-bed (Fig. 3, 4; Tables 3, 4 and 5).

The macrofauna of the Upper Whitcliffe Beds, though not uniform throughout, is collectively distinct. It is characterised by articulate brachiopods (Protochonetes ludloviensis, Microsphaeridiorhynchia nucula, Salopina lunata), encrusting, boring and stick bryozoans (Ceramopora sp., Rhopalonaria sp., Leioclema sp.), bivalves (Goniophora cymbaeformis, Fuchsella amygdalina) and the gastropod Loxonema obsoletum.

The fauna of the overlying Downton Castle Formation is conspicuously dominated by ostracods (Frostiella groenvalliana, Londinia kiesowi, Cytherellina

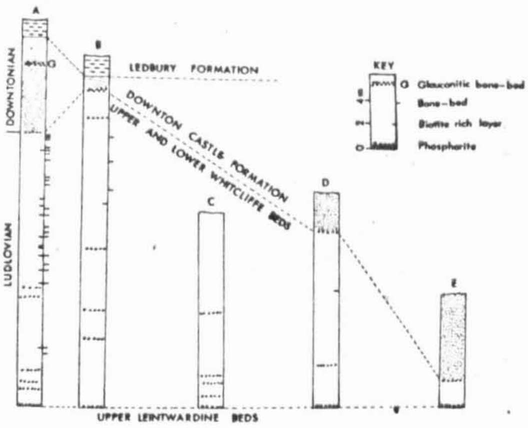


Fig. 2 Lithofacies in the Southern half of the bone-beds outcrop. A. Brookend, B. Tites Point; C. Newnham, D. Wood Green, E. Gorsley. Compiled after Cave & White (1971, 1978), Lawson (1953). Note that the number of bone-bed and phosphorite layers increases southward and the apparent correlation of biotite rich layers and bone-beds at Brookend. The Ledbury formation consist here of red siltstones and mudstones containing caliche horizons. The Downto Castle Formation consists of laminated sandstones at its base (Plate 2B) grading up into a glauconitic bone bed and parallel laminated siltstones rich in plant debris (Plate 2A). The base of the Formation is marked by a phosphorite layer resting on an eroded surface (Plate 2B). The Underlying Whitcliffe Beds are lenticular bedded calcareous siltstones (Plate 2B) which are often bioturbated and contain thin bone-beds in their upper portion (Plate 2 E, F). The lower portions of the Whitcliffe Beds consist of laminated siltstones alternating with shell, bone-bed and phosphorite layers (e.g. Plate 2C).

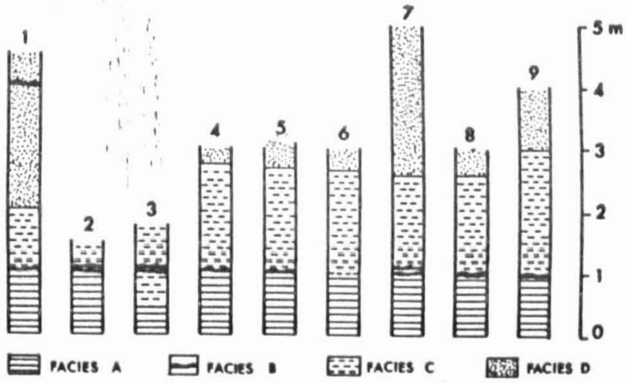


Fig. 3. Lithofacies in the Northern half of the bone-beds outcrop. 1, Willey, 2, Brockton, 3, Shipton, 4, Aston Munslow, 5, Corfton, 6, Siefton, 7, Ludlow, 8, Deepwood, 9, Downton.

Facies A - Lenticular bedded shelly calcareous often bioturbated siltstones.

Facies B - Bone-Beds in lenticular and wavey bedded siltstones.

Facies C - Rippled and lenticular bedded limenitic siltstones, sandstones and mud cracks, shell sheets and local channels.

Facies D - Trough cross bedded, and rippled sandstones.

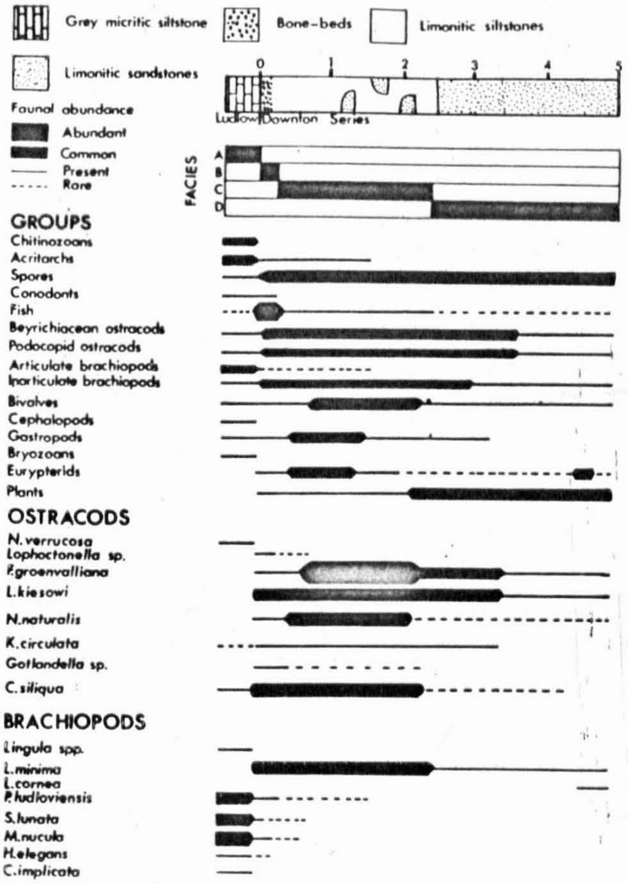


Fig. 4. Profile across the Ludford lane section showing the distributionof sediments and faunal groups. Note the transitional nature of faunas particularly brachiopods just across the series boundary.

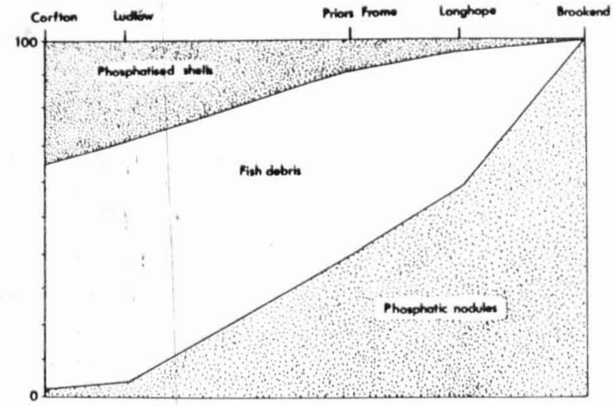


Fig. 5. Section showing the composition of phosphatic clasts in the Ludlow Bone-Bed in a transect from Corfton to Brookend.

TABLE 1.

Table 1 is included in the pocket of this thesis

Table 2. The Upper Ludlovian and Lower Downtonian faunas at Tites Point. Sediments in the section have been described by Cave and White (1972). The position of individual bone-beds and phosphorites in the section is given in Fig. 2. The fauna recorded in this table is stored in the Institute of Geological Sciences at London under the Museum numbers D.E.X. 1108-1328. Note that some bits of theladont and acanthodia fish skins are associated with the bone-beds. The Whitcliffian sediments (located between 2.24 and 3.20 m) increase in clay and organic content towards the top of the section. Bone-bed density and vertebrate remains appear to be more abundant in the upper parts of the Whitcliffian. Many of the *Nuculites* spp. observed were in burrows and *in situ*. The base of the Downtonian is irregular and channelled, and marked by a bone-bed, the Ludlow Bone-Bed. The overlying sandstones are rich in plate debris and glauconite. The Downtonian fauna occurs between 23.20 and 24.90 m.

Height in metres above the base of the section

BRACHIOPODS	0	2.25	3.67	10.02	15.67	17.83	23.20	24.90
Atrypa recticularis	1	-	-	-	-	-	-	
Dayia navicula	4	-	3	-	-	-	-	
Howellella elegans	5	-	-	-	-	-	-	
Lingula cornea J. de C. Sowerby	-	-	-	-	-	-	1	
Lingula lewisii J. de C. Sowerby	-	-	-	-	1	-	-	
Microsphaeridiorhynchus nucula	17	3	7	20	-	1	-	
Orbiculoidea rugata	-	-	162	18	6	7	-	
Protochonetes ludloviensis	4	16	27	261	68	88	-	
Protochonetes cf. *novascoticus* (McLearn)	-	-	-	-	-	1	-	
Salopina lunata	2	7	10	34	20	37	-	
Schizocrania striata	-	-	-	2	-	-	-	
Hyattidina canalis	2	-	-	-	3	3	-	
BIVALVES								
Fuchsella amygdalina	5	1	2	-	-	-	-	
Goniaphora cymbaeformis	-	-	2	-	25	-	-	
Grammysia sp.	-	-	-	-	3	1	-	
Nuculites antiques	-	1	1	-	39	94	-	
Nuculites ovata	-	-	-	-	2	2	-	
Paracyclas sp.	2	3	-	-	-	-	-	
GASTROPODS								
Loxonema obsoletum	2	3	-	-	4	6	-	
Hormotoma sp.	-	2	-	-	-	1	-	
CEPHALOPODS								
Kionoceras angulatum	-	1	1	-	-	-	-	
'*Orthoceras*' sp.	-	-	1	5	12	9	-	
OTHER MOLLUSCS								
Bucanopsis expansus	-	-	1	-	-	-	-	
Hyolithes forbesi	-	-	1	-	1	3	-	

[illegible] sp.	-	2	-	-	-	1	-
CEPHALOPODS							
Kionoceras angulatum	-	1	1	-	-	-	-
'Orthoceras' sp.	-	-	1	5	12	9	-
OTHER MOLLUSCS							
Bucanopsis expansus	-	-	1	-	-	-	-
Hyolithes forbesi	-	-	1	-	1	3	-
BRYOZOAN COLONIES							
Leioclema sp.	10	-	8	-	-	1	-
ECHINOIDS							
Sea urchin spines	-	-	1	-	-	-	-
Pentagonal crinoid columnals	-	-	1	-	3	-	-
Circular crinoid columnals	4	10	13	-	19	14	-
ANNELIDS							
Keilorites sp.	-	-	-	-	-	-	-
Serpulites sp.	4	6	9	3	-	1	-
Skolithodonts	1	-	-	-	-	1	-
Clionoides sp.	-	-	25	-	11	-	-
TRILOBITES							
Calymene sp.	1	-	-	-	-	-	-
MISCELLANIA							
Cornulites sp.	-	-	-	-	-	1	-
Ozarkodina sp.	-	-	1	-	-	1	-
FISH							
Acanthodian debris	-	1	1	1	1	1	1
Cythaspis banksi Banks	-	-	2	-	-	10	20
Thelodont debris	-	1	1	1	1	1	1
Gomphonches tenuistriata	-	-	-	-	-	-	2
Gomphonchus murchisoni	-	-	1	-	-	-	-
Sclerodus sp.	-	-	1	-	-	-	1
OSTRACODS							
Cavellina sp.	-	-	-	-	-	-	11
Cytherellina siliqua	-	-	1	-	1	1	2
Hebellum cf. tetragonum	-	8	-	1	-	-	-
Hermannia cf. marginata (Jones)	-	-	-	-	-	-	8
Scaldinnella cf. simplex	-	6	-	1	-	-	-
PLANTS AND EURYPTERIDS							
Eurypterids	-	-	-	-	-	2	-
Nematophyton sp.	-	-	-	-	-	1	1
Pachytheca sp.	-	-	-	-	-	2	124
Sample size	69	67	280	345	215	287	159

Table 3. Faunas across the Ludlow-Downton series. Boundary at Ludlow. Note the transition fauna just above the boundary.

	Ludlovian				Downtonian						
	38	25	15	0	10	20	41	67	89	19	147 c
BRACHIOPODS											
Craniops implicata	19	39	1	4	2	-	-	-	-	-	
Howellella elegans	2	1	6	3	-	-	-	-	-	-	
Lingula sp. nov.	1	4	4	7	-	-	-	-	-	-	
Lingula lata	3	19	9	11	-	-	-	-	-	-	
Lingula minima	-	-	-	82	49	64	49	18	10	-	
Microsphaeridiorhynchus nucula	42	8	6	106	-	-	-	-	-	-	
Orbiculoidea rugata	-	1	1	-	1	-	-	-	-	-	
Protochonetes ludloviensis	224	14	19	49	2	-	-	-	-	-	
Salopina lunata	179	142	65	330	4	-	-	-	-	-	
BIVALVES											
Fuchsella amygdalina	-	-	1	-	-	-	-	-	-	-	
Goniophora cymbaeformis	1	2	-	2	-	-	-	-	-	-	
Modiolopsis complanata	-	-	-	-	-	19	-	3	35	122	
Nuculites ovata	-	1	-	2	-	-	-	-	1	-	
Pterinea retroflexa	1	-	-	4	-	-	-	-	-	-	
'Pterinea' tenuistriata	-	1	-	2	-	-	-	-	-	-	
Solenamya sp.	-	-	-	-	-	2	-	-	-	1	
GASTROPODS											
Cymbularia carinata	-	-	-	-	-	1	-	-	-	-	
Loxonema conicum (J. de C. Sowerby)	-	-	-	1	-	-	-	-	-	-	
Loxonema gregarium	-	-	-	4	2	27	2	3	4	-	
Loxonema obsoletum	-	-	1	5	-	1	-	-	-	-	
Tubocheilus helicites	-	-	-	31	1	21	-	-	15	6	
OTHER MOLLUSCS											
Bucanopsis expansus	-	1	-	3	-	-	-	-	-	-	
Leurocycloceras sp.	-	1	-	-	-	-	-	-	-	-	
OSTRACODS											
Calcaribeyrichia torosa	1	-	-	-	-	-	-	-	-	-	
Cytherellina siliqua	-	-	-	1	-	-	2	-	18	7	
Frostiella groenvalliana	-	-	-	81	24	93	14	22	29	74	
Hebellum cf. tetragonum	-	-	-	80	-	3	4	-	1	-	
Kurresaaria circulata	-	-	-	5	8	8	-	-	-	1	
Londinia kiesowi	-	-	-	90	38	70	22	6	87	6	
Lophoctonella sp.	-	-	-	2	-	-	-	-	-	-	
Nynamella sp.	-	-	-	19	1	2	-	-	-	1	
Nodibeyrichia verrucosa Shaw	1	-	-	4	-	-	-	-	-	-	
BRYOZOAN COLONIES											
Leioclema sp.	-	-	-	2	-	-	-	-	-	-	
Rhopalonaria sp.	1	1	-	1	-	-	-	-	-	-	
OTHER FOSSILS											
Cornulites sp.	-	-	-	3	-	-	-	-	-	-	
Eurypterid fragments	-	-	-	7	26	70	-	1	2	1	
Calcareous tubes	-	-	-	-	-	-	-	4	3	1	
Ozarkadina sp.	-	-	-	-	1	-	-	-	-	-	
Pachythecea sp.	-	-	-	-	6	7	-	-	-	-	
Plant debris	-	-	-	1	1	1	1	1	1	1	
Serpulites sp.	-	-	-	-	1	-	-	-	-	-	
Sample size	484	235	113	860	166	388	93	57	205	221	

Table 4. Faunas across the Ludlow - Downtonian boundary at Aston Munslow.
C = common P = present

POSITION RELATIVE TO BOUNDARY (m)

	LUDLOVIAN				DOWNTONIAN			
	-2.0	-1.67	-0.75	0	0.06	0.4	1.2	1.54
BRACHIOPODS								
Craniops implicatus	-	-	4	133	-	-	-	
Lingula lata	3	7	36	7	-	-	-	
Lingula minima	-	-	-	40	116	467	6	
Lingula sp nov.	-	4	1	-	-	-	-	
Howellella elegans	-	4	17	29	-	-	-	
Microsphaeridiorhynchus nucula	2	12	14	115	-	-	-	
Orbicoidea rugata	-	14	6	27	-	-	-	
Protochonetes ludloviensis	5	64	151	347	5	-	-	
Salopina lunata	15	132	329	316	-	-	-	
BIVALVES								
Fuchsella amygdalina	-	3	-	-	-	-	-	
Goniophora cymbaeformis	-	-	-	-	1	-	-	
Leodispis cf. barrowsi Reed	-	-	-	2	3	4	-	
Modiolopsis complanata	-	-	-	30	80	26	-	
Nuculites ovata	-	-	-	-	2	-	-	
Pteronitella reticularis	-	-	-	2	-	-	-	
GASTROPODS								
Cymbularia carinata	-	-	-	3	2	-	-	
Loxonema obsoletum	-	14	-	-	-	-	-	
Naticopsis sp.	-	1	-	-	-	-	-	
'Platyschisma' williamsi	-	-	-	3	-	-	-	
Turbocheilus helicites	-	-	-	47	16	6	-	
OTHER MOLLUSCS								
Hyolithes forbesi	-	2	-	2	-	-	-	
Leurocycloceras sp.	-	1	4	-	-	-	-	
Orthoceras sp.	1	-	-	2	-	-	-	
BRYOZOAN COLONIES								
Rhophalonaria sp.	-	-	-	-	3	-	-	
OSTRACODA								
Calcaribeyrichia torosa	-	-	-	3	-	-	-	
Cytherellina siliqua	-	4	3	8	3	13	-	
Lerpiditia cf. marginata (Jones)	-	-	-	-	-	1	-	
Londinia cf. kiesowi Krause	-	-	-	-	1	5	-	
ANNELIDS								
'Serpulites' longissimus	-	-	-	3	-	-	-	
ECHINOIDS								
Crinoid columnals	-	1	-	-	-	-	-	
FISH								
Sclerodus sp.	-	-	1	-	-	-	-	
Thelodus parvidens Ag.	-	-	-	C	4	2	-	
Gomphonchus tenuistriata	-	-	-					
Gomphonchus murchisoni	-	-	-	1				
Thelodent skin fragment	-	-	-	-	-	2	-	
PLANTS								
Nematophyton sp.	-	-	-	-	-	7	-	
Pachytheca sp.	-	-	-	5	4	15	-	
OTHERS								
Glauconitic fecal pellets	-	-	P	P	-	-	-	
Eurypterid fragments	-	-	-	-	-	5	5	
Calcareous tubes	-	-	-	1	2	-	-	
Total Fauna	26	263	567	1140	268	564	11	

Table 5: Faunas of the Upper Ludlow Downton Series at Willey, Much Wenlock. Sample and basal units indicated here have been described in detail by White & Coppack (1978). The fauna recorded in this table by the author is stored in the Institute of Geological Sciences, London under the Museum numbers D.E.X. 8517-8755

Height in section (m)

	Ludlow				Downton Series												
	,05	1.15	0.	0.	0.90	0.97	1.61	1.81	2.13	2.66	3.00	3.09	3.16	3.26	3.31	4.05	4.12
BRACHIOPODS																	
Craniops inplicatus	-	3	11	-	-	-	-	-	-	-	-	-	-	-	-	-	
Howellella elegans	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Lingula lata	-	3	-	5	-	-	-	-	-	-	-	-	-	-	-	-	
Lingula minima	-	-	13	722	18	12	1	8	46	6	-	1	97	120	106	15	
Lingula cornea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	
Microsphaeridiorhynchus nucula	73	35	26	-	-	-	-	-	-	-	-	-	-	-	-	-	
Orbiculoidea rugata	4	5	1	-	-	-	-	-	-	-	-	-	-	-	-	-	
Protochonetes ludloviensis	19	9	10	-	-	-	-	-	-	-	-	-	-	-	-	-	
Salopina lunata	127	25	56	-	-	-	-	-	-	-	-	-	-	-	-	-	
GASTROPODA																	
Cymbularia carinata	-	-	-	-	-	-	-	-	-	-	-	1	-	11	-	-	
Loxonema conicum (J. de C. Sowerby)	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	
Loxonema gregarium	-	-	-	2	3	8	-	-	-	13	-	1	1	162	-	-	
Hormatoma sp.	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Turbocheilus helicites	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	
CEPHALOPODA																	
Leurocyclocerus sp.	5	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	
Orthoceras sp.	7	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Litulites ibex	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
BIVALVES																	
Goniophora cymbaeformis	3	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Grammysia sp.	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Ledopsis cf. burrowsi	-	-	-	-	-	-	-	9	-	-	-	-	1	2	-	-	
Modiolopsis complanata	-	-	8	53	55	17	-	1	1	-	-	-	56	82	18	2	
Nuculites antiques	13	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	
Nuculites ovata	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	
Pteronitella cf. retroflexa	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	

Ptychopteria aff. tenuistriata	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Solenamya sp.	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-
OTHER MOLLUSCS																
Hyolithes forbesi	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ANNELIDS																
Ildraites sp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Serpulites spp.	28	24	2	-	-	5	-	-	-	-	-	-	-	-	-	-
BRYOZOAN COLONIES																
Ceranopora sp.	3	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leioclema sp.	9	3	3	-	-	-	-	-	-	-	-	-	-	-	-	-
OSTRACODS																
Cavellina sp.	3	1	-	34	-	1	-	7	44	-	-	-	-	2	-	-
Cytherellina siliqua	1	-	2	71	5	5	-	7	143	-	-	-	-	7	24	3
Calcaribeyrichia torosa	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Londinia kiesowi	-	-	3	126	3	8	3	13	19	-	-	-	-	37	86	21
Hebellum cf. tetragonum	-	-	1	39	-	5	1	17	50	-	-	-	-	9	2	-
Nynamella sp.	1	-	-	197	20	32	11	75	630	1	-	-	2	19	-	1
? Jefinia sp.	1	-	-	2	-	8	-	1	13	-	-	-	-	1	-	1
Frostiella groenvalliana	-	-	-	121	53	264	38	107	601	1	-	3	42	318	237	58
~~Commutated~~ Comminuted ostracod shells	-	-	-	-	-	-	-	3028	-	-	-	-	-	-	-	-
ECHINOIDS																
Crinoid columnals	41	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
FISH DEBRIS																
Thelodont skin	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Acanthodian fragments	39	1	40/cm^2	-	-	-	-	-	-	-	-	-	-	-	-	-
Logania ludlowiensis Gross	1	-	11/cm^2	27	48	36	-	-	8	3	-	1	1	897	951	67
Thelodus parvidens	38	5	23/cm^2	20	6	3	-	-	-	1	-	-	1	3	2	-
Thelodus biocostus Hoppe	-	-	1/cm^2	-	-	-	-	-	-	-	-	-	-	-	-	-
Gomphonchus tenuistriata	-	-	-	3	2	-	-	-	-	-	-	5	2	-	-	-
Gomphonchus murchisoni	-	-	-	-	-	3	-	-	-	-	-	1	2	2	4	1
PLANTS																
Pachytheca sphaerica	-	-	-	-	7	4	-	-	-	-	-	-	-	-	-	-
Nematophyton sp.	-	-	-	P1	-	-	P	P	P	-	-	-	-	-	-	-
OTHERS																
Small calcareous tubes	-	-	-	59	1	5	-	3	4	-	-	-	-	-	-	-
Euryplerid fragments	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Zoophychus sp.	-	-	-	-	4	5	-	-	-	-	-	-	-	-	-	-
Sample size	428	133	147	1483	237	525	54	3276	1559	25	-	12	204	1723	1431	169

siliqua) inarticulate brachiopods (Lingula minima, Lingula cornea), bivalves (Modiolopsis complanata) and gastropods (Loxonema gregarium, Cymbularia carinata, Turbocheilus helicites).

In the northern outcrops, particularly in the Ludlow - Munslow region the change in faunas is gradational (Tables 3 and 4). This is shown by the appearance of a 25 to 65 cm thick Whitcliffian - Downtonian transitional faunal zone, just above the bone-bed. The gradual north-westerly appearance of this transitional zone appears to parallel the progressive north-westerly disappearance of phosphatic pebbles in the deposit (Fig. 5) and marks the gradual north-westerly termination of the proposed discontinuity.

Biostratigraphic proof of a discontinuity at the Ludlow Bone-Bed is lacking (Siveter, 1974, 1978; Aldridge, 1975) mainly because biostratigraphically useful fossils (e.g. ostracods, conodonts etc.) are rare or long ranging and their distribution within the British Whitcliffian is poorly understood. Consequently, it is difficult to correlate the British Whitcliffian with Baltic, Bohemian, Estonian, Nova Scotian or even Lake District sections with detailed stratigraphic precision (cf. Kaljo, 1978).

2. Physical evidence

In most localities physical evidence of a discontinuity is lacking and even within a section the Ludlow Bone-Bed is frequently difficult to trace. For example at Ludlow there is no direct sedimentary evidence of a disconformity (Fig. 6, Plate 1, Fig. A).Although some minor scouring is present at the bed junction, burrows immediately below the bone-bed are infilled with quartz, silt or vertebrate debris, perhaps suggesting that the carbonate substrate was semilithified at the time of bone-bed deposition. However, in the Brookend bore hole and at Tites Point, the base of the Ludlow Bone-Bed appears to be marked by an erosion surface (Plate 1, Fig. B; Cave & White, 1971).

Among the most interesting features associated with the proposed discontinuity is the presence of phosphate pebbles in the bone-bed (Plate 2, Fig. B) as at May Hill (Lawson, 1955) and Gorsley (Lawson, 1954). They occur as rounded ellipsoids and irregular masses (Fig. 7; Plate 1 D,F,G,H,I,J) composed

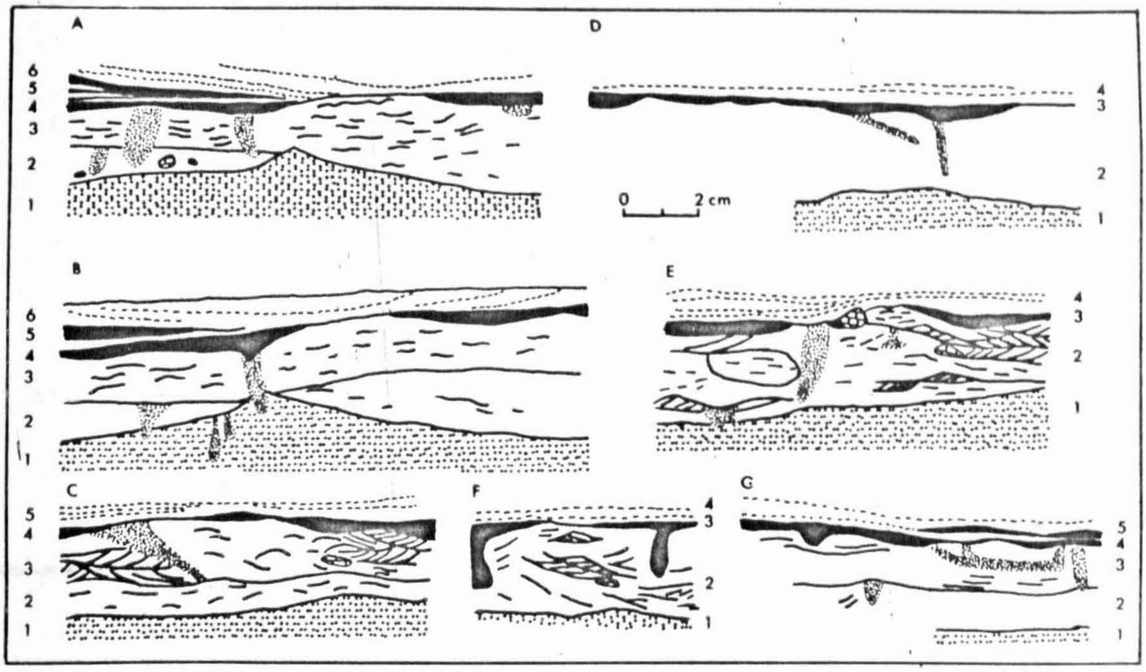


Fig. 6. Traces of structures visible in vertical sections across the Ludlow Bone-Bed at Ludlow. Layer 1 = bioturbated siltstones. In Figs. 6A, B, C, G layer 3 also forms part of this unit. The burrows are infilled with coarse quartz siltstone. The bone-bed (layer 3 in Fig. 6 D, E, F and 4/5 in A, B, C, G) locally infills burrows Fig. 6 F, and small hollows on the sediment surface Fig. 6 D and occasionally forms an integral part of rippled strata Fig. 6 A, B. The sediments overlying the bone-bed may be rippled or parallel laminated. Locally e.g. Fig 6 E the bone-bed contains micrite clasts.

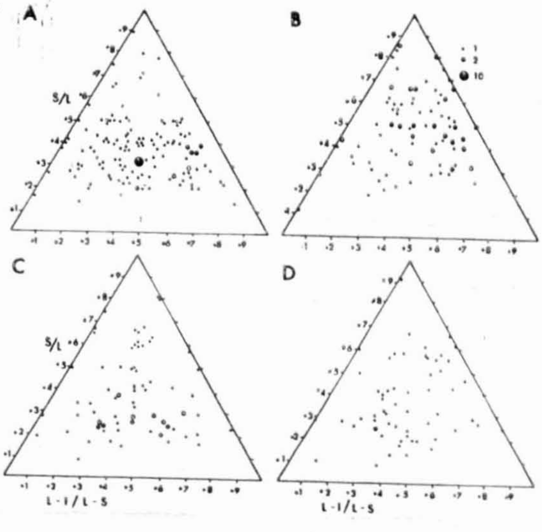


Fig. 7. Sphericity form diagrams of the phosphate nodules in the Ludlow Bone-Bed at A = Longhope, B = Priors Frome, C = Netherton, D = Ludlow.

Table 6. Composition (%) of phosphatic steinkerns in the Ludlow Bone-Bed at a number localities.

SPECIES	LOCALITY			
	NETHERTON	LUDLOW	LONGHOPE	PRIORS FROME
1. BRACHIOPODS				
Lingula sp.	-	17.6	20.0	4.5
Orbiculoidea rugata	17	5.8	20.0	0.9
Protochonetes sp.	-	-	-	0.9
Salopina sp.	-	11.7	-	1.8
2. MOLLUSCS				
Bucanopsis expansus	-	5.8	-	2.7
Cymbularia carinata	-	-	-	4.5
Hyolithes forbesi	5	-	30	1.8
Loxonema gregarium	83	11.7	15	74.7
Nuculites cf. *ovata*	-	-	-	0.9
Orthoceras sp.	-	-	-	0.9
'*Platyschisma*' *williamsi*	-	-	-	0.9
Tentaculites sp.	-	-	-	1.8
Turbocheilus helicites	-	-	10	-
3. OTHERS				
Crinoid stem	1	47.0	-	1.8
Pachytheca sp.	-	-	-	0.9
'*Serpulites*' *longissimus*	4	-	5	-

of carbonate apatite (Fig. 8; Cave & White, 1972; Antia, 1979a). They are black, brown or cream in colour and are usually small (2-10 mm in length), but occasionally reach 2-3 cm in length.

In thin section, these pebbles contain variable amounts of angular quartz silt, and fish debris (Plate 1, Fig. F-J). Some of these pebbles partially or completely enclose articulated phosphatic shells; particularly those belonging to Lingula sp. and Orbiculoidea sp. Other species are preserved as phosphate-replaced shells (e.g. crinoid stems), or as phosphatic internal or external moulds of gastropods monoplacophorans, hyolithids, articulate brachiopods and bivalves. The steinkern composition of the Ludlow Bone-Bed at a number of localities is indicated in Table 6.

Since both modern phosphate nodules and steinkerns tend to form within the sediment (Baturin, 1970) and the presence of borings on some of the nodules and steinkerns (Antia & Whitaker, 1979; Antia, 1979a) indicates surface exposure (Baird, 1978) it is probable that these nodules testify to an erosion event (cf. Baturin,1970; Kennedy & Garrison, 1975; Baird, 1978).

Composition of the phosphatic pebbles

10 gms of phosphatic pebbles from the Ludlow Bone-Bed at Longhope were processes using both X.R.F. and X.R.D. analyses. The X.R.F. analysis (Table 2) showed that the pebbles were made of phosphate and contained quantities of silica and iron and manganese. The composition of these nodules is similar to the composition of phosphorites actively forming or occurring on the modern sea floor and some fossil phosphorite and phosphatic pebbles in bone-beds (see Table 7). The nodules in the Ludlow Bone-Bed contain a honeycomb internal structure (Antia & Whitaker, 1979; Antia, 1979a) similar in both morphology and magnitude to the clay structure of the contempory sediments (Antia, 1979a). Since it has been suggested (Antia, 1979a,b; Antia & Whitaker, 1979) that the phosphorites formed by organophosphates binding with and eventually replacing the original honeycomb clay lattice structure of the sediment in which they formed, the high iron and magnesium concentrations (Table 7) could be remnants

Table 7. Composition of phosphorite nodules from (1) West African continental shelf (Baturin, 1971a), (2) Peru-Chilean continental shelf (Burnett, 1977), (3) Agulhas Bank (Parker, 1974), (4) Californian continental shelf (Dietz et al., 1942), (5) The Pacific Ocean (Bezrukov & Shirchov, 1969), (6) The Muschelkulk Grenzbonebed (Reif, 1971), (7) The Ludlow Bone-Bed (this study). Note the apparent similarity in composition between the nodules.

Elements	1	2	3	4	5	6	7
SiO_2	0.15	22.13	12.84	n.d.	11.9	0.42	16.44
Al_2O_3	0.04	5.15	1.85	1.47	1.7	n.d.	3.79
Fe_2O_3	0.20	2.85	8.24	n.d.	1.1	1.44	4.78
MgO	1.70	1.07	1.35	n.d.	0.3	0.50	4.69
CaO	46.42	33.93	37.29	44.91	44.0	50.10	38.23
Na_2O	n.d	0.85	0.67	n.d	0.6	0.84	0.42
H_2O	n.d	1.3	1.29	n.d	0.5	0.34	0.89
P_2O_5	32.74	23.61	16.18	28.15	30.5	31.50	25.76
S	n.d	0.16	0.40	n.d	0.7	n.d	n.d
F	3.02	2.22	2.10	3.08	3.1	n.d	n.d
TiO_2	n.d	n.d	n.d	n.d	0.001	0.09	n.d
MnO	n.d	n.d	n.d	n.d	0.003	0.38	n.d

Table 8. Composition of phosphate nodules in the Ludlow Bone-Bed at Longhope as determined by point counting.

	NODULE										
CLAST & TYPE	1	2	3	4	5	6	7	8	9	10	TOTAL
Quarts grains	50	20	40	10	43	37	14	12	35	34	29.5%
Organic fragments	10	12	10	20	4	12	18	35	15	12	14.8%
Phosphate/clay matrix	15	53	45	60	18	48	64	45	40	44	42.7%
Fish scales	-	10	5	5	2	3	-	6	2	4	3.5%
Muscovite	-	-	-	-	-	-	-	-	-	2	0.2%
Phosphate replaced shells	25	-	5	25	-	-	-	-	-	-	5.5%
Phosphatic shells	-	5	-	-	3	-	4	2	8	4	2.6%

of the original clays. The low K_2O values (Table 7) suggest that any authogenic glauconite has probably ~~reverted~~ been converted to apatite during diagenesis (cf. Birch, 1979).

The X.R.D. analysis (Fig. 8) shows that quartz and carbonate apatite are the dominant constituents of the pebbles. This is partially confirmed by the point count analysis of the pebbles (Table 8). Thin sections and probe slides of 33 phosphate pebbles were examined. Of these, 3 of the pebbles contained a number of earlier formed phosphate pebbles within their mass (e.g. Plate 1, Fig.F5). Similar pebbles have been recorded from recent phosphorites off California (Dietz <u>et al</u>., 1942) and South Africa (Parker, 1971b; Birch, 1979). Five of the pebbles showed signs of an original sedimentary bedding. These bedding structures (seen only on the probe slides) show contacts between laminae rich in fish scales and ?clay laminae, and fine quartz silt and clay laminae.

Two of the pebbles appear to have nucleated around crinoid stems (Plate 1, Fig. J). The sediment around these stems is a quartz silt rich in acritarchs anc chitinozoans held together by a carbonate apatite cement. The crinoid stem is preserved as carbonate apatite containing some small quartz grains and acritarchs suggesting that perhaps the crinoid stem had been dissolved and replaced by a quartz-poor, acritarch-rich clay, which was subsequently altered to carbonate apatite. Clastic pseudomorphing of fossils, by clays, sands and silts, followed in some cases by phosphatisation, is not uncommon, as has been demonstrated by many authors (e.g. Murchison, 1839; Wells, 1944; Duffin & Gadzicki, 1977; Baird, 1978; Antia & Whitaker, 1979; Hanken, 1979). Twelve of the pebbles contained <u>Trypanites</u> borings (Plate 1, Fig. I). Some of these borings have been infilled with quartz silt and fish scales. In others they have been infilled with clay which has been subsequently phosphatised. The walls of some of these borings are lined with acritarchs. <u>Trypanites</u> borings have been illustrated by Dietz <u>et al</u>., (1942) on recent Californian phosphorite pebbles and described by Baird (1978) on some Devonian phosphate pebbles.

Most of the pebbles had a slightly darker rim on their outer margin.

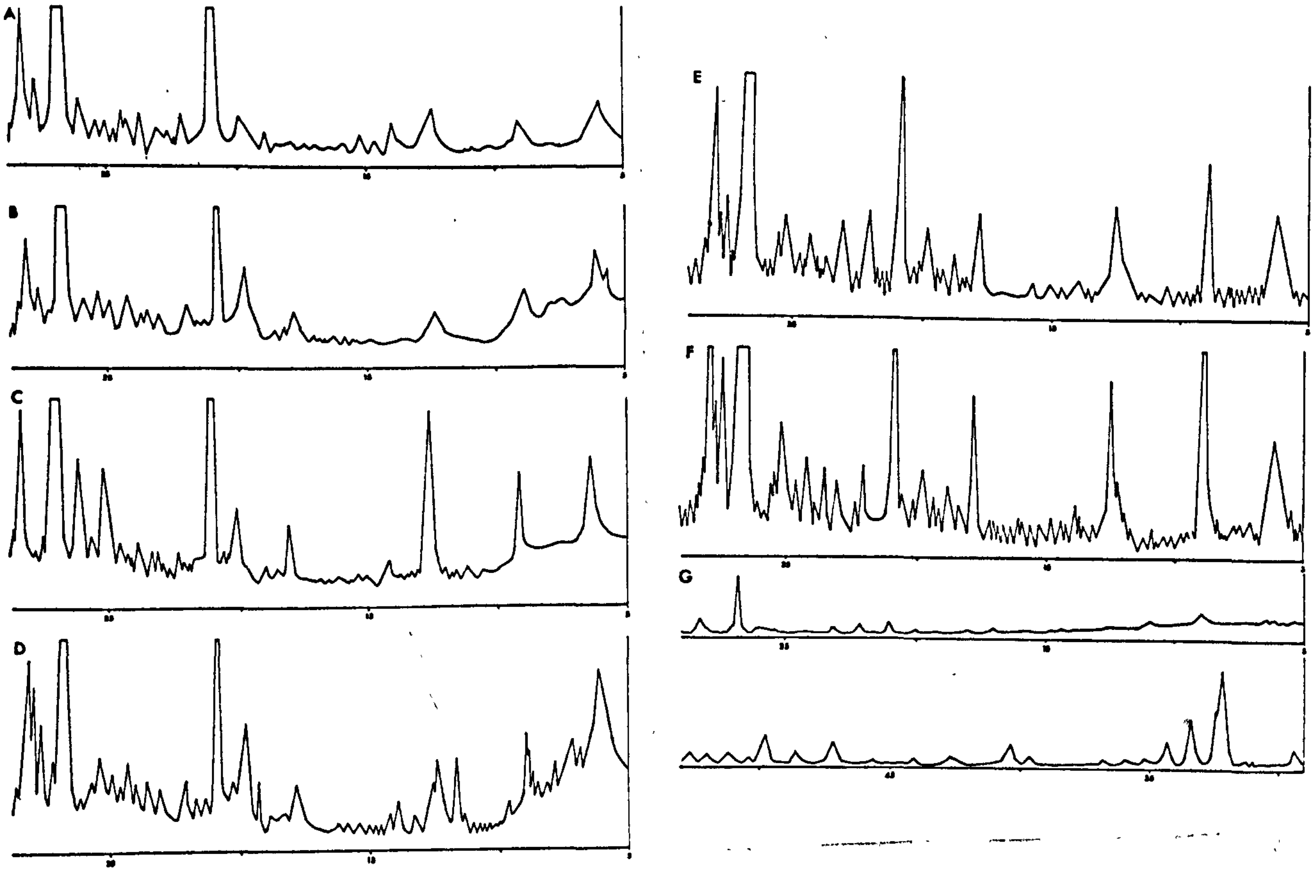


Fig. 8 X.R.D. Traces of a phosphate nodule and the Netherton Section. Base line gives 20 valves.

A Netherton Section (cf. Fig. 11) 230 cm above base - contains chlorite, quartz, apatite, calcite.

B Netherton Section 218 cm above base - contains chlorite, limonite, apatite, quartz.

C Netherton Section 210 cm above base - contains chlorite, pyrite/limonite, apatite, quartz.

D Netherton section 204 cm above base - contains chlorite, pyrite, quartz, gypsum.

E Netherton section 170 cm above base - contains thuringite, calcite and quartz.

F Netherton section 140 cm above base - contains thuringite, calcite and quartz.

G Phosphate nodule from Longhope, contains quartz, carbonate, apatite and? illite

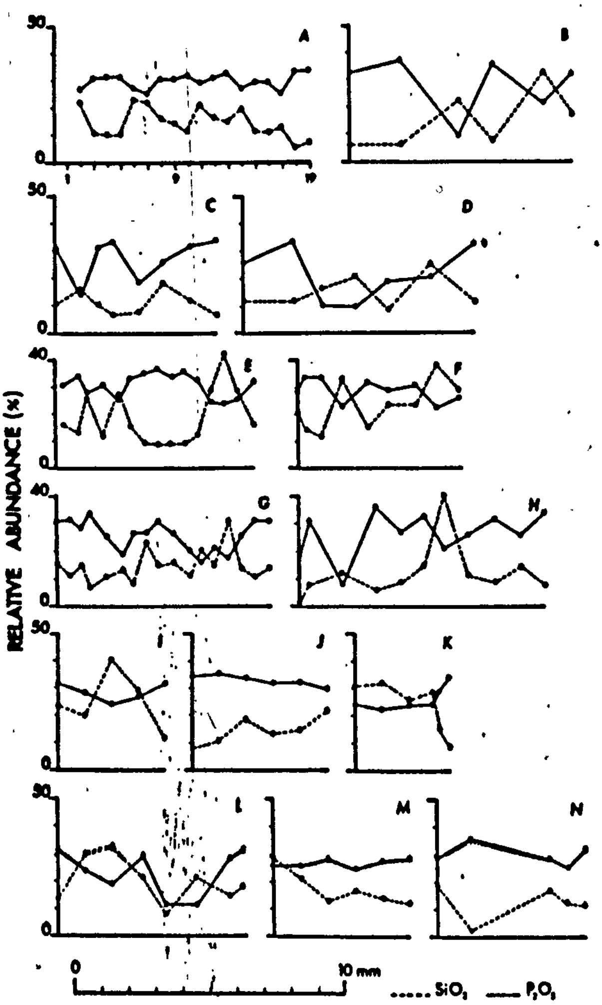

RELATIVE ABUNDANCE (%)
30
0
1
9
19
A
B
50
0
C
D
40
0
E
F
40
0
G
H
50
0
I
J
K
30
0
L
M
N
0
10 mm
SiO₂
P₂O₅

Fig. 9 Microprobe transects of Phosphorite nodules showing the relative abundance of SiO_2 and P_2O_5.

(a) Content of SiO_2 and P_2O_5 around the rim of the pebble illustrated in Fig. 10. Nos. 1 - 19 correspond to probe spots in Fig. 10 and Table.9.

(b) Transect of pebble in Fig. 10. Spots 19, 28, 22, 33, 25, 12. Note core and rim phosphate rich, light interior phosphate poor.

(c) Transect of pebble in Fig. 10. Spots 36 - 29. Note phosphate rich rim and core, light interior phosphate poor.

(d) Transect of pebble in Fig. 10. Spots 17, 20, 21, 22, 32, 23, 16 note phosphate rich rim, phosphate poor centre.

(e) Transect pebble (details Appendix 1a) Apparent uniform P_2O_5 composition.

(f) Transect pebble (details Appendix 1b) Apparent uniform P_2O_5 composition.

(g) Transect pebble (details Appendix 1c) Pebble has dark rim and patchy light interior. Note that P_2O_5 content is higher in the pebbles margins.

(h) Transect pebble (details Appendix 1d) - note fluctuating P_2O_5 content in uniformly dark pebble.

(i) Transect pebble (details Appendix 1e) - note slight phosphate enrichment around the margins.

(j) Transect pebble (details Appendix 1f) with an apparent uniform P_2O_5 composition.

(k) Transect pebble (details Appendix 1g) Pebble is uniformly dark but appears to be P_2O_5 enriched on one of its margins.

(l) Transect pebble (details Appendix 1h). Pebble is P_2O_5 inriched in its margins. Pebble also has a dark rim.

(m) Transect pebble (details Appendix 1i) Pebble is uniform in its P_2O_5 composition and colour.

(m) Transect pebble (details Appendix 1j) Pebble is uniform in its P_2O_5 composition and colour.

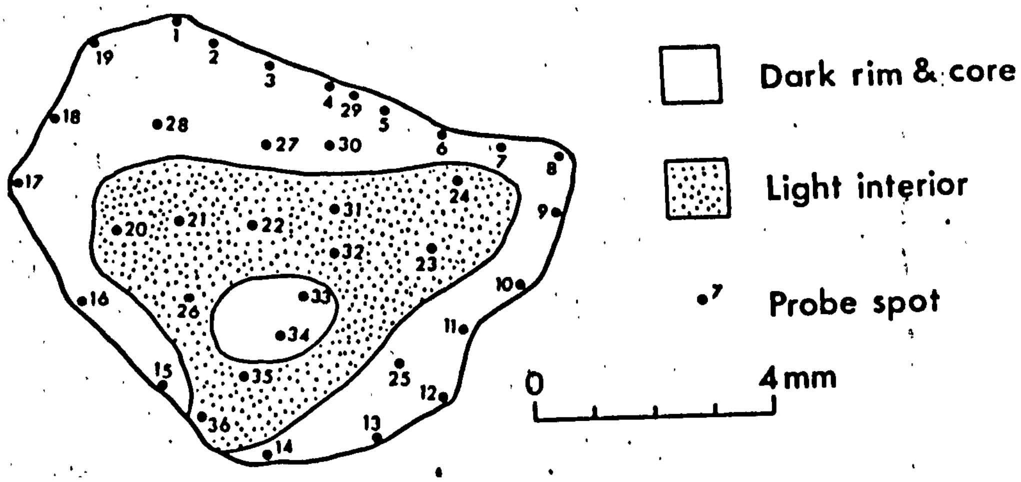


Fig. 10 Position of probe spots on a phosphate nodule from the Ludlow Bone-Bed at Longhope. Analyses are given in Table 9.

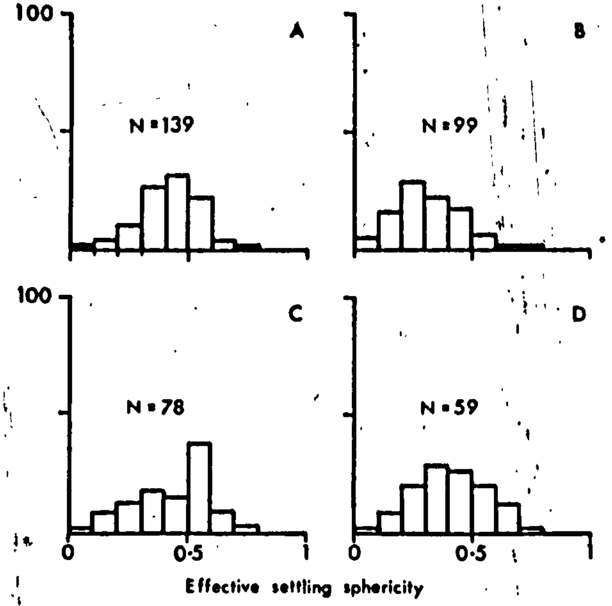


Fig. 11 Graph of frequency (%) against effective settling sphericity for phosphate nodules from (A) Longhope, (B) Priors Frome, (C) Netherton, (D) Ludlow.

This rim is concordant with the pebbles edge and even follows borings into the pebble. Birch (1979) has shown that similar margins on phosphate pebbles from the Aghulas Bank are enriched in apatite. However, in recent Californian phosphorites and the Muschelkalk Grenzbonebed, similar rims are enriched in manganese (Dietz _et al_., 1942; Reif, 1971), while in the Western Pacific the rims represent crusts of iron and manganese oxides which have intergrown with phosphatic minerals (Heezen _et al_., 1973). The phosphatic pebbles from the Ludlow Bone-Bed contain some manganese in their rims, which are also enriched.

A microprobe analysis using a diffuse beam of some phosphatic pebbles from the Ludlow Bone-Bed at Longhope showed that the amount of phosphate in a pebble's rim remained fairly constant (Fig. 9a) and that individual pebbles contained patches on their outer margin which are enriched in manganese and/or iron (Table 9).

It also showed that the dark outer margins present on some nodules were phosphate enriched (Fig. 9) and that the dark cores of some nodules were similarly enriched in phosphate (Fig. 9, Fig. 10). Pebbles of an apparently uniform visual composition appeared to have a fairly uniform chemical composition (Fig. 9, Table 9, also Appendix).

Many of the pebbles contain a large proportion of organic debris (Table 8). Although no spores were observed in the nodules, the following acritarchs and chitinozoans were tentatively identified in thin sections. They are _Filisphaeridium_ sp., _Onondagella_ sp., _Visbysphaera_ sp., _Protoleisphaeridium_ sp., _Duvernaysphaera_ sp., _Diexallophasis_ sp., _Ancyrochitina_ cf. _pedavis_, and _Sphaerochitina_ cf. _sphaerocephala_. Antia (1979b) suggested that many of the phosphorite pebbles formed in subtidal anoxic organic rich clays similar to those found at Netherton. These clays contain variable amounts of organic material, averaging about 25% of their bulk. Much of this organic debris is unidentifiable. However, acritarchs and rare chitinozoans (?_Ancyrochitina_ sp.) were observed. The more common acritarchs included _Onondagella_ sp., _Diexallophasis_ sp. and _Visbysphaera_ sp. In some of the phosphate pebbles the acritarch faunas are dominated by single species, e.g. _Onondagella_ sp. and _Visbysphaera_ sp.

Table 9. Microprobe analyses of a phosphate nodule from the Ludlow Bone-Bed at Longhope. The position of each probe spot on the nodule is given in Fig. 10. Probes 1 - 18, 29, 36 are on the nodules edge. Profiles across the nodule are given in Fig. 9.

Sample	Na	Mg	Al	Si	P	K	Ca	Mn	Fe
1	0.83	-	5.00	74.03	-	2.29	0.14	-	0.71
2	0.74	0.40	5.08	23.15	27.25	2.07	36.50	-	2.10
3	1.17	0.67	4.20	10.93	31.33	0.66	41.2	-	3.06
4	0.51	0.30	2.98	10.60	32.17	0.65	44.53	0.20	2.29
5	0.44	0.37	2.14	10.08	31.76	0.40	43.17	0.26	1.98
6	0.75	0.31	4.38	23.56	27.08	0.81	36.32	-	2.53
7	1.72	0.29	7.58	21.94	25.49	1.04	33.03	-	3.48
8	0.44	0.45	2.28	15.93	30.53	0.52	41.04	-	3.74
9	-	0.31	3.51	14.05	30.85	1.04	41.64	0.24	2.91
10	0.46	0.29	1.94	11.74	31.36	0.50	43.67	-	2.71
11	0.50	0.30	2.44	20.85	29.24	0.61	39.21	-	2.56
12	-	0.43	1.45	15.79	30.49	0.29	41.70	-	2.20
13	0.63	0.37	2.34	14.24	32.16	0.19	42.46	-	2.92
14	0.70	0.34	6.06	19.44	26.56	1.16	36.54	-	3.70
15	-	0.92	3.00	11.93	29.61	0.50	40.30	-	5.41
16	0.82	0.36	2.69	11.46	29.28	0.45	40.53	0.20	5.25
17	0.74	0.650	5.12	12.61	25.58	1.70	35.27	-	6.38
18	0.58	-	1.24	4.72	33.88	0.28	49.54	-	1.90
19	0.49	0.26	0.81	7.81	33.61	0.20	46.19	0.24	2.4
20	0.45	0.25	3.80	12.29	34.54	1.92	44.19	-	0.73
21	-	0.34	3.67	16.82	10.34	0.77	14.35	0.69	2.18
22	0.57	0.788	4.59	21.93	8.17	0.67	13.05	0.29	3.01
23	0.89	0.43	5.35	25.60	20.81	1.12	29.19	-	3.15
24	1.03	0.50	5.26	22.79	24.42	0.45	33.96	0.22	5.78
25	0.81	0.417	4.42	30.71	21.73	1.01	30.02	-	2.00
26	0.61	1.07	5.70	17.29	14.33	1.02	19.37	-	2.77
27	-	0.28	2.58	10.66	34.98	0.56	45.87	-	1.00
28	-	0.53	2.46	5.68	36.93	0.21	48.00	-	1.31
29	0.55	-	1.45	6.93	34.00	0.18	46.30	-	1.16
30	0.62	-	3.77	12.61	32.45	0.71	43.09	-	1.00
31	0.42	0.48	2.70	19.06	26.79	0.52	36.55	0.29	1.86
32	-	0.45	2.65	8.94	19.73	0.53	27.08	0.30	2.54
33	0.50	-	2.47	7.56	34.09	0.55	46.41	0.20	0.88
34	0.61	0.35	2.52	10.33	32.13	0.52	45.37	-	1.08
35	-	0.46	5.77	14.81	14.52	1.65	19.70	0.36	2.15
36	0.87	0.43	3.04	11.54	31.06	0.47	41.53	-	3.64

Process of phosphatization

Secondary phosphatization of calcium carbonate in the Ludlow Bone-Bed is rare. The fossil articulate brachiopod shells seen in the Bone-Bed are consistently unphosphatized and it appears that fossil material was in general unaffected by phosphatization. Even shells of hyolithids and gastropods which may have been made of less stable aragonite are unphosphatized. It should be noted that these fossils only occur as phosphatic internal moulds and casts in this Bone-Bed. Although similar observations have been made elsewhere in phosphatic rocks in the geological column (e.g. Parker, 1971b; Kennedy & Garrison, 1975; Duffin & Gadizicki, 1977; Baird, 1978), they contrast sharply with the widespread phosphatization of skeletal carbonates noted in modern Florida, Peruvian and Agulhas phosphorites (Veeh et al., 1973; Manheim et al., 1974; Burnett & Gomberg, 1977; Birch, 1979). The reason or reasons for the general absence of calcium phosphate replacement of aragonite shells in some phosphorite and bone-bed deposits are not presently known. However, it is interesting to note that on the Agulhas Bank (S. Africa) the calcareous shells are replaced by glauconite prior to phosphatization (Birch, 1979), while in the West Pacific calcareous shells appear to be replaced directly by apatite (Heezen et al., 1973).

At the present time phosphate pebbles are currently forming as concretions through interstitial precipitation of calcium phosphate in near surface ocean floor sediments off the west coast of Africa and South America (Baturin, 1969, 1970, 1971a,b; Veeh et al., 1973; Burnett, 1974, 1977). These sediments are both anoxic and carbonate depleted organic rich siliceous muds and as such differ greatly from the carbonate rich silts on which the Ludlow Bone-Bed is commonly found, (Fig. 8, e,f). However, at three localities of the bone-bed visited by the author, Netherton (British National Grid reference SO 936 874), Priors Frome (SO 577 391) and Longhope (so 691 191), it is contained within or rests on a black clay, which is enriched in organic debris and at Netherton contains gypsum crystals (Antia, 1979b). These bone-beds are enriched in phosphate pebbles when compared with bone-beds elsewhere (e.g. at

Table 10. Numeric composition of Bone-Bed residue. Locality 1 = Deepwood, 2 = Rushall, 3 = Usk, 4 = Longhope, 5 = Priors Frome (clayey bone-bed), 6 = Lye, 7 = Netherton, 8 = Brockton, 9 = Ludow, 10 = Aston Munslow, 11 = Crofton, 12 = Longhope (clayey Bone-bed), 13 = Netherton (clayey bone-bed).

CLAST TYPE	LOCALITY 1	2	3	4	5	6	7	8	9	10	11	12	13
Thelodus parvidens	201	507	257	296	860	125	147	172	856	432	769	258	178
Logania ludlowiensis	7	51	45	39	76	73	542	243	123	125	31	64	384
Gomphonchus tenuistriata	–	2	–	–	–	–	37	2	2	3	7	–	11
Gomphonchus murchisoni	–	1	–	–	–	–	–	–	–	6	3	–	2
Lingula sp.	–	3	1	–	–	–	71	–	–	14	–	–	30
Orbiculoidea sp.	12	40	18	–	134	11	–	7	146	25	64	–	3
Serputites sp.	2	4	3	2	28	–	–	60	36	38	254	–	4
Phosphate nodues	28	5	–	29	192	–	3	–	21	62	11	134	90
Distomodus dubius	–	–	1	–	–	–	–	–	–	1	–	–	–
Ozarkodina sp.	–	–	–	17	–	–	–	–	2	12	–	23	–
Thelodus trilobatus	–	–	–	–	–	–	28	1	4	–	3	16	33
Matoporus tricauns	–	–	–	–	–	–	1	–	–	–	–	–	4
Thelodus pugniformis	–	–	–	–	3	–	1	–	2	3	–	6	–
Thelodus costatus	–	–	–	–	2	–	46	–	3	5	–	–	60
Thelodus bicostatus	–	–	–	–	–	–	–	1	1	–	–	–	1
Pachytheca sp.	–	–	–	–	–	–	–	–	–	–	–	–	3
Acanthodina debris	–	–	–	–	–	–	–	–	158	–	248	–	10
Cythaspis sp.	–	–	–	–	–	–	–	–	–	–	2	–	–

Ludlow) -- see Table 10. It has been suggested (Antia, 1979b) that these sediments indicate a general change in the chemistry of the Silurian sea, which may have been caused by a change in current source or alternatively have resulted from the influence of a massive southward migrating delta-estuary fluvial complex (Antia, 1979c).

The net change is considered (Antia, 1979b) to have resulted in Ca^{2+} CO^{2-} depletion and oxygen enrichment of the sea. Such conditions would probably result in an enlargement of the plankton and fish populations, dissolution of micritic shelf sediments and the slow deposition of organic rich muds.

The variability of substrates under the Ludlow Bone-Bed is such that four possible geochemical explanations for the phosphatic pebbles in the Ludlow Bone-Bed could exist. These explanations are:-

1. Formation by colloid aggregation;
2. Direct replacement of clay and micrite;
3. Direct replacement of micrite;
4. Direct precipitation in anoxic porewaters;

and may be described in more detail as follows:-

1. Colloid aggregation

It has been suggested (Kazakov, 1937; Bailey & Atherton, 1969) that apatite can precipitate out of natural sea water. However, it should be noted that the conditions necessary for apatite precipitation also favour carbonate and glauconite precipitation (Bailey & Atherton, 1969; Gulbrandsen, 1969; Burnett, 1977; Birch, 1979). Perhaps the most recent proponents of direct inorganic precipitation of phosphorite nodules are Bailey & Atherton (1969). They suggest (op. cit. p.1428) that clay colloids and colloidal apatite flocculate as a result of chance encounters in suspension. Colloidal aggregation continues till the combined mass is sufficient for the pellet to settle out of the water layer immediately above the sediment. Further colloids would be preferentially attracted to the surface of the proto-apatite pellet by ionic imbalances, associated with the particles comprising the pellet. Pellet growth would cease when colloidal attraction and bonding is insufficient to prevent dislodgement of colloidal particles from the pellets surface during agitation. This theory of phosphorite formation is considered to provide an unacceptable explanation for the phosphatic pebbles in the Ludlow Bone-Bed because (1) such colloid particles have so far never been observed and as little is known about the behavior of phosphatic colloid particles is saline waters the whole theory must at the present time be regarded as speculation. (2) the inclusion of primary bedding structures, abundant quartz, fish debris, acritarchs, chitinozoans and shell debris in these Silurian phosphatic pebbles and the general absence of concentric ring growth structures within them, further mitigates against colloid aggregation as a mechanism for their formation.

2. Direct replacement of clay and micrite

Some recent phosphorites may have arisen (Birch, 1979) from the inorganic replacement of micrite and partial lithification of the upper sedimentary layers of the sea floor. Phosphatic pebbles formed in this manner contain (Birch, 1975) an apatite groundmass containing a finely ($<1 \mu m$) interspersed glauconite (up to 4% K_2O). These pebbles are derived from the disaggregation of the lithified or semilithified bottom sediment and contain allochthonous constituents typical of shell sediments, such as quartz grains and residual carbonate fragments. The resultant pebbles tend to be well sorted and rounded (Lloyd & Fuller, 1965) and are concentrated in lag-placer deposits where finer, less dense or less resistant materials were winnowed away (Birch, 1979). Such pebbles contain an apatite enriched dark rim which is concordant to the pebble margin (Birch, 1979).

This model forms an attractive explanation for the gensis of the phosphate pebbles in the Ludlow Bone-Bed, because (1) in most localities the bone-bed rests on micritic silts, (2) many of the pebbles contain dark outer rims and (3) the phosphatic pebbles are well sorted (Fig. 11) suggesting that they may have been concentrated within a lag deposit. However, it should be noted that phosphatic pebbles formed by this mechanism are frequently enriched in glauconite (Birch, 1979) and that glauconite appears (Table 7, Fig. 8) to be absent from the Silurian pebbles. This problem can be overcome if necessary, since the common clay in the Ludlow Bone-Bed and underlying sediments is a chlorite complex, which may have been derived originally (March, 1976) from montmorillonite (cf. Pettijohn et al, 1973), and the common clay which is replaced by apatite and glauconite in this model is illite (Birch, 1979). It is therefore possible that direct replacement of chlorite or montmorillonite clay will not always lead to the apatite pebbles becoming enriched in glauconite.

3. Direct replacement of micrite

It has been demonstrated (Ames, 1959; Simpson, 1964) that alkaline phosphatic solutions (e.g. sodium and potassium phosphate) will replace calcite with a carbonate-apatite of variable composition. Both the replacement rates and composition of the resulting apatite are dependant on solution pH and PO_4^{3-} content in relation to HCO_3 concentration and temperature. The conditions of phosphorite formation from micrite are considered (Ames, 1959; p.839 Simpson, 1964) to be

1. A non-depositional environment.
2. Limy sediments available for replacement.
3. Ca - saturated sea water and sediment pore waters.
4. pH of 6.1 or greater.
5. PO_4^{3-} concentration of 0.1 pp.m or greater.

Micrite replacement by phosphate of carbonate nodules or intraclasts can also occur. In such instances replacement of the clast proceeds from its surface towards its centre resulting in the formation of a well developed phosphate enriched rim on the clasts outer margin (Ames, 1959).

Carbonate nodule formation within micritic sediment followed by excavation, concentration, and phosphatization, could account for many of the partially phosphatized micritic clasts of the Wenlockian and Leintwardinian of the Welsh Borderlands which contain phosphate rims and in some instances are completely phosphatized (e.g. Hancock, 1976; pers. com. 1978; Cherns, 1977). This model could also account for the genesis of the carbonate apatite nodules of the Whitcliffian at Tites Point and the Brookend Bore-hole (Cave & White, 1972, 1978) as many of these nodules appear to have a micritic centre and a phosphate enriched outer rim (Plate 2, Fig. C) which is frequently bored (Plate 2, Fig. D).

However, this model does not explain the high density of fish remains and organic debris (Table 8) present in the phosphatic pebbles of the Ludlow Bone-Bed. As the micritic sediments of the Whitcliffian (Table 8) tend to contain few fish scales and little organic debris.

4. Direct precipitation in anoxic porewaters

The only two known sites of actively forming phosphorite concretions at the present time (Baturin et al, 1972, Burnett, 1977) occur in regions of marine upwelling (Baturin, 1969; Burnett, 1979). They involve the phosphatization of anoxic organic rich mud a few centimetres below the sediment-water interface followed by later excavation of these 'newly formed' concretions and subsequent lithification on the sediment surface (Baturin, 1969, 1970, 1971a, b; Burnett, 1977). In these sediments apatite grows on the surfaces of biogenic clasts (Burnett, 1977) and within sediment pore spaces (Baturin & Dubinchuk, 1974). Although some replacement of clacite occurs (Baturin & Dubinchuk, 1974) much of the phosphatization is strictly localised within the sediment producing nodular rather than laminar phosphate growth (Baturin, 1970; Burnett, 1974). Phosphorite concretions commonly nucleate around biogenic clasts (e.g. Baird, 1978) or within biogenic clasts such as gastropod or biovalve shells (Baturin, 1970; Kennedy & Garrison, 1975). Such concretions frequently contain abundant fish, and plankton debris (Baturin, 1970) and are often associated with both vertebrate sand leses (Baturin, 1970 p.93) and vertebrate rich sediments containing up to 9.5% fish debris (Diester-Hauss & Schrader, 1979). It is interesting to note that in regions of episodic marine upwelling a positive correlation between the presence of a downwelling front and high densities of phosphorite nodules and fish debris in the sediment has been observed (Diester-Hauss & Schrader, 1979).

As already mentioned it is unlikely that the phosphate nodules in the Ludlow Bone-Bed formed by colloid aggregation. Although the direct replacement of clay and for micrite models explain the high concentrations of quartz grains in them (Table 8) and the dark rims on their margins, they fail to explain why the nodules contain an abundance of fish scales and organic debris. The presence of minor illite peaks on the XRD analysis (Fig. 8) at 20 valves of 8.8, 17.7, 26.8 is interesting, since illite is the only clay mineral which is commonly found in phosphorite nodules elsewhere in the geological column (e.g. Guldrandsen, 1966; Rooney & Kerr, 1967; Weaver & Wampler, 1972; Weaver & Beck, 1977; Birch, 1979).

Much of the illite in these other nodules is probably detritial (Weaver & Wampler, 1972), however, the abundance of montimorillonite and comparative ~~parity~~ paucity of illite in the adjacent sediments containing the nodules (Rooney & Kerr, 1967; Griffin et al, 1968; Weaver & Wampler, 1972; Weaver & Beck, 1977) may suggest that all other clay minerals are unstable in the micro-environment in which the phosphate grains formed and have been destroyed or altered to illite (Weaver & Wampler, 1972). The clay matrix of the Ludlow Bone-Bed contains three clay minerals Kaolinite, Chlorite and montmorillonite (Antia, 1979a, b; Antia & Whitaker, 1979). Chlorite (Fig.10) is the most abudant clay mineral in this bone-bed and is presumed to have formed as primary montmorillonite, which has been altered during diagenesis to a chlorite, illite complex. Small quantities of both chlorite and illite can be seen adhering to the surface of some of the quartz grains in the bone-bed under the scanning electron microscope.

The high fish and organic content of the nodules suggests that they formed in a region of high plankton productivity in which the waters were probably both oxygenated and undersaturated with respect to calcium carbonate (Antia, 1979b). Such a region probably received little detrital input and phosphorous was concentrated in the sediment by dead and decaying organisms. In the slightly basic environments presumed to have existed in the sediment much of the phosphate should be present as H PO_4^{2-} (Gulbrandsen, 1969) and/or an organic-phosphate complex (Antia, 1979b). In the nodules much of the phosphate has precipitated in a honeycomb structure (Antia, 1979a; Antia & Whitaker, 1979) which closely resembles the habit of clays in the Bone-Bed (Antia, 1979a, pl.18c) and suggests that the phosphate nodules may have formed by a clay absorption process (cf. Dean & Rubins, 1947; Pomeroy et al., 1965). The mechanics of phosphate absorption by clay are not entirely resolved. However, it has been shown (Perkins, 1945) that the amount of phosphate absorbed by montmorillonite increases greatly as its pH increases from 4 to 9 and that the compounds $AlPO_4.2H_2O$, $FePO_4.2H_2O$ are formed with Al and Fe obtained from the clays surface (Hemwall, 1957). As the pH of the sediment increases, Ca becomes more effective at fixing PO_4 than Al, Mg or Fe (Perkins, 1947). The resulting apatite would probably pseudomorph after the original clay structure of the sediment (Antia & Whitaker, 1979; Antia, 1979b) and the high Mg and Fe concentrations in the nodules (Table 7) may be residual elements from the original clays of the nodule or result from an ionic substitution of Mg and Fe for Ca in the apatite structure during diagenesis (McConnel, 1973; Cruft et al., 1965).

This model of phosphate nodule formation requires the presence of dark organic rich muds containing both fish debris and phosphorite nodules. Such clays are present in the Ludlow Bone-Bed (Lawson, 1953; Antia, 1979b) and their regional distribution indicated in Fig. 1. Since the West African, Agulhas Bank and Californian phosphorites, phosphate nodule formation is concentrated in localised areas (Parker, 1971, 1975; Parker & Siesser, 1972; Summerhayes, 1973; Birch, 1979; Baturin, 1970; D'Anglejan, 1967, 1968) with subsequent erosion and transport spreading the nodules over a wide area on the sea bed, a similar situation could have occurred in the Silurian Ludlow Bone-Bed with fish scales accumulating in the onshore regions and phosphatic vertebrate rich muds in more offshore regions. The gradual decrease in fish scale abundance and increase in phosphate nodule abundance from the lithobonebeds in the Much Wenlock Ludlow District to the clayey pelbonebeds and phosphorites of the Mayhill-

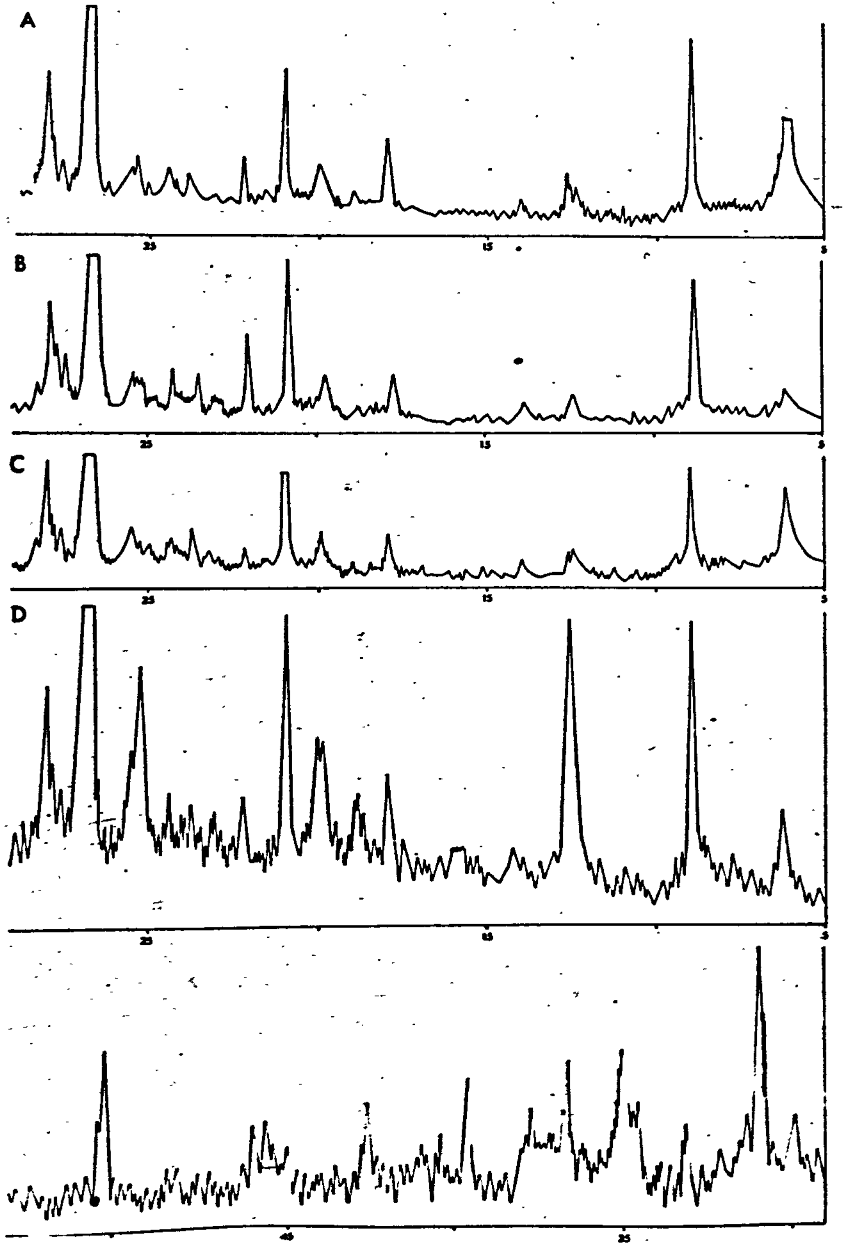


Fig. 12

X.R.D. Traces of soft clay layers at

A. Broadstone Farm (Upper Whitcliffe Beds)

B. Aslon Munslow (ca. 1.5 m below the Ludlow-Downton boundary).

C. Ludlow (6 cm above the Ludlow-Downton series boundary. These layers all contain Chlorite (2θ peaks ca. 6.10, 12.5, 19.9, 25.4), muscovite/sengiente (2θ peaks 8.9, 17.8, 23.7, 28.0), and quartz (e.g. 2θ peaks 20.9, 26.7).

D. Clayey siltstone layer in the Brookend Borehole about 100 m below the surface (Upper Whitcliffe Beds). Minerals in order of abundance are quartz (2θ peaks 26.7, 20.95, 50.2, 36.6, 41.5, 40.3, 45.4), ripidolite (2θ peaks 12.6, 25.2, 35.1, 50.2, 36.6, 34.6, 39.6, 37.7, 18.8, 6.3, 31.4, 33.9, 45.0), saleeite (2 peaks 9.0, 36.6, 25.5, 17.9, 39.6, 41.5, 27.6, 29.9, 31.4, 33.9, 40.4), chloritoid (2 peaks 31.0, 28.0, 36.6, 20.0, 19.8, 39.6, 41.5, 37.7, 27.6, 18.8, 23.0, 24.4, 29.9, 33.1, 32.1, 40.4, 40.9, 45.0, 45.9), and plagioclase (2 peaks 28.0, 35.1, 36.6, 25.5, 27.6, 18.8, 22.2, 23.0, 23.7, 24.4, 39.9, 31.4, 33.9, 15.8).

Brookend district lends some credence to this idea (Fig. 1).

Source of clays in the phosphatic clay deposits

The clays in the Ludlow Bone-Bed could have a number of sources. They could be derived from (1) bentonites, (2) the in situ weathering of detrital igneous material such as feldspars and micas, or (3) from the input of fresh terrigenous material.

1. Bentonites

K-bentonites rich in biotite have been recorded from throughout the Welsh Borderlands (Marsh, 1976) and from the Whitcliffian (Cave & White, 1978). These montmorillonite rich deposits are commonly reworked after deposition to produce clayey siltstones or even biotite enriched lag concentrates (cf. Marsh, 1976). In the Brookend Borehole (Fig. 2) and elsewhere in the Woolhope - Mayhill - Malverns region, there is an apparent correlation between biotite rich layers and bone-beds. This correlation has been commented on elsewhere (Tucker, 1960; Antia, 1979a) and may indicate that the fish in the bone-bed were killed by volcanic ash (and associated chemicals) descending through the water column after a local eruption. Subsequent winnowing of the sediment may have removed the fine clays from the surface layers and decomposition of the fish soft parts would have resulted in disarticulation and disaggregation of their body scales. The resulting sediment would be enriched in both biotite and fish scales and would be termed a bone-bed.

In the Ludlow Bone-Bed at Ludlow, a soft pliable silty clay is locally present. This clay is morphologically similar to a clay 1.2 m below the Ludlow Bone-Bed at Aston Munslow and about 60 cm below the top of a section through the Upper Whitcliffe Beds in the road cutting opposite Broadstone Farm, near Shipton (G.R. SO 545 903). These latter two deposits have a flat base, are 2-3 cm thick and have a flat top. They are considered here to represent a reworked bentonite similar to those described by Marsh (1976) from elsewhere in the Ludlovian. The similarity in mineral composition (Fig. 12) between the three clays suggests that they may have a common source, and that the Ludlow

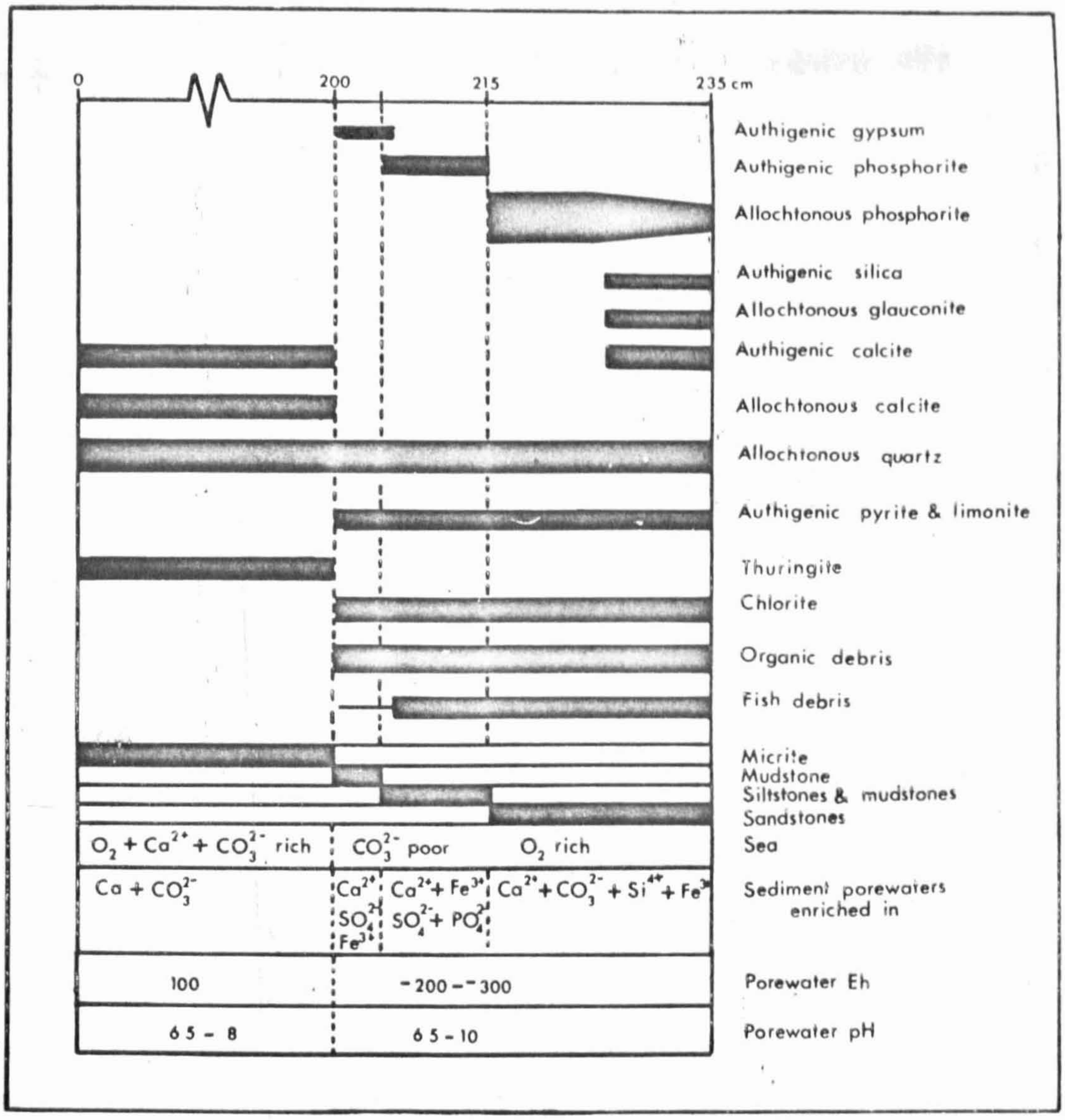


Fig. 13. Profile of the Netherton section showing the distribution of authigenic and allochthonous minerals, sediment type, the interpretation of sediment pore waters Eh, pH and mineralogy, and an interpretation of sea water chemistry. The clay minerals recorded are thuringite (a chlorite mineral) and a group of undifferentiated chlorite X.R.D. traces for different points in the section are given in Fig. 8.

Bone-Bed may owe its origin in part to local Silurian vulcanicity. It is interesting to note that all three clays contain, in addition to chlorite, quartz and muscovite, traces of a mineral which may be sengiorite. This mineral contains small quantities of uranium and vanadium, both of which are commonly concentrated in bones and phosphorite nodules (Gulbransen, 1966; Tasgrev & Nikitia, 1970; Burnett, 1974 etc.). The chlorite probably formed by the diagenetic alteration of an original montmorillonite clay (cf. Pettijohn et al., 1973). It is interesting to note Fig. 8, 13 that in a section containing two very different pore water microenvironments, the 'montmorillonite' has been altered to two different chlorite clays.

2. Detrital material

Some of the clays in the Ludlow Bone-Bed and associated phosphatic clays might have originated from the decomposition of feldspars and micas (cf. Pettijohn et al., 1973). This is partially confirmed by the presence of kaolinite (Antia & Whitaker, 1979; Antia, 1979a) and illite in the Bone-Bed. However, at the present time it is impossible to assess the contribution of detrital igneous grains by decomposition to the clay population.

3. Input of fresh terrigenous material

It is unlikely that significant contributions to the clays were made from a fresh source at the end of the Whitcliffian, because both Whitcliffian and Dowtonian sediments contain abundant chlorite (e.g. Fig. 8; 13).

Consequently the probable source for many of the clays in both the Whitcliffian and Downtonian is considered here to be volcanic ashes and bentonites. The decomposition of micas and feldspars undoubtedly contributed to the clay population, but their contribution is considered here to be minor.

Palaeoecology of the Bone-Bed

No burrows have been recorded in the Ludlow Bone-Bed. However, at Ludlow rare specimens of Goniophora cymbaeformis J. de C. Sowerby occur in situ in the bone-bed (Antia, 1979a). In the phosphorite rich clays at Netherton both in situ Pachytheca sphaerica and black laminae produced by blue green alga are present (Plate 1, Fig. D). The black algal laminae appear to encrust relict bedding traces within the phosphorite rich clays (Plate 1, Fig. D) and have like Pachytheca been heavily impregnated by calcite during diagenesis.

The Pachytheca (Plate 1, Fig. B; D) are interesting because they appear to be encrusting on a quartz grain nuclei. This suggests that Pachytheca may have been a marine sedentary encrusting alga which encrusted small sand grains lying on the surface of anoxic organic rich muds (cf. Appendix).

Reconstruction of faunal and taphonomic events leading to the formation of the Ludlow Bone-Bed

1. Pre-discontinuity

Prior to the formation of the bone-bed, a number of important events are considered to have occurred. The first and perhaps most important was a change in the chemistry of the Silurian shelf sea. This change (Antia, 1979b) to more oxygenated calcium carbonate undersaturated environment from a calcium carbonate saturated environment was sudden and appears to have affected the whole of the Welsh Borderlands. The lack of fresh detritus associated with the change suggests that it may result from sea floor current switching, perhaps turning the region into one of marine upwelling (cf. Diester - Hauss & Schrader, 1979) or alternatively it could result from (Antia, 1979c) a decrease in salinity or alteration of the chemical balance of the sea caused by the gradual southward migration over the Welsh Borderlands of a massive delta/estuary complex which reached its acme later in the Dittonian (Allen, 1974).

Either of these changes would have probably resulted in both an increase in the plankton productivity of the surface waters, and an increased organic contribution to the sediment (Antia, 1979b; Diester Hauss & Schrader, 1979). The former increase would have probably resulted in a greatly increased fish population in the overlying waters (Walsh, 1976; Dugdale, 1976; Parsons, 1976) and a high vertebrate skeletal contribution to the sediment. Locally this change would have resulted in the deposition of thin organic rich anoxic muds with very slow deposition rates. Subsequent diagenetic reactions (cf.

Arrhenins, 1962; Robert & Chamley, 1974; Siesser & Rogers, 1976; Briskin & Schreiber, 1978) would probably have led to the formation of authigenic gypsum in some of these muds (Antia, 1979b) and eventually phosphorite nodule and steinkern formation (Antia, 1979b) within the sediment pore waters. Within these muds representative examples of the in situ fauna would probably have been phosphatised. The fauna recorded in the steinkerns from these muds (Table 6) includes crinoid stems, Lingula's, Orbiculoidea's, gastropods and hyoliths, and differs from the fauna in the underlying Whitcliffian sediments in containing few articulate brachiopods (cf. Calef & Hancock, 1974; Lawson, 1975), and from the overlying Downtonian sediments in containing no abundant ostracods and bivalves (cf. Elles & Slater, 1906; Shaw, 1969; Siveter, 1978).

The phosphatised crinoids, hyoliths, gastropods and brachiopods were benthic species (cf. Franzen, 1974; Marek & Kochelson, 1976; Peel, 1977; Cherns, 1977, 1979), which probably lived in or on the anoxic environment presented by the dark muds.

2. Erosion event

Since much of the Ludlow Bone-Bed occurs as a well sorted grain supported sediment (cf. Antia, 1979), it is probable that many of the anoxic muds were removed by erosion and the fish remains and phosphatic nodules within them concentrated as a bone-bed on the sediment surface, prior to the deposition of the Downton Castle Formation. These lag concentrates were well sorted by currents and vertebrate contributions may have been added to them as a result of both fish mass mortalities and normal fish mortalities. Although in the May Hill - Brookend district the Ludlow Bone-Bed may mark a pronounced discontinuity, in the Ludlow to Much Wenlock district it represents part of a continuous regressive sequence of intertidal sedimentation (Allen, 1974; Antia, 1979a; Antia & Whitaker, 1979) accumulating as vertebrate sand patches in the lower part of a mudflat in which the vertebrate and phosphatic material had been swept onshore by storms and currents. Perhaps an analogous modern example are the vertebrate sands on the Mellum mudflats in West Germany (Shäfer, 1966, 1972).

The apparent absence of the Ludlow Bone-Bed from much of the basinal Whitcliffian sediments to the west of the lower Palaeozoic Church Stretton Growth Fault (Davies & Cave, 1976) in Kerry, Bucknell, Knighton and Clun (Stamp, 1918; Earp, 1938, 1980; Holland, 1958) may either be a result of poor exposure at the critical Ludlovian - Dowtonian junction as has been partially demonstrated by Palmer (1971), or relate to the higher rates of sedimentation (Holland & Lawson, 1963) and differing palaeocurrent directions of this region (Bailey & Rees, 1972).

ACKNOWLEDGEMENTS

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PLATE 1.

A. The Ludlow-Downton boundary at Corfton showing that the Ludlow Bone-Bed forms an integral part of rippled strata (x 2) - negative print

B. <u>Pachytheca</u> <u>sphaerica</u> Hooker, <u>in situ</u> growing from a quartz grain. The same specimen is situated in the middle top part of Fig. D (x 12.5) - negative print.

C. The Ludlow Bone-Bed at Lye. Note its erosive base (x 2) - negative print.

D. Phosphate rich clayey bone-bed at Netherton. Note mud pellets and phosphate nodules in a quartz sand. The think white lines and layers of fossil blue green algae encrusting along an ancient bedding plane. (x 3) - negative print.

E. Ludlow-Downton boundary at Ludlow. Note bioturbated top Ludlovian overlain by a thin scatter bone-bed (terminology after Sykes, 1977) and laminated Downtonian siltstones (x 2) - negative print.

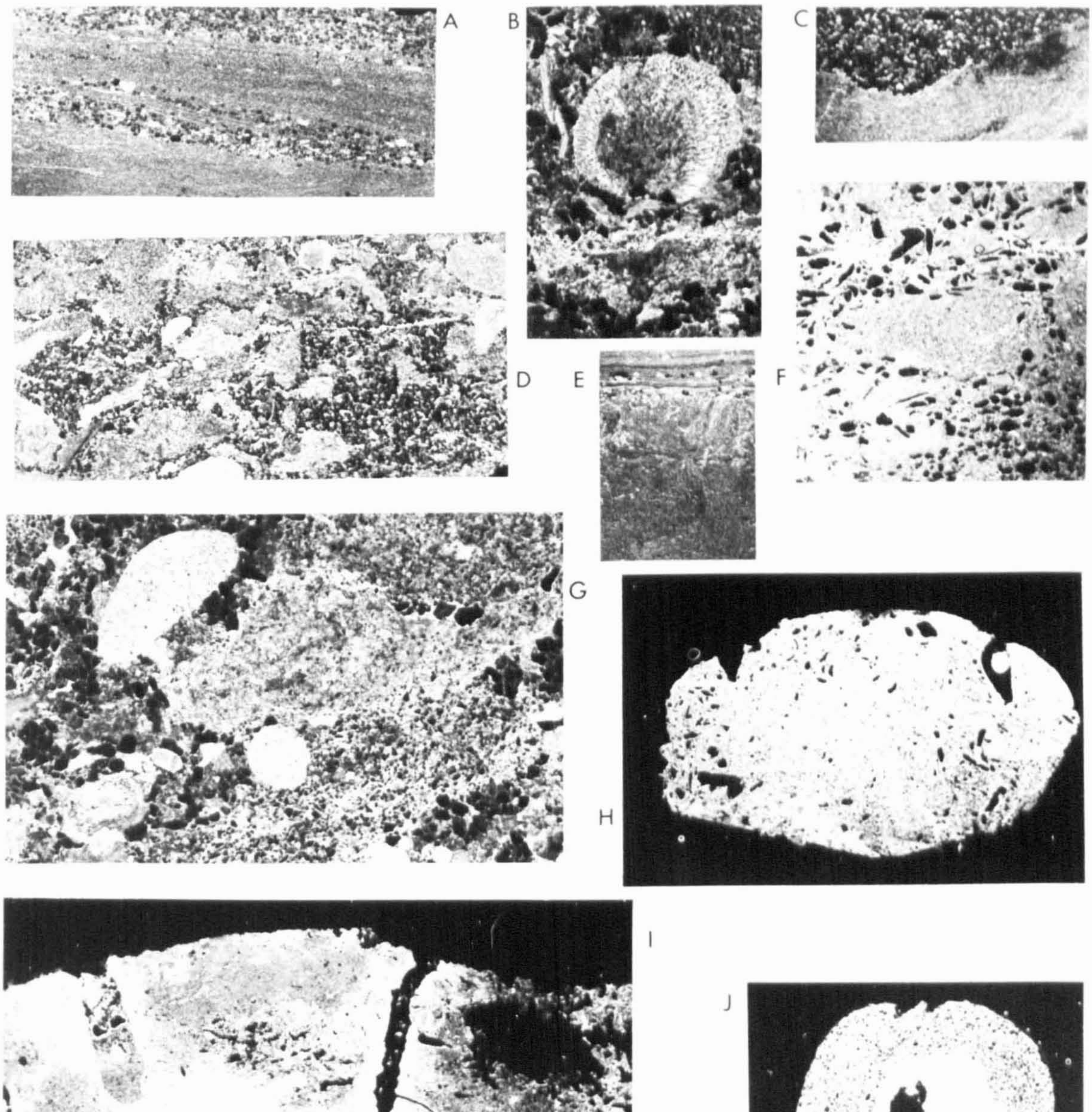
F. Negative print of part of a phosphate nodule showing its composite peletal structure of mud pellets surrounded by fish debris enriched phosphatic muds. (x 10) - negative print.

G. Detail of phosphate rich clayey bone bed at Netherton. Note abundant quartz grains, mud pellets with diffuse margins and phosphate pebbles with distinct margins (x 12) - negative print.

H. Negative print of a bored phosphate nodule from the Ludlow Bone-Bed at Longhope (x 12).

I. Negative print of another bored phosphate nodule from the Ludlow Bone-Bed at Longhope. Note the 2 <u>Trypanites</u> borings, one of which has been infilled with phosphatised mud. The other has a light coloured inner margin which is lined with acritarchs and other organic debris. The white patches in the photomicrograph are enriched in organic debris and microplankton (x 15).

J. Negative print of a quartz rich phosphate nodule which nucleated around a crinoid stem. The crinoid stem has since been replaced by a phosphatised mud containing quartz silt and microplankton (x 8).


A
B
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J

PLATE 2. The Brookend Borehole.

A. A glauconite rich bone-bed in the Downton Series (I.G.S. specimen No. CV 3307d) from 15 m above the base of the Downtonian. The glauconite pellets in this bone-bed are probably analagous with recent glauconite pellets found off the Agulhas at the present time and described in detail by Birch <u>et al</u> (1976). All the glauconite grains appear to have a uniform dark green colour, are unsutured and generally well rounded.

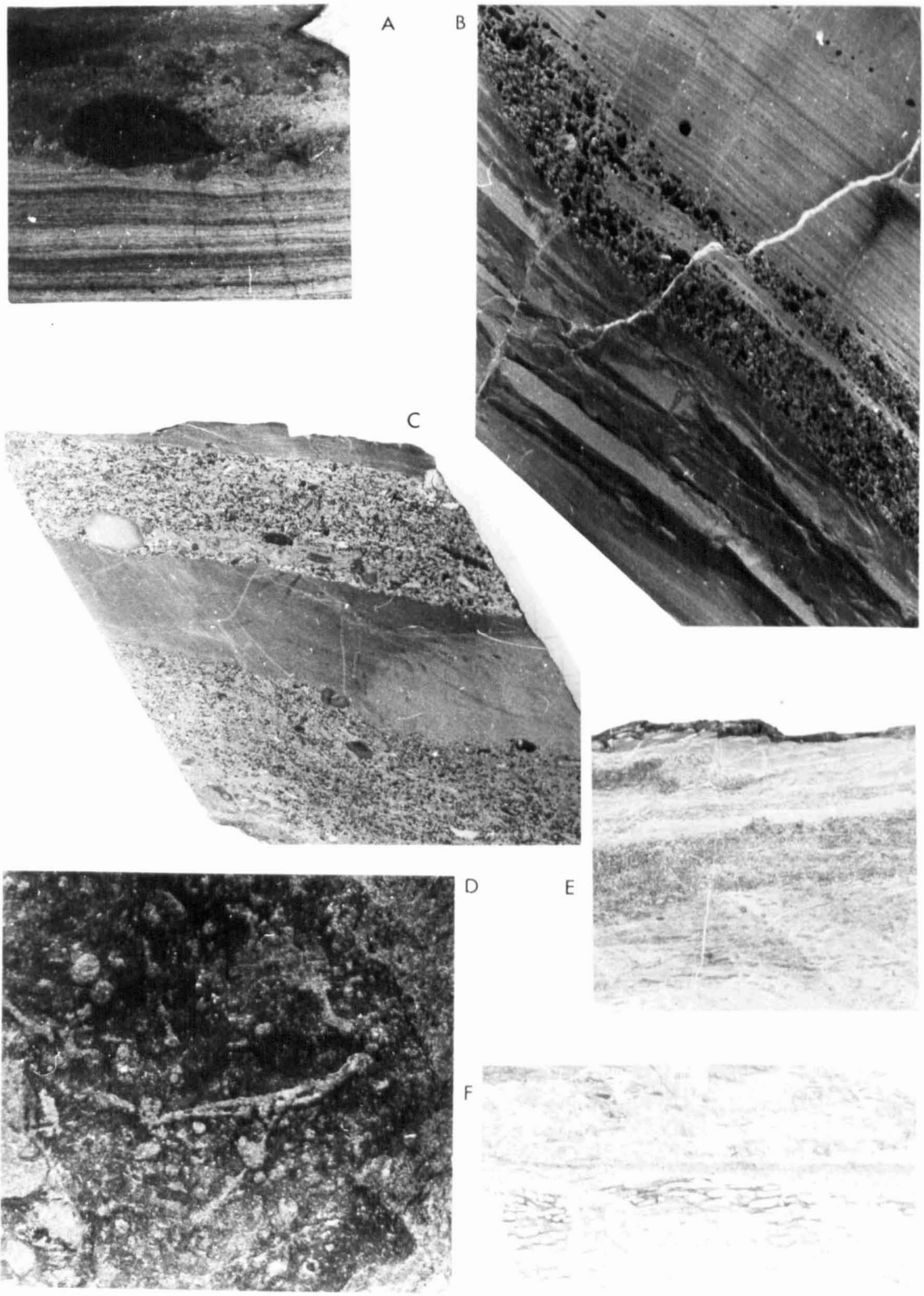
B. The Ludlow Bone-Bed. Note minor microfaulting in the overlying sandstone, and the erosive base at the base of this phosphorite layer. The underlying lenticular bedded silts and muds are carbonate rich (I.G.S. specimen No. CV 3434).

C. Bone-Bed in the lower part of the Whitcliffe Beds occurring as a shelly vertebrate rich layer containing phosphate nodules and partially phosphatised micrite pebbles. These layers rest on bioturbated muddy siltstones.

D. Bored phosphate pebble from the Lower Whitcliffe Beds.

E. Bone-Bed in Upper Whitcliffe Beds.

F. Bone-Bed in Bioturbated Upper Whitcliffe Beds.


A
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Appendix I Edge to edge Microprobe transects for the phosphate pebbles in Fig. 9e - m.

All element abundances were calculated as oxides by the microprobe.

(a) Pebble transect Fig. 9e, indicating relative abundances (%) of 9 elements

Distance from pebble edge (mm)

	0	0.3	0.8	1.2	1.8	2.3	2.8	3.3	3.8	4.3	4.8	5.3	5.8	6.3	6.9	7.4
Na	-	-	-	-	-	-	-	-	-	-	-	-	0.91	0.71	-	-
Mg	-	0.39	0.26	-	0.64	1.58	0.40	0.50	0.56	0.45	0.62	0.47	0.84	0.25	1.10	0.86
Al	3.08	2.51	4.15	1.38	3.84	5.93	3.36	3.23	3.19	4.04	3.20	3.84	8.64	2.53	5.77	2.99
Si	65.99	16.24	12.62	27.22	11.35	27.23	15.21	9.81	9.29	9.72	9.46	12.55	28.21	42.76	29.25	14.78
P	-	31.86	34.00	28.90	31.81	26.64	33.50	35.37	37.07	34.27	36.60	33.33	24.43	24.20	26.21	32.83
K	0.72	0.19	0.73	0.26	0.72	0.92	0.66	0.69	0.57	0.77	0.52	0.68	1.34	0.62	1.28	0.37
Ca	0.39	40.7	43.13	35.74	40.79	32.76	41.84	45.73	46.35	43.76	46.02	42.33	29.22	28.6	31.94	41.4
Mn	1.22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fe	1.06	4.25	1.81	0.75	1.77	3.44	1.11	1.17	0.96	2.50	1.26	3.06	2.31	0.80	1.89	2.78

(b) Pebble transect Fig. 9f, indicating relative abundances (%) of 9 elements

	0	0.4	0.9	1.7	2.6	3.4	4.3	5.1	5.9
Na	0.47	-	-	1.43	-	-	0.43	-	-
Mg	0.55	0.40	0.39	0.46	0.58	1.21	0.48	0.40	0.276
Al	4.28	3.69	4.49	7.95	5.18	5.03	4.50	4.24	3.960
Si	21.87	14.84	11.65	33.54	15.12	24.20	23.12	39.63	29.29
P	29.54	34.92	34.59	23.96	32.43	29.81	30.81	22.96	27.72
K	0.79	0.58	0.76	1.06	0.83	0.84	0.72	0.81	0.85
Ca	37.30	43.92	42.84	29.58	41.41	36.23	37.87	27.76	34.31
Mn	-	-	-	-	-	-	-	-	-
Fe	3.63	1.20	2.77	1.74	1.95	1.73	1.31	1.07	2.42

(c) Pebble transect, Fig. 9g, indicating relative abundances (%) of 9 elements

	Distance from pebble edge (mm)																
	0	0.5	0.9	1.3	1.9	2.5	2.9	3.4	3.8	4.4	5.0	5.4	5.9	6.4	6.9	7.4	8.0
Na	0.41	-	0.69	0.41	-	0.53	-	0.67	-	0.48	-	1.84	0.66	2.14	-	0.39	0.46
Mg	0.43	0.58	0.46	0.56	0.49	0.53	0.34	0.34	0.29	0.54	0.89	0.35	0.54	0.32	0.61	0.54	0.35
Al	3.91	4.32	5.14	2.77	4.05	5.57	1.93	5.07	3.85	4.94	4.52	6.58	5.15	5.61	5.61	3.85	2.78
Si	15.17	11.52	15.25	7.24	11.35	13.94	8.43	24.47	15.08	16.27	11.13	20.10	15.55	30.59	13.41	11.62	13.80
P	31.23	31.20	28.61	34.29	25.15	19.72	27.57	27.90	30.78	27.03	20.17	16.22	21.25	17.94	25.47	31.17	31.07
K	0.75	0.79	0.91	0.58	0.81	1.34	0.38	0.99	0.83	0.82	0.67	1.33	0.91	0.53	1.11	0.66	0.68
Ca	40.85	41.92	38.38	45.65	33.99	25.16	35.87	34.82	39.95	34.67	25.46	21.06	28.96	23.80	34.70	42.30	42.26
Mn	-	-	-	-	0.24	0.74	-	-	0.69	-	4.20	0.53	-	-	-	0.20	0.21
Fe	2.23	2.10	2.14	1.97	2.08	2.57	1.28	1.74	1.3	1.99	3.06	1.21	3.87	1.78	2.92	1.79	1.15

(d) Pebble transect, Fig. 9h, indicating relative abundances (%) of 9 elements

	Distance from pebble edge (mm)										
	0	0.4	1.6	2.8	3.8	4.6	5.3	6.2	7.2	8.2	9.2
Na	0.47	0.46	-	-	0.42	0.45	-	-	0.42	-	0.58
Mg	0.43	0.41	0.39	-	0.42	0.59	-	1.22	0.35	0.33	0.47
Al	1.15	2.51	3.11	1.24	2.97	3.13	4.62	3.99	2.39	4.81	2.25
Si	2.83	8.90	12.91	5.74	9.93	15.79	40.36	12.32	9.01	14.31	7.97
P	19.4	31.11	8.09	36.44	27.4	33.20	21.70	27.58	31.65	25.83	34.43
K	0.14	0.90	0.65	0.32	0.57	0.66	1.06	0.34	0.48	2.25	0.98
Ca	25.77	41.11	10.62	46.30	35.60	42.06	27.42	36.78	41.97	31.69	44.87
Mn	1.89	-	0.24	0.29	0.52	-	-	-	-	-	-
Fe	1.03	1.13	1.77	1.00	2.14	1.09	1.72	4.53	3.50	14.86	1.81

(e) Pebble transect, Fig. 9i, indicating relative abundances (%) of 9 elements

	Distance from pebble edge (mm)				
	0	1.0	2.0	3.0	4.0
Na	0.56	1.72	-	0.80	-
Mg	0.28	0.42	0.31	-	0.51
Al	3.62	6.60	2.48	2.69	3.5
Si	24.57	20.53	41.46	29.19	13.62
P	32.01	28.27	24.83	28.68	32.02
K	0.37	0.66	0.87	0.29	0.83
Ca	38.39	34.64	29.93	35.75	42.18
Mn	-	0.61	0.27	-	-
Fe	2.16	2.65	0.83	1.89	2.54

(f) Pebble transect, Fig. 9j, indicating relative abundances (%) of 9 elements

	Distance from pebble edge (mm)					
	0	1.0	2.0	3.0	4.0	5.0
Na	0.44	-	-	0.87	-	-
Mg	0.30	0.41	0.51	0.50	0.26	0.61
Al	3.85	2.41	2.66	4.44	2.77	3.04
Si	8.17	11.13	19.76	14.94	15.08	22.02
P	35.30	36.02	34.14	33.31	33.80	30.37
K	0.75	0.38	0.42	0.66	0.41	0.54
Ca	44.69	45.10	42.00	41.68	41.93	36.47
Mn	-	-	-	-	-	0.21
Fe	0.83	1.00	0.98	1.69	3.84	2.42

(g) Pebble transect, Fig. 9k, indicating relative abundances (%) of 9 elements

Distance from pebble edge (mm)

	0	1.0	2.0	2.9	3.0	3.4
Na	-	1.03	-	0.69	0.88	0.76
Mg	0.33	0.78	0.58	0.29	1.23	0.29
Al	2.65	4.56	3.75	5.16	5.39	2.64
Si	31.82	32.69	26.15	29.22	15.98	9.91
P	25.38	23.11	26.95	25.91	29.22	34.36
M	0.43	0.72	0.9	1.28	0.88	0.34
Ca	33.58	30.69	35.36	34.01	38.99	45.81
Mn	-	-	0.29	0.26	-	-
Fe	1.34	2.04	1.67	1.06	2.45	1.14

(h) Pebble transect, Fig. 9l, indicating relative abundances (%) of 9 elements

Distance from pebble edge (mm)

	0	1.0	2.0	3.1	4.1	5.1	6.4	6.8
Na	-	-	4.86	-	-	-	-	-
Mg	0.58	0.27	0.83	0.69	0.21	0.39	1.33	0.35
Al	2.37	3.79	13.44	5.44	1.71	4.10	5.89	2.61
Si	13.00	30.61	33.54	21.64	8.00	21.37	15.76	17.14
P	32.58	24.32	19.06	29.	11.36	11.12	29.12	32.53
K	0.40	0.89	0.83	1.12	0.38	0.52	0.88	0.37
Ca	41.85	28.66	23.79	36.29	14.13	13.16	35.81	40.78
Mn	-	-	-	-	-	-	-	-
Fe	3.08	9.37	2.39	2.97	0.31	4.40	6.19	3.39

(i) Pebble transect, Fig. 9m, indicating relative abundances (%) of 9 elements.

Distance from pebble edge (mm)

	0	1.0	2.0	3.0	4.0	4.5
Na	0.44	0.75	0.62	0.91	0.43	0.44
Mg	0.53	0.54	0.65	1.40	1.39	0.44
Al	2.35	4.82	4.07	6.38	3.39	3.58
Si	28.42	21.25	13.66	17.17	14.90	13.25
P	26.13	26.80	29.81	25.12	28.31	29.10
K	0.42	1.33	0.87	1.04	0.48	0.79
Ca	34.76	35.94	41.65	34.86	37.76	41.03
Mn	-	-	-	-	-	0.20
Fe	1.65	2.90	1.64	3.81	5.27	2.40

(j) Pebble transects, Fig. 9n, indicating relative abundances (%) of 9 elements.

Distance from pebble edge (mm)

	0	1.20	4.10	4.80	5.60
Na	-	-	0.60	0.58	-
Mg	-	-	0.64	0.59	0.30
Al	3.02	0.23	3.10	3.08	3.04
Si	19.30	2.37	17.78	12.38	12.41
P	29.63	36.60	29.98	26.82	33.30
K	0.56	-	0.49	0.46	0.50
Ca	39.69	49.10	38.19	33.57	42.61
Mn	0.36	-	-	-	-
Fe	0.94	0.64	1.72	14.53	1.10

APPENDIX II

The systematic position and environmental distribution of *Pachytheca sphaerica*.

Pachytheca sphaerica Hooker was an Upper Silurian/Lower Devonian (Wenlock to Tedinnian) alga which is found in marine sediments in the Welsh Borderlands, U.K. It may be described as a carbonaceous sphere, varying in diameter from 1 to 7 mm, with a smooth external surface.

Internally it consists of a central medulla and a radially striated tubular cortex. This cortex consists of a series of filaments, each contained within an open ended tubular hexagonal sheath. These sheaths have a diameter in the order of 50 to 100μ (Kidston and Lang, 1924, Plate 53, Fig.4). They are radially arranged and densely packed (Lang, 1937, Plate 14, Fig. 121; Antia and Whitaker, 1978, Fig. 4). Individual sheaths thicken towards their bases and occasionally exceed 700 in length. Periodically the effect of internal growth lines is produced by false branching forming concentric zones determined by the bases of a new generation of sheaths (see Lang, 1937, Plate 14, Figs. 121, 124). Individual pachythecids may show three or more such zones. Bounding the cortex is thin sheet of mucilage (Antia and Whitaker, 1979, Fig. 4). The central medulla is commonly found infilled with sediment. This infill is usually composed of diagenetic clay, phosphate, or calcite, Occasionally, pachythecids contain quartz grains or fish scales in their centres.

Pachytheca is currently thought to have been a cyanophytid alga of uncertain affinities within the group (Corsin, 1945; Lang, 1945; Johnson, 1951; Schmidt, 1958). However, (1) the presence of multicellular filaments within a cortical sheath suggests a taxonomic position within the tribe Hormogoneae (cf. Prescott, 1969, p.143) and (2) the presence of a spherical colony with a smooth outer surface, containing densely packed radiating trichomes encased in sheaths which taper from base to apex and show false branching, may indicate that *Pachytheca* should be assigned to the order Riveriales, family Rivulariaceae (cf. Drouet, 1951; Prescott, 1969).

Within the Rivulariaceae, Pachytheca bears a close resemblance to the genera Gloeotrichia and Rivularia. All three genera share the following features (1) they all occur as smooth black mucilagenous spheres containing an internal cortex of radially arranged and densely packed filaments within sheaths, (2) the filaments all taper towards their bases and show false branching, (3) the impression of internal growth rings is given by successive generations of false branching forming concentric zones determined by the basal heterocysts of the new trichomes (Fritsch, 1945; Prescott, 1969).

At the present time Rivularia is a sedentary intertidal marine alga found just below the splash zone (Prescott, 1969), while Gloetrichia is both epiphytic and planktonic (Prescott, 1969). Lang (1937, 1945) considered Pachytheca sphaerica to inhabit both subtidal marine and fluvial environments.

Following detailed palaeoecological and sedimentological studies of the Upper Silurian of the Welsh Borderlands (Hobson, 1960; Allen, 1974; Calef and Hancock, 1974; Antia and Whitaker, 1979; Antia, 1979a, b, c and in prep.), it may be possible to locate a preferred habitat for the species.

In 26 sections in the Ludlow to Birmingham (U.K.) region of the Welsh Borderlands the fauna and flora was examined at 10 - 50 cm intervals, and the sediment in which they occurred examined and placed within a depositional environment.

The sections sampled have the following British National Grid References - SO 457740, 928846, 936874, 578939, 563917, 545903, 523875, 512865, 502862, 597853, 496851, 482839, 474833, 475818, 458798, 456750, 445750, 445742, 460740, 492743, 511742, 522741, 497726, 485724; SJ 315078, 313073.

The environments examined (see Reineck and Singh, 1975; Antia, 1979a for details of the sedimentary features characterizing each environment) contained Pachytheca sphaerica in the densities and abundances indicated in Table 11. This table shows that Pachytheca was absent from the subtidal environment, but present in the intertidal environment. In the lower shore face it was common in the shelly lag concentrates infilling channels in the mudflats. It occurred very rarely in the surrounding mudflats. In the beach sands and silts Pachytheca occurred only

Table 11. The environmental distribution of *Pachytheca sphaerica* in the Upper Ludlow and Lower Downtonian. Its abundance in phosphorite rich black clays is not indicated here.

1 = No. of samples; 2 = No. of samples with *Pachytheca*; 3 = Mean density of *Pachytheca*; 4 = Maximum density of *Pachytheca*.

3 & 4 expressed as density per m^2 bedding plane surface area.

Environments outlined here have been recorded by Allen (1974), Antia & Whitaker (1979), Antia (1979).

Environment	1	2	3	4
1. Subtidal calcareous muds and silts containing a brachiopod fauna	345	0		
2. Bone-beds in low intertidal zone	41	5	0.4	8.5
3. Mudflats (a) lower shore zone	68	0		
(b) upper shore zone	14	1	0.1	4.6
4. Upper Shore Zone - Mudmounds				
(a) channels	8	8	6.3	11.1
(b) mounds	16	0		
5. Upper Shore Zone - Beach				
(a) sand and silt	22	0		
(b) Organic debris layers	8	7	244.1	583.5
6. Back shore zone - Lagoonal muds and silts				
(a) muds and silts	24	0	1754	2010
(b) organic debris layers	4	4		

in association with layers rich plant (algal) debris. In the lagoonal marsh back shore sediments, Pachytheca occurs abundantly in thin laminae rich in organic debris. Its high density presence in the lagoon and beach sediments may suggest that it lived in this environment (cf. Lingwood, 1976), but the organic debris layers in which it commonly occurs could be transported strand line deposits (cf. Reineck and Singh, 1975).

Its in situ occurrence in the phosphatic clays at Netherton (Plate 1. Fig. B) suggests that the latter hypothesis may be more correct. Pachytheca is common in the soft organic rich phosphatic clays of the Lower Downtonian and also occurs occasionally in non calcareous clayey layers of the Whitcliffian (Table 1). It is therefore possible that Pachytheca lived offshore in a subtidal environment and that during postmortem decomposition its central medulla became infilled with gases, making the pachythecid buoyant and allowing it to be transported to a position high in the littoral zone. During subsequent diagenesis the medulla could have been infilled with calcite or apatite [illegible]

REFERENCES

AEPLER, R, 1974 Der Rhätsandstein von Tübingen - ein Kondensiertes Delta. N. Jb. Geol. Palaeont. Abh. 142, 113-162.

ALDRIDGE, R.J. 1975 The Stratigraphic distribution of conodonts in the British Silurian. Jour. Geol. Soc. Lond. 131, 607-618.

ALLEN, J.R.L. 1962 Discussion to paper by J.H.McD. Whitaker, The Geology of the area around Leintwardine, Herefordshire, Q. Jl. Geol. Soc. Lond. 118,349.

ALLEN, J.R.L. 1974 Sedimentology of the Old Red Sandstone (Siluro-Devonian) in the Clee Hills Area, Shropshire, England. Sediment. Geol. 12, 73 -

ALLEN, J.R.L. & DINELEY, D 1976 The succession of the Lower Old Red Sandstone (Siluro-Devonian) along the Ross-Tewkesbury Spur Motorway (M50), Hereford and Worcester. Geol. J. 11 p.1-14

ALLEN, P. 1975 Wealden on the Weald - a new Model. Proc. Geol. Ass. 86, 389-437

AMES, L.L. 1959 The genesis of carbonate apatites. Econ. Geology 54, 829-841

ANTIA, D.D.J. 1979a Bone-Beds: A review of their classification, occurrence, genesis, geochemistry, diagenesis, palaeoecology, weathering and microbiotas Mercian Geol. 7, 93-174

ANTIA, D.D.J. 1979b Authigenic gypsum in marine sediments - a comment. Marine Geol. 31, M1-M4

ANTIA, D.D.J. 1979c Comments on the faunas and environments across the Ludlovian-Downtonian boundary (Upper Silurian) at Siefton, Salop. Geol. J. 14, 127-134

ANTIA, D.D.J. & SYKES, J.H. 1979. The surface textures of on quartz grains from a Rhaetian Bone-Bed, Blue Anchor Bay, Somerset. Mercian Geol. 7, 205-210

ANTIA, D.D.J. & WHITAKER, J.H. McD. 1979 A scanning electron microscope study of the genesis of the Upper Silurian Ludlow Bone-Bed. In Whalley, W.B. (ed) Scanning electron microscopy in the study of sediments. Geo Abstracts Ltd. Norwich. 119-176

ARKELL, W.J. 1933 The Jurassic system in Great Britain. Clarendon Press, Oxford, 681p

ARRHENIUS, G. 1962 Pegalic sediments. In Hill, M.N. (ed.) The Sea, 3. Wiley, New York. 655-727.

BAILEY, R.J. & ATHERTON, M.P. 1969 The petrology of glauconitic sandy chalks. J. sed. Petrology. 39, 1420-1431.

BAILEY, R.J. & REES, A.I. 1972 A magnetic fabric study of Late Whitcliffian (U. Silurian) siltstones from the Welsh Borderland. Geol. J. 8, 179-188.

BAIRD, G.C. 1976 Coral encrusted concretions: a key to recognition of a 'shale on shale' erosion surface. Lethaia 9, 293-302.

BAIRD, G.C. 1978 Pebbly phosphates in shale: A key to the recognition of a widespread submarine discontinuity in the Middle Devonian of New York. J. Sed. Pet. 48, 545-556.

BAIRD, G.C. & FÜRSICH, F.T. 1975 Taphonomy and biologic progression associated with submarine erosion surfaces from the German Lias. N.Jb. Geol. Palaeont. Mh. 1975, 321-338.

BANKS, R.W. 1856 Tilestones or Downton sandstone in the neighbourhood of Kington and their contents. Q. Jl. Geol. Soc. Lond. 12, 93-101.

BATURIN, G.N. 1969 The authigenic phosphorite nodules in recent sediments of the South West African shelf, Dokl. Akad. Nauk. S.S.S.R. Earth Sci. Sect. 189, 227-230.

BATURIN, G.N. 1970 Recent authigenic phosporite formation on the south West African Shelf. Institute of Geological Sciences, London, Report No.70/13 p. 87-97

BATURIN, G.N. 1971a The stages of phosphorite formation on the ocean floor. Nature Phys. Sci. 232, 61-62.

BATURIN, G.N. 1971b Formation of phosphate sediments and water dynamics. Oceanology 11, 372-376.

BATURIN, G.N. and BEZRUKOV, P.L. 1979 Phosphorites on the sea floor and their origin. Mar. Geol. 31, 317-336.

BATURIN, G.N. & DUBINCHUK, V.T. 1974 Microstructures of Agulhas Bank phosphorites. Marine Geology 16, M63-M70.

BATURIN, G.N., MERKULOVA, K.I. & CHALOV, P.I. 1972. Radiometric evidence for recent formation of phosphatic nodules in marine shelf sediments. Marine Geology 13, M37-M41.

BEZRUKOV, P.L. AND RUSHCHENKO, R.F., MURDMAA, I.O., AND SKORNYAKOVA, N.S. Phosphorite of the Ocean Floor in the Central Pacific. Dokl. Acad. Nauk SSSR Earth Sci. Sect. 185 p.189-191.

BIRCH, G.F. 1979 The nature and origin of mixed apatite/glauconite pellets from the continental shelf off South Africa. Marine Geology 29, 313-334.

BIRCH, G.F., WILLIS, J.P. AND RICKARD, R.S. 1976 An electron microprobe study of glauconites from the continental margin off the West Coast of South Africa Marine Geology 22, 271-283.

BRISKIN, M. & SCHREIBER, B.C. 1978 Authigenic gypsum in marine sediments. Marine Geology 28, 37-49.

BROWN, B.J. & FARROW, G.E. 1978 Recent dolomitic concretions of Crustacean Burrow origin from Loch Sunart, West Coast of Scotland. J. Sed. Pet. 48 p 825-834.

BURNETT, W.C. 1974 Phosphate deposits from the sea floor off Peru and Chile: radiochemical and geochemical investigations concerning their origin. Ph.D. thesis. Hawaii Institute of Geophysics Honolulu Hawaii 164p

BURNETT, W.C. 1977 Geochemistry and origin of phosphorite deposits from off Peru and Chile. Geol. Soc. Amer. Bull. 88 p.813-823.

BURNETT, W.C. & GOMBERG, D.N. 1977 Uranium oxidation and probable subaerial weathering of phosphatised limestone from the Pourtalés Terrace. Sedimentology 24, 291-302.

CALEF, C.E. & HANCOCK, N.J. 1974 Wenlock and Ludlow Communities in Wales and the Welsh Borderlands, Palaeontology 17, 779-810.

CAVE, R. & WHITE, D.E. 1972 The exposure of Ludlow rocks and associated beds at Titles Point near Newnham, Gloucestershire. Geol. J. 7, 239-254.

CAVE, R. & WHITE, D.E. 1978 Stratigraphy of the Brookend (Vine Farm) Bonehole. Ludlow Research Group Bull. No.25, p.44-45.

CHERNS, L. 1977 The paleocology of the lower Leintwardinian (Upper Silurian) of the Welsh Borderlands and Wales. Ph.D. thesis. University of Glasgow.

CHERNS, L. 1979 The environmental significance of Lingula in the Ludlow Series of the Welsh Borderland and Wales. Lethinia 12, 35-46.

CORSIN, P. 1945 Les algues de l'eodevonien de Vimy (P-de-C). Mem. Soc. Sci. de l'Agriculture et des Arts de Lille (France) Ser. 5, 9, 86 pp.

CRUFT, E.F. & INGAMELLS, C.O. & MUTSSON, J. 1965 Chemical analysis and the stoichiometry of apatite Geochim. et Cosmochim. Acta. 29, 581-597.

DAVIES, W. & CAVE, R. 1976 Folding and cleavage determined during sedimentation. Sediment. Geol. 15, 89-133.

D'ANGLEJAN, B.F. 1967 Origin of marine phosphorites off Baja, California, Marine Geology 5, 15-44.

D'ANGLEJAN, B.F. 1968 Phosphate diagenesis of carbonate sediments as a mode of in situ formation of marine phosphorites. Observations in a cove from the Eastern Pacific. Canadian Jour. Earth Sci. 5, 81-87.

DEAN, L.A. & RUBINS, E.J. 1947 Anion exchange in soils: 1 Exchangeable phosphorous and the anion exchange capacity. Soil Sci. 63, 377-387.

DIESTER-HAASS, L. & SCHRADER, H.-J. 1979 Neogene coastal upwelling history of northwest and southwest Africa. Marine Geology 29 p. 37-54.

DIETZ, R.S., AMERY, K.O., AND SHEPARD, F.P. 1942 Phosphorite deposits on the sea floor off Southern California. Geol. Soc. America Bull. 53, 815-848.

DUFFIN, G.J. & GAZDZICKI, A. 1977. Rhaetian fish remains from the Tatra Mountains. Acta Geologica Polonica. vol. 27, 333-348.

DUGDALE, R.C. 1976 Nutrient cycles. In Cushing, D.H. & Walsh, J.J. (eds) The ecology of the seas. Blackwell, London. p.141-172.

DROUET, F. 1951 Cyanophyta p.159-166. In Smith, G.M. (ed.) Manual of Phycology Chronica Botanica Co., Waltham, Mass., U.S.A.

EARP, J.R. 1938 The higher Silurian rocks of the Kerry District. Q. Jl. Geol. Soc. Lond. 94, 125-160.

EARP, J.R. 1940 The geology of the south-western part of the Clun Forest. Q. Jl. geol. soc. Lond. 96, 1-11.

ELLES, G.L. & SLATER, I.L. 1906 The highest Silurian rocks of the Ludlow District. Q.Jl. Geol. Soc. Lond. 62, 195-122.

EVANS, A.M. 1979 The East Midlands Aulacogen of Caledonian age. Mercian Geol. 7, 31-42.

FRANZEN, C. 1977 Crinoid holdfasts from the Silurian of Gotland. Lethaia 10, 219-234.

FRITSCH, F.E. 1945 Structure and reproduction of the algae. Cambridge Univ. Press.

FÜRSICH, F.T. 1979 Genesis, environments and ecology of Jurassic hardgrounds. N. Jb. Geol. Palaeont. Abh. 158, 1-63.

GARDINER, C.I. 1927 The Silurian Inlier of Woolhope, Herefordshire. Q. J. Geol. Lond. 83, 501-530.

GREIG, D.C., WRIGHT, J.E., HAINS, B.A., MITCHELL, G.H. et. al. 1968 The geology of the country around Church Stretton, Craven Arms, Wenlock Edge, and Brown Clee. Mem. Geol. Surv. U.K. 1-379.

GRIFFIN, J. WINDOM, H.L., & GOLDBERG, E.D. 1968 The distribution of clay minerals in the World Ocean. Deep-Sea res. 15, 433-459.

GULBRANSEN, R.A. 1966 Chemical composition of phosphorite of the Phosphoria Formation. Geochim. et Cosmochim. Acta 30, 769-778.

GULBRANSEN, R.A. 1969 Physical and chemical factors in the formation of marine apatite. Econ. Geology 64, 365-382.

HANKEN, N.-M. 1979 Sandstone pseudomorphs of aragonite fossils in an Ordovician vadose zone. Sedimentology 26p 135-142.

HEEZEN, B.C., MATTHEWS, T.L., CATALANO, R., NATLAND, J., COOGAN, A., THARP, M.,& RAWSON, M. 1973. WESTERN PACIFIC GUYOTS. In Heezen, B.C., MacGregor, I.D., et al., Initial Reports of the Deep Sea Drilling Project, 20, 653-724.

HEMWALL, J.B. 1957 The role of soil clay minerals in phosphorous fixation. Soil Sci. 84, 101-108.

HOBSON, J.S.C. 1960 *The sedimentary petrology of the Downton Castle Sandstone Formation in Wales and the Welsh Borderland.* Ph.D. thesis, University of Birmingham.

HOLLAND, C.H. 1958 The Ludlovian and Downtonian rocks of the Knighton District, Radmorshire. *Q.Jl. Geol. Soc. Lond.* 114, 449-

HOLLAND, C.H. & LAWSON, J.D. 1963 Facies patterns in the Ludlovian of Wales and the Welsh Borderlands. *Geol. J.* 3, 269-288.

HOLLAND, C.H., LAWSON, J.D. & WALMSLEY, V.G. 1963 The silurian rocks of the Ludlow District, Shropshire. *Bull. Br. Mus. Nat. Hist. (Geol)* 8, 93-171.

HUDSON, J.D. 1966 Hugh Miller's Reptile Bed and the *Mytilus* Shales Middle Jurassic, Isle of Eigg, Scotland. *Scot. Jl. Geol.* 2, 265-281.

JOHNSON, J.H. 1951 Fossil Algae 193-201. *In* Smith, G.M. *Manual of Phycology.* Chronica Botanica Co. Waltham, Mass. U.S.A.

KALJO, D. 1978 The Downtonian or Pridiolian from the point of view of the Baltic Silurian. *Eesti NSV Teaduste Akadeemia Toimelised 27 Koide Geologia* 1 p.5-10

KAZOKOV, A.V. 1937 The phosphorite facies and the genesis of phosphorites. *U.S.S.R. Sci. Inst. Fertilizers Insectofungicides, Trans,* No.142, p.93-113.

KENNEDY, W.J. & GARRISON, R.E. 1975 Morphology and genesis of nodular phosphates in the Cenomanian Glauconitic Marl of South East England: *Lethaia* 8, 339-360.

KENNEDY, W.J. & KLINGER, H.C. 1972 Hiatus concretions and hardgrounds in the Cretaceo of Zululand. *Palaeontology* 15, 539-549.

KENNEDY, W.J., LINDHOLM, R.C., HELMOLD, K.P. & HANCOCK, J.M. 1977 Genesis and diagenesis of hiatus - and breccia - concretions from the mid-Cretaceous of Texas and Northern Mexico. *Sedimentology* 24, 833-844.

KIDSTON, R. AND LANG, W.H. 1924 Notes of fossil plants from the Old Red Sandstone of Scotland. II Nematophyton Forfarease Kidston, sp. III On two species of *Pachytheca* (P. *media* and *P. fasiculata*) based on the characters of the algal filaments. *Trans. Roy. Soc. Edin.* 53, 603-614.

KING, W.W. & LEWIS, W.J. 1912. The Uppermost Silurian and Old Red Sandstone of South Staffordshire. *Geol. Mag.* 49, 437-443, 484-491.

KOLODNY, Y. & KAPLAN, K.R. 1970 Isotopes in sea floor phosphorites. Geochim. et. Cosmechim. Acta. 34, 3-24.

LANG, W.H. 1937 On the plant-remains from the Downtonian of England and Wales. Phil. Trans. Roy. Soc. Lond. B227, 245-291.

LANG, W.H. 1945 Pachytheca and some anomalous early plants (Prototaxites, Nematothallus, Parka, Foerstia, Orvillea n.g.)

LAWSON, J.D. 1954. The Silurian Succession at Gorsley (Herefordshire). Geol. Mag. 99, 227-237.

LAWSON, J.D. 1955. The geology of the May Hill inlier. Q. Jl. Geol. Soc. Lond. 111, 85-116.

LAWSON, J.D. 1975. Ludlow Benthonic assemblages. Palaeontology 18, 509-525.

LLOYD, A.T. & FULLER, A.O. 1965. Glauconites from shallow marine sediments off the South African coast. S. Afr. J. Sci. 61, 444-448.

LUTZE, G.F. 1967 Ein . Emersions-Horizout. im Bathonium von Hildesheim. Senckenbergiana Leth. 48, 535-548.

MANHEIM, F., ROWE, G.T. & JPIA, D. 1975. Marine phosphorite formation off Peru. Jour. Sed. Petrology. 45, 243-251.

MAREK, L. & YOCHELSON, E.L. 1976 Aspects of the biology of Hyolitha (mollusca). Lethaia 9, 51-64.

MARSH, R. 1976 Silurian stratigraphy and mineralogy in the Welsh Borderlands and Central Wales. unpub. Ph.D. thesis. Leicester University.

McCONNELL, D. 1973 Apatite. New York. Springer Verlag, 111p.

McKELVEY, V.E. 1967 Phosphate deposits. U.S. Geol. Survey Bull. 1252-D, p D1-D27.

McKERROW, W.S. & ZEIGLER, A.M. Silurian paleogeographic development of the Proto-Atlantic Ocean. 24th Int. Geol. Congr. Montreal. g, 4-10.

MURCHISON, R.I. 1839. The Silurian system, founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester, and Stafford; with descriptions of the coal-fields and overlying formations. London. J. Murray 768p 37 pls.

MURCHISON, R.I. 1859. Siluria. J. Murray. London

PALMER, D.C. 1972. The geology of the Long Mountain, Montgomeryshire and Shropshire. Ph.D. thesis, Trinity College, Dublin.

PALMER, T.J. & FURSICH, F.T. 1974. The ecology of a Middle Jurassic hardground and crevice fauna. Palaeontology. 17, 507-524.

PARKER, R.J. 1971a. The petrography and major element geochemistry of phosphorit nodule deposits on the Agulhas Bank, South Africa. South Africa Natl. Comm. Oceanog. Research and Marine Geology Progress Bull. 2, 94p.

PARKER, J.R. 1975. The petrology and origin of some glauco-conglomeratic phosphorites from the South African continental margin. J. sed. Pet. 45, 230-242.

PARKER, R.J. & SIESER, W.G. 1972. Petrology and origin of some phosphorites from the South African continental margin. J. sed. Pet. 42, 434-440.

PEARSON, T. R. 1977. The structure of life in the sea. In Cushing, D. H. & Walsh, J. J. The ecology of the seas. p.81-97.

PEEL, J.S. 1977. Systematic and palaeoecology of the Silurian gastropods of the Arisaig Group, Nova Scotia. Biol. Skr. 21, (2), 89pp.

PERKINS, A.T. 1945. Phosphate fixation by soil minerals V. time of reaction. Soil Sci. Soc. Amer. Proc. 25, 102-106.

PERKINS, A.T. 1977. Phosphate solubility in relation to cations and ptt: Magnesium. Soil Sci. Soc. Amer. Proc. 63, 1-78.

PETTIJOHN, F.J., POTTER, P.E. & SIEVER, R. 1973. Sand and Sandstone. Springer-Verlag. New York. 616p.

PHILLIPS. W.E.A., STILLMAN, C.J. & MURPHY, T.A. 1976. A Caledonian plate tectonic model. Jl. geol. Soc. Lond. 132, 579-609.

PHILLIPS, J. 1898. The Malvern Hills, compared with the Palaeozoic districts of Abberley, Woolhope, May Hill, Tortworth, and Usk. Mem. geol. Surv. U.K. 2, 1-

PHIPPS, C.B. & REEVE, F.A.E. 1964. Stratigraphy and geological history of the Malvern, Abberley and Ledbury Hills. Geol. J. 5, 339-368.

POMPERDY, L.R., SMITH, E.E. & GRANT, C.M. 1965. The exchange of phosphate between estuarine water and sediments. Limnol. Oceanog. 10, 167-172.

PRESCOTT, C.W. 1969. Algae: A review. Nelson, London, 436p.

REIF, W, -E. 1971. Zur genese der Muschelkalk - Keuper - Grenzbonebeds. N. Jb. Geol. Palaont. Abh. 139, 369-404.

RICHARDSON, L. 1901. Mesozoic geography of the Mendip Archipelago. Proc. Cotteswold Nat. Fld. Club. 14, 59-69.

ROBERT, C. & CHAMLEY, H. 1974. Gypse et sàpropels profonde de Mediterranea orientale. C.R. Acad. Sci. Paris (ser. D). 278.

ROONEY, T. P. & KERR, P. F. 1967. Mineralogic nature and origin of phosphorite, Beaufort County, North Carolina. Geol. Soc. Am. B-11. 78 731-748.

SCHMIDT, W. 1958. Pflanzen - Reste aus der tonschiefer-Gruppe (unteres Siegen) des Soegerlandes II. Pachytheca reticulata Corsin aus den Betzdorfer Schichten nebst neuen Bechachtungen an Pachytheca. Palaeontolgraphica B, 104, 1-38.

SIESSER, W.G. & ROGERS, J. 1976. Authigenic pyrite and gypsum in Southwest African continental slope sediments. Sedimentology 23, 566-577.

SIMPSON, D.R. 1964. The nature of the alkali carbonate apatites. Am. Mineral 49, 363-376.

SIVETER, D. J. 1974. The Superfamily Ecyrichiacen (Ostracoda) from the Silurian and Devonian systems of Britain. Unpub. Ph.d. Thesis. Leicester Univ.

SIVETER, D.J. 1978. The Silurian. In. Bate, R. & Robinson, E. (eds.) A stratigraphical index of British Ostracoda. Geol. J. spec. Issue No. 8. p.57-100.

SHAFER, W. 1966. Aktuopalidontologische Beobachtungen 6. Otolithen - Anreicherungen. Natur. u. Museum. 96 (11) 429-438.

SHAFER, W. 1972. Ecology and Palaeontology of marine environments. Oliver & Boyd, Edinburgh. 567p.

SHAW, R.W.L. 1969. Beyrichiacean ostracods from the Downtonian of Shropshire. Geologiska Forenigens i Stockholm Forhandlinger. 91, 52-72.

SOLLAS, W. J. 1979. On the Silurian district of Rhymney and Pen-y-lan, Cardiff. Q. Jl geol. Soc. Lond. 35, 475-507.

SQUIRRELL, H. C. 1958. New occurrences of fish remains in the Silurian of the Welsh Borderland. Geol. Mag. 95, 328-332.

SQUIRRELL, H.C. & TUCHER, E.V. 1960. The geology of the Woolhope inlier (Herefordshire). Q. Jl geol. Soc. Lond. 116, 151-185.

SQUIRRELL, H.C. & WHITE, D.E. 1978. Stratigraphy of the Silurian and Old Red Sandstone of the Cennen Valley and adjacent areas, South-east Dyfed, Wales. Rep. Inst. Geol. Sci. No.78/6, 1-45.

STAMP, L.D. 1918. The highest Silurian rocks of the Clun-Forest district. Q. Jl geol. Soc. Lond. 74, 221-246.

STAMP. L.D. 1923. The base of the Devonian with especial reference to the Welsh Borderland. Geol. Mag. 60, 276-282, 331-116, 367-376, 385-412.

STEACHAN, A. & CANTRILL, T. C. 1912. The geology of the South Wales Coalfield Part III. The country around Cardiff. Mem. Geol. Surv. Eng. and Wales. Sheet 263. London H.MS.O.

SUMMERHAYES, C. P. 1973. Distribution, origin and economic potential of phosphatic sediments from the Agulhas Bank, South Africa. Trans. Geol. Soc. S. Afr., 76, 271-277.

SYKES, J.H. 1977. British Rhaetian Bone-Beds. Mercian Geol. 6, 117-140.

TUCKER, E.V. 1960. Ludlovian biotite bearing banks. Geol. Mag. 97, 245-249.

VEEH, H.H., BURNETT, W.C. & SOUTAR, A. 1973. Contempory phosphorite on the continental margin off Peru. Science 181, 845-847.

VOIGT, E. 1968. Uber Hiatus-Konkretionen (dargestellt an Beispielen aus dem Lins) Geol. Rundasch. 58, 281-296.

WALMSLEY, V. G. 1958. The geology of the Usk inlier (Monmouthshire). Q. Jl geol. Soc. Lond. 483-521.

WALSH, J.J. 1976. Models of the sea. In. Cushing, D.H. & Walsh, J.J. (eds) The ecology of the sea. P.383-408.

WEAVER, G.E. & BECK, K.C. 1977. Miocene of the S.E. United States: a model for chemical sedimentation in a peri-marine environment. Sediment. Geol. 17, 1-234.

WEAVER, C.E. & WAMPLER, J.M. 1972. The illite-phosphate association. Geochim. Cosomochim. Acta. 36, 1-13.

WELLS, T.W. 1944. Middle Devonian bonebeds of Ohio. Bull. Geol. Soc. Am. 55, 273-302.

WHITE,, D.E. & COPPACK, B.C. 1976. A new section showing the junction between the Ludlow and Downton series in the Much Wenlock area, Shropshire. Bull. Geol. Surv. G.B. No. 62, p.25-32.

WICKES, W.H. 1908. Pebble swallowing animals. Proc. Bristol Nat. Soc. 5, 23-31.

WILLS, L.J. 1975. A Palaeogeological map of the Lower Palaeozoic floor below the cover of Upper Devonian, Carboniferous and later Formations with inferred and speculative reconstructions of the Lower Palaeozoic and Precambrian rocks in adjacent areas. Geol. Soc. Lond. Mem. No. 8.

WILLS, L.J. 1977. A conjectural palaeogeological map of Wales and England south of the latitude of Manchester and North of the Variscan Front as in End-Silurian times (395-400 m.y.a.). Geol. Soc. Lond. Mem. No. 8.

YASYREV, A.P. 1969. Gold in Mesozoic nodular phosphate deposits of the Russian Platform. Dokl. Akad. Nank. SSSR. 185 p.183-186.

YASYREV, A.P. 1971. Concretionary phospharite of the Russian Platform - An Intermediate Gold Collector in Placer Formation. Dokl. Akad. Nank. SSSR Earth Sci seot. 199. p.206-208.

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15

THE SURFACE TEXTURES OF QUARTZ GRAINS FROM A RHAETIAN BONE-BED, BLUE ANCHOR BAY, SOMERSET.

by

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Summary

The surface textures of detrital quartz grains in a Rhaetian bone-bed at Blue Anchor Bay, Somerset, have been investigated using a scanning electron microscope. The results show that there is a systematic change from the base to the top of the bed in the nature of the textures displayed by the quartz grains. Those from the basal, clay-rich parts of the bed feature solution pits, while grains from the upper clay-poor parts of the bed display well developed euhedral overgrowths. The differences are attributed to in-situ diagenesis.

Introduction

Quartz grains in Rhaetian bone-beds are usually abraded and well rounded. They have been recorded from many localities, ranging across England and Wales, including Barnstone (Nottinghamshire), Barrow-upon-Soar (Leicestershire), Westbury (Gloucestershire), Chilcompton (Somerset) and Lavernock (Glamorgan). Further examples including locality details have been presented by Sykes (1977). Rare bipyramidal quartz crystals have been recorded from Rhaetian bone-beds (Kent, 1970, p.365) at a number of localities including Barnstone (Duffin, 1978, pers.com.) and Blue Anchor Bay (Antia, 1979a, pl. 18, fig. f). Such crystals arise as the result of quartz overgrowths around an original quartz nucleus. They have been recorded from a number of bone-beds including those of the Silurian in Britain (Antia & Whitaker, 1978, p.121, 123-127; Antia, 1979b, pp.115, 169) and bone-beds in the Devonian of the U.S.A. (Wells, 1944, p.283).

In Silurian bone-beds (e.g. the Ludlow Bone-Bed) some of the euhedral crystals pre-date the formation of the deposit and bear surface abrasion features (Antia & Whitaker, 1978, p.132, 133, 135, 136). Others have no abrasion features and nucleate around quartz grains, suggesting that they have grown in the bone-bed after its deposition. At the present time there are no adequate descriptions of euhedral quartz crystals from a Rhaetian bone-bed and consequently it is not known if they were reworked from a previous sediment or whether they have grown in situ in the bone-bed. Reworked grains should be identified by their abraded surfaces.

Conversely, if the quartz euhedra were precipitated in the sediment after it was deposited, then a complete continuum ranging from original quartz grains and silica coated quartz nuclei through to perfect euhedral quartz crystals could be expected to occur, in which quartz euhedra increase in abundance towards the more porous base or top of the deposit. If, however, the relative abundances of the various diagenetic quartz morphotypes remain constant throughout the deposit then they could either have been derived from an older deposit (cf. Wilson, 1979) or have formed as diagenetic precipitates within the bone-bed. This study seeks to determine which of the explanations is most applicable to the quartz euhedra in the bone-bed under review.

Stratigraphy

Exposures of the Rhaetian beds at Blue Anchor Bay have been described by Richardson (1911, p.17) and also by Elliot (1953) and Macfayden (1970, p.225). Richardson recorded three bone-beds:- 'Basal Bone-bed' (no. 33), 'The Clough' (no. 27) and 'The Bone-bed' (no. 15) near the top of the Westbury beds.

In a recent investigation into the nature of British Rhaetian bone-beds (Sykes, 1977), a large number of quartz crystals were

Table 1. Description of bone-bed, parts 'a' to 'e'

Part	Thickness	Description
e	up to 120mm	A massive, calcareous sandstone, enriched in vertebrate remains.
d	50mm	A calcareous sandstone, enriched in vertebrate remains and containing thin layers of black shale limestone.
c	70mm	Alternating layers of black shales and sandstones with vertebrate remains.
b	up to 30mm	A layer of 'beef' calcite (CaCo3).
a	18mm	A calcareous, sandy bone-bed containing shell and silt laminae.

Table 2. Distribution of crystalline pyrite and quartz crystal faces in the coarse fraction of the bone-bed

Part	Without crystal faces	With crystal faces	Crystalline pyrite
e	23%	74%	3%
d	33%	62%	5%
c	73%	19%	8%
a	94%	0%	6%

noticed in part of the uppermost bone-bed (Richardson's bed 15) at Blue Anchor Bay (ST 042432). This bone-bed is 0.28 m thick and has been divided into five distinct parts (Table 1) (Sykes, 1977, p.231). Samples from parts 'a, c, d, & e' were disaggregated in acetic acid, washed and dried. The finer particles were removed by washing the grains in petroleum spirit and the coarser fraction (above 250 microns) separated by sieving. Several random samples were taken from each part and examined under a binocular microscope. The number of grains in each sample were counted in respect to their possession or lack of crystal faces also with regards to the amount of crystalline pyrite present. In each part of the bed averages of the relative contents were calculated over the various samples and the amounts expressed in percentages (Table 2).

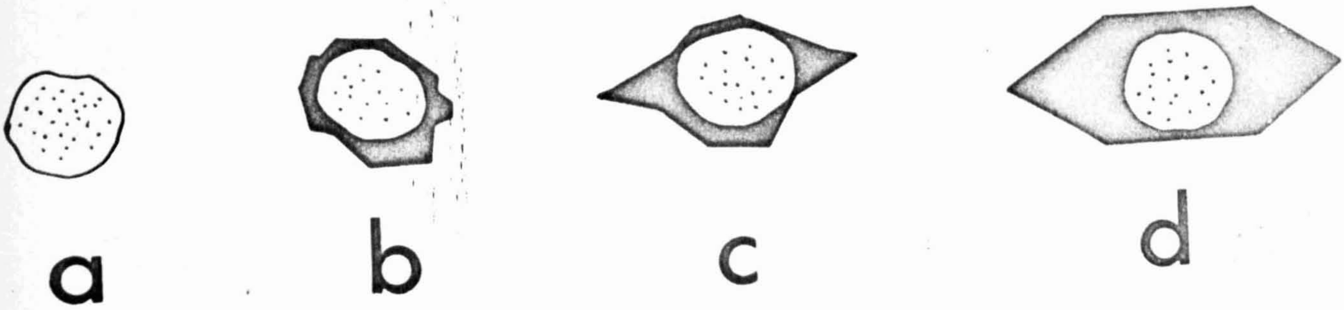
Scanning electron microscope (S.E.M.) analysis

Fifty quartz grains were randomly selected from each part of the bed listed in Table 2. These grains were then mounted on the S.E.M. stubs with either silver dug (parts d & e) or Pritt (parts a & c) and gold splatter coated to a thickness of 350 Å. The grains were then examined on a Cambridge 600 S.E.M.. After examination the grains were removed from the stubs and cleaned using first acetone and then hydrogen peroxide. Most of the grains are now deposited with the Ludlow Museum; specimen nos.

Most of the external surfaces of the quartz grains were covered by diagenetic overgrowths which appear to have been precipitated on more rounded quartz nuclei. Some of the grains are affected by silica solution which has removed the primary abrasive features and caused pitting. The exoscopic features of the grains are described as follows.

1. Primary crystal overgrowths, pl. 1 , figs. 1, 2 & 3

Many of the quartz grains observed from parts 'd' and 'e' possess euhedral crystal faces. These vary in shape from compact



Explanation of text figure 1

Deduced stages in the development of quartz euhedra

fig. a. Original quartz grain (shape unknown).

fig. b. Quartz grain coated with silica sheets producing crystal faces on the grains surface (most common in parts 'a' and 'c').

fig. c. Polarisation of crystal growth and the development of crystal faces (most common in parts 'd' and 'e').

fig. d. Development of prism faces connecting the pyramid faces (most common in parts 'd' and 'e').

grains in elongate, bipyramidal, euhedral crystals, some of which have prism faces. Some of the compact grains have crystal faces without a clear crystallographic orientation, while some of the more euhedral grains have prism faces which are poorly defined or are smothered by bulbous overgrowth.

The quartz grains show three stages of diagenetic overgrowth around an original, compact spheroidal quartz grain (text-fig. 1, fig. A).

<u>a</u> Silica sheet layering on the external surface of the quartz grain (pl. I , fig. 7, text-fig. 1, fig B). These sheets are in optical continuity with the host quartz grain.

<u>b</u> Polarisation of quartz growth to produce a c-axis aligned along the quartz grain and to allow development of pyramidal crystal faces at either end of the grain (pl. I , fig. 3, text-fig. 1, fig. C).

<u>c</u> Enlargement of the pyramidal faces until the pyramid diameter equals or exceeds the grain diameter. This is followed by development and growth of the prism faces (text-fig. 1, fig. D).

2. <u>Secondary crystal overgrowths (pl. I , figs. 6 & 8)</u>

On one quartz grain from part 'c', a small euhedral crystal growth was observed encrusting a primary overgrowth crystal face (pl. I , fig. 8). On another grain from the same part of the bed a more complex pattern of secondary crystal overgrowth was observed (pl. I , fig. 6). On some grains the growth of silica sheets appears to post-date the development of euhedral crystal faces within the bone-bed (pl. I figs. 4, 7 & 9).

3. <u>Diagenetic solution (pl. I , fig. 5)</u>

Silica solution features are present throughout the bone-bed though they are most pronounced at its base, in part 'a'. A thin section of this part (Sykes, 1977, pl. 16, fig. 5) shows that most of the silica solution features appear to be related to the growth of the calcite matrix during 'late' diagenesis.

Typical examples of pitting due to silica solution within the bone-bed are illustrated in plate 1, fig. 5.

Discussion

The association of pyrite, apatite and black shale has been noted in bone-beds throughout the geological record and may indicate the presence of high negative Eh (-200 to -300) and a pH of 6 to 8 in the sediment pore waters during diagenesis (Baturin, 1971, p.61; Burnett, 1974, 1977, p.820-821; Antia, 1979a, pp.107, 124). If this sediment was also undersaturated with respect to Ca^{2+} and CO_3^{2-} ions, then diagenetic gypsum and/or quartz may have precipitated within the sediment (Burnett, 1974, 1977, p.821; Briskin and Schreiber, 1978, pp.47-48; Antia, 1979b, p.M1, M3).

Observations (Sykes, 1977, p.232) show that the mean grain size of the sand fraction of the bone-bed increases upwards. This trend, coupled with a decrease in its clay and limestone content towards its top (Sykes, 1977, p.231), shows that the initial post-depositional porosity of the bone-bed probably also increased towards its top. The increase in porosity coincides with a change in quartz grain shape (Table 2) and a decrease in the incidence of solution features.

A possible explanation is that silica was removed from some of the quartz grains and clay minerals in the bone-bed by upward percolating pore waters and concentrated in the upper porous layers of the bone-bed beneath the overlying impervious clays. In this context it is interesting to note that clay minerals may actually enhance solutions of quartz (see Blatt, Middleton & Murray, 1972; Pettijohn et al., 1972) ~~(Sand and sandstone)~~ and that the presence of a clay mineral matrix will inhibit growth of cement. The pore water solutions may then have become supersaturated with respect to silica and precipitated as silica sheets in the lower porosity layers of the bone-bed (parts 'a' and 'c') and quartz crystals in the higher porosity layers (parts 'd' and 'e'). Silica may also have been derived from the impermeable clays overlying and underlying the bone-bed.

Elsewhere in the geological column similar relationships appear to occur between porosity and quartz crystal growth. For example, the Ludlow bone-bed at Netherton (King & Lewis, 1912) grades upwards from vertebrate rich clays to a vertebrate sand (Antia, 1979b). These vertebrate sands had a higher initial porosity than the vertebrate rich clays and they contain diagenetic, euhedral, quartz crystals. Such crystals are not present in the lower porosity clays.

Conclusions

The quartz grains in a Rhaetian bone-bed at Blue Anchor Bay, Somerset, have diagenetic quartz overgrowths. These overgrowths are restricted to silica sheets in the lower porosity, vertebrate rich clays and limestones but form euhedral crystal overgrowths in the higher porosity, vertebrate rich quartz sands of the upper layers of the bone-bed.

Acknowledgements

D.D.J.A. thanks N.E.R.C. for its financial support, and Prof. B.E. Leake for the use of facilities at Glasgow University. We thank Mr. M. Ghummed ([illegible]) for critically reading the manuscript.

Explanation of Plate No. 1

1 - 9 Quartz grains and surfaces from a Rhaetian Bone-bed at Blue Anchor Bay.

1 Angular, compact, high sphericity grain (x 80).

2 Modified, compact grain, showing the development of crystal faces (x 80).

3 Compact grain completely enclosed within a quartz overgrowth (x 80).

4 Silica sheeted surface (x 600).

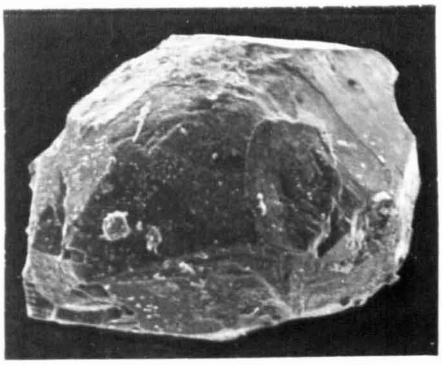
5 Silica surface showing solution pits (x 600).

6 Quartz overgrowth on a grain (x 500).

7 Silica sheeting on a grain surface (x 600).

8 Quartz overgrowth on a grain surface (x 1000).

9 Silica sheeting on a grain surface - note the various angles of the sheet faces (x 700).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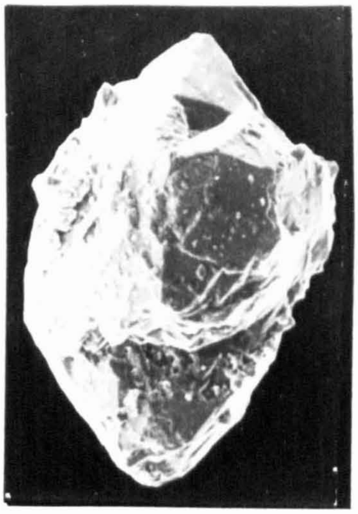
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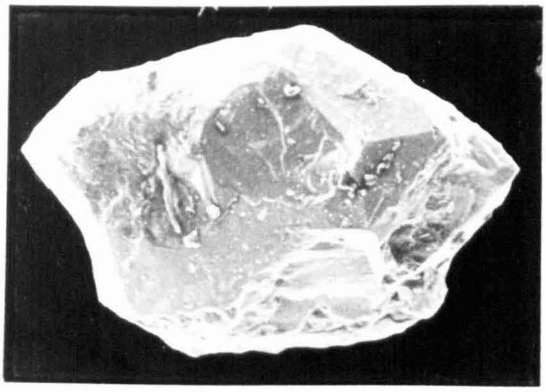
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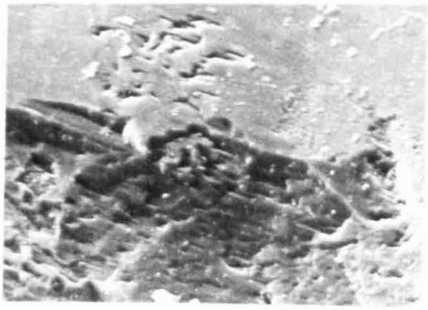
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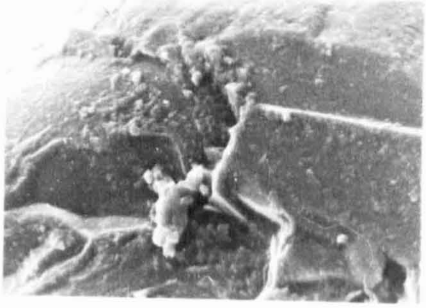
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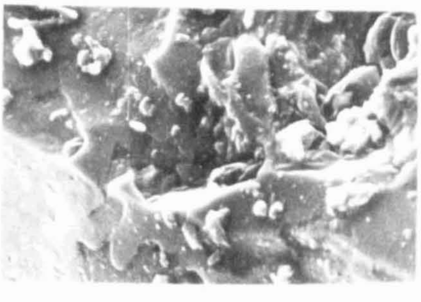
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References

ANTIA, D.D.J. 1979a. Bone-beds: A review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering and microbiotas. Mercian Geol., vol. 7, pp. 93-174.

ANTIA, D.D.J. 1979b. Authigenic gypsum in marine sediments - a comment. Marine Geol., vol. 32, pp. M1-M4.

ANTIA, D.D.J. and WHITAKER, J.H. McD. 1979. A scanning electron microscope study of the genesis of the Upper Silurian Ludlow Bone-bed. In W.B. Whalley (ed.) Scanning Electron Microscopy in the study of sediments. Geo. Abstracts Ltd, Norwich, pp. 179-136.

BATURIN, G.N. 1971. Stages of phosphorite formation on the sea floor. Nat. Phys. Sci., vol. 232, pp. 61-62.

BLATT, H., MIDDLETON, G. and MURRAY, R. 1972. Origin of sedimentary rocks. Prentice Hall, New Yersey, 634 p.

BRISKIN, M. and SCHREIBER, B.C. 1978. Authigenic gypsum in marine sediments. Marine Geol., 28, pp. 37-49.

BURNETT, W.C. 1977. Geochemistry and the origin of phosphorite deposits from off Peru and Chile. Bull. Geol. Soc. Amer., vol. 88, pp. 813-823.

ELLIOT, G.F. 1953. The conditions of formation of the Lower Rhaetic at Blue Anchor Bay, Somerset, and the Western European Rhaetic generally. Proc. geol Soc. Lond., vol. 64, pp. 32-35.

KENT, P.E. 1970. Problems of the Rhaetic in the Midlands. Mercian Geol., vol. 3, pp. 361-373.

KING, W.W. and LEWIS, W.J. 1912. The uppermost Silurian and Old Red Sandstone of South Staffordshire. Geol. Mag., 49, 437-443, 484-491.

MACFAYDEN, W.A. 1970. Geological highlights of the West country, 296 p.

PETTIJOHN, F.J., POTTER, P.E. and SIEVER, R. 1972. Sand and sandstone. Springer-Verlag, New York, 618p.

RICHARDSON, L. 1911. On the Rhaetic and contiguous deposits of West, Mid. and East Somerset. Q. Jl. geol. Soc. Lond., vol. 67, pp. 1-72.

SYKES, J.H. 1977. British Rhaetic Bone-beds. Mercian Geol., vol. 6, pp. 197-240.

WELLS, J.W. 1944. Middle Devonian Bone-beds of Ohio. Bull. Geol. Soc. Am., vol. 55, pp. 273-302.

WILSON, P. 1979. Surface features of quartz sand grains from the Brassington Formation. Mercian Geol., vol. 7, pp. 19-30.

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16

Preparation techniques for the S.E.M. examination of palaeontological and sedimentological material.

by

S.S.J. Al-Sheikhly and D.D.J. Antia

The scanning electron microscope (S.E.M.) is a very useful palaeontological and sedimentological tool, which can be used to aid palaeontological, diagenetic and sedimentological studies.

In this article the preparation techniques used by the authors for taxonomic, palaeontological, diagenetic and sedimentological studies are outlined, to assist future S.E.M. workers.

Methods

All samples were broken down using a jaw crusher to fragments less than 1 cm^3 and put in an appropriate preparation medium.

I Acetic acid preparations

(a) Used to extract non-carbonate material from calcareous sediments, e.g. fish scales, conodonts, phosphatic pebbles, etc.

(b) Place the sample into a 30% acetic acid solution (CH_3COOH) so that it is submerged and leave for 3 to 14 days in a fume cupboard. If a crust forms on the surface of the acid after a few days the solution needs to be replaced by fresh acid.

(c) Wash and sieve.

(d) If the sample is particularly clayey the sieved residue should be placed for a few hours in 30% hydrogen peroxide (H_2O_2) solution, to clean it.

II Hydrogen peroxide preparations

(a) Used to extract carbonate material (e.g. ostracods, foraminifera etc.) from marls, limestones and clastics.

(b) Submerge about 200 gms of sample in 400 ml of 30% H_2O_2 solution, with 3-5 pellets of sodium hydroxide in a 1000 ml beaker. Shale will effervesce vigorously and may require a larger container or a smaller sample size (say 50 gms) to stop the sample bubbling out of the beaker. Leave hard material (e.g. limestones and sandstones) standing overnight and soft material (e.g. shales and muds) standing for 2-3 hours in a fume cupboard.

(c) Boil the sediment - H_2O_2 solution for about 3-4 hours if it is a hard rock. Alternatively if it is a soft sludge at this stage sieve the sample through a 65 μ sieve to remove the clays. Then boil with a fresh 20% H_2O_2 solution for 1-2 hours. The boiling beakers should be periodically topped up with water.

(d) Wash and sieve.

III. Paraffin method

(a) This method is used to extract delicate material from soft shaley often hydrocarbon rich sediments.

(b) Cover the sample in paraffin and leave to stand for 4 to 6 hours.

(c) Filter the sample to remove the paraffin for re-use.

(d) Wash the sample onto a 65μ sieve to remove the solid paraffin residue.

(e) Boil the sample in water in a fume cupboard for 30 to 60 mintues.

(f) Wash and sieve.

The processed residue is collected on a number of sieves (e.g. 65μ, 125μ, 250μ, and 1000μ sizes) and dried in an oven at 200°C. This residue is then picked under a binocular microscope. Residues off the -

(1) 65μ sieve contain chitinozoans, fish debris, shell debris, megaspores, foraminifera, juvenile ostracods, quartz grains etc.

(2) 125μ sieve as above, but with small adult ostracods, and fish scales.

(3) 250μ sieve. This is the best sample size for adult ostracods, foraminifera and mineral crystals.

(4) 1000μ sieve. Large ostracods, fish debris, foraminifera, bivalves, brachiopods etc.

If the specimens to be examined on the S.E.M. are not clean enough the following cleaning methods can be used.

I Dacon method

After the specimen has been soaked in Dacon overnight, any remaining dirt particles can be removed using a fine sable hair brush or a needle which consists of a thin tapering piano wire attached to a handle.

II Hydrogen peroxide method

After the specimen has been soaked in 20% H_2O_2 solution for 1-3 hours the remaining dirt particles are removed as above. The soaking duration is dependent on the strength of the specimen and the thickness of the dirt coating.

III Ultra sonic method

(a) Put the specimen in a small glass vial and fill with water.

(b) Set the ultra sonic instrument at 50-55,000 cycles per second. Immerse the vial for less than one second in the ultrasonic field. Repeat again if required. The specimen should be examined after each immersion. (Delicate specimens may be damaged by this cleaning method, similarly prolonged immersion may result in a recrystallisation of the specimen).

S.E.M. studies fall into three basic groups, viz. (1) taxonomic studies, (2) general studies, (3) statistical studies. Each study has its own mounting requirements. Taxonomic specimens generally require specific orientations of specimens, while in general and statistical studies orientation is less important.

Specimens have to be mounted (glued onto) an S.E.M. stub (a 1 cm diameter holder) before they can be viewed under the S.E.M. The advantages and disadvantages of a varietyof mounting mediums are discussed below.

I. Pritt

Pritt is a cheap quick drying solid adhesive made by Henkel Ltd. of West Germany and is sold in most newsagents. It is the best S.E.M. mounting adhesive the authors have found for specimens less than 2 mm in length. . To use (a) smear the stub with a thin film of adhesive (b) put the specimen on the adhesive using a damp brush under a binocular microscope within fifteen mins. (c) dry the stub under a desk lamp or any other heat source for 30 minutes. (d) scratch the surface of the glue to improve the surface contact between the stub and coated specimens (e) coat the specimens (f) examine specimens under the S.E.M. (g) to remove a specimen from the stub - (1) immerse it in a drop of water under the binocular microscope (2) and remove it from the stub using a wet brush.

II. Kaiser's gycerol gelatin for microscopy.

Like Pritt this adhesive allows easy removal of specimens from the stubs. However, the preparation of stubs using this mounting medium is more complex. To use -

(a) take some developed exposed photographic paper and stick it to the stub using double sided sellotape. The stub should completely overlap the photographic paper.

(b) paint the edge of the photographic paper and the adjacent exposed stub with silver paint, to improve conductivity between the stub and coated specimens.

(c) smear the photographic paper with glycerol gelatin.

(d) mount the specimen on the glycerol using a damp brush within a few days.

(e) dry under a source of heat for 30 minutes.

(f) coat and examine under the S.E.M.

(g) to remove the specimens use a drop of water and a brush.

This method is for specimens less than 2 mm in length.

III. Kodaflat

This adhesive is manufactured by Kodak and is useful for mounting specimens less than 2 mm in length.

To use -

(a) Smear the stub with a thin layer of Kodaflat.

(b) Put the specimen on the Kodaflat using a damp brush under a binocular microscope within about 10 minutes.

(c) Leave the stub to dry for 12 to 24 hours.

(d) Coat and examine.

(e) To remove the specimen from the stub use acetone to dissolve the Kodaflat. Then soak the removed specimen in a container of acetone for 5 minutes to remove any remaining Kodaflat.

IV. Durafix

This adhesive is manufactured by Rawlplug Co. Ltd. a subsidiary of Burmah Company. Its main use is for mounting specimens larger than 0.5 mm.
To use -

(a) Put a small drop of durafix on the stub.

(b) Put the specimen on the durafix under binocular microscope within 15 seconds of applying the durafix to the stub, but after 5 seconds.

(c) Leave the stub to dry for 12 to 24 hours.

(d) Coat and examine.

(e) To remove the specimen use the same procedure as for Kodaflat.

V Silver dug.

This adhesive is supplied by Cambridge instruments. Its main use is for mounting specimens larger than 0.5 mm. It provides better results under the S.E.M. than durafix. Its method for use is the same as for durafix. Specimens can be removed from the stubs using glycerine and a needle, or by immersing the whole stub in acetone for five minutes to dissolve the silver dug.

After a specimen has been mounted on a stub it should be coated with gold or aluminium in a coating machine. The thickness of the coatings required depends on the material but as a general rule, fossils and grains require a 500 Å thickness coating while sediment requires a 750Å coating.

A specimen removed from an S.E.M. stub should be soaked in 20% H_2O_2 for up to 2 hours (dependent on the condition of the specimen) to clean it.

Of the techniques which are outlined, acetic acid extraction is recommended for phosphatic fossils while H_2O_2 extraction is recommended for carbonate fossils. The paraffin extraction technique is regarded as being too dangerous for common laboratory usage.

The ultrasonic cleaning technique is regarded as being likely to damage specimens. Of the mounting mediums, Pritt is highly recommended since it is simple to use, quick drying and cheap. It also has the advantage in taxonomic photographic work of producing a good readily obtainable black background. Silver dug is beyond doubt the best mounting medium we have used for large specimens.

There are other extraction and mounting techniques which we have not used. These include the use of dilate hydrochloric acid to remove foraminifera from limestone (Conkin et al 1968) and the use of an ultrasonic method to remove ostracods from chert (Tillman & Murphy, 1978).

For further details of palaeontological techniques we recommend Kummel & Raup (1965).

The uses for which we have used the S.E.M. for are -

(1) Taxonomical work on ostracods.

(2) The development of a weathering scale on fish debris.

(3) A study of abrasive features on quartz grains and fish debris.

(4) A study of sediment and grain diagenesis.

(5) An examination of microborings.

Other uses for which the S.E.M. can be used include a study of microtrace fossils, other microfossil groups, progressive destruction of grains, environmental interpretations of sediment based on abrasive and weathering features, metamorphic cleavage studies, metasomatic studies, weathering and crystallisation studies of igneous and metamorphic rocks.

LITERATURE CITED

Conkin, J.E., Conkin, B.M. and Kanis, W.F., 1968; Mississippian foraminifera of the United States, Part 3 - The limestones of the Chouteau Group in Missouri and Illinois, Micropaleontology, Vol.14, No.2, pp.133-178 Pls.1-4.

Kummel, B. and Raup, D., 1965; Handbook of Paleontological techniques, Freeman & Co., 852 p.

Tillman, J.R. and Murphy, S.E., 1978; Ostracodes of the Superfamily Hollinacea from Middle Devonian rocks of Central Ohio, J. Paleontology, v.52, pp.411-439.

17

i) Leggott, J.K.

ii) British Lower Palaeozoic Black Shales and their Palaeo-oceangraphic significance

iii) May 2 1979

iv) David D.J. Antia, Department of Geology, Glasgow University, Glasgow, Scotland.

Dr. Leggott suggests that the Ludlow-Pridioli boundary can be and has been correlated with certainty in the Lake District, Welsh Borderlands, and Ireland. This suggestion is clearly fallacious because the criteria for the recognition of the boundary in the U.K. have only recently been outlined (e.g. Kaljo, 1978), and insufficient palaeontological work has been done to allow these criteria to be applied. If, however, Dr. Leggott meant the Ludlow-Downton boundary, correlation is still a problem, since Squirrell & White (1978) have shown that middle Ludlovian sediments can contain supposedly diagnostic (Siveter, 1978) Downtonian ostracods.

He also asserts that the black shales contain little or no land derived organic debris. This is surprising as much of the organic debris in modern black shales is land derived, and terrestrial algae, cuticular and vascular plants are considered to have inhabited the Lower Palaeozoic land (cf. Gray & Boucot, 1977).

He notes only one occurrence of Lower Palaeozoic phosphatic black shales in the Welsh Borderland region, though others have been recorded (e.g. ~~[illegible]~~, 1957; Antia, 1979), and he suggests that they are analagous to those forming today under oxygen deficient waters off west facing continental margins. However, he neglects to inform us if they formed on an overriding plate between the land and the trench like the modern Peruvian examples (Burnett, 1977) or on a passive Atlantic type margin like the West African examples (Baturia <u>et al</u>., 1972), and fails to comment on their environmental significance with respect to the genesis of the Carodocian black shale in which they occur. This is important because phosphorites found in black shales can either form by the replacement of micrites or the anoxic clays in which they are found (cf. Birch, 1979; Burnett, 1977; Antia, 1979). In both instances at the present time different environmental scenarios exist for the 'black shale' formations.

References

Antia, D.D.J. 1979. Authigenic gypsum in marine sediments - a comment. Marine Geol. 31, M1 - M4

Baturin, G.N., Merkulova, K.I. & Chalov, P.I. 1972. Radiometric evidence for recent formation of phosphatic nodules in marine shelf sediments. Marine Geol. 13, M37-M41.

Birch, G.F. 1979. The nature and origin of mixed apatite/glauconite pellets from the continental shelf off South Africa. Marine Geol. 29, 313-334.

Gray, J. & Boucot, A.J. 1977. Early vascular land plants; proof and conjecture. Lethaia 10, 145-174.

Burnett, W.C. 1977. Geochemistry and origin of phosphorite deposits from off Peru and Chile. Geol. Soc. Amer. Bull. 88, 813-823.

Kaljo, D. 1978. The Downtonian or Pridolian from the point of view of the Baltic Silurian. Eesti Nsv. Tead. Akad. Toim. 27, Köide Geol. (1) 5-10.

Siveter, D.J. 1978. The Silurian. In Bate, R. & Robinson, E. (eds) A stratigraphical index of British ostracoda. Geol. J. spec. issue No. 8, p.57-100.

Squirrell, H.C. & White, D.E. 1978. Stratigraphy of the Silurian and Old Red Sandstone of the Cennen Valley and adjacent areas, south-east Dyfed, Wales. Rep. Inst. Geol. Sci. No. 78/6.

i) Leggott, J.K.

ii) British Lower Palaeozoic Black Shales and their Palaeo - Oceanographic Significance.

iii) 2 May 1979

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Dr. Leggott notes no black shale type sequences within the Ludlovian and Pridolian of Wales and the Welsh Borderlands. However, Pridolian (sensu Kaljo 1978) sediments contain thin black shale horizons (e.g. Antia 1979) rich in gypsum, organic debris and phosphatic nodules. In the Clun Forest - Knighton - Builth Wells region some 2 km thickness of black shales were deposited during the Ludlow. Both these shale sequences have different environmental origins but neither is related to a eustatic transgression; in fact McKerrow (1979) has proposed a eustatic regression during this time period. The Ludlovian sequence of black shales were deposited in a 'deep', fault bounded, subsiding basin whose bottom waters appear to have been very low in oxygen during most of this time. The latter can be deduced both from the finely laminated, unburrowed nature of the sediments and their lack of indigenous benthic fauna.

A benthic fauna has been recorded from the basin but it is confined to slump or turbidite beds (i.e. it is transported) or to sediments representing occasional brief periods of bottom water oxygenation.

During the Eltonian, Bringewoodian and Lower Leintwardinian up to 1.6 km of marine 'varved' rhythmite sediments (including intercalated slumps and turbidites) were deposited. These rhythmites consist of regular alternations of less than 1 mm thick light coloured carbonate rich laminae and black or dark grey organic, clay rich laminae which are probably seasonal in nature. The dark laminae may even contain what are apparently pyrite framboids (Holland 1958, p.451). Similar sediments are found today in areas where the bottom waters are anoxic (cf. Reineck & Singh, 1973).

During the Upper Leintwardinian (about 0.1 km thick) megavarves were deposited in the Clun-Knighton region. These megavarves consist of unfossiliferous silt/clay rhythmites (5-20 cm thick) alternating with blue grey carbonate rich layers. The latter are burrowed, as is the contact with the underlying dark layer; the lighter coloured units contain an apparently indigenous benthic fauna (of articulated *Dayia navicula*). Degens *et al.* (1978) have described similar megavarves from the Black Sea area where they arise during fluctuations between oxic and anoxic bottom conditions.

In the Lower Whitcliffian a sequence (about 0.4 km thick) of terrigenous rhythmites (whose laminae are less than 1 mm thick) with interbedded turbidites and allodapic limestones were deposited. Again bottom conditions appear to have been anoxic.

We have described the upper Silurian Welsh Basin succession in some detail to indicate that the situation is far more complex than Dr. Leggett has suggested ~~indicated~~. During the late Silurian compression effects resulting from the closure of the Iapetus Ocean (McKerrow and Ziegler 1972) and the Midlands aulacogen (Evans 1979) gave rise to a basin which was bounded on its eastern and western sides by faults (eg.Ziegler 1970). Tectonic compression resulted in the floor of this basin subsiding beyond the reach of normal surface circulation so that the bottom waters were largely poorly oxygenated during this time, resulting in the deposition of black shales. Occasionally relatively brief periods of oxygenation resulted in the disruption of the rhythmite sediments by biological and current activity. The Pridolian black shales are considered (Antia 1979) to have formed immediately after a major change in sea water chemistry.

We conclude that lower Palaeozoic black shales were formed under a variety of conditions, which are not necessarily related to eustatic transgressions.

References

ANTIA, D.D.J. 1979. Authigenic gypsum in marine sediments - a comment. *Marine Geol.* 31, M1-M4.

DEGENS, E.T., STOFFERS, P., GOLUBIC, S. & DICKMAN, M.D. 1978. Varve chronology: estimated rates of sedimentation in the Black Sea deep basin. *Initial Reports of the Deep Sea Drilling Project*, 42, 499-508.

EVANS, A.M. 1979. The East Midlands Aulacogen of Caledonian age. *Mercian Geol.* 7, 31-42.

HOLLAND, C.H. 1958. The Ludlovian and Downtonian rocks of the Knighton district, Radnorshire. *Q. Jl geol. Soc. Lond.* 114, 449-482.

KALJO, D. 1978. The Downtonian or Pridolian from the point of view of the Baltic Silurian. *Eesti Nsv Tead. Akad. Toim. 27. Köide Geol.* 5-10.

McKERROW, W.S. 1979. Ordovician and Silurian changes in sea level. *Jl geol. Soc. Lond.* 136, 137-145.

McKERROW, W.S. & ZIEGLER, A.M. 1972. Silurian palaeogeographic development of the proto-Atlantic Ocean. *24th Int. geol. Congr., Montreal*, 6, 4-10.

REINECK, H. & SINGH, I.B. 1973. *Depositional sedimentary environments.* Springer-Verlag.

ZIEGLER, A.M. 1970. Geosynclinal development of the British Isles during the Silurian period. *J. Geol.* 78, 445-479.

APPENDIX

The Appendix to this thesis contains :-

1. The revised Lockley & Antia manuscript for Palaeontology,
2. Data tables (in the thesis pocket) for the sections examined in Mortimer Forest in Paper 1.
3. Size distribution charts of *Thelodontites corftonensis* at Ludlow, Priors Frome, and Corfton.
4. A paper published in Paleobiology on the effect of shell transport in the Essex Chenier Plain, England. This latter paper is included because it gives an insight into the effect of shell transport on the composition of shell assemblages in a Recent intertidal environment, which bears many superficial similarities to the intertidal environments of the basal Downtonian. The chenier plain environment may eventually prove to be a good analogue of the basal Downtonian. However, at the present time insufficient research has been done to allow a valid interpretation and comparison of the Downtonian intertidal environments, with Recent intertidal environments like the chenier plain environment.

POSSIBLE DISPERSAL MECHANISMS ACCOUNTING FOR ANOMALOUS OCCURRENCES OF THE LOWER PALAEOZOIC BRACHIOPOD SCHIZOCRANIA

by

Martin G. Lockley & David D. J. Antia

Abstract Rare occurrences of Ordovician and Silurian species of the inarticulate brachiopod Schizocrania (Trematidea) in facies where they are not normally indigenous is explained by illustrating that the orthoconic cephalopod shells to which these inarticulates are attached may have drifted considerable distances prior to their deposition and entombment in onshore sediments.

Introduction During the course of respective studies of Upper Llanvirn, Ordovician (MGL) and Whitcliffian, Silurian (DDJA) successions in the Anglo Welsh region, the authors independently noted rare occurrences of orthocones with Schizocrania attached to both the inner and outer walls of their body chambers; in both cases the entombing clastic sediments are of a coarse arenaceous type associated with demonstrably shallow-water facies assemblages which include transported shell deposits and disconformities (Williams 1953 and Antia 1979).

Since the Anglo Welsh Schizocrania usually occur abundantly only in argillaceous offshore sediments we consider that, although they are predictably rare in these onshore sediments, some explanation must be sought for their association, in significant numbers, with the orthocones to which they are attahced. Havlicek (1972 p.230) reported that the Upper Ordovician trematid Ptychopeltis incola Perner from Bohemia .. "lived attached only to the shells of orthocone nautiloids"; he also noted that its ancestor P. hornyi Havlicek sometimes encrusted orthocones. We consider therefore that these intriguing examples of apparent host-specific relationships may be paralleled elsewhere amongst the Trematidae (e.g. Schizocrania) by similar associations between host and encruster.

Material The Upper Llanvirn orthocone, an incomplete, poorly-preserved internal mould (diameter ca. 18 mm) of unknown taxonomic affinity, was recovered from calcareous benthos-dominated, arenaceous shell beds in the upper part of the Flags and Grits Member of the Ffairfach Group exposed at Coed Duon, 3 km south of Llangadog, Dyfed (Grif Ref. SN 709256) where it lay parallel to bedding. The orthocone has three specimens of *Schizocrania* cf. *salopiensis* Williams attached to the inner surface of the body chamber; the brachial valves all face inwards (Fig. 1A) but show no obvious preference for any particular attachment site although two of the specimens are alined sub-parallel to each other near the anterior end.

The Whitcliffian orthocones are represented by two poorly preserved fragmentary internal moulds of *Orthoceras* sp. (diameters ca. 20 mm and 30 mm respectively) from the Lower Whitcliffe Beds of Mortimer Forest, south of Ludlow (Grid Ref. SO 497725) and the Upper Whitcliffe Beds near Broadstone Farm (SO 544900). The older specimen (Fig. 1B) is extensively bored by bryozoa and has *three specimens of* *Schizocrania striata* (Sowerby) attached to the anterior part of its external surface. The specimens all occur closely adjacent to each other on the exposed section of the orthocone mould which faces downward from the undersurface of a bedded unit; relative to the final entombment position of the orthocone the *Schzocrania* specimens occur on its "underside" and following the dissolution of the cephalopod shell have become impressed onto the preserved mould. The younger (Upper Whitcliffian) orthocone has five poorly preserved specimens of *S. striata* attached to the inner surface of its body chamber; the specimens are aligned transversely, parallel to the phragmacone edge (Fig. 1C).

The lectotype (Geol. Surv. Mus. no. 6631) of *S. striata* (Sowerby) from the Leintwardinian-Whitcliffian beds of Delbury, Salop (Grid Ref. SO 501854) is the only other known British *Schizocrania* which we have discovered attached to an orthoconic nautiloid; although this specimen is also attached to the phragmacone (Fig. 2a, b) it differs from the other examples in its larger size (length 9 mm) and posterior attachment site.

Observations All twelve of the Schizocrania specimens, found in association with these orthocones, exhibit only their convex brachial valves facing away from the cephalopod shell surface. Schizocrania is known to attach to substrates by its flat pedicle valve (Rowell in Williams et al. 1965 p.H283). However, it is a recurrent empirical observation that pedicle valves are exceptionally rare, being either altogether absent from assemblages or hidden from view beneath the brachial valve; indeed S. salopiensis Williams (1974 p.44) was until recently (Lockley and Williams 1980 in press) known only from its brachial valve.

The three orthocone specimens shown in Fig. 1 indicate that the anterior edge of the phragmacone was the preferred encrustation site for all but two of the Schizocrania specimens. The orientation of these Schizocrania inside the phragmacone and on the shell exterior is apparently not random since all adjacent shells are alined with their umbones pointing in approximately the same direction (i.e. transverse or oblique to the orthocones' long axis).

The orthocones may have been encrusted (A) whilst they were alive and mobile, (B) whilst dead and floating, (C) whilst dead and semi bouyant, being washed around on the sea floor, (D) whilst dead and settled on the sea floor and, finally, (E) whilst being reworked. Although determination of criteria for deducing encrustation sequences is too complex to be considered within the scope of this paper it is worth noting that a different pattern, density, composiition and diversity of encrusting faunas may be expected at each stage (A - E) of a cephalopods pre-entombment history.

In addition to the abundant material recorded from the Mesozoic (e.g. Seilacher 1960) and the few Lower Palaeozoic examples referred to by (Holland 1971 and Havlicek 1972) we have noted Ordovician and Silurian collections containing several varied and undescribed examples of orthocone encrustation (e.g. National Museum of Wales specimen NMW 79. 5G. Map. loc. 771; Hunterian Museum specimens S. 25129 / 1-3 & S. 25114 a/b).

Schizocrania is ornamented by numerous radial capillae (Williams 1974 p.44) each of which, according to Williams & Rowell in Williams et al. (1965 p.H81) would support a setal follicle at the commissure. Sudarson (1969 p.65) noted that Discinisca larvae have well developed principle setae and that "there may be a prolonged larval stage ... with chaetae increasing in number to facilitate floatation". Both the Schizocrania species discussed here exhibit high capillae densities at the same growth stage (i.e. 10 - 12 per mm, 5 mm anteromedianly of the dorsal umbones) and probably therefore had at least a juvenile epiplanktic stage.

Interpretation of orthocone encrustation patterns

Holland (1971) and Havlicek (1972) respectively have favoured the interpretation that articulate and inarticulate brachiopods attached to living orthocones. We consider that although this may have been true for brachiopods with an inferred epiplanktic mode of life, e.g. Sericoidea and Aegiria (Bergstrom 1968) and setiferous Trematidae, such as those referred to by Havlicek (1972) and noted herein it is unlikely that the normally benthic gregarious Microsphaeridiorhynchus nucula, referred to by Holland (1971), would have attached to living nektic orthocones.

Since modern spirorbids are known to be host specific and capable of seeking a preferred attachment site and orientation (Knight-Jones 1951), it is almost certain that the occurrence of fossil spirorbids alined along the growth margins of orthocones (Holland 1971) indicates a comparable relationship. This may mean that the similar alinment of Schizocrania specimens noted here (Fig. 1) could be indicative of a similar host specific relationship. Such a contention tends to be supported by our observation that the Anglo-Welsh Schizocrania have not been found attached to any other host organisms and would also offer possible explanations for the virtual absence of pedicle valves, which could have either remained attached to a host when the brachial valve disarticulated, or become obscured, during fossilization, by the substrate to which they were attached.

Indeed, in the light of the present limited evidence, the possibility that they were also attached to an algal substrate (cf. Bergstrom 1968) cannot be overlooked.

The Schizocrania on the internal surface of the body chambers of the Llanvirn and Upper Whitcliffian specimens indicate encrustation beginning no earlier than the post mortem drifting phase (following decay of mantle lining the body chamber) but prior to the infilling of the phragmocone. The Lower Whitcliffian orthocone however could have been encrusted at any one of a number of stages in its history as a live or dead mobile organism; however, since the Schizocrania are attached to its underside they must have settled and had time to grow prior to its final entombment in this position. The S. striata lectotype must have become attached to the posterior and of its phragmacone substrate after the separation of the body chamber from the remaining posterior part of the shells (i.e. at a late stage in the orthocones' post-mortem history).

Distribution of Schizocrania

The Llanvirn orthocone and Schizocrania discussed here are virtually the only representatives of these taxa known from the predominantly arenaceous and rudaceous Ffairfach Group of the Llandeilo area. Since S. salopiensis is common in penecontemporaneous, argillaceous successions elsewhere in South Wales and the Welsh Borderlands (Williams 1974, Bassett et al. 1974 p.9 and Lockley and Williams 1980 in press) where the fauna is dominated, or exclusively represented by neritic and pelagic faunas (i.e. trilobites, graptolites and cephalopods), it is reasonable to assume that the unique (or "exotic") Ffairfach occurrence may have been related to the drifting or migration of a stray cephalopod beyond the normal limits of its indigenous environment. Such post-mortem drifting of modern cephalopods is well known (e.g. Hewitt & Pedlay 1978).

Similarly Schizocrania striata is rare in the Whitcliffe Beds of the Ludlow region where it constitutes only about 0.01 to 0.005% of the total fauna with specimens generally occurring in a fragmentary condition and random orientations.

It is more common in unbioturbated, parallel-laminated, alternating light and dark siltstones (rhythmites) of deeper water facies (e.g. Upper and Lower Leintwardinian Beds, Holland *et al*. 1963, p.154 and Lawson 1973, p.274) and is recorded only rarely in shallow water bioturbated siltstones (Facies B *sensu* Antia 1979). In this case, therefore, again it seems possible that the two more heavily encrusted Whitcliffian cephalopods drifted into inshore deposits from an offshore source, although limited evidence also points to later phases of encrustation.

Williams (1969 p.143) discussed the potential range of larval dispersal and its bearing on brachiopod migration during the Ordovician. Clearly his suggested figure (up to 250km) is only a fraction of the range potential for brachiopods capable of encrusting live or drifting orthocones. Since the Llanvirn occurrence of *Schizocrania* reported here is as old as any hitherto known record of the genus in the Anglo Welsh region (Williams 1974 p.45; Bassett *et al*. 1974 p.9; Lockley & Williams 1960 *in press*) consideration must be given to the potentialities of such mechanisms.

Trematid hosts

Encrusting Trematidae such a *Schizocrania*,*Drabodiscina* and *Ptychopeltis* appear to be host specific. *S*. *salopiensis*, *S*. *striata* and *P*. *incola* have hitherto only been observed attached to orthoconic nautiloids generally presumed to have been alive or floating at the time of their encrustation. Other members of the family, e.g. *Ptychopeltis hornyi* Havlicek and *Drabodiscina grandis* Barrande, are commonly attached to conularids which are considered by Havlicek (1972) to have been mobile during life, and the American species *Schizocrania filosa* Hall frequently attached to the brachiopod *Rafinesquina* (Cooper 1956 & Rowell *in* Williams *et al*, 1965). With respect to trematid-nautiloid associations, it is intriguing to note that Titus and Cameron (1976) record *S*. *filosa* only in their deep water *Geisonoceras* (Orthocerida) community. Since Dr. R. A. Hewitt and Mrs. D. Evans (Pers. comm. 1979) inform us that they know of no Silurian or

Ordovician examples of cephalopod encrustation by brachiopods other than those reported here, we conclude that although the examples discussed here are rare they are none the less reminiscent of host specific relationships.

Conclusions

Faunal associations with abundant Schizocrania in the Ordovician and Silurian of the Anglo Welsh region are almost invariably confined to argillaceous deep water facies where species of the genus are represented almost exclusively by assemblages of brachial valves. Such exceptionally disproportionate valve ratios, which have never been adequately explained or investigated, are considered to result from the probable encrustation relationships inferred above which might account for the obscuring or removal of pedicle valves.

Known associations between trematid encrusters and hosts such as those reported here and elsewhere (e.g. Havlicek 1972 and Rowell in Williams et al. 1965) point to some form of host specific relationship between representatives of this family and other larger invertebrate hosts. Whether such relationships could be termed symbiotic, commensal or parasitic is unclear since, although an encrusting trematid would neither obviously incapacitate or benefit a living host, we currently lack evidence which conclusively demonstrates that hosts were encrusted during life. With respect to this issue, however, we can establish that encrustation of orthocones, which may in some cases have begun during their life, often began no earlier than the post mortem drifting phase, and may have continued or begun at a time when the orthocones were resting or rolling on the sea floor. Since encrustation of many of these orthocones could not have taken place when they were in the final "resting" position it must have occurred during the middle phases of their pre-entombment history.

Although these considerations theoretically allow for considerable scope in the interpretation of "probable time of encrustation" several factors point to its early occurrence in the orthocones life and post mortem history. (1) The encrusting Schizocrania noted here are not currently known to attach to non-orthocone skeletal components within the deposits from which they were recovered and are therefore likely to have settled preferentially on orthocone shells - prior to their final deposition. (2) The apparent high density, orderly clustering of Schizocrania towards the anterior of the phragmacone suggests that possibly the orthocone was colonized as a specific host whilst it was floating. (3) Since both Schizocrania and its nautiloid hosts are normally indigenous to sparsely fossiliferous, low density offshore facies, it is proable that encrustation occurred in an offshore region before the orthocones finally became entombed in more diverse, fossiliferous, onshore facies where Schizocrania is invariably rare. This inference is supported by the observation that the setiferous Schizocrania may well have been adapted to a prolonged larval stage which would have enhanced its chances of encountering a suitable encrustation site, e.g. an orthocone or other indigenous organism. If this were the case and Schizocrania even occassionally encrusted orthocones in a manner analagous to the attachment of epiplanktic aegeromenids to buoyant organisms noted by Bergstrom (1968), then the combined effect of nautiloid mobility during life (e.g. migration) and drifting after death would offer an explanation for occurrences such as those noted here and point to an important potential brachiopod dispersal mechanism.

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We should like to thank Dr. G. E. Farrow and Dr. R. A. Hewitt for critically reading manuscripts and suggesting many improvements; Dr. M. G. Bassett, Dr. A. Williams, Dr. J. D. Lawson, Mr. D. Atkins and Mrs. D. Evans also assisted us by providing aid and useful comments. Both authors acknowledge the receipt of N.E.R.C. grants.

References

Antia, D. D. J. 1979. Bone-Beds: A review of their classification, occurrence, genesis, geochemistry, ecology, diagenesis, weathering and micro-biotas. Mercian Geol. 7(2), 93-174, 6 pls.

Bassett, D. A., Ingham, J. K. and Wright, A. D. (Eds). 1974. Field excursion guide to type and classical sections in Britain. (Ordovician System Symposium, Birmingham 1974). The Palaeontological Assoc. London. pp.66.

Bergstrom, J. 1968. Some Ordovician and Silurian Brachiopod Assemblages. Lethaia. 1. p.230-237.

Cooper, G. A. 1956. Chazyan and related brachiopods. Smithson. Misc. Coll. Washington. 127, 1-1245, pls. 1-169.

Havlicek, V. 1972. Life habit of some Ordovician inarticulate brachiopods. Vestnik ustred ust geol. 47, 4. 229-233.

Hewitt, R. P. and Pedley, H. M. 1978. The preservation of the shells of *Sepia* in the Middle Miocene of Malta. Proc. Geol. Ass. 89(3), 227-237.

Holland, C. H. 1971. Some conspicuous participants in Palaeozoic symbiosis. Sci. Proc. R. Soc. Dublin. Ser. A 4(2), 15-26.

Holland, C. H., Lawson, J. D. and Walmsley, V. G. 1963. The Silurian rocks of the Ludlow district, Shropshire. Bull. Brit. Mus. (Nat. Hist.), Geol. 8, 95-171.

Knight-Jones, E. W. 1951. Gregariousness and some other aspects of the settling behaviour of *Spirorbis*. J. Marine Biol. Ass. U.K. 30, 202-222.

Lawson, J. D. 1973. Facies and faunal changes in the Ludlovian rocks of Aymestry, Herefordshire. Geol. J. vol. 8, Pt. 2, 247-278.

Lockley, M. G. & Williams, A. 1980. (in press). Lower Ordovician Brachiopods from Mid and South Wales. Bull. Br. Mus. Nat. Hist. [Geol.]

Seilacher, A. 1960. Epizoans as a key to Ammonoid Ecology. J. Palaeont. 34, 189-93.

Sudarson, A. 1969. Brachiopod larvae from the west coast of India. Proc. Ind. Acad. Sci. 68B, 59-68.

Titus, R. & Cameron, B. 1876. Fossil Communities of the Lower Trenton Group (Middle Ordovician) of Central and North Western New York State. J. Palaeont. 50, 1209-25.

Williams, A. 1969. Ordovician faunal provinces with reference to brachiopod distribution in Wood, A. (Ed.). The Pre-Cambrian and Lower Palaeozoic rocks of Wales. Univ. of Wales Press, Cardiff.

---------- 1974. Ordovician Brachiopods from the Shelve district, Shropshire. Bull. Brit. Mus. (Nat. Hist.) Geol. Supp. 11, 1-163, pls. 1-28.

Williams, et al. in Moore, R. C. (Ed.). 1965. Treatise on invertebrate palaeontology Part H. Brachiopoda. Univ. Kansas Press.

Williams, A. 1953 The geology of the Llandeilo district, Carmarthenshire, Q. Jl geol. Soc. Lond. 108, 177-208.

Explanation of Figures

(1) Scale drawings of Schizocrania encrusted orthoconic nautiloids from Upper Llanvirn strata exposed near Llangadog, Mid Wales (A) and from Lower (B) and Upper (C) Whitcliffe strata exposed near Ludlow, Salop. All Schizocrania specimens have British Museum numbers and are depicted by the same diagrammatic representation regardless of which side of the orthocone mould they appear attached to; length width measurements, listed bottom right, should be regarded as only approximate where bracketed.

(2) Lateral (A) and postero lateral (B) views of lectotype of Schizocrania striata Sowerby showing its phragmacone attachment site (both x3).

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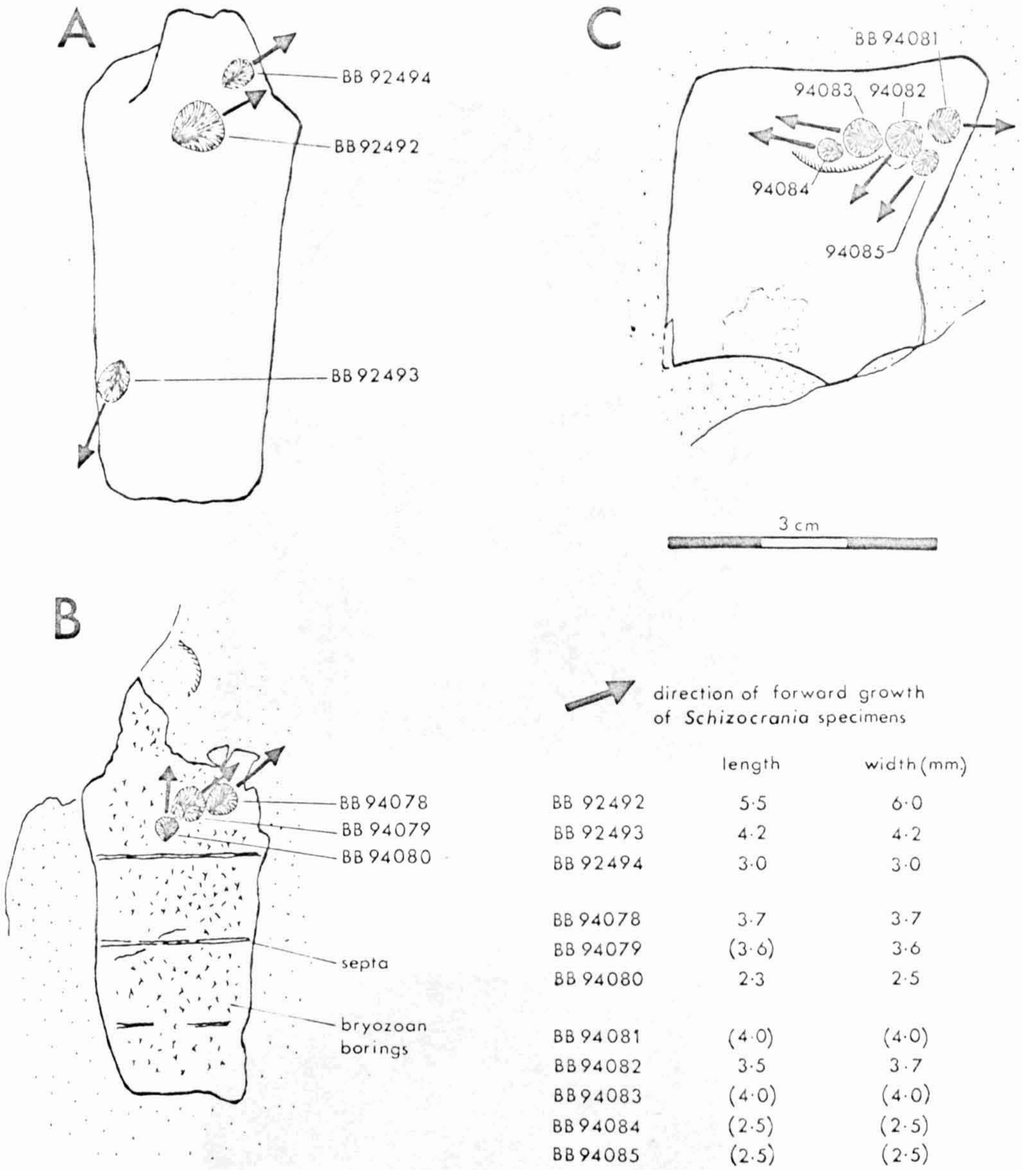

direction of forward growth of *Schizocrania* specimens

	length	width (mm)
BB 92492	5·5	6·0
BB 92493	4·2	4·2
BB 92494	3·0	3·0
BB 94078	3·7	3·7
BB 94079	(3·6)	3·6
BB 94080	2·3	2·5
BB 94081	(4·0)	(4·0)
BB 94082	3·5	3·7
BB 94083	(4·0)	(4·0)
BB 94084	(2·5)	(2·5)
BB 94085	(2·5)	(2·5)

Lakey & Antia Fig. ①.

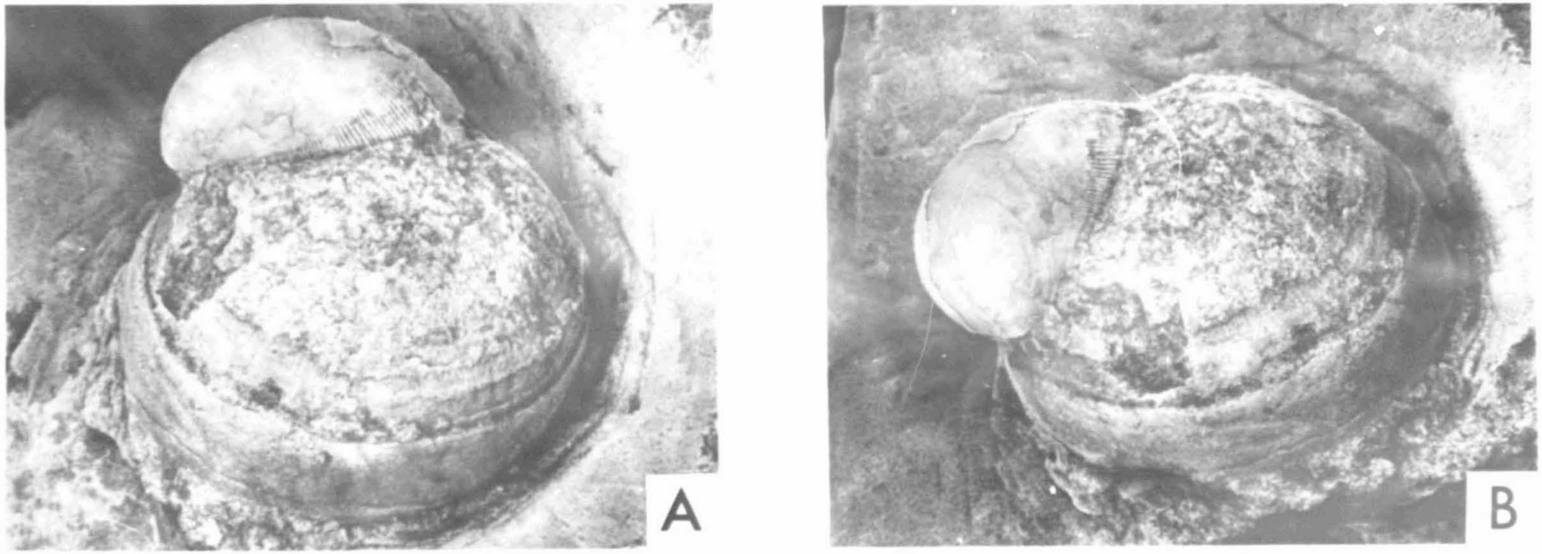

Fig. 2

Also in thesis pocket

Paleobiology. 1977. vol. 3, pp. 404–414.

A comparison of diversity and trophic nuclei of live and dead molluscan faunas from the Essex Chenier Plain, England

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Abstract.—The rarefaction graphs and trophic nuclei of dead molluscan shell cumulates and their associated live molluscan fauna from seven 'ecological' habitats in the Essex Chenier Plain facies are examined and compared. The results show that while the trophic nuclei of the live and dead faunas tend to be dissimilar, the rarefaction graphs indicate that the dead fauna will be more diverse than the live, though changes in the diversity of the live fauna tend to be mirrored in the dead fauna.

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Introduction

In many recent palaeoecological studies much has been made of the statistical methods used by modern marine ecologists. Yet little has been done to determine the validity of these methods in the analysis of recurrent fossil assemblages (Scott and West 1976). The two statistical methods which will be examined here are the rarefaction graph (a measure of ecological diversity) and the trophic nucleus.

The rarefaction graph was conceived by Sanders (1968) as a means of comparing the diversities of similar ecological habitats at varying depths and latitudes. Its advantage over previous diversity measurements is that it takes account of sample size and allows the diversity of different sized collections to be compared graphically at a collection size common to each. Sanders (1968) showed that while individuals are added to a collection at an arithmetic rate, species are added at a logarithmic rate. Furthermore, he showed that diversity can best be described as a species abundance curve, rather than the absolute number of specimens in a sample and that each particular environment has its own characteristic rate of species increment, with its rarefaction curves lying within particular fields.

Since the rarefaction method was originally proposed, it has received heavy theoretical criticism in some statistical studies (Fager 1972; Simberloff 1972; Heck et al. 1975; Clifford and Stephenson 1975; Antia and Wood 1977), while at the same time gaining increasing usage in palaeoecological (Calef 1972; Stanton and Evans 1972; Calef and Hancock 1974; Duff 1975; Antia and Wood 1977; Fursich 1977; Watkins 1978), evolutionary (Raup 1975), and ecological studies (Sanders 1968; Sanders and Hessler 1969; Boesch 1971; Young and Rhoads 1971; Stout and Vandermeer 1975). Hurlbert (1971), Fager (1972), Simberloff (1972) and Clifford and Stephenson (1975) following a re-analysis of Sanders' (1968) data suggest that the rarefaction method is wrong since it tends to overestimate true species richness (diversity) of the fauna. However, since species richness ($E(s)$) can be calculated directly (Hurlbert 1971; Heck et al. 1975) a modified rarefaction graph based on explicit $E(s)$ values will be used here to provide a correct rarefaction plot. The formulae by which the graphs (Fig. 2) were calculated are given as follows:

$$E(s) = s - \sum_{i=1}^{s} (1 - N_i/N)^n \qquad (1)$$

$$\begin{aligned} E(v) = \sum_{i=1}^{s} [(1 - N_i/N)^n 1 - (1 - N_i/N)^n] \\ + 2\sum_{j=2}^{s} [(1 - N_i/N - N_j/N)^n \\ - (1 - N_i/N)^n (1 - N_j/N)^n], \end{aligned} \qquad (2)$$

Where $E(s)$ = species richness; $E(v)$ = species richness variance; N_i = species population size for i = 1...S; N = total number of individuals; S = number of species; n = required sample size.

The formulae for calculating $E(s)$ and

$E(v)$ given here (after Harris 1959; Heck et al. 1975) were used in preference to other formulae given in Heck et al. (1975) and Calef (1972) since when computing the rarefaction plots, the vast majority of calculated points occurred in situations where (n) was so much smaller than N, that drawing n individuals randomly approximated to sampling with replacement (cf. Heck et al. 1975).

Although marine ecological diversity is dependent on a large number of variables which include temperature, local evolution rates, predation rates, nutrient availability, salinity, latitude, depth of water and habitat area (Sanders 1968; Sanders and Hessler 1969; Slobodkin and Sanders 1969; Schopf 1972; Porter 1972; Valentine 1973; Barbour and Brown 1973), some palaeoecologists, when using the rarefaction graph, have assumed that one or more of these variables is more important than the rest; for example Duff (1975) assumed that latitude and temperature are the primary controls on ecological diversity when he used the graph to suggest that the Oxford clay of Central England was deposited in the Boreal Province; in contrast Calef and Hancock (1974) assumed depth to be the primary control on ecological diversity when they used the graph to investigate depth relationships between different Wenlockian and Ludlovian benthonic communities. However, though the validity of the latter usage has been questioned (Lawson 1975) on sedimentological and palaeontological grounds, little has been published illustrating the relationship between actively forming shell deposits and the local ecology.

In any fossil assemblage or ecological community it is usual for a small number of species numerically to dominate the fauna. These species have been variously defined as the prevalent species (Curtis 1959; Calef and Hancock 1974) or the trophic nucleus (Turpaeva 1948; Neyman 1967; Walker 1972; Rhoads et al. 1972; Duff 1975; Fursich 1977). The prevalent species comprise the 'top species' in a faunal assemblage and are determined with respect to their proportional abundance and ubiquity by methods outlined elsewhere (Calef and Hancock 1974). The trophic nucleus is defined as the numerically dominant species which comprise 80% of the fauna (Neyman 1967 p. 151). Both indices are useful in ecological studies; the former shows how widespread a species is in a community, while the latter illustrates the relative abundance of the species and the importance of the various trophic groups.

The facies chosen for this study was that of the Essex Chenier Plain, since the results will be directly applicable to the author's current palaeoecological study of the intertidal (chenier?) Downtonian (Upper Silurian) sediments of the Welsh Borderlands, England.

The chenier plain facies was originally defined by Price (1955) as a number of 'shallow based, perched sandy ridges resting on clay along a marshy or seaward facing tidal shore with other beach ridges stranded in the the marsh behind' but was later modified by Greensmith and Tucker (1967, 1975) to include perched gravel ridges.

The taphonic nature of the dead shell assemblages is considered here only to the extent of determining a shell's completeness since in many recent palaeoecological analyses the amount of abrasion undergone by fossil shells is either indeterminable, as in some rottenstone faunas, or not considered (cf. Watkins, in press; Pickerill 1976; Lawson 1975; Calef and Hancock 1974). Also since many recent statistical palaeoecological studies (e.g. Watkins, in press) do not consider whether or not the faunal 'community' examined at a particular locality is in situ, this aspect has been ignored in sampling.

Methods

Three cheniers within the Blackwater Estuary were examined (Fig. 1). They were the Gore Spit Chenier (TL928082), the Mersea Stone Chenier (TM075154) and the Sales Point Chenier (TM032087) of Greensmith and Tucker (1975). At each chenier the main habitats were examined. These habitats have been partially defined by Davis (1964, 1965 a, b, c, 1967), Davis and Milligan (1964), Greensmith and Tucker (1967), and Greensmith et al. (1973 and will be described in detail by the author in a separate publication.

At each habitat the molluscan fauna was sampled by taking a random area (usually between one and three square metres) and sieving all the sediment in the area down to a depth of 50 cm with a one millimetre mesh sieve. In practice sieving was continued till the number of live molluscan shells in each

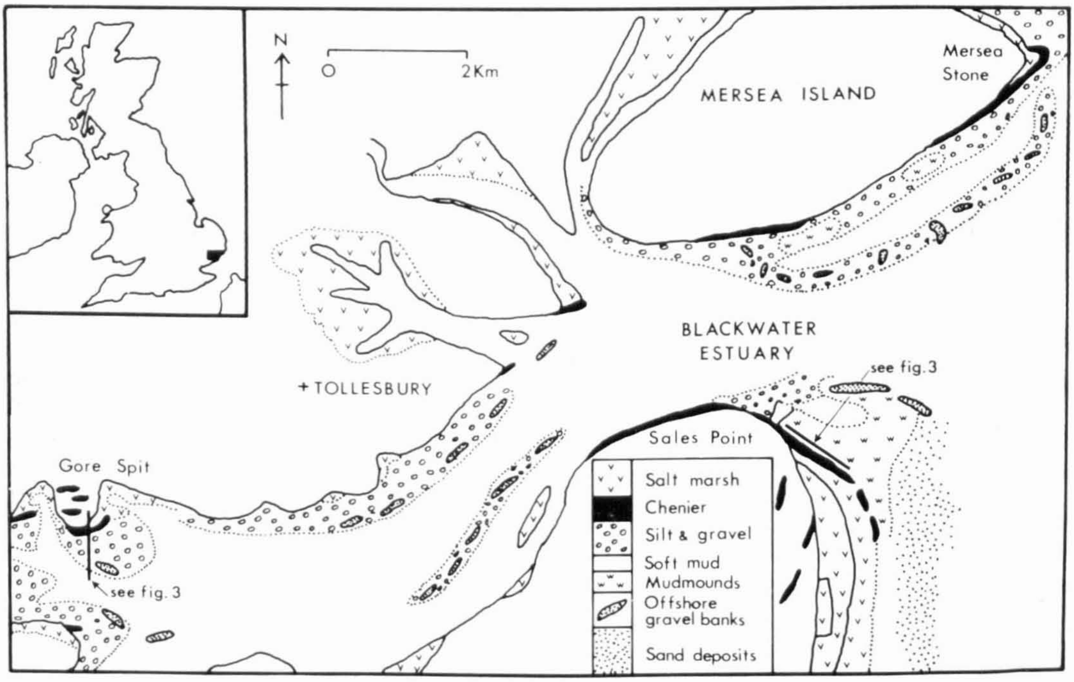

FIGURE 1. Sketch map of the Blackwater Estuary showing sediment distribution. (Inset map shows the relative position of the Blackwater Estuary within the British Isles.)

sample exceeded 500 individuals. A similar number of entire dead molluscan shells were also sampled at each sampling point. The trophic nuclei and rarefaction graphs for each sample were then determined and the results are presented in Table 1 and Fig. 2.

A sample size of 500 individuals was chosen in this instance in order to minimise sampling error (Clifford and Stephenson 1975) and to allow comparison with smaller samples obtained in palaeoecological studies from similar ancient environments.

The Trophic Nucleus of the Fauna

After examination of the data in Table 1, six points of interest are immediately apparent.

(1) The facies can be divided on the bases of morphology and sedimentology into seven ecological habitats labelled A–G in Table 1.

(2) The cheniers themselves contain no live molluscan fauna.

(3) The trophic nucleus of the live fauna bears little relationship in composition to that of its associated shell cumulate, except in the ripple drifted mud habitats where there is no molluscan epifauna and the dead shells are in life position.

(4) The trophic nuclei all contain less than 6 species.

(5) In the majority of habitats, species of the gastropod *Littorina* comprise a dominant part of the trophic nucleus of the live fauna, while in the associated dead shell cumulates the bivalve *Cerastoderma edule* is the dominant member.

(6) Species occurring in the trophic nucleus of the live fauna may be completely unrepresented in the trophic nucleus of the shell cumulate and vice versa.

The abundance of *Cerastoderma edule* in the shell cumulates is an enigma, since the species is not abundant in the live fauna of any of the habitats studied (except in the offshore mudmound habitat—G.R. TM042088). However, in disagreement with Greensmith (1977) who suggests an intertidal origin for the shell cumulates, the faunal evi-

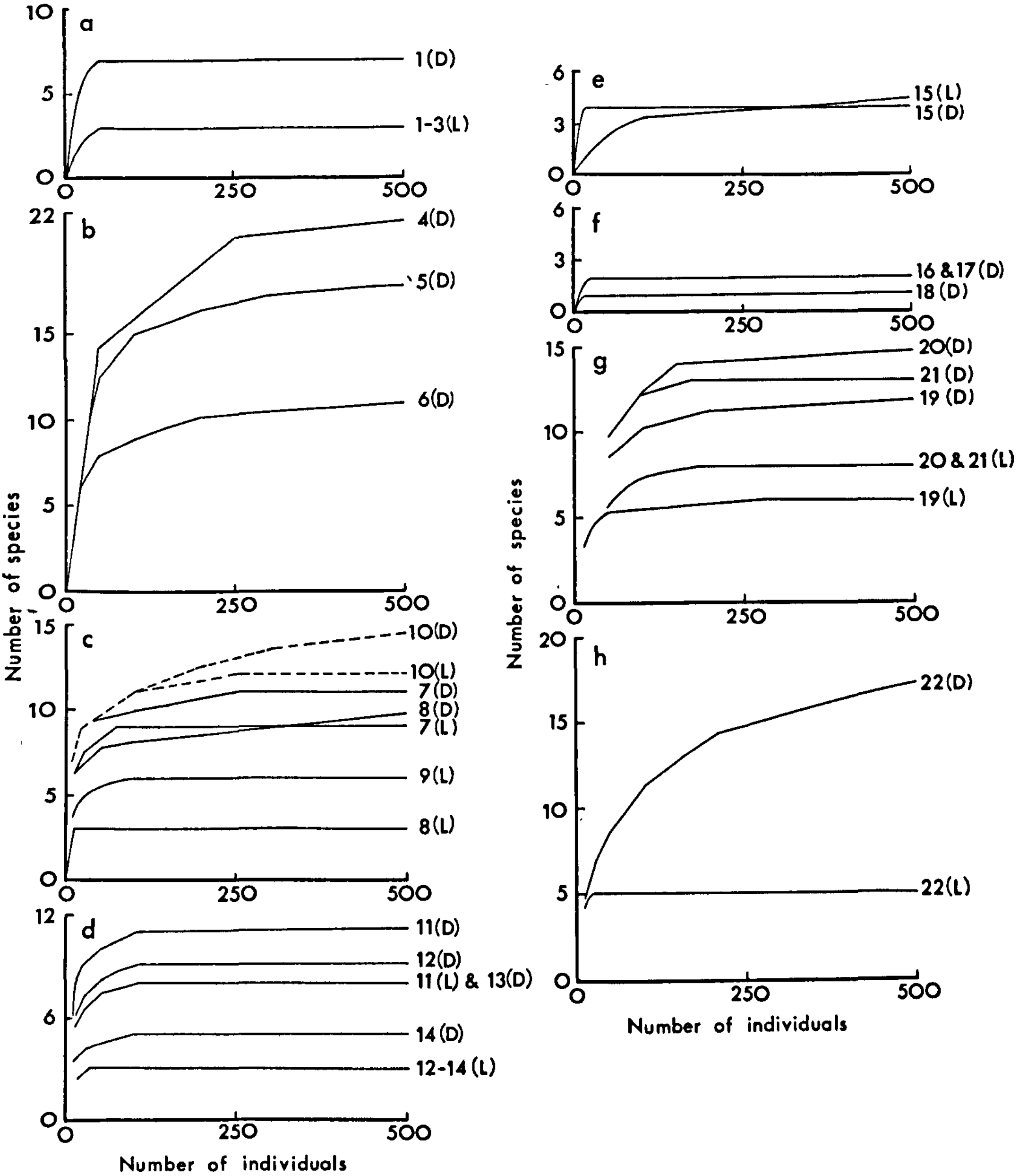

FIGURE 2. Rarefaction graphs for each sample. Broken line indicates that the sample was sublittoral. L = live molluscan fauna; D = molluscan fauna of associated shell cumulate. (a) Salt marsh habitat grid references: 1 = TL928083; 2 = TM072155; 3 = TM036079. (b) Chenier habitat grid references: 4 = TM032087; 5 = TM073154; 6 = TL915082. (c) Silt and gravel habitat grid references: 7 = TL930080; 8 = TM074155; 9 = TL924088; 10 = TL928073. (d) Shell pebble and muddy sand habitat grid references: 11 = TR032088; 12 = TM035090; 13 = TR033086; 14 = TR037087. (e) Ripple drifted mud habitat grid references: 15 = TM037086. (f) Mudmound habitat grid references. 1. Fauna from the mounds: 16 = TM034087; 17 = TM042088; 18 = TM034085. (g) 2. Fauna from the channels: 19 = TM034085; 20 = TM042088; 21 = TM034087. (h) Offshore shell bank habitat grid reference: 22 = TM039091.

TABLE 1. Molluscan species present in the trophic nucleus of each habitat examined (based in part on Greensmith and Tucker 1975). Results expressed where possible as percentage of total population. Note the differences in composition of the trophic nuclei of the live and dead faunas. – = absence of species from the trophic nucleus, + = species present in the trophic nucleus, where the exact abundance is uncertain, * = after Greensmith & Tucker (1967).

		FAUNA IN THE TROPHIC NUCLEUS											
HABITATS		*Buccinum undatum* (Linn.)	*Cerastoderma edule* (Linn.)	*Crassostrea angulata* (Lamarck)	*Crepidula fornicata* (Linn.)	*Hydrobia* spp.	*Lepidochitona cinereus* (Linn.)	*Littorina* spp.	*Macoma balthica* (Linn.)	*Mytilus edulis* (Linn.)	*Ostrea edulis* (Linn.)	*Scrobicularia plana* (da Costa)	Height of station above M.L.W.M. in metres
A. *Salt Marsh*													
1. Gore Marsh	(Live)	–	–	–	–	+	–	–	+	–	–	+	1.7
(TL928083)	(Dead)	–	+	–	–	–	–	–	–	+	+	–	
2. Sales Point	(Live)	–	–	–	–	–	–	91	–	–	–	–	1.8
(TM036079)	(Dead)					NOT RECORDED							
3. Mersea Stone	(Live)	–	–	–	–	–	–	100	–	–	–	–	1.8
(TM072155)	(Dead)					NOT RECORDED							
B. *Chenier*													
(No live observed)													
1. Gore Spit (TL915082)	(Dead)	–	46	7	–	–	–	–	–	23	7	–	2.1
2. Sales Point (TM032087)	*(Dead)	–	70	–	–	–	–	10	–	–	–	–	2.8
3. Mersea Stone (TM073154)	(Dead)	–	46	–	–	23	–	–	–	11	–	–	2.9
C. *Silt and Gravel*													
1. Gore Spit													
TL924088	(Live)	–	–	–	–	–	–	92	–	–	–	–	1.5
TL928073	(Live)	–	–	–	78	–	6	–	–	–	–	–	1.4
	(Dead)	22	–	–	61	–	–	–	–	–	–	–	
TL930080	(Live)	–	11	–	18	–	–	31	–	23	–	–	0.9
	(Dead)	–	22	–	11	–	–	–	13	15	–	19	
2. Mersea Stone													
TM074155	(Live)	–	–	–	–	–	–	+	+	–	–	+	1.4
	(Dead)	–	+	–	–	+	–	–	–	–	–	+	
D. *Shell, pebble and muddy sand*													
TM035090	(Live)	–	–	–	–	–	–	81	–	–	–	–	1.3
	(Dead)	–	53	–	–	–	–	17	–	21	–	–	
TM037087	(Live)	–	–	–	–	–	–	92	–	–	–	–	1.2
	(Dead)	–	63	–	–	–	–	27	–	–	–	–	
TM033086	(Live)	–	–	–	–	–	–	91	–	–	–	–	1.3
	(Dead)	–	45	–	–	–	–	21	–	14	–	–	
TM032088	(Live)	–	–	–	11	–	–	57	–	15	–	–	1.2
	(Dead)	–	28	–	17	–	–	13	–	19	–	8	
E. *Ripple drifted mud*													
TM037086	(Live)	–	–	–	–	–	–	–	–	–	–	92	0.8
	(Dead)	–	–	–	–	–	–	–	–	–	–	96	

TABLE 1.—(Continued).

		FAUNA IN THE TROPHIC NUCLEUS											
HABITATS		*Buccinum undatum* (Linn.)	*Cerastoderma edule* (Linn.)	*Crassostrea angulata* (Lamarck)	*Crepidula fornicata* (Linn.)	*Hydrobia* spp.	*Lepidochitona cinereus* (Linn.)	*Littorina* spp.	*Macoma balthica* (Linn.)	*Mytilus edulis* (Linn.)	*Ostrea edulis* (Linn.)	*Scrobicularia plana* (Da Costa)	Height of station above M.L.W.M. in metres
F. *Mudmounds*													
1. Dead fauna from mounds													
TM042088		–	–	–	–	–	–	–	–	–	–	95	0.4
TM034087		–	–	–	–	–	–	–	–	–	–	85	1.1
TM034085		–	–	–	–	–	–	–	–	–	–	100	1.4
2. Fauna from channels													
TM042088	(Live)	–	18	–	14	–	–	20	16	23	–	–	
	(Dead)	–	42	–	–	–	–	12	–	18	–	8	
TM034087	(Live)	–	–	–	–	–	–	83	–	–	–	–	
	(Dead)	–	41	–	–	–	–	14	8	16	–	7	
TM034085	(Live)	–	–	–	–	–	–	87	–	–	–	–	
	(Dead)	–	46	–	–	–	–	22	–	8	–	11	
G. *Offshore shell bank*													
TM039091	(Live)	–	–	–	–	–	–	66	–	17	–	–	0.4
	(Dead)	–	40	–	8	–	–	14	–	18	–	–	

dence presented here (Tables 1 and 2) suggests that much of the fauna in the shell cumulates may have a subtidal origin (also Tucker, pers. com., 1977) having been swept onshore primarily by wave action and secondarily by tidal currents, as in the Solway Chenier Plain (Farrow, pers. com., 1977), from two main sources; (1) the Blackwater Estuary itself, as can be inferred from the presence of *Crassostrea angulata* and *Ostrea edulis* in the trophic nucleus of the Gore Spit Chenier (Table 1)—see Davis (1965a, 1967) and Barnes and Coughlan (1971) for details regarding the numerical distribution of these species in the Blackwater Estuary; and (2) the open sea benthos as is indicated by the presence of the marine species *Neptunea antiqua* (Linn.) and *Glycimeris glycimeris* (Linn.) in the shell cumulates of the offshore shell bank at Sales Point, Bradwell (TM039091).

The Rarefaction Graphs of the Fauna

The rarefaction graphs for the different habitats (Fig. 2) consistently show a higher diversity dead molluscan fauna associated with a less diverse live molluscan fauna at each sample locality (Table 3), except in the ripple-drifted mud habitat, where both live and dead molluscan shells are only found infaunally in life position and hence have the same faunal diversity. Two other trends were also observed (1) lateral changes in diversity can occur within a habitat, for example the shell, pebble and muddy sand habitat of the Sales Point region (Figs. 2 & 3a), and (2) diversity decreases as the fauna proceeds up the littoral zone as at Gore Spit (Fig. 2 & 3b). However, general diversity gradients may contain a superimposed varietal component since diversity also appears to decrease with decreasing topographic complexity of the

TABLE 2. Rank order distribution of species in corresponding live and dead faunas, for samples of 500 individuals. A key to localities is given in Fig. 2. * Indicates species usually confined to a subtidal habitat in life. Note the differences in species rank orderings presented by the live and dead faunas; also note the high percentages of subtidal species in the dead shell faunas.

	LOCALITIES																									
SPECIES	1L	1D	7L	7D	8L	8D	10L	10D	11L	11D	12L	12D	13L	13D	14L	14D	15L	15D	19L	19D	20L	20D	21L	21D	22L	22D
Abra alba (Wood)*	–	–	–	–	–	–	3	4	–	–	–	–	–	–	–	–	–	–	–	–	–	15	–	–	–	12
Acanthodoris pilosa (Muller)*	–	–	–	–	–	–	10	13	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Barnea candida (L.)	–	–	–	7	–	–	–	–	8	10	–	9	–	–	–	–	3	3	–	9	–	11	–	7	–	8
Buccinum undatum L.*	–	–	–	10	–	10	8	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10
Cardium exiguum L.*	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	–	–	–	7
Cerastoderma edule (L.)	–	3	4	1	–	1	12	–	5	1	–	1	–	1	–	1	4	4	6	1	2	1	6	1	–	1
Chlamys varia (Muller)*	–	–	–	8	–	–	–	8	–	9	–	–	–	–	–	–	–	–	–	–	–	–	–	9	–	–
Crassostrea angulata (Lamarck)*	–	4	–	9	–	–	9	11	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Crepidula fornicata (L.)	–	5	3	5	–	4	1	1	4	3	–	–	–	–	–	–	–	–	–	6	5	6	–	11	4	4
Ensis sp.*	–	–	–	–	–	–	–	–	–	11	–	–	–	–	–	–	–	–	–	–	–	10	–	13	–	–
Gibbula cineraria L.	–	–	–	–	–	–	6	12	–	–	–	–	–	–	–	–	–	–	–	–	–	12	–	–	–	17
Hydrobia ulvae (Penn.)	2	–	9	–	–	3	–	–	–	8	–	–	–	7	–	–	–	–	–	10	–	7	–	6	–	–
H. ventrosa (Mont.)	–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lepidochitona cinereus (L.)	–	–	–	–	–	–	2	–	6	–	3	–	–	–	–	–	–	–	3	–	6	–	5	–	5	–
Littorina littorea (L.)	–	6	1	–	1	6	5	6	1	4	1	3	1	2	1	2	1	1	1	2	4	3	1	3	1	3
L. littoralis (L.)	–	–	–	–	–	–	–	14	–	–	–	–	–	–	–	–	–	–	–	–	7	–	4	–	2	5
L. saxatilis (Olivi)	–	7	6	–	–	–	–	–	3	–	–	8	3	6	3	4	–	–	2	7	–	–	–	–	–	–
Macoma balthica (L.)	1	–	7	4	2	5	–	10	–	5	–	–	–	4	–	–	–	–	5	5	3	4	3	4	–	9
Modiolus modiolus (L.)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9	–	–	–	–
Mya arenaria L.	–	–	5	–	–	9	–	3	–	–	–	–	–	–	–	–	–	–	–	–	8	8	–	–	–	13
M. truncata L.	–	–	–	–	–	–	–	15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mytilus edulis L.	–	1	2	3	–	–	–	–	2	2	2	2	2	3	2	3	–	–	4	4	1	2	2	2	3	2
Nassarius reticulatus L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11
Nucula nucleus (L.)*	–	–	–	–	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ostrea edulis (L.)*	–	2	–	6	–	7	7	–	–	7	–	6	–	8	–	–	–	–	–	8	–	13	–	8	–	6
Petricola pholadiformis (Lamarck)*	–	–	–	–	–	–	–	5	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Scrobicularia plana (da Costa)	3	–	8	2	3	2	–	–	7	6	–	5	–	5	–	–	2	2	–	3	–	5	7	5	–	14
Teredo navilis L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–	–	–
Urosalpinx cinerea (Say)*	–	–	–	–	–	–	11	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	–	15
Venerupis aurea (Gmelin)*	–	–	–	–	–	–	–	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
% species designated by*	0	29	0	40	0	20	50	60	0	27	0	38	0	13	0	0	0	0	0	10	0	27	0	31	0	41

TABLE 3. Species richness variances $E(v)$ and absolute values where $n = 100\,E(d)$ and $n = 500\,E(s)$, and the difference between live and dead fauna expressed in the form (EsL-D) and (EsL-D)/s where s = total number of species present. Key to samples given in Fig. 2. Note (1) that the species richness variance (col. 2) tends to be higher in the dead faunas than in the corresponding live. (2) Less than 50% of the samples showed no increase in the number of species present (col. 6) when the sample size was increased from 100 individuals (col. 4) to 500 individuals (col. 3). (3) The number of species in the live and dead faunas (col. 3) are different (col. 5); these differences tend to be most marked with respect to the total number of species present in a sample (col. 7) which is taken from a habitat low in the intertidal zone (22).

(1) Sample	(2) E(v)	(3) E(s)	(4) E(d)	(5) EsL-D	(6) (Es-Ed)	(7) EsL-D/s
1L	0.634	3.000	3.000		0.000	
1D	0.751	7.000	7.000	4.000	0.000	0.4
2D	0.481	3.000	3.000		0.000	
3D	0.577	3.000	3.000		0.000	
4D	0.459	20.558	14.296		6.262	
5D	0.733	16.902	12.739		4.163	
6D	0.646	10.568	7.908		2.660	
7L	0.822	9.000	9.000		0.000	
7D	0.853	11.000	10.008	3.000	0.992	0.2
8L	0.654	3.000	3.000		0.000	
8D	0.770	9.634	8.327	6.634	1.307	0.7
9L	0.689	6.000	5.914		0.086	
10L	0.459	12.000	10.949		1.051	
10D	0.578	14.488	10.653	2.288	3.835	0.1
11L	0.744	8.000	8.000		0.000	
11D	0.828	11.000	11.000	3.000	0.000	0.2
12L	0.486	3.000	3.000		0.000	
12D	0.715	9.000	8.833	6.000	0.167	0.6
13L	0.297	3.000	3.000		0.000	
13D	0.735	8.000	8.000	5.000	0.000	0.6
14L	0.233	3.000	3.000		0.000	
14D	0.547	5.000	5.000	2.000	0.000	0.5
15L	0.086	4.496	3.389		1.107	
15D	0.646	4.055	4.011	0.441	0.044	0.1
16D	0.254	2.000	2.000		0.000	
17D	0.095	2.000	2.000		0.000	
18D	0.000	1.000	1.000		0.000	
19L	0.393	6.000	5.394		0.606	
19D	0.731	11.994	10.386	5.994	1.608	0.5
20L	0.840	8.000	8.000		0.000	
20D	0.744	15.000	12.949	7.000	2.451	0.4
21L	0.369	8.000	7.156		0.844	
21D	0.772	13.000	12.400	5.000	0.600	0.3
22L	0.718	5.000	5.000		0.000	
22D	0.737	17.272	11.125	12.272	6.147	0.7

environment. For instance the topographically complex inner mudmounds of Sales Point (TM034085 Fig. 2) are more diverse than the less complex ripple drifted muds slightly further offshore (TM037086 Fig. 2). A similar effect has been observed by Kohn (1968) in the Indian Ocean among gastropods of the genus *Conus* in both inter and subtidal habitats and by MacArthur (1964, 1968) among woodland birds.

Conclusions

The chenier plain deposits of the River Blackwater are divided into seven ecological habitats, each of which contain a low diversity molluscan fauna, associated with a slightly higher diversity actively forming shell cumulate. This environment was used to test the validity of two statistical indices which are gaining increasing popularity in palaeoecological studies (the concept of the trophic nucleus and the rarefaction curve) by comparing the local molluscan fauna with its associated shell cumulates. From this comparison a number of points relevant to the palaeoecologist arise.

(1) Rarefaction graphs tend to give a higher diversity value for the associated

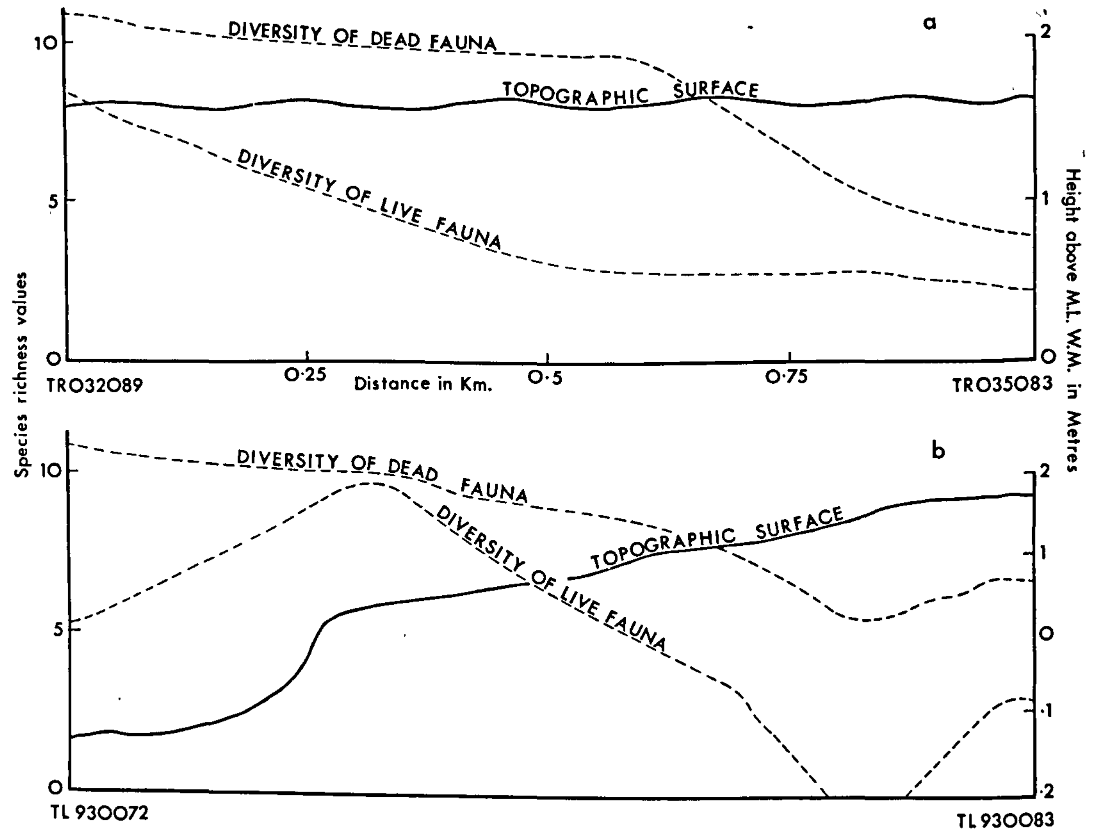

FIGURE 3. The relationship of diversity (species richness) to topography in two areas (where species richness is defined in terms of the number of species per 500 individuals); illustrating (a) variations in diversity within the shell pebble and muddy sand habitat of Sales Point and (b) variations in diversity across the littoral zone at Gore Spit. TR numbers should read as TM.

shell cumulate than they do for the live molluscan fauna. Thus, diversity values produced by the rarefaction method in palaeoecology will tend to overestimate, rather than underestimate, the original diversity of the fauna.

(2) Changes in molluscan diversity of the local fauna, recorded by rarefaction methods, tend to mirror similar diversity changes in the associated shell cumulates.

(3) The composition of the trophic nucleus of the indigenous fauna is often very different from that suggested by the associated shell cumulates.

Thus it would appear from this study that the palaeoecologist studying a fossil chenier could be reasonably confident in interpreting diversity changes but not so in interpreting the trophic nuclei of the fauna.

Acknowledgments

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Literature Cited

ANTIA, D. D. J. AND B. A. WOOD. 1977. Some aspects of the palaeoecology of the E_1b zone of the Edale Shales (Namurian) in the Edale Valley, Derbyshire. Mercian Geol. *6*(3):~~In Press.~~ p.179-196.

BARBOUR, D. S. AND J. H. BROWN. 1974. Fish species diversity in lakes. Am. Nat. *108*:473–489.

Barnes, R. S. K. and J. Coughlan. 1971. A survey of the bottom fauna of the Blackwater Estuary: 1970. Essex Nat. *32*:263–276.

Boesch, D. F. 1971. Distribution and structure of benthic communities in a gradient estuary. Ph.D. Dissertation. Virginia Institute of Marine Science; Virginia.

Calef, C. E. 1972. Palaeoecological and stratigraphical studies of the Ludlow in Wales and the Welsh Borderlands. Ph.D. Thesis. Oxford University; Oxford.

Calef, C. E. and N. J. Hancock. 1974. Wenlock and Ludlow marine communities in Wales and the Welsh Borderland. Palaeontology. *17*:779–810.

Clifford, H. T. and W. Stephenson. 1975. An Introduction to Numerical Classification. 229 pp. Academic Press; London.

Curtis, J. T. 1959. The Vegetation of Wisconsin. 657 pp. University of Wisconsin Press; Madison, Wisconsin.

Davis, D. S. 1964. The physical and biological features of the Mersea flats. Central Electricity Research Lab. Note No. RD/L/NI31/164. 14 pp.

Davis, D. S. 1965a. A study of the bottom fauna of the Blackwater Estuary: 1960–1963. Central Electricity Research Lab. Report No. RD/L/R 1300. 54 pp.

Davis, D. S. 1965b. Biology of the Bradwell shore. Central Electricity Research Lab. Note No. RD/L/N 3/65. 24 pp.

Davis, D. S. 1965c. The biological effects of Bradwell power station: precommissioning studies on the fauna of Bradwell Creek. Central Electricity Research Lab. Note No. RD/L/N 2/65. 18 pp.

Davis, D. S. 1967. The marine fauna of the Blackwater Estuary and adjacent waters, Essex. Essex Nat. *32*:2–61.

Davis, D. S. and G. M. Milligan. 1964. Bradwell biological investigations: seaweeds of the Blackwater Estuary. Central Electricity Research Lab. Note No. RD/L/N 41/64. 20 pp.

Duff, K. L. 1975. Palaeoecology of a bituminous shale—the Lower Oxford Clay of central England. Palaeontology. *18*:443–482.

Fager, E. W. 1972. Diversity, a sampling study. Am. Nat. *106*:293–310.

Fursich, F. T. 1977. Corallian (Upper Jurassic) marine benthic associations from England and Normandy. Palaeontology. *20*:337–386.

Greensmith, J. T. 1977. Carbonate bodies in Essex marshlands. Geol. Soc. London. News Letter. *6*(2):22.

Greensmith, J. T. and E. V. Tucker. 1967. Morphology and evolution of inshore shell ridges and mudmounds on modern intertidal flats, near Bradwell, Essex. Proc. Geol. Assoc. *77*:329–346.

Greensmith, J. T. and E. V. Tucker. 1975. Dynamic structures in the Holocene chenier plain setting of Essex, England. Pp. 251–272. In: Hails, J. and A. Carr, eds. Nearshore Sediment Dynamic and Sedimentation.

Greensmith, J. T., R. G. Blezard, C. R. Bristow, R. Markham, and E. V. Tucker. 1973. The Estuarine Region of Suffolk and Essex. Geol. Assoc. Guide No. 12, 41 pp.

Harris, B. 1959. Determining bounds on integrals with application to cataloguing problems. Ann. Math. Stat. *30*:521–548.

Heck, K. L., G. V. Belle, and D. Simberloff. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. Ecology. *56*:1459–61.

Hurlbert, S. H. 1971. The non-concept of species diversity: A critique and alternative parameters. Ecology. *52*:557–586.

Kohn, A. J. 1968. Microhabitats abundance and food of *Conus* on atoll reefs in the Maldive and Chagos Islands. Ecology. *49*:1046–1062.

Lawson, J. D. 1975. Ludlow Benthonic Assemblages. Palaeontology. *18*:509–525.

MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. Am. Nat. *98*:387–397.

MacArthur, R. H. 1968. The theory of the niche. In: Lewontin, R. C., ed. Population Biology and Evolution. Syracuse Univ. Press; Syracuse, New York.

Neyman, A. A. 1967. Limits to the application of the Trophic group concept in benthonic studies. Oceanol. Acad. Sci. U.S.S.R., *7*:149–155.

Pickerill, R. R. 1976. Significance of a new fossil locality containing a Salopina community in the Waweig Formation (Silurian-uppermost Ludlow/Pridoli) of South West New Brunswick. Can. J. Earth Sci. *13*:1328–31.

Porter, J. W. 1972. Predation by *Acanthaster* and its effect on coral species diversity. Am. Nat. *106*: 487–492.

Price, W. A. 1955. Environment and formation of the chenier plain. Quaternaria. *2*:75–86.

Raup, D. M. 1975. Taxonomic diversity estimation using rarefaction. Paleobiology. *1*:333–342.

Rhoads, D. C., I. G. Speden, and K. M. Waage. 1972. Trophic group analysis of Upper Cretaceous (Maestrichtian) bivalve assemblages from South Dakota. Bull. Am. Assoc. Petrol. Geol. *56*:1100–1113.

Sanders, H. L. 1968. Marine Benthic diversity: a comparative study. Am. Nat. *102*:243–282.

Sanders, H. L. and R. R. Hessler. 1969. Ecology of the deep sea benthos. Science. *163*:1419–1424.

Schopf, T. J. M., ed. 1972. Models in Paleobiology. 250 pp. W. H. Freeman and Co.; San Francisco.

Scott, R. W. and R. R. West. 1976. The structure and classification of palaeocommunities. Hutchinson & Ross; Stroudsburg, Pennsylvania.

Simberloff, D. 1972. Properties of the rarefaction diversity measurement. Am. Nat. *106*:414–418.

Slobodkin, L. B. and H. L. Sanders. 1969. On the contribution of environment predictability to species diversity. Pp. 71–81. In: Woodwell, G. M. and H. H. Smith, eds. Diversity and Stability in Ecological Systems. Brookhaven Sympos. Biol. 22; Upton, New York.

Stanton, R. J. and I. Evans. 1972. Community structure and sampling requirement in paleoecology. J. Paleontol. *46*:845–858.

STOUT, J. AND J. VANDERMEER. 1975. Comparison of species richness for stream inhabiting insects in tropical and mid latitude streams. Am. Nat. *107*: 295–302.

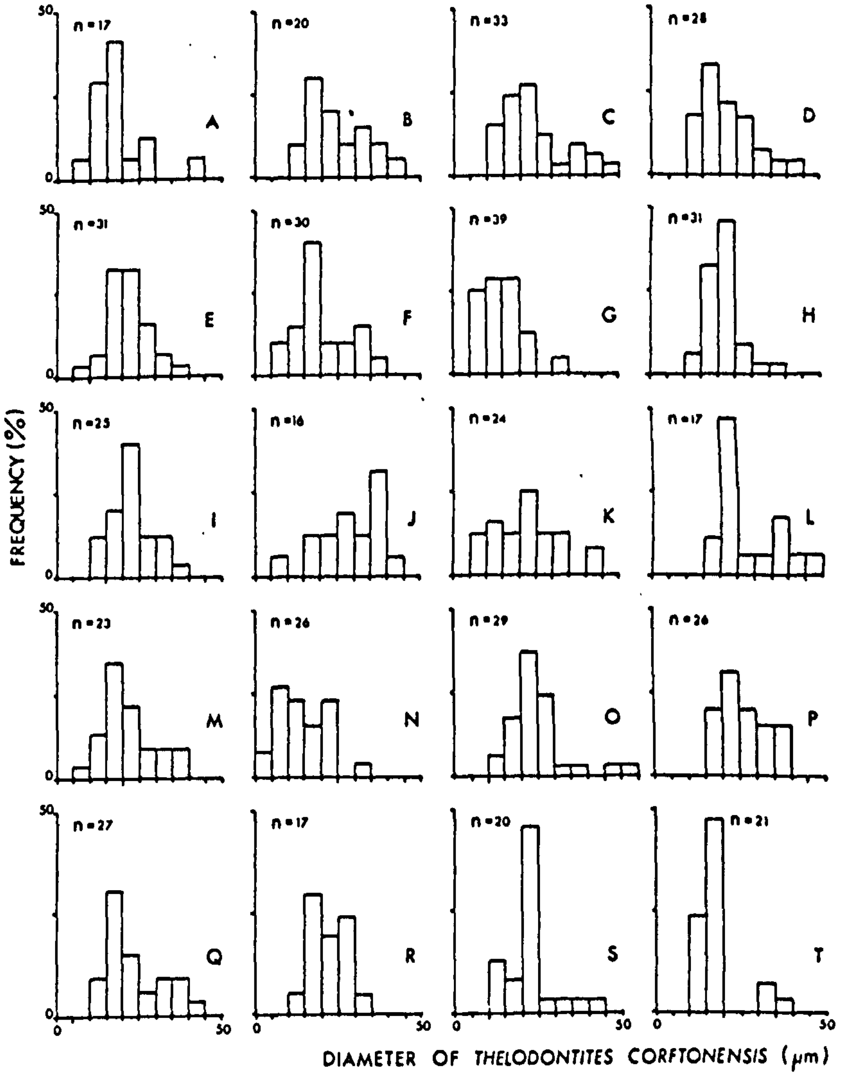
TURPAEVA, E. P. 1948. The feeding of some benthic invertebrates of the Barents Sea. Zool. Zh. Ukr. 27.

VALENTINE, J. W. 1973. Evolutionary palaeoecology of the marine biosphere. 510 pp. Prentice-Hall; New Jersey.

WALKER, K. R. 1972. Trophic analysis: a method for studying the function of ancient communities. J. Paleontol. *46*:82–93.

WATKINS, R. 1978. Benthic community organisation in the Ludlow series of the Welsh Borderland. Bull. Brit. Mus. In Press.

YOUNG, D. K. AND D. C. RHOADS. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. I. A transect study. Mar. Biol. *11*:242–254.



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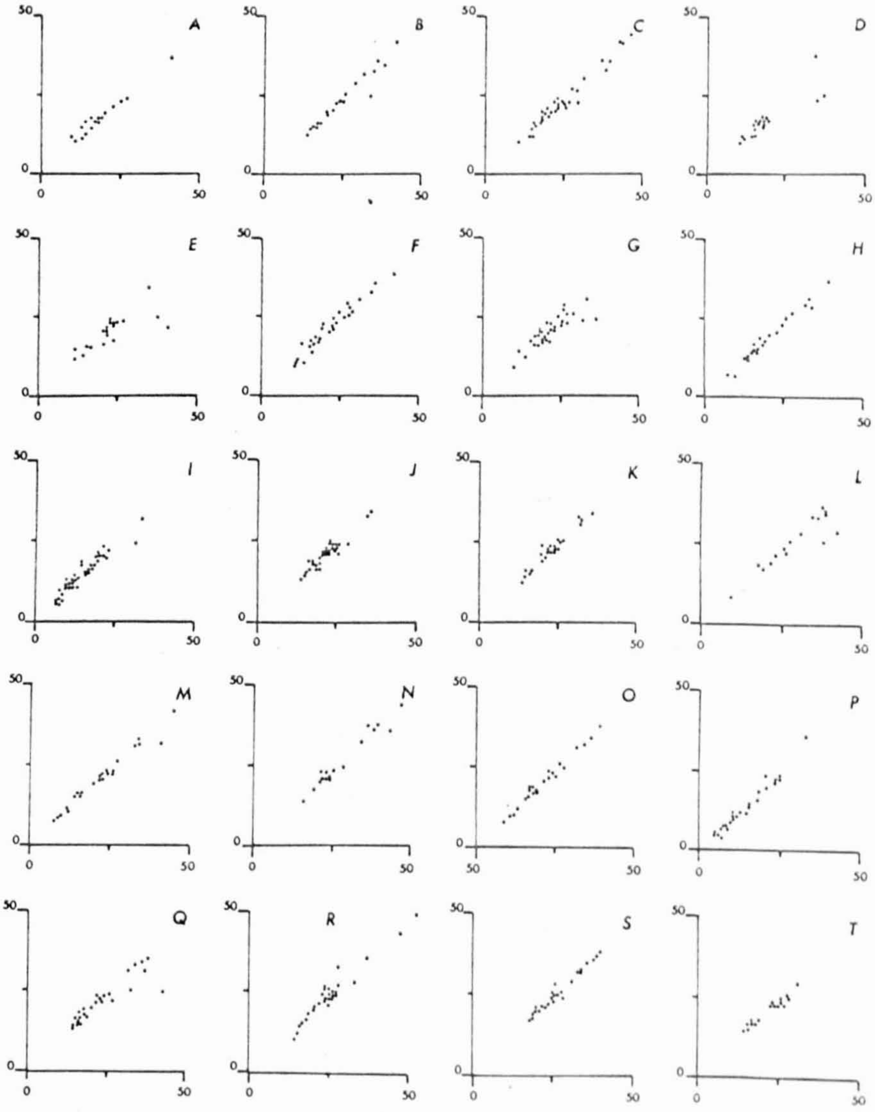
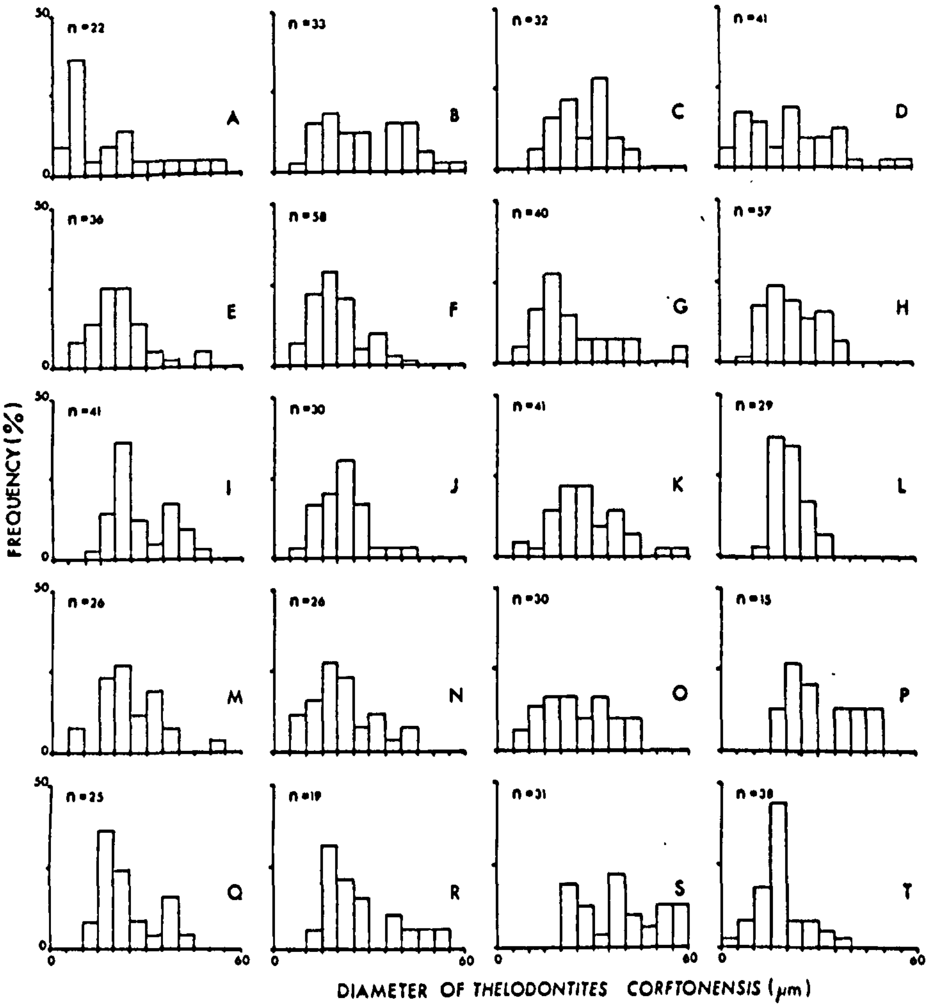
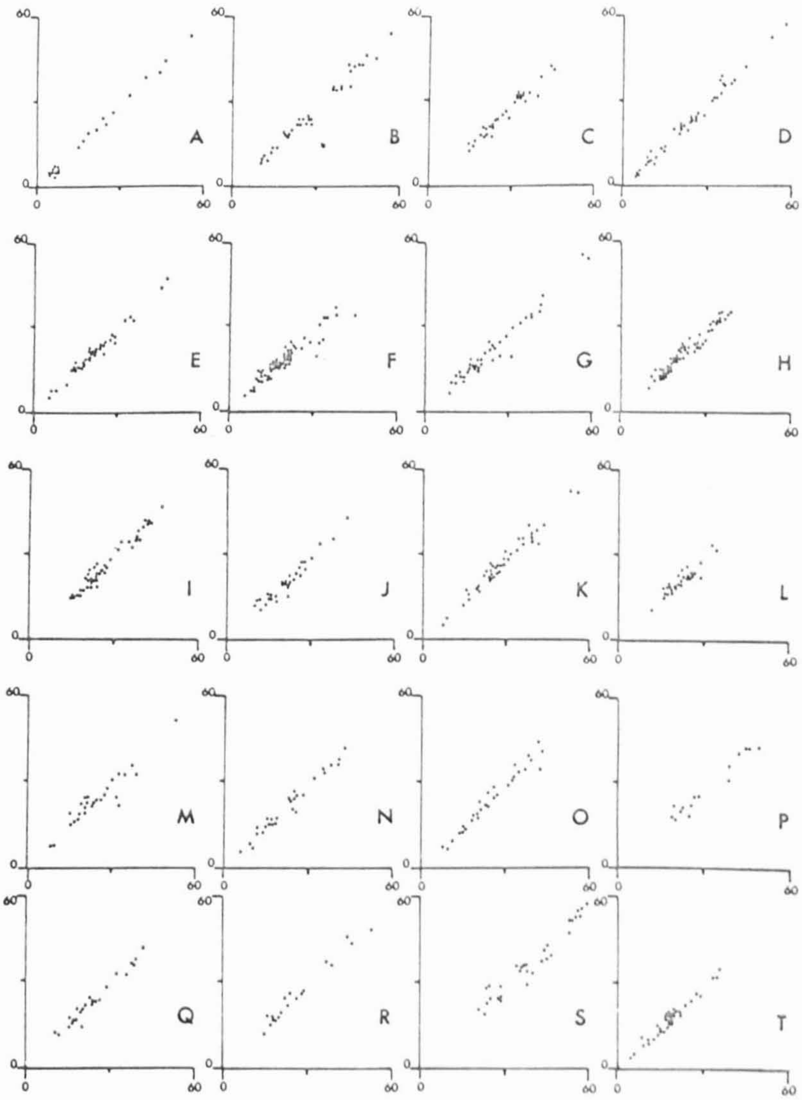


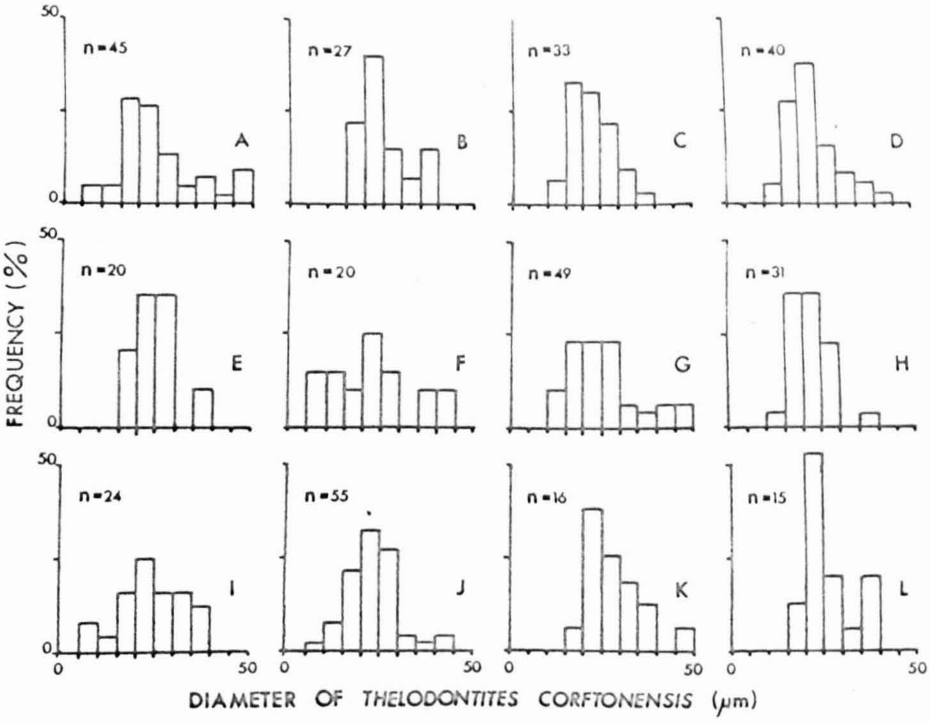
Plot of maximum length against width of *Thelodontites corftonensis* on 20 scales of *Thelodus parvidens* from the Ludlow Bone-Bed at Priors Frome.



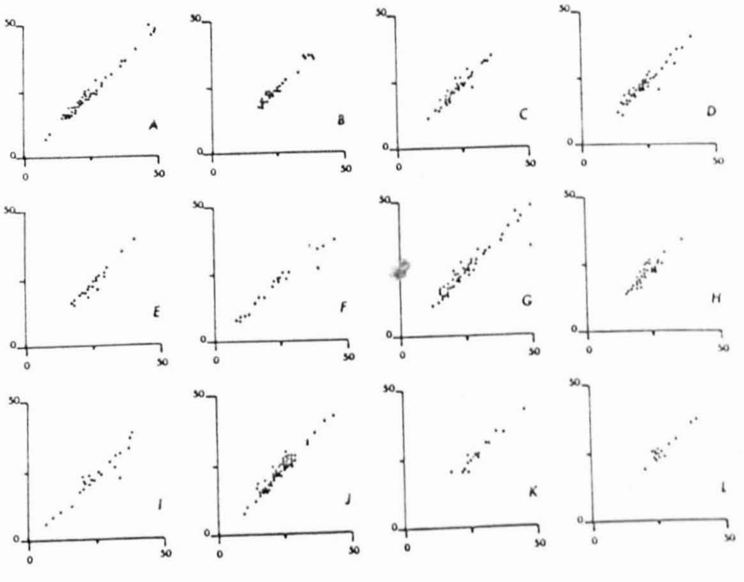
Size/Frequency histograms for Thelodontites corftonensis borings on 20 Thelodus parvidens scales, from the Ludlow Bone-Bed at Corfton. Further details of these borings are given in paper 11.



Plot of maximum length against width of *Thelodontites corftonensis* on 20 scales of *Thelodus parvidens* from the Ludlow Bone-Bed at Corfton.



Size/Frequency histograms for Thelodontites corftonensis borings on 12 Thelodus parvidens scales from the Ludlow Bone-Bed at Ludlow.



Plot of maximum length against width of Thelodontites corftonensis on 12 scales of Thelodus parvidens from the Ludlow Bone-Bed at Ludlow.

THE SURFACE TEXTURES OF QUARTZ GRAINS FROM A RHAETIAN BONE-BED, BLUE ANCHOR BAY, SOMERSET

BY D. D. J. ANTIA AND J. H. SYKES

MERCIAN GEOLOGIST VOL. 7 No. 3 1979 pp. 205-210,
TEXT FIG. 1, PLATE 23

THE SURFACE TEXTURES OF QUARTZ GRAINS FROM A RHAETIAN BONE-BED, BLUE ANCHOR BAY, SOMERSET.

by

D.D.J. Antia and J.H. Sykes

Summary

The surface textures of detrital quartz grains in a Rhaetian bone-bed at Blue Anchor Bay, Somerset, have been investigated using a scanning electron microscope. The results show that there is a systematic change from the base to the top of the bed in the nature of the textures displayed by the quartz grains. Those from the basal clay-rich parts of the bed feature solution pits, while grains from the upper clay-poor parts of the bed display well developed euhedral overgrowths. The differences are attributed to *in-situ* diagenesis.

Introduction

Quartz grains in Rhaetian bone-beds are usually abraded and well rounded. They have been recorded from many localities, ranging across England and Wales, including Barnstone (Nottinghamshire), Barrow-upon Soar (Leicestershire), Westbury (Gloucestershire), Chilcompton (Somerset) and Lavernock (Glamorgan). Further examples including locality details have been presented by Sykes (1977). Rare bipyramidal quartz crystals have been recorded from Rhaetian bone-beds (Kent, 1970, p.365) at a number of localities including Barnstone (Duffin, 1978, pers. com.) and Blue Anchor Bay (Antia, 1979a, pl.18, fig.f). Such crystals arise as the result of quartz overgrowths around an original quartz nucleus. They have been recorded from a number of bone-beds including those of the Silurian in Britain (Antia & Whitaker, 1978, pp.121, 123-127; Antia, 1979a, pp.115, 169) and bone-beds in the Devonian of the U.S.A. (Wells, 1944, p.283).

In Silurian bone-beds (e.g. the Ludlow Bone-Bed) some of the euhedral crystals predate the formation of the deposit and bear surface abrasion features (Antia & Whitaker, 1978, pp.132, 133, 135, 136). Others have no abrasion features and nucleate around quartz grains, suggesting that they have grown in the bone-bed after its deposition. At the present time there are no adequate descriptions of euhedral quartz crystals from a Rhaetian bone-bed and consequently it is not known if they were reworked from a previous sediment or whether they have grown *in-situ* in the bone-bed. Reworked grains should be identified by their abraded surfaces.

Conversely, if the quartz euhedra were precipitated in the sediment after it was deposited, then a complete continuum ranging from original quartz grains and silica coated quartz nuclei through to perfect euhedral quartz crystals could be expected to occur, in which quartz euhedra increase in abundance towards the more porous base or top of the deposit. If, however, the relative abundances of the various diagenetic quartz morphotypes remain constant throughout the deposit then they could either have been derived from an older deposit (cf. Wilson, 1979) or have formed as diagenetic precipitates within the bone-bed. This study seeks to determine which of the explanations is most applicable to the quartz euhedra in the bone-bed under review.

Stratigraphy

Exposures of the Rhaetian beds at Blue Anchor Bay have been described by Richardson (1911, p.17) and also by Elliot (1953) and Macfayden (1970, p.225). Richardson recorded three bone-beds: 'Basal Bone-bed' (no. 33), 'The Clough' (no. 27) and 'The Bone-bed' (no. 15) near the top of the Westbury beds.

In a recent investigation into the nature of British Rhaetian bone-beds (Sykes, 1977), a large number of quartz crystals were noticed in part of the uppermost bone-bed (Richardson's bed 15) at Blue Anchor Bay (ST 042432). This bone-bed is 0.28 m thick and has been divided into five distinct parts (Table 1) (Sykes, 1977, p.231). Samples from parts 'a, c, d, & e' were disaggregated in acetic acid, washed and dried. The finer particles were removed by washing the grains in petroleum spirit and the coarser fraction (above 250 microns) separated by sieving. Several random samples were taken from each part and examined under a binocular microscope. The number of grains in each sample were counted in respect to their possession or lack of crystal faces also with regards to the amount of crystalline pyrite present. In each part of the bed averages of the relative contents were calculated over the various samples and the amounts expressed in percentages (table 2).

Scanning electron microscope (S.E.M.) analysis

Fifty quartz grains were randomly selected from each part of the bed listed in Table 2. These grains were then mounted on the S.E.M. stubs with either silver dug (parts d & e) or Pritt (parts a & c) and gold splatter coated to a thickness of 350 Å. The grains were then examined on a Cambridge 600 S.E.M.. After examination the grains were removed from the stubs and cleaned using first acetone and then hydrogen peroxide. The majority of the grains are now deposited with the Ludlow Museum; specimen nos. SHRCM G05501-4.

Most of the external surfaces of the quartz grains were covered by diagenetic overgrowths which appear to have been precipitated on more rounded quartz nuclei. Some of the grains are affected by silica solution which has removed the primary abrasive features and caused pitting. The exoscopic features of the grains are described as follows.

1. Primary crystal overgrowths, pl.23, figs.1,2 & 3

Many of the quartz grains observed from parts 'd' and 'e' possess euhedral crystal faces. These vary in shape from compact grains to elongate, bipyramidal, euhedral crystals, some of which have prism faces. Some of the compact grains have crystal faces without a clear crystallographic orientation, while some of the more euhedral grains have prism faces which are poorly defined or are smothered by bulbous overgrowth.

The quartz grains show three stages of diagenetic overgrowth around an original, compact spheroidal quartz grain (text-fig. 1, fig.A).

a Silica sheet layering on the external surface of the grain (pl. 23, fig.7, text-fig.1, fig.B). These sheets are in optical continuity with the host quartz grain.

b Polarisation of quartz growth to produce a c-axis aligned along the quartz grain and to allow development of pyramidal crystal faces at either end of the grain (pl.23, fig.3, text-fig.1, fig.C).

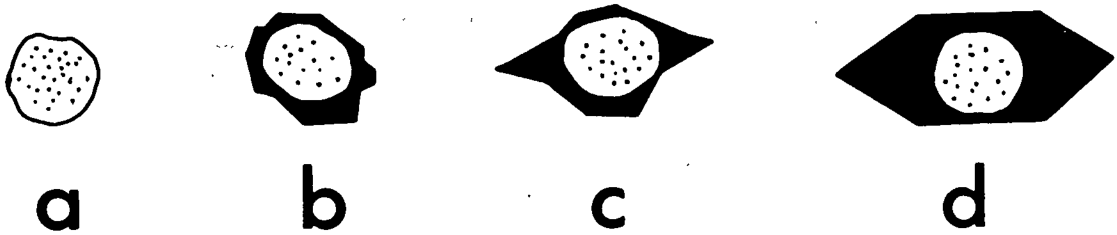
c Enlargement of the pyramidal faces until the pyramid diameter equals or exceeds the grain diameter. This is followed by development and growth of the prism faces (text-fig.1, fig.D).

Table 1. Description of bone-bed, parts 'a' to 'e'

Part	Thickness	Description
e	up to 120 mm	A massive, calcareous sandstone, enriched in vertebrate remains.
d	50 mm	A calcareous sandstone, enriched in vertebrate remains and containing thin layers of black shale limestone.
c	70 mm	Alternating layers of black shales and sandstones with vertebrate remains.
b	up to 30 mm	A layer of 'beef' calcite ($CaCo_3$).
a	18 mm	A calcareous, sandy bone-bed containing shell and silt laminae.

Table 2. Distribution of crystalline pyrite and quartz crystal faces in the coarse fraction of the bone-bed

Part	Without crystal faces	With crystal faces	Crystalline pyrite
e	23%	74%	3%
d	33%	62%	5%
c	73%	19%	8%
a	94%	0%	6%



Text-fig. 1. Deduced stages in the development of quartz euhedra

Fig. a. Original quartz grain (shape unknown).

Fig. b. Quartz grain coated with silica sheets producing crystal faces on the grain's surface (most common in parts 'a' and 'c').

Fig. c. Polarisation of crystal growth and the development of crystal faces (most common in parts 'd' and 'e').

Fig. d. Development of prism faces connecting the pyramid faces (most common in parts 'd' and 'e').

2. Secondary crystal overgrowths (pl.23, figs.6 & 8)

On one quartz grain from part 'e', a small euhedral crystal growth was observed encrusting a primary overgrowth crystal face (pl. 23, fig.8). On another grain from the same part of the bed a more complex pattern of secondary crystal overgrowth was observed (pl.23, fig.6). On some grains the growth of silica sheets appears to post-date the development of euhedral crystal faces within the bone-bed (pl.23, figs.4,7 & 9).

3. Diagenetic solution (pl.23, fig.5)

Silica solution features are present throughout the bone-bed though they are most pronounced at its base, in part 'a'. A thin section of this part (Sykes, 1977, pl.16, fig.5) shows that most of the silica solution features appear to be related to the growth of the calcite matrix during 'late' diagenesis.

Typical examples of pitting due to silica solution within the bone-bed are illustrated in pl.23, fig.5.

Discussion

The association of pyrite, apatite and black shale has been noted in bone-beds throughout the geological record and may indicate the presence of high negative Eh (-200 to -300) and a pH of 6 to 8 in the sediment pore waters during diagenesis (Baturin, 1971, p.61; Burnett, 1977, p.820-821; Antia, 1979a, pp.107, 124). If this sediment was also undersaturated with respect to Ca^{2+} and CO_3^{2-} ions, then diagenetic gypsum and/or quartz may have precipitated within the sediment (Burnett, 1977, p.821; Briskin and Schreiber, 1978, pp.47-48; Antia, 1979b, p.M1, M3).

Observations (Sykes, 1977, p.232) show that the mean grain size of the sand fraction of the bone-bed increases upwards. This trend, coupled with a decrease in its clay and limestone content towards its top (Sykes, 1977, p.231), shows that the initial post-depositional porosity of the bone-bed also probably increased towards its top. The increase in porosity coincides with a change in quartz grain shape (Table 2) and a decrease in the incidence of solution features.

A possible explanation is that silica was removed from some of the quartz grains and clay minerals in the bone-bed by upward percolating pore waters and concentrated in the upper porous layers of the bone-bed beneath the overlying impervious clays. In this context it is interesting to note that clay minerals may actually enhance solutions of quartz (see Blatt, Middleton & Murray, 1972; Pettijohn *et al.*, 1972) and that the presence of a clay mineral matrix will inhibit growth of cement. The pore water solutions may then have become supersaturated with respect to silica and precipitated as silica sheets in the lower porosity layers of the bone-bed (parts 'a' and 'c') and quartz crystals in the higher porosity layers (parts 'd' and 'e'). Silica may also have been derived from the impermeable clays overlying and underlying the bone-bed.

Elsewhere in the geological column similar relationships appear to occur between porosity and quartz crystal growth. For example, the Ludlow Bone-Bed at Netherton (King & Lewis, 1912) grades upwards from vertebrate rich clays to a vertebrate sand (Antia, 1979b). These vertebrate sands had a higher initial porosity than the vertebrate rich clays and the contain diagenetic, euhedral, quartz crystals. Such crystals are not present in the lower porosity clays.

Conclusions

The quartz grains in a Rhaetian bone-bed at Blue Anchor Bay, Somerset, have diagenetic quartz overgrowths. These overgrowths are restricted to silica sheets in the lower porosity, vertebrate rich clays and limestones but form euhedral crystal overgrowths in the higher porosity, vertebrate rich quartz sands of the upper layers of the bone-bed.

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References

ANTIA, D.D.J. 1979a. Bone-beds: A review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering and microbiotas. *Mercian Geol.*, vol.7, pp.93-174.

ANTIA, D.D.J. 1979b. Authigenic gypsum in marine sediments - a comment. *Marine Geol.*, vol.32, pp.M1-M4.

ANTIA, D.D.J. & WHITAKER, J.H. McD. 1978. A scanning electron microscope study of the genesis of the Upper Silurian Ludlow Bone-Bed. In W.B. Whalley (ed.) *Scanning Electron Microscopy in the study of sediments*. Geo. Abstracts Ltd., Norwich, pp.119-136.

BATURIN, G.N. 1971. Stages of phosphorite formation on the sea floor. *Nat. Phys. Sci.*, vol.232, pp.61-62.

BLATT, H., MIDDLETON, G. & MURRAY, R. 1972. *Origin of sedimentary rocks.* Prentice Hall, New Jersey, 634 p.

BRISKIN, M. & SCHREIBER, B.C. 1978. Authigenic gypsum in marine sediments. *Marine Geol.*, vol.28, pp.37-49.

BURNETT, W.C. 1977. Geochemistry and the origin of phosphorite deposits from off Peru and Chile. *Bull. Geol. Soc. Amer.*, vol.88, pp.813-823.

ELLIOT, G.F. 1953. The conditions of formation of the Lower Rhaetic at Blue Anchor Bay, Somerset, and the Western European Rhaetic generally. *Proc. geol Soc. Lond.*, vol.64, pp.32-35.

KENT, P.E. 1970. Problems of the Rhaetic in the Midlands, *Mercian Geol.*, vol.3, pp.361-373.

KING, W.W. & LEWIS, W.J. 1912. The uppermost Silurian and Old Red Sandstone of South Staffordshire. *Geol. Mag.*, vol.49, pp.437-443, 484-491.

MACFAYDEN, W.A. 1970. *Geological highlights of the West country*, 296 p.

PETTIJOHN, F.J., POTTER, P.E. & SIEVER, R. 1972. *Sand and Sandstone.* Springer-Verlag, New York, 618 p.

RICHARDSON, L. 1911. On the Rhaetic and contiguous deposits of West, Mid. and East Somerset. *Q. Jl geol. Soc. Lond.* vol.67, pp.1-72.

SYKES, J.H. 1977. British Rhaetic Bone-beds. *Mercian Geol.*, vol.6, pp.197-240.

WELLS, J.W. 1944. Middle Devonian Bone-beds of Ohio. *Bull. Geol. Soc. Am.*, vol.55, pp.273-302.

WILSON, P. 1979. Surface features of quartz and grains from the Brassington Formation. *Mercian Geol.*, vol.7, pp.19-30.

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Explanation for Plate 23

1 - 9 Quartz grains and surfaces from a Rhaetian Bone-Bed at Blue Anchor Bay

1 Angular, compact, high sphericity grain (x 150).

2 Modified, compact grain, showing the development of crystal faces (x 80).

3 Compact grain completely enclosed within a quartz overgrowth (x 80).

4 Silica sheeted surface (x 600).

5 Silica surface showing solution pits (x 600).

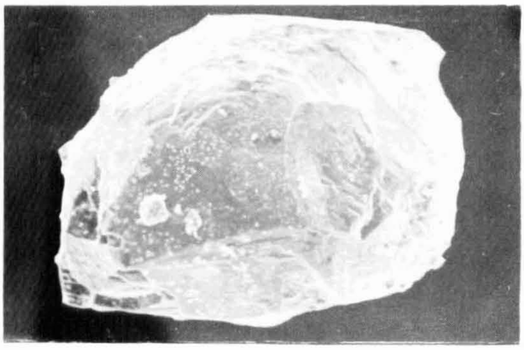
6 Quartz overgrowth on a grain (x 500).

7 Silica sheeting on a grain surface (x 600).

8 Quartz overgrowth on a grain surface (x 1000).

9 Silica sheeting on a grain surface - note the various angles of the sheet faces (x 700).

Plate 23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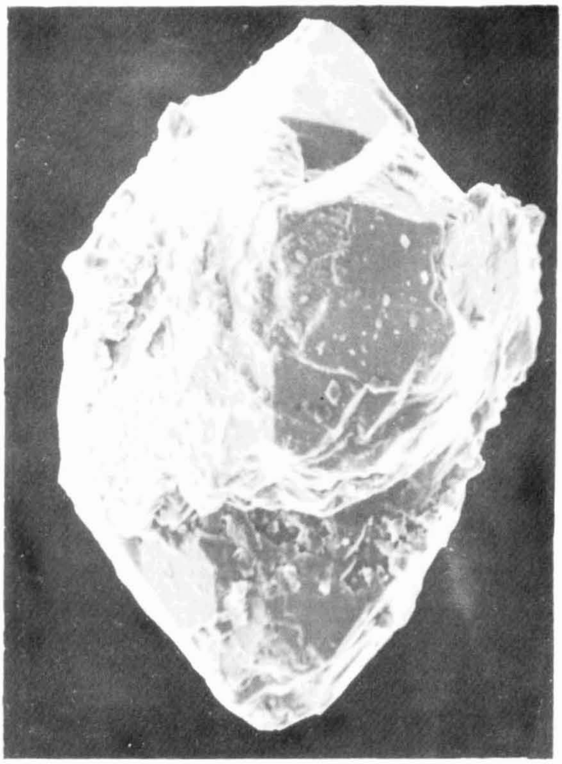
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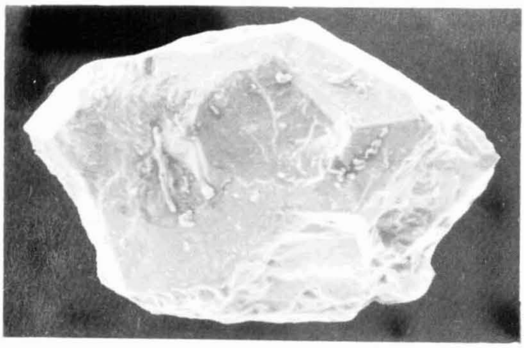
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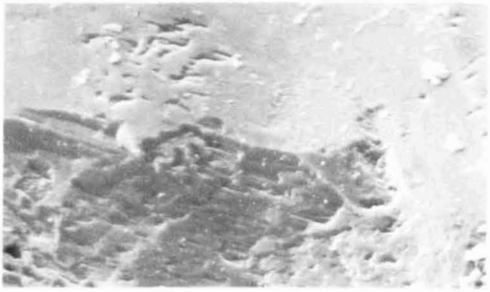
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Antia & Sykes-surface textures of quartz grains.

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Comments on the environments and faunas across the Ludlovian-Downtonian Boundary (Upper Silurian) at Siefton, Salop

David D. J. Antia

A new temporary section across the Ludlovian-Downtonian boundary (Upper Silurian) at Siefton (Nr Craven Arms), Salop, England, is described. The sediments present in the section were deposited in both intertidal and subtidal marine environments. The shelly faunas across the section are recorded and considered to be transported assemblages. Both burrowing and boring trace fossils occur in the presumed subtidal environments. Evidence for a late Whitcliffian marine transgression, following a marine regression is presented.

During August 1977 a temporary roadside trench produced in the course of extensive road repairs at Siefton (GR. SO 475833–478835) exposed the Ludlow-Downton boundary (Upper Silurian). The faunas and sediments present in the trench section were recorded and are described here in Tables 1 and Figure 1. The section observed contained a vertical thickness of 6.14 m of sediment (Fig. 1) and extends from the Upper Whitcliffe Beds (Upper Ludlovian) into the Downton Castle Formation (basal Downtonian).

The first appearance of the ostracod *Frostiella groenvalliana* is taken to indicate the base of the Downtonian in the section (cf. Martinsson 1967; Shaw 1969). This species makes its first appearance in the section about 1·4 m below its top and indicates that the Ludlovian–Downtonian boundary occurs at this point in the section. The fauna (Table 1) above the boundary is of typical Downtonian aspect (cf. Elles and Slater 1906), while the fauna (Table 1) below contains some species (e.g. *Lingula minima* and *Londinia kiesowi*) which are commonly found in the Downtonian (see Elles and Slater 1906; Shaw 1969), as well as typical Whitcliffian forms (cf. Holland, Lawson and Walmsley, 1963).

The sediments recorded in this section (Fig. 1) can be assigned to four facies.

Facies A—Lenticular bedded silts and clays (sensu Reineck and Singh 1973), containing well sorted shell sheets composed almost entirely of a single species. For example one shell sheet contained *Pteronitella retroflexa* shells covering about 80% of the substrate. These shells had a leptokurtosic size distribution (Fig. 2a). Some wavey bedding (sensu Reineck and Singh 1973) is also present in the facies. The lenticular bedded nature of the sediments indicates that they were deposited in a tidally influenced environment (Reineck and Singh 1973 p. 101) in which periods of tidal currents alternated with periods of quiescent or slack water. The

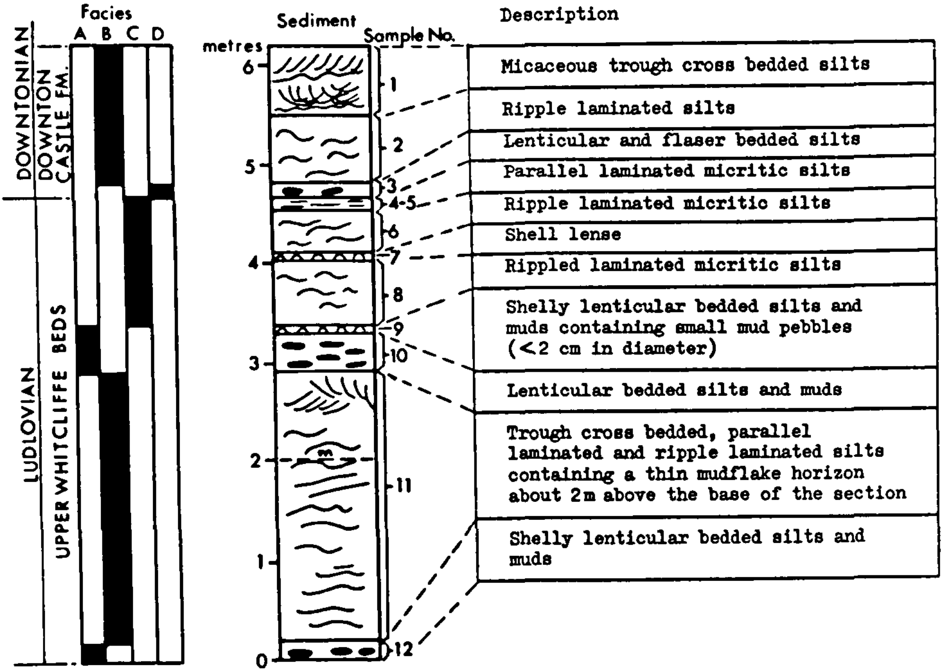

Fig. 1. Distribution of sediments and facies across the Ludlovian/Downtonian boundary at Siefton. Sample Nos. refer to the faunal collections in Table 2. An explanation of the facies is given in the text.

climbing ripple lamination effect produced by the lenticular bedding, contains in-drift ripple laminae (sensu McKee 1965) in which the ripple stoss side is absent and its lee side is preserved, suggesting that the suspension load/bed load ratio was low (cf. Jopling and Walker 1968). The ripple trough/crest axes were striking at angles of between 200° and 245°. Local erosion surfaces are common and these are frequently densely strewn with concave down orientated shells. The shell cover of the substrate on these layers varies from 65 to 90%.

Frequently the original structure of the sediment has been destroyed by bioturbation. The most abundant trace fossil types can be referred to the ichnogenera ?*Chondrites*, ?*Dendrotichium* and ?*Lophoctenium*. However a number of burrows (Fig. 1b, c) not unlike the three dimensional burrows produced by modern annelids (cf. Ronan 1977), are present in the facies. These burrows (Fig. 2b, c) have a burrow diameter of between 1 and 2 mm, a burrow height of between 15 and 30 mm, a burrow complex width of between 10 and 25 mm, a burrow complex length of between 20 and 35 mm and between 4 and 10 terminal shafts. These burrows were probably produced by a deposit feeding 'polychaete worm', 2 to 5 cm in length (M. Pye, personal communication). It may be that many of the traces doubtfully assigned here to the ichnogenera *Lophoctenium*, *Chondrites* and *Dendrotichium* were formed by these 'polychaetes' during their reworking (for food) of the uppermost 5–10 cm of the contemporary sediment substrate. These polychaete burrow complexes occur in densities of between 200 and 350 per metre square of bedding plane surface area.

Table. 1. Fossils across the Ludlow/Downton boundary at Siefton. Numbers indicate the frequency of occurrence of shells and shell fragments. See Fig. 1 for the position of each layer in the section.

SPECIES	DOWNTON							LUDLOW SERIES				
						LAYER						
	1	2	3	4	5	6	7	8	9	10	11	12
Brachiopods												
Craniops implicatus (J. de C. Sowerby)	—	—	—	—	—	—	2	—	—	—	—	2
Howellella elegans (Muir-Wood)	—	—	—	—	—	—	4	—	2	—	—	44
Lingula sp.	—	—	—	—	—	—	—	—	—	1	—	—
Lingula minima (J. de C. Sowerby)	82	119	112	—	—	—	—	—	—	—	11	—
Microsphaeridiorhynchus nucula (J. de C. Sowerby)	—	—	—	—	1	2	27	—	13	35	—	18
Orbiculoidia rugata (J. de C. Sowerby)	—	—	1	—	—	—	—	—	—	—	—	1
Protochonetes ludloviensis (Muir-Wood)	—	—	—	—	36	—	305	—	159	303	—	3
Salopina lunata (J. de C. Sowerby)	—	—	—	—	3	—	38	—	24	64	—	36
Bivalves												
Goniophora cymbaeformis (J. de C. Sowerby)	—	—	—	—	—	—	—	—	2	—	—	—
Modiolopsis complanata	2	—	2	—	1	—	—	—	—	—	—	—
Pteronitella retroflexa (Wahlenberg)	—	—	—	—	—	—	—	—	—	1	—	29
Fuchsella amygdalina (J. de C. Sowerby)	—	—	—	—	—	—	—	—	—	9	—	4
Solenomya sp.	—	—	—	—	—	—	—	—	—	—	4	—
Gastropods												
Loxonema gregarium (J. de C. Sowerby)	1	—	—	—	—	2	—	—	—	—	—	—
?*Umbospira helicites* (J. de C. Sowerby)	—	—	1	—	—	—	—	—	—	—	—	—
Cephalopods												
Leurocycloceras sp.	—	—	—	—	—	—	—	—	—	—	—	2
Eurypterids												
Hughmilleria sp. (?)	—	—	—	—	—	—	—	—	—	—	1	—
Pterygotus sp.	—	3	12	—	—	—	—	—	—	—	1	—
Ostracods												
Calcaribeyrichia torosa (Jones)	1	—	—	—	—	—	—	—	—	—	—	—
Cytherellina siliqua (Jones)	1	1	3	—	—	—	—	—	—	—	—	—
Nyhamnella naturalis (Sarv)	—	—	1	—	—	—	—	—	—	—	—	—
Londinia kiesowi Krause	—	—	9	—	—	—	—	—	—	—	1	—
Frostiella groenvalliana Martinsson	7	—	18	—	—	—	—	—	—	—	—	—
Cavelina sp.	1	—	—	—	—	—	—	—	—	—	—	—

Table 1.*–cont.*

SPECIES	DOWNTON			LUDLOW SERIES								
	LAYER											
	1	2	3	4	5	6	7	8	9	10	11	12
Bryozoans												
Leioclema sp. (colonies)	—	—	—	—	—	—	—	—	—	1	—	—
(zooecia)	—	—	—	—	—	—	—	—	—	362	—	—
Plants												
Gloeotrichia sphaerica (Hooker)	1	5	1	—	—	—	—	—	—	—	—	—
Vertebrates												
Logania ludlowiensis Gross	5	—	5	—	—	—	—	—	—	—	—	—
Thelodus parvidens Ag.	277	8	297	—	—	—	—	—	—	—	—	—
'Onchus' tenuistriatus Ag.	3	—	—	—	—	—	—	—	—	—	—	—
Total fauna counted	381	136	462	—	41	4	376	—	200	775	18	139
Bedding plane surface area examined (m^2)	0·2	0·3	0·1	2	0·5	3	0·03	6	0·07	0·09	7	0·15

The high density of the 'polychaete' burrows and the highly bioturbated nature of the sediment, locally destroying all its internal structure indicates (Reineck 1967) that the sedimentation rate was normally slow and that little contemporary erosion occurred. However, both the shell sheets and lenticular bedding indicates that the environment represented by this facies was affected by turbulent conditions. (Reineck and Singh 1973). This apparent paradox can be resolved if the sediments were deposited in a subtidal region of slack water currents in which slit lenticles were periodically deposited as a result of unusually strong tides (e.g. spring tides), locally giving the sediment a lenticular bedded appearance. The deposition of the shell sheets could have resulted from either tidal current or storm activities.

Many of the shells in this facies are bored. At the present time two boring types have been recognised. The first consists of discontinuous grooves 2–4 mm in length, 0·2–0·5 mm in depth and 0·5–1 mm in width. These are considered by Ben Akpan (personal communication) to have been formed by a boring annelid. The second form consists of a branching network of pores (0·2–0·4 mm in diameter) interconnected by fine tubes (0·2–0·9 mm in length), and may have been produced by sponges (Akpan, personal communication). The distribution and boring style of these two trace fossil types on some *P. retroflexa* shells is illustrated in Figure 2d. A more detailed account of these borings will be presented elsewhere.

Facies B—In-phase climbing ripple-laminated (sensu McKee 1965) fine grained sands and parallel laminated silts containing some erosion surfaces, grading up into trough cross bedded and channelled silts and sands, containing some layers rich in platy mudclasts up to 35 m in length. This facies can be assigned to the Downton Castle Fm. Facies D described by Allen (1974) which is considered (Allen 1974) to have been deposited in the high intertidal zone.

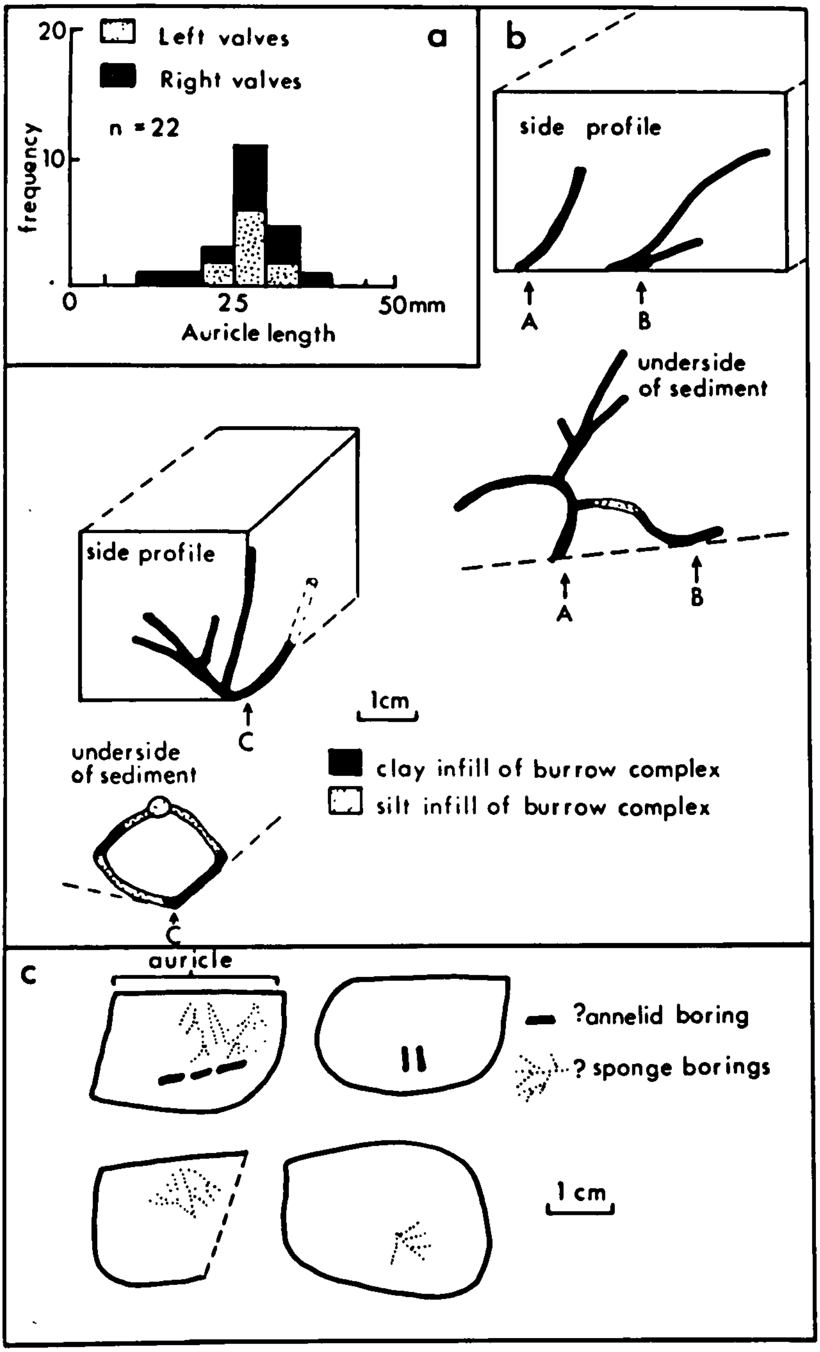

Fig. 2. (a) Size distribution of *Pteronitella retroflexa* on the surface of a shell sheet. Their Left valve/right valve ratio is 0·76. (b) Side and basal profiles of two complex burrow systems from facies A. (c) Traces of four shells of *P. retroflexa* showing the two types of shell boring. About 65% of the shells had ?sponge borings and 45% had ?annelid borings. All specimens illustrated in this figure are from facies A, layer 12 of the section (see Table 1) and have been deposited in Ludlow Museum.

Facies C—In-phase climbing wave rippled silts with clay drapes, interbedded with parallel laminated silts and shell sheets. Ripple mark axes are orientated at between 220° and 260° (wavelength 6–14 cm, amplitude 6–14 mm). Some layers contain interference wrinkle marks (ridge thickness 0·5–1·5 mm, wavelength 2·5–3 mm, amplitude 0·2–0·5 mm, orientation 270° to 350°, shape-asymmetrical to symmetrical with a rounded crustal region). The ripple marks are occasionally asymmetrical (depositing current came from the southeast) and tend to have well developed bifurcating ripple crests. These asymmetric ripples have stoss side length of 6–8 cm, a lee side length of 4–5 cm and a slip face of 2–3·5 cm. Many of the sediment surfaces contain antiripplets. Some of the rippled surfaces show load structures at their base. The presence of wrinkle marks suggests that the sediment was formed in an intertidal environment (Singh and Wunderlich 1978). This is confirmed by the presence of antiripplets, which are formed (Reineck and Singh 1973) by the capture of wind blown sand on a water saturated sediment surface. They suggest that the wind travelled from the northeast to the southwest. The strike of these antiripplets is between 270° and 280°. Some rare trails are present on the sediment surfaces. The shell layers appear to have infilled small hollows in the substrate and contain an internal cross laminated structure, and a "parallel" laminated upper surface. Shell size measurements for one shell layer are given in Figure 3.

Facies D—Interbedded rippled (wavelength 2–6 cm, amplitude 3–6 mm) and parallel laminated silts containing rare laminae rich in shell debris, phosphate nodules and fish debris. The sediments are probably best assigned to the Downton Castle Formation Facies B, which Allen (1974) and others (Antia and Whitaker, 1979; Antia 1979a) consider to have been deposited in the lower part of the intertidal zone. The fish debris and phosphate nodule rich layers probably formed as lag concentrates within the intertidal zone (cf. Allen and Tarlo 1963; Allen 1974; Antia and Whitaker 1979; Antia 1979a).

The phosphate nodules occur as compact rounded grains 4 to 15 mm in length. Similar grains occurring at the top of the Ludlovian Series elsewhere are considered (Antia 1979a) to have formed within the sediment of a subtidal environment and been subsequently excavated and concentrated in a variety of vertebrate rich sediments. If the phosphate nodules occurring in this facies formed in a subtidal environment, then their presence in presumed intertidal sediments indicates that there was some onshore transport of subtidal material into the intertidal zone. This suggestion is further supported by the presence of subtidal brachiopods (see Calef and Hancock 1974; Fürsich and Hurst 1974) in the intertidal sediments of Facies C. Many recent studies (e.g. D'Anglejan 1967; Shafer 1972; Antia 1977) have demonstrated that fish bones, phosphate nodules and shells can be transported from a subtidal environment into both intertidal and supratidal environments.

The order of facies up the section is A–B–A–C–D–B, and suggests that the sequence represents an initial shallowing up sequence from a subtidal environment into an intertidal environment (initial Facies A–B transition—see Fig. 1), followed by a small marine transgression (Facies B–A transition–see Fig. 1). This marine transgression was followed by continued marine regression resulting in the facies A–C–D–B transitions (see Fig. 1), in which each successive facies represents a shallower subtidal or a more emergent intertidal environment.

The absence of an in situ shelly fauna and the apparent faunal change (Table 1) within the intertidal zone may coincide with either a substrate preference for sandy conditions by lingulids confining them to Facies B and D or it may coincide with the

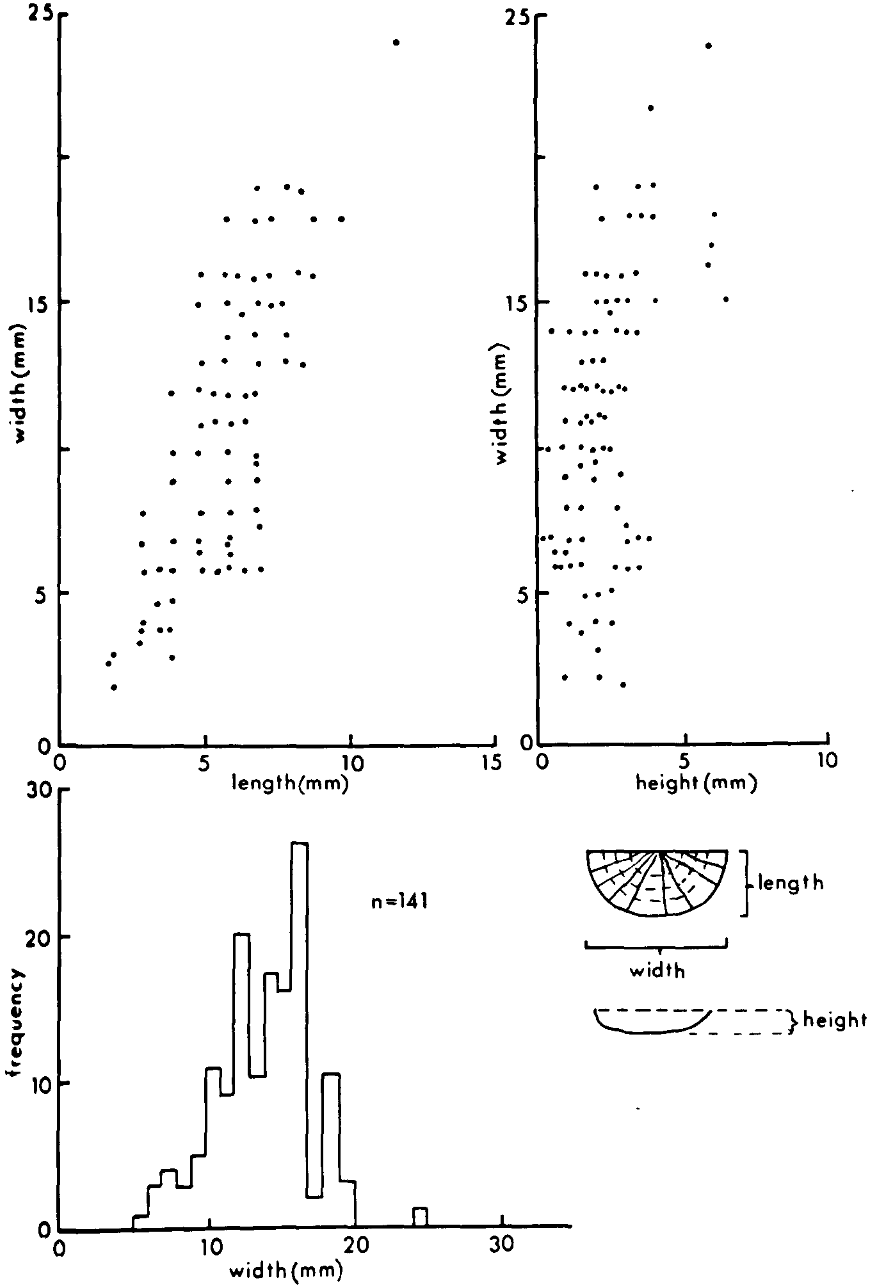

Fig. 3. Size measurement of *Protochonetes ludloviensis* from a shell bed in facies C, layer 7.

change in the chemical nature of the upper Silurian sea from a carbonate saturated sea to a highly oxygenated, carbonate undersaturated sea which has been described elsewhere (Antia 1979b). This change might relate to the gradual southward advancement of the fluvial environment whose sediments eventually engulfed the Ludlow–Much Wenlock region during the late Downtonian and early Dittonian (Allen 1974).

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References

Allen, J. R. L. 1974. Sedimentology of the Old Red Sandstone (Silurian–Devonian) in the Clee Hills area, Shropshire, England. *Sedimentary Geology* **12,** 73–167.

— and L. B. Tarlo, 1963. The Downtonian and Dittonian facies of the Welsh Borderland. *Geol. Mag.* **100,** 129–155.

Antia, D. D. J. 1977. A comparison of diversity and trophic nuclei of live and dead molluscan faunas from the Essex Chenier Plain, England. *Paleobiology* **3,** 404–414.

— 1979a. Bone-Beds: A review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering and microbiotas. *Mercian Geol.* **7,** 93–174.

— 1979b. Authigenic gypsum in marine sediments—a comment. *Marine Geol.* 30 (in press).

— and J. H. McD. Whitaker. 1979. A scanning electron microscope study of the genesis of the upper Silurian Ludlow Bone Bed. pp. 119–136 *In* W. B. Whalley (ed.) *Scanning electron microscopy in the study of sediments.* Geoabstracts Ltd. Norwich.

Calef, C. E. and N. J. Hancock. 1974. Wenlock and Ludlow marine communities in Wales and the Welsh Borderland. *Palaeontology,* **17,** 779–810.

D'Anglejan, B. F. 1967. Origin of marine phosphorites off Baja, California. *Marine Geol.* **5,** 15–44.

Elles, G. J. and I. L. Slater. 1906. The highest Silurian rocks of the Ludlow District. *Jl geol. Soc. Lond.* **62,** 195–220.

Fürsich, F. T. and J. M. Hurst. 1974. Environmental factors determining the distribution of brachiopods. *Palaeontology* **17,** 879–900.

Holland, C. H., Lawson, J. D. and V. G. Walmsley. 1963. The Silurian rocks of the Ludlow district, Shropshire. *Bull. Br. Mus. Nat. Hist.* (geol.) **8,** 95–171.

Jopling, A. V. and R. G. Walker. 1968. Morphology and origin of ripple drift cross lamination, with examples from the Pleistocene of Massachusetts. *J. Sediment. Petrol.* **38,** 971–984.

Martinsson, A. 1967. The succession and correlation of ostracode faunas in the Silurian of Gotland. *Geol. Foren. Stockholm Forb.* **89,** 350–386.

McKee, E. D. 1965. Experiments on ripple lamination. In Middleton, G. V. (ed.). Primary Sedimentary structures and their hydrodynamic interpretation. *Soc. Econ. Palaeontologists & Mineralogists Spec. Pub.* **12,** 66–83.

Reineck, H. E. 1967. Paramter von Schichtung und Bioturbation. *Geol. Rundschau.* **56,** 420–438.

— and I. B. Singh. 1973). *Depositional sedimentary environments.* Springer. Berlin 439 p.

Ronan, T. E. Jr. 1977. Formation and palaeontological recognition of structures caused by marine annelids. *Paleobiology* **3,** 389–403.

Shafer, W. 1972. *Ecology and palaeoecology of marine environments.* Oliver and Boyd Edinburgh 586 p.

Shaw, R. W. L. 1969. Beyrichiacean ostracodes from the Downtonian of Shropshire. *Geol. For. Stockh. Forb.* **91,** 52–72.

Singh, I. H. and Wunderlich, F. 1978. On the terms wrinkle marks (Runzelmarken), millimetre ripples and miniripples. *Senckenbergiana marit.* **10,** 75–83.

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A SCANNING ELECTRON MICROSCOPE STUDY OF THE GENESIS OF THE UPPER SILURIAN LUDLOW BONE BED

* D. D. J. Antia & ** J. H. McD. Whitaker

ABSTRACT

The Ludlow Bone Bed horizon (Basal Downtonian) consists of a rippled thelodont sand formed low in the intertidal zone as a lag concentrate. SEM examination of the clasts reveals an abundance of thelodont scales, acanthodian and brachiopod fragments with accessory phosphorite and quartz. About 20% of the thelodonts are markedly abraded and these often contain borings comparable to recent intertidal algal borings. Many quartz grains bear authigenic, euhedral, bipyramidal overgrowths formed within the sediments. These overgrowths show varying degrees of abrasion, indicating that there was local reworking of the original subtidal sediment and concentration of the abraded quartz euhedra, fish debris, phosphatic shell fragments and internal moulds and casts to form the bone beds. Grain edges may be plastered with cryptocrystalline silica and fungal filaments on the grains surfaces may be silicified, before final sediment stabilisation.

Both worn and unworn euhedra may show a second generation of diagenetic overgrowths after sediment stabilisation and burial.

INTRODUCTION

The Ludlow Bone Bed forms an historically important geological horizon (Griffiths 1973), once considered to represent the Silurian/Devonian boundary (Stamp 1923). At present it marks the junctions of the Ludlow and Downtown (Pridoli) series (Upper Silurian) and the junctions of the Whitcliff and Temeside stages (Holland *et al* 1963; Allen 1974).

Although the Ludlow Bone Bed is described as two distinct layers (Elles & Slater 1906) found within the marked roadside cleft at Ludlow, detailed work by one of us (DDJA, unpublished) has revealed the presence of 8 separate bone beds and shown the cleft to be diachronous. Within its main outcrop the bone bed may be described at Aston Munslow, Corfton, Deepwood, Brockton, Ludford, Netherton, Orleton,

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Shipton and Willey, as a thin (0.1 - 13 cm thick) rippled discontinuous unimodal sand (mean grain size approx. 0.25 mm) with a gingerbread appearance, comprised largely of thelodont scales (up to 1000 scales per cm^2 bedding plane surface area) and acanthodian fragments; with secondary phosphatic brachiopod fragments, small phosphatic concretions, pachythecids, eurypterids, ceratiocarids, conodonts and quartz grains. Nonphosphatised brachipods (chiefly *Protochonetes ludloviensis, Howellella elegans, Craniops implicata, Salopina lunata, Lingula sp. nov., and Microsphaeridiorhynchia nucula,* ostracods (chiefly *Nodibeyrichia verrucosa, Frostiella groenvalliana*, Londinia arisaigenesis* Cytherellina siliqua, Kummerowia* sp., Jefina* sp., Cavellina sp., Poniklacella sp., and Thilipsura* sp*), bivalves (chiefly *Modiolopsis complanata*, Pteronitella retroflexa, and Fuchsella amygdalina),* gastropods (chiefly *Loxonema gregaria*, L. obsoleta, Umbospira (Platyschisma) helicites* Platyschisma williamsi*, and Cymbularia carinata*),* and cephalopods (chiefly *Leurocycloceras whitcliffense)* accumulate as ripple hollow infill above and below the bone bed layers. Asterized species are only found above the basal bone bed horizon. In places (Brockton SO 578938, Shipton 563917, and Ludford 512742) the bone bed can clearly be seen to form an integral part of flaser-bedded strata, thus implying an intertidal origin for the bone bed as suggested by Allen (1974), and implied by Antia (1977), instead of a subtidal origin as a shallow marine shelf sediment (Hain 1969; Reif 1976; personal communication 1976) or a storm generated sheet (Watkins, in press).

Studies have concentrated on the thelodonts (DDJA using gold coated (75 nm thickness for sediment, 50 nm thickness for clasts) specimens on a Cambridge 600 SEM) and quartz grains (JHMcDW using aluminium coated (25 nm thickness) specimens on an ISI 60 SEM), although other clasts have been examined.

The quartz grains,thelodonts, phosphatic nodules and acanthodian debris examined were extracted (by DDJA) by acid treatment, using the techniques outlined by Turner (1973) from Ludford Lane (SO 512742) and Aston Munslow (SO 512865). Sediment samples consisted of untreated rock chips.

NON-CALCAREOUS CLASTS FROM THE BONE BED

The basal thelodont layer at Ludford consists largely of thelodonts (ca. 90%). Within the bone bed facies (Facies A - Allen 1974), for example (1) the bone bed horizon 6 at Ludford (512742) is dominated by phosphatized *Gomphonchus* spp. spine fragments; (2) *Thelodus parvidens* forms the dominant clast in the lower bone beds, but is replaced in the higher bone beds by *Logania ludlowiensis* as the dominant clast, (3) the bone bed contains varying amounts of debris acanthodian and phosphorite eg. 50% at Deepwood (Holland *et al* 1963); and Corfton lane (SO 497852), Ludford Lane 20% Aston Munslow (SO 512865), 1% Corfton - Sun Inn (SO 496851), (4) the density of quartz grains is also variable (expressed as number per gram of sediment)

(a) 12 at Ludford, (b) 0 at Deepwood), (c) 0.4 at Aston Munslow.

(1) Thelodonts

Two specimens dominate the thelodont fauna (1) *Thelodus parvidens* (70 - 95%) and *Logania ludlowiensis* (5 - 30%). They occur chiefly as unabraded scales (Figs 1, a-e and 3d) though some scales show attrition marks, borings and some degree of abrasion (Figs 1f, g, k and 3a). The borings appear to be similar to recent intertidal algal borings found in carbonate clasts at Sales Point, Bradwell, Essex (See Antia 1977 for location) (Figs 1h, i; 3c). Many of the clasts are imbricated and randomly orientated.

(2) Acanthodian fragments

These occur as broken, worn, often recrystallised fragments of *Scolithus pustiliferous* and other fishes (Fig 2, m-o).

(3) Conodont fragments

An extensive low diversity conodont fauna has been recorded from the Ludlow bone bed (Aldridge 1975). However, this study has only recorded worn fragments of *Ozarkodina confluens* and *Distomoda dubius* from the bone bed at Aston Munslow (identified by Alridge 1977, personal communication).

(4) Brachiopod fragments

Occur as worn fragments of *Orbiculoidea rugata* Fig 1m, n) (no other forms have been recorded) as about 1% of the bone bed by volume at Aston Munslow.

(5) Phosphorite deposits

Phosphorite nodules occur as the internal moulds and casts of *Loxonema gregaria, Cymbularia carinata* and *Orthoceras* sp. (Fig 1o, p). Some contain algal borings (Fig 1s) and consist of replaced authigenic clays containing angular quartz grains (Fig 1t) while others are comprised of faecal pellets (Fig 1q, r).

(6) Eurypterid fragments

Eurypterid debris forms a minor part of the deposits and is made up largely of *Pterygotus* spp. (Fig 1u).

(7) Quartz grains

Quartz grains form a minor component of the bone beds, and range from euhedral bipyramidal (ca. 15%) to spherical rounded grains (ca. 5%) (Fig 2a-d). The euhedral grains occur as hexagonal bipyramidal forms either with sharp or worn edges (Figs 2e-h) often with later diagenetic overgrowths (Fig 2i-l). Many of the subrounded grains show euhedral faces (Figs 2b, i, u and 3e). The grains may be pitted or polished (Fig 3e) and are often covered by siliceous filaments (Figs 2u and 3e, f). These filaments are of late stage origin since they transgress across pitted and fractured surfaces (Fig 2q-r). They often display triple junctions, with junction angles approximating to 120° (Fig 1t, w) and may possibly represent silicified fungal hyphae cf. Edwards & Perkins (1974). Some of the quartz

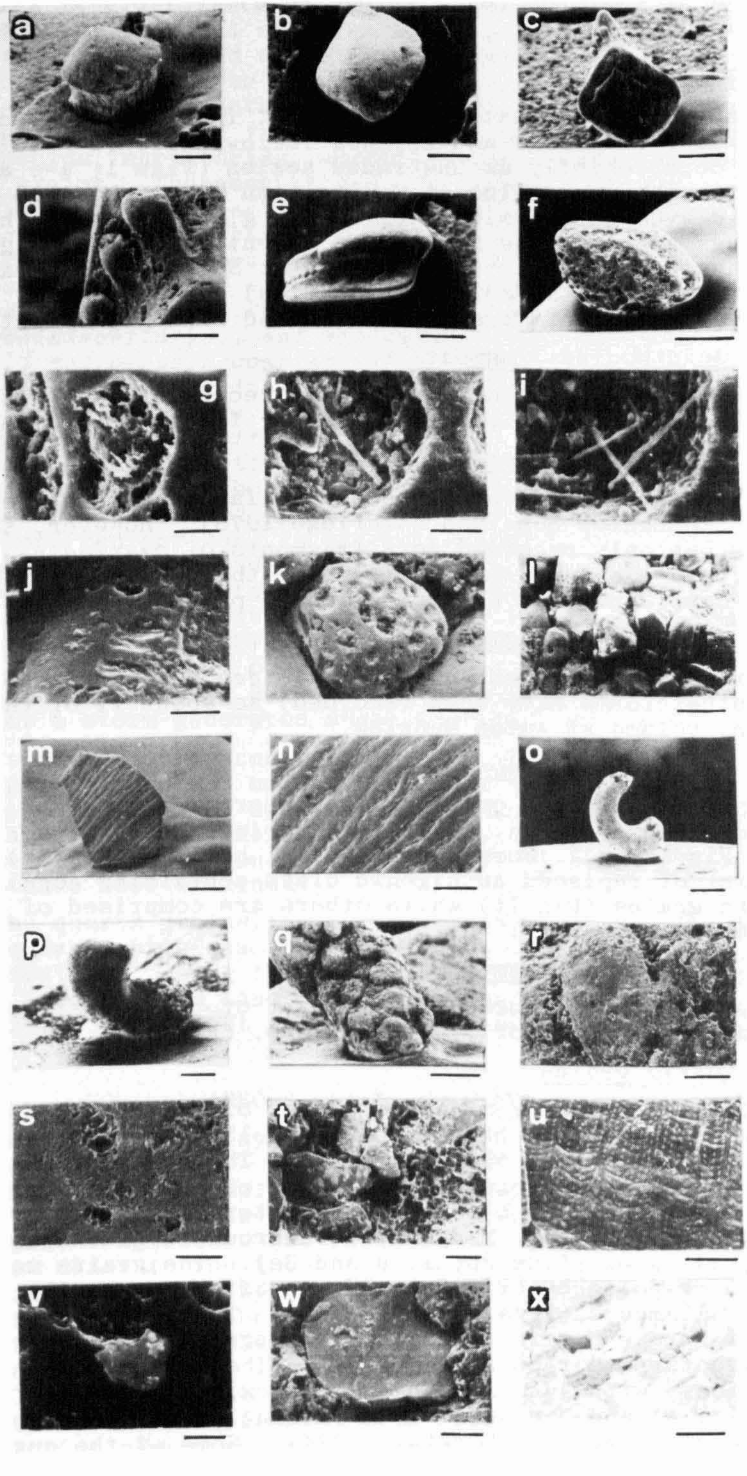
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Figure 1 Number in parenthesis = Scale Bar length. Unabraded thelodont scales. (a) *Thelodus parvidens* (100 µ), (b) *Thelodus parvidens* - dorsal view (100 µm), (c) *Logania ludlowiensis* - upper body scale (100 µm), (d) *Logania ludlowiensis* - lower body scale (20 µm), (e) detail of latter (100 µm). Worn thelodonts (f) Rounded worn bored thelodont (*T. parvidens* - note boring density on the spongy cusp of the denticle the crown of this denticle (not shown) has almost no borings (200 µm), (g) Detail of a boring with a raised cusp in its centre indicating uneven dissolution of the thelodont during its formation (20 µm), (h & i) Recent algal dissolution pits in a carbonate grain from the low intertidal (rippled mud facies) of Sales Point, Bradwell, Essex - note the presence of algal filaments - see also Plate 3c (15 µm), (j) Attrition marks on a *Logania ludlowiensis* denticle (10 µm), (k) Well rounded, worn, bored, thelodont (*T. parvidens*) in sediment - note close packed nature of the clasts and that the thelodont has been worn after as well as before it was bored (100 µm), (l) Bedding plane surface of the bone bed - note imbricated nature of the clasts (200 µm), (m) Shell fragment of *Orbiculoidea rugata* (200 µm), (n) Detail of the ornamented surface (20 µm), (o) Internal case of ?*Cymbularia carinata* (200 µm), (p) Internal cast of ?*Loxonema gregaria* (200 µm), (q) Internal cast of ?*Orthoceras semipartitum* made largely of faecal pellets (200 µm), (r) Detail of faecel pellets (40 µm), (s) ?Algal borings on the surface of *L. gregaria cast* (10 µm), (t) Internal structure of an internal cast of *L. gregaria* - note quartz grains (2) and replaced clays (1) (20 µm), (u) Surface of a *Pterygotus* sp. fragment (50 µm), (v) Kaolinite grain on the surface of a bored thelodont (20 µm), (w) Worn mica grain (20 µm), (x) Diagenetic quartz in Upper Whitcliffe sediment (20 µm).

grains contain small pits with raised rims (Figs 2u and 3e, j,k). These are probably pressure solution cavities formed at the junction of two grains of different chemical compositions. Some of the quartz shards (Fig 3f) may be derived from bentonites. On some of the quartz grains 'spherulite' and doughnut-like structures are present (Fig 2x, y).

Thus the quartzes show the following diagenetic and depositonal phases/forms:

a) Original unaltered (probably β) quartzes occurring as well-rounded grains and angular shards (Figs 2a and 3f)

b) Secondary euhedral (α) quartzes formed as overgrowths nucleated around the initial quartz (Fig 2d, 1). These overgrowths were probably formed in a clay rich

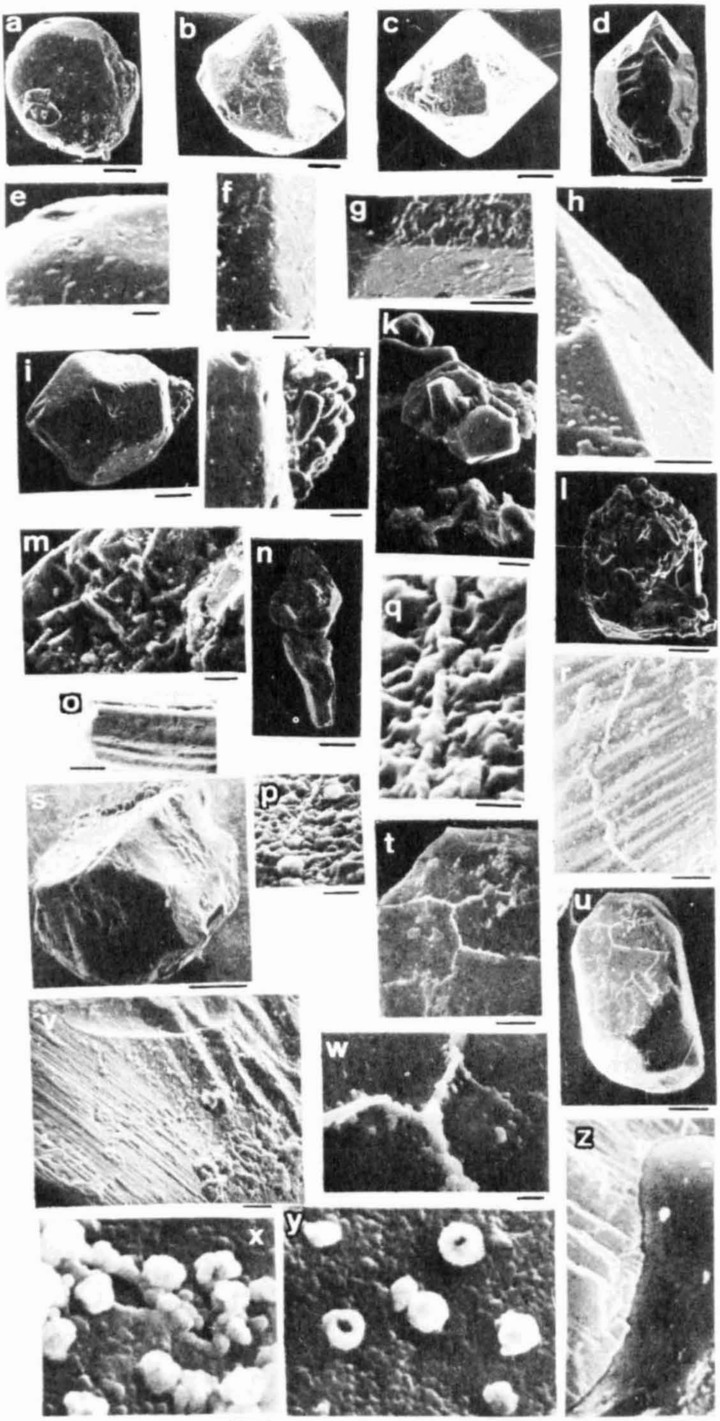
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Figure 2 Number in parenthesis = Scale Bar length. Quartz grains. (a) Well rounded quartz grain (100 µm), (b) Worn quartz grain with some euhedral faces (100 µm), (c) Euhedral bipyramid (100 µm), (d) Euhedral quartz grain with unworn edges (100 µm), (e.h) Rounded to sharp grain edges for grains (a-d) (20 µm), (i) Rounded euhedral quartz grain with secondary unworn euhedral overgrowths (100 µm), (j) Detail of overgrowths (50 µm), (k) Detail of euhedral overgrowths on an unworn quartz grain (20 µm) (1) the unworn grain (100 µm), (m) Detail of recrystalised surface of an acanthodian fragment (20 µm), (n) The acanthodian fragment showing post prefossilisation wear and post sediment stabilisation recrystalisation (100 µm), (o) Part of an *Onchus muchisoni* spine (Acanthodian) (100 µm), (p) Siliceous ?fungal filament on the pitted surface of quartz grain (20 µm), (q) Detail of the filament (4 µm), (r) Detail of a filament on the fractured surface of a quartz grain (Plate 3f) (20 µm), (s) A feldspar grain (25 µm), (t) Detail of filaments on the surface of a quartz grain (25 µm), (u) The worn euhedral quartz grain covered in filaments (50 µm), (v) Detail of the cleavage on the feldspar grain (s) (10 µm), (w) Detail of a filament triple junction (2 µm), (x) Quartz spherulites and rosettes on the surface of a quartz grain (2 µm), (y) Quartz 'doughnuts' on the surface of a quartz grain (2 µm), (z) Thelodont denticle (t) in calcite cement (c) (30 µm).

carbonate sediment, since Al-Sheikly (personal communication 1977) has shown that the lower the clay content of a carbonate sediment the larger the hexagonal prism faces of the (diagenetic) bipyramidal euhedral overgrowths.

c) Exhumed rolled quartzes - varying degrees of abrasion (Figs 2a-c, i, u and 3e).

d) Stabilisation of the grain in the sediment was followed by subsequent fungal overgrowths. Later movement of silica from the porewaters replaced the fungal walls (Figs 2p-r, t, u, w) and provided thin silica sheet overgrowths on some grains (Fig 31) to give a polished appearance.

e) Late phase diagenetic precipitation of secondary quartz overgrowths on the primary overgrowths (Fig 2i-1)

The Ludlow bone bed is not unique in containing euhedral quartz overgrowths since they have also been recorded in the Rhaetic Bone Bed (Sylvester-Bradley & Ford 1968), and the Kiddville bone bed of Kentucky (Foersete 1906; Wells 1944, p 285).

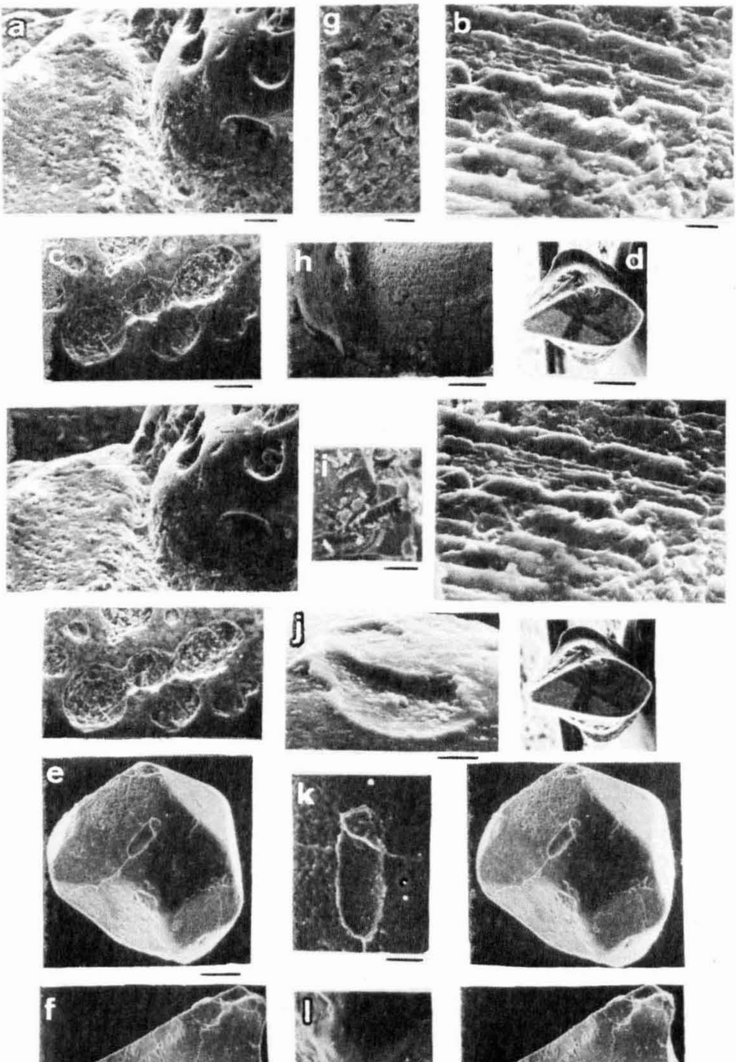
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Figure 3 NB. The individual picture of stereopairs on this page have been interposed to save space. Number in parenthesis = Scale Bar length. (a) Junction of a rounded bored thelodont (*P. parvidens*) with a worn quartz grain. Note- pitting on the quartz grain and the clay rim around the thelodont - stereopair (40 µm), (b) Well cleaved calcite cement - stereopair (10 µm), (c) Algal dissolution hollows (borings) on a recent carbonate grain from Sales Point, England - note morphological similarity to the thelodont borings - stereopair (50 µm), (d) *Logania ludlowiensis* scale - variant - note almost unworn condition of the scale - stereopair (100 µm), (e) Quartz euhedra showing worn edges, quartz plastering (1), pressure solution pits and filaments - stereopair (100 µm), (f) Quartz shard cut by filaments (Detail Plate 2r) - stereopair (200 m), (g-i) *Pachytheca spaerica* - a round spherical algae (up to 6 mm in diameter) comprised of an inner layer of tubes radiating from a centre (the external surface expression of the tube illustrated in (g) (20 µm). The internal mass of tubes is covered by a thin outer layer (h (100 µm) shows the junction of the two layers) which contains small tubes with an annular structure, (i) (10 µm) Pressure solution pits bordered with a clay rim are shown in j and k (50 µm/ 40 µm), (k) A quartz plastered edge is shown in 1 (50 µm).

Feldspar grains derived from ?bentonites occur rarely (1 grain recorded) in the Ludlow Bone Bed at Ludford Lane (Figs 2s, v).

(9) Sediment

Below the bone bed diagenetic calcite and quartz comprise much of the sediment (Fig 1x). In the bone bed carbonate (Figs 2z and 3b) and kaolinite grains (Figs 1v) dominate the matrix with accessory muscovite grains (Fig 1w).

DISCUSSION

The Ludlow Bone Bed is an unusual, but by no means unique, accumulation of fish debris (cf. Reif 1976). It was formed as a littoral lag concentrate on or about the low watermark in a chenier environment (Antia 1977 - in preparation). Although a discussion of the environmental location of the bone bed is not the purpose of this paper, the source of the fish debris deserves some mention. Many theories for the origin of this debris have been proposed and are summarised by Griffiths (1973). In general theories range from the suggestion of mass mortality to condensation. In contrast to these theories we would like to propose the following schematic model for the clast source and intertidal formation of the Ludlow Bone Bed with the schematic environments illustrated in Fig 4.

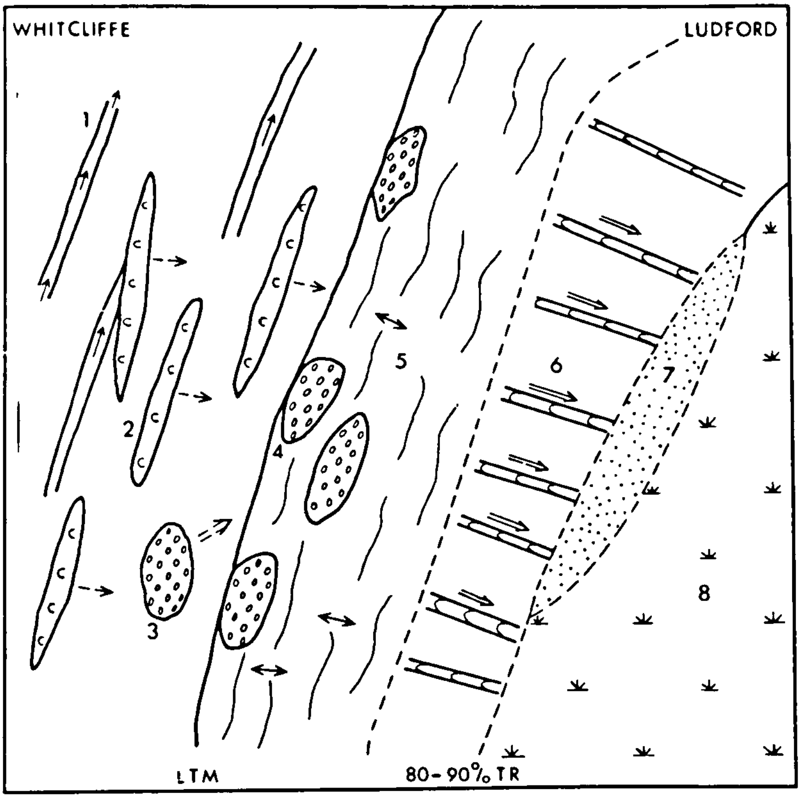

Figure 4 Detailed schematic environmental model (approx. 1 km wide) based on the type Whitcliffe and Ludlow/Downtonian boundary sections at Whitcliffe (507742) and Ludford Lane (512742) for the environments present during the Late Whitcliffe - Early Downtonian in the Ludlow Region. Arrows indicate directions of sediment movement. L.T.M. = Low Water Mark. T.R. = Tidal Range.
1) Subtidal shallow channels (<1m wide x <30 cm deep) with some concentrated shell debris at base (507742).
2) Migrating subtidal shell mega ripples (amplitude approx 4 - 15 cm wavelength 3 - 10 m) made of worn brachiopod shells *Protochonetes* sp. *Microphaeridiorhynchia* sp. and *Salopina* sp.) containing an extant fauna of podocopid ostracoda and bryozoans (507742). Some of these mega ripples have cut across and infilled the subtidal channels (506743).
3) Small subtidal patches (often rippled) of Thelodont-rich clays or shelly silts formed by a winnowing effect by the currents on the excavated material from the channels (512865).

<u>Figure 4</u> (Contd) 4) Intertidal bone bed (Thelodont sand) often forming an integral part of flaser-bedded strata and commonly overlying rippled shell patches and *Chondrites* rich muds.

5) Intertidal rippled mudflats (markedly flaser bedded) often containing small thelodont sand patches infilling burrows or forming part of flaser-bedded strata. The *in situ* fauna on these mudflats included endobyssate colonies of *Modiolopsis* sp. and shallow burrowing brachipods *(Lingula minima)*.

6) Mud mounted topography (512742, 512865), intertidal, formed by the temporary re-excavation of the lower rippled mudflats (5). Individual channels can be traced in excess of 10 m (512742). The extant fauna of these channels included *Umbospira* sp. and *Frostiella* sp.

7) Perched trough cross bedded sand sheets (?chenier sands) which sometimes bury the underlying channels of the mud-mounted topography (512742). They contain no extant fauna - and may be supratidal in nature.

8) ?High intertidal - supratidal marsh sediments consisting of fine grained parallel laminated silts, rich in plant debris/fragments, the algae *Pachytheca* Fig 3g-i) and rare disarticulated ostracods (512742).

1) Subtidal setting - carbonate-clay-silt substrate with a burrowing soft bodied fauna and calcareous epifauna.
   - (a) Fish die (with normal natality and mortality rates operative) and lie on substrate surface. Either normal decomposition of the soft parts occurs phosphatising the derman scales on the fish (Burnett 1974) or anaerobic burial of the fish occurs with subsequent phosphatisation (Burnett 1974).
   - (b) Since complete thelodont fishes have not been recorded in the Whitcliffe near Ludlow, even though their scales are abundant (>0-50 per m^2), it is unlikely that the scales were disarticulated prior to burial. In modern Peruvian subtidal sediments both phosphate and silica precipitate out at about 15 cm depth in the substrate (Burnett 1974). It is also possible that similar chemical processes were operative in the subtidal Whitcliffe sediments. If they were, then it is envisaged that the euhedral quartz overgrowths formed at this stage in addition to unphosphatised scales becoming phosphatised and phosphatic concretions forming internally in gastropod and cephalophod shells.
   - (c) Local chanelling and bioturbation within the Whitcliffe may have excavated the quartz grains and phosphatic debris, prior to their washing onshore by local currents and wave action. Both channels and bioturbation are common in the Whitcliffe eg. Aston Munslow (511876 & 512865),

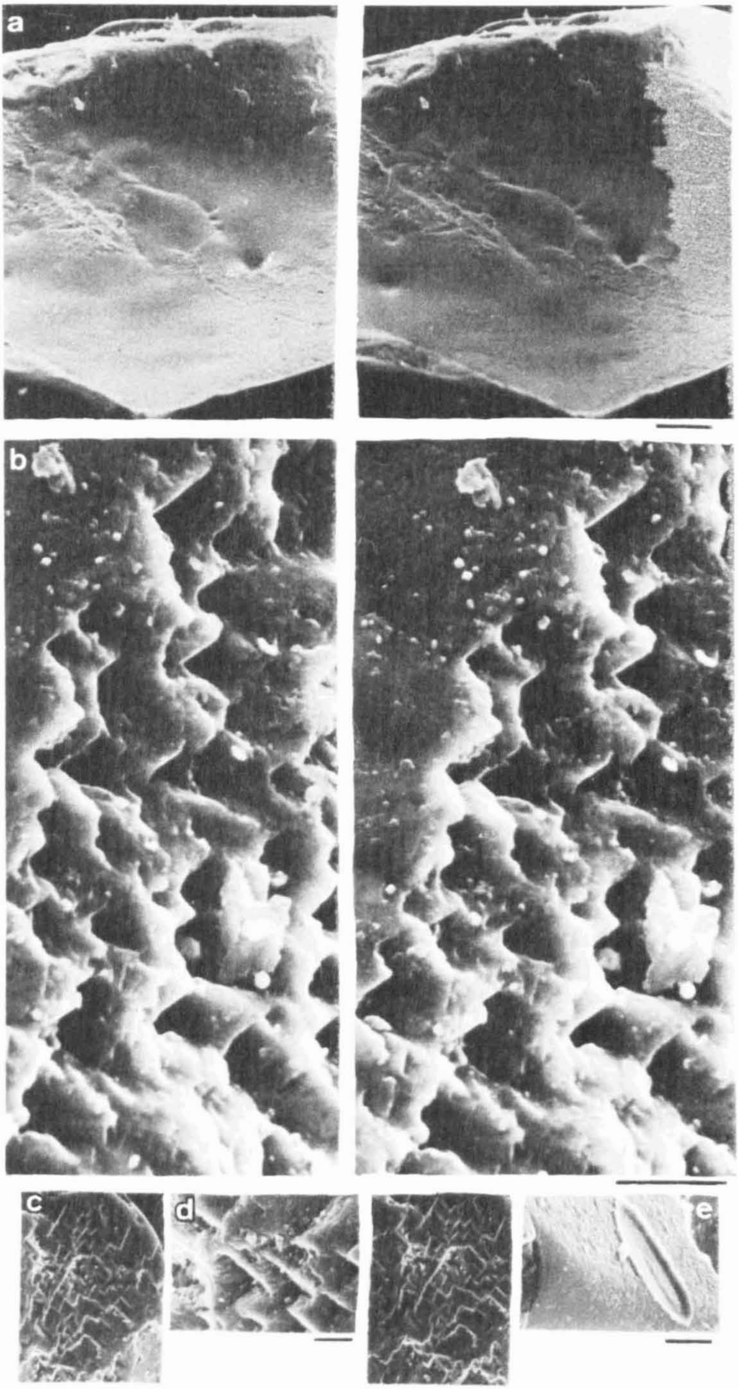
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Figure 5 a) Rounded quartz grain from the Ludlow Bone Bed Ludford Lane, showing a cryptocrystalline silica plastering which covers both the edges and surfaces of the grain and post dates the development of the tabular plates on the grain. Scale Bar = 75 μm
b) Tabular plates on a quartz grain surfaces (L.BB. Ludford Lane). Note 1) the two preferred orientations of plate edge formation, 2) that the plates form parallel to the crystal surfaces, 3) some of the plate edges are fractured possibly indicating abrasive effects on the plate. Scale Bar = 3 μm.
c) Large well-formed tabular plates on a quartz grain surface (L.BB., Corfton Lane) form parallel to the crystal surface. Scale Bar = 40 μm (Stereopair)
d) Detail of plates figures in Fig 5c. Scale Bar = 10 μm
e) Rounded edge of a quartz grain (L.BB., Corfton Lane) note the distribution of the tabular 'micro' plates. Scale Bar = 10 μm

Bourton (595964), Brockton (577939), Callaughton (617975), Hillpike (438760), Ludford (512742), Ludlow (504745 & 491743), Medley (477833), Munslow (522875) and Mortimer Forest (495719 & 496727).

2) Littoral environments - Flaser-bedded muds and silts forming rippled mudflats containing a high density low diversity fauna of ostracods, modiolopsids, lingulids and umbospirids.

(a) Bone bed debris concentrated and swept into pockets by tide and current. The white phosphatic debris (thelodont scales) was colonized by boring algae (the black phosphatic debris (*Gomphonchus* sp. and Brachiopod shells) was not bored, probably because they contained no collagen (Reif 1977, personal communication) when the thelodonts were colonized. A high energy origin for the bone bed is indicated since coprolites (an essential attribute of a low energy bone bed (Reif 1977, personal communication) are rare or absent. Supposed coprolites from the Ludlow bone bed in the Aepler collection (Tübingen University), when viewed in thin section can be shown to be carbonised limonite mudpellets rich in angular quartz grains and articulate brachiopod shell fragments.

(b) Period of silt/mud deposition - caused by increased sediment load in the estuary? - possibly seasonal in origin.

(c) Repetition of process to produce next bone bed layer, or continuation of mudflat facies depending on stage in the regression cycle.

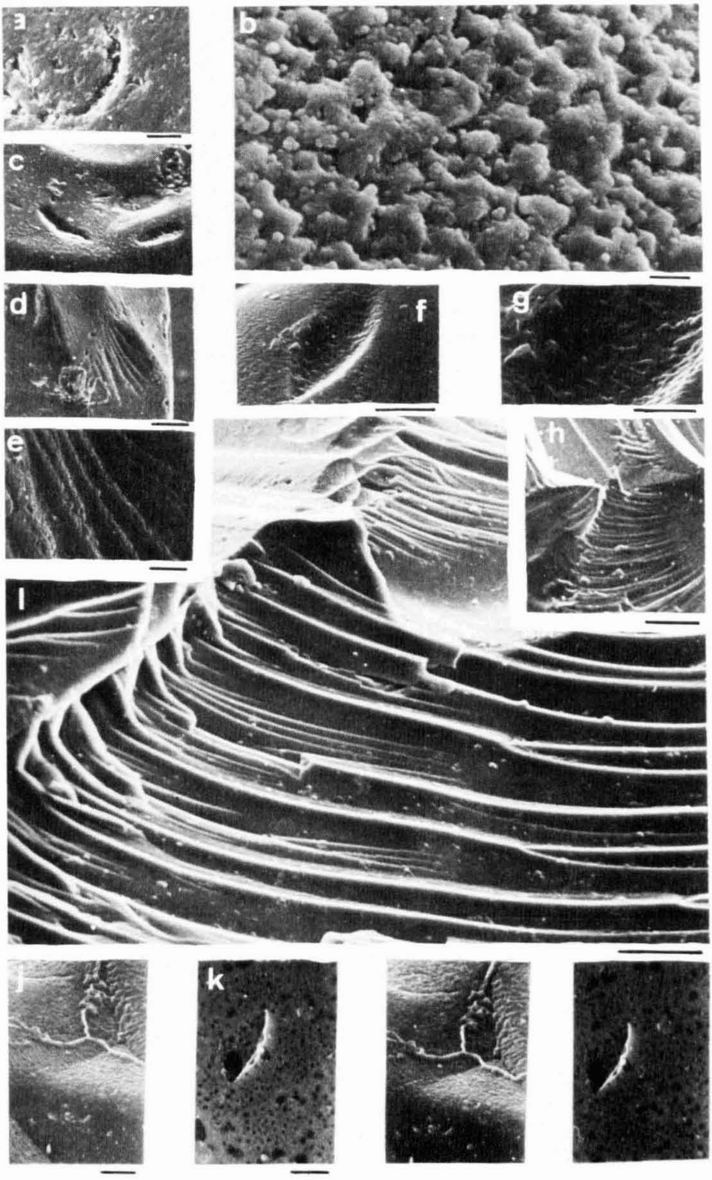
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Figure 6 a) Crescentic chip mark (L.BB. Corfton Lane). Scale Bar = 40 µm
b) Tabular plates (L.BB. Aston Munslow - grain illustrated Fig 3e) which have been modified percolating pore waters and contain quartz spherulites. Scale Bar = 2 µm
c) Crescentic chip marks (L.BB. Corfton Lane). Scale Bar = 40 µm
d) Surface of a quartz grain showing a fracture (L.BB. Corfton Lane). Scale Bar = 40 µm
e) Detail of fracture; note the tabular micro-plates on the fracture surface. Scale Bar = 10µm
f) Crescentic chip mark (L.BB. Corfton Lane) Scale Bar = 40 µm
g) Detail of chip mark (Fig 6f) showing micro-plates in the chip. Scale 1 cm = 20 µm
h) Fracture in a quartz grain produced by mechanical crushing (L.BB. Ludford Lane). Scale Bar = 100 µm
i) Detail of the fracture. Scale Bar = 10 µm
j) Detail of a quartz grain surface showing the relationship of the quartz plates to grain rounding. (L.BB. Corfton Lane). Note the filament with a triple junction. Scale Bar = 10 µm (Stereopair)
k) Chip mark on a smooth crystal surface (L.BB. Corfton Lane). Scale Bar = 10 µm. (Stereopair)

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REFERENCES

Aldridge, R.J., 1975, The stratigraphic distribution of conodonts in the British Silurian. *Journal of the Geological Society of London,* 131, 607-618

Upper Silurian Ludlow Bone Bed

Allen, J.R.L., 1974, Sedimentology of the Old Red Sandstone (Siluro-Devonian) in the Clee Hills area, Shropshire, England. *Sedimentary Geology,* 12, 73-167

Antia, D.D.J., 1977, A comparison of diversity and trophic nuclei of live and dead molluscan faunas from the Essex Chenier Plain, England. *Paleobiology,* 3, 404-414

Burnett, W.C., 1974, *Phosphate deposits from the sea floor off Peru and Chile: radio-chemical and geochemical investigations concerning their origin.* PhD thesis, Hawaii Institute of Geophysics, Honolulu, Hawaii, 164 pp

Edwards, B.D. & Perkins, R.D., 1974, Distribution of microborings within continental margin sediments of the South Eastern United States. *Journal of Sedimentary Petrology,* 44, 1122-1135

Elles, G.L. & Slater, I.L., 1906, The highest Silurian rocks of the Ludlow district. *Quarterly Journal of the Geological Society of London,* 62, 195-220

Foersete, A.F., 1906, The Silurian, Devonian and Irvine formations of East-Central Kentucky. *Kansas Geological Survey Bulletin,* 7, 369 pp

Griffiths, A.L., 1973, *Aspects of nineteenth-century stratigraphy in the Welsh Borderlands, with particular reference to rocks at the Silurian-Devonian boundary.* MSc. thesis, London University External

Hains, B.A., 1969, *The geology of the Craven Arms area.* Institute of Geological Sciences, London, 70 pp

Holland, C.H., Lawson, J.D. & Walmsley, W.G., 1963, The Silurian rocks of the Ludlow District, Shropshire. *Bulletin British Museum (Natural History),* 8, 93-172

Reif, W.-E., 1976, Sedimentologie und Genese von Bonebeds In: Seilacher, A (ed), *Palaökologie. Konstruktionen, Sedimentologie, Diagenese und Vergesellschaftung von Fossilien.* (Bericht 1970 - 1975 des Sonderforschungs-berichers 53, Tübingen). *Zentralblatt. Geologie und Paläontologie.* Teil II, (H.5/6), 252-255, Stuttgart

Stamp, L.D., 1923, The base of the Devonian with special reference to the Welsh borderland. *Geological Magazine,* 6), 276-336, 367-372, 385-410

Sylvester-Bradley, P.C. & Ford, T.D., 1968, *Geology of the East Midlands.* Leicester University Press

Turner, S., 1973, Siluro-Devonian thelodonts from the Welsh Borderlands. *Journal of the Geological Society of London,* 129, 557-584

Watkins, R., Benthic community organization in the Ludlow series of the Welsh Borderland. *Bulletin British Museum (Natural History) Geology. In press.*

Wells, J.W., 1944, Middle Devonian bone beds of Ohio. *Bulletin of Geological Society of America,* 55, 273-302

QUESTIONS

Q: P. Bull, Swansea University
How can you tell that some of the rounding of the euhedral crystal edges is not due to a cryptocrystalline silica plastering?

Q: D. H. Krinsley, Arizona State University
One can determine if the edges of quartz grains have been abraded by recognising plates on these edges. Plasting of silica should cover edges and surfaces.

A: D. D. J. Antia
Although Dr. Krinsley's statement answers Dr. Bull's question, it would perhaps be best to clarify the answer with a series of illustrated examples and comments:

On the recognition of abrasive rounding versus rounding by cryptocrystalline silica plastering in quartz grains.

If a quartz grain edge is rounded because it has been plastered by cryptocrystalline silica then its surface will appear to be very smooth (Fig 31, Fig 5a) much smoother than on an unplastered crystal (grain) edge (Fig 2e-h, Fig 5e). Plastering by cryptocrystalline silica may be confined to only the edges of the grain (Fig 3e, 1) or cover both grain edges and surfaces (Fig 5a). In the bone bed plastering occurs as a post depositional, early diagenetic stage, post dating the formation of tabular plates on the grains (Fig 5a).

However, if a grain has suffered abrasive rounding then three features will usually be present on the grains surfaces.

1) Tabular plates over the grains surface
2) Crescentic abrasive chip marks
3) Rounded (but not smooth) edges and fracture marks

Tabular plates on quartz grains in the Ludlow Bone Bed are orientated parallel to the crystal (grain) surfaces (Fig 5b, c, d) and are of varying sizes ranging from 3 - 40 µm in length (Fig 5b, c, d).

Crescentic chip marks occur on the quartz grains (Fig 6a, c, f, g, k) on either smooth crystal faces (Fig 6k) or on 'smooth' surfaces covered by small tabular plates (<5 µm) - Fig 6a, c, f, g, Many of these chip marks also contain a lining of tabular plates (Fig 6f, g) perhaps indicating that the grains had been abraded post chipping?

The grain edges of abrasively rounded grains tend to be smooth surfaces, made irregular, by the presence of tabular plates on their edges (Fig 5e, Fig 6j). Similar features are noticed on fractured quartz grains (Fig 6d, e) where the development of plates has given the fracture edges a rounded appearance (Fig 6e). This rounded appearance contrasts sharply with the angularity of fresh fractures produced by the mechanical crushing of samples (Fig 6h, 1).

Since plates are not present on grains which have only suffered mechanical abrasion (Fig 6h, i) it seems likely that their origin may be related to syn-depositional differential dissolution of the quartz grain surfaces, and/or early post depositional dissolution in the porewaters predating the deposition of cryptocrystalline silica on the grains (Fig 5a). Similar interpretations of the tabular plates on quartz grains have been made by Weaver & Beck (1977, *Sedimentary Geology,* 17, pp 1-234; cf. pp 161-162)

However, some of the tabular plates on grains plastered with cryptocrystalline silica show evidence for solution rounding of the plates (Fig 6b). These plates may have acted as crystalline growth nuclei for the many quartz rosettes present on their surfaces (Fig 6b).

It is therefore suggested that the tabular plates arise as a result of syndepositional chemical solution processes which may modify pre-existing mechanical abrasion features such as chip marks and fractures. The presence of plates on a quartz grain aids the abrasive mechanical weathering processes, since it may require less energy to remove a small 'cleavage like' plate from a grain than to chip or fracture it. Such tabular plates, once formed may be modified by pore solutions after sediment stabilisation, and act as nuclei for later diagenetic crystal growths.

Marine Geology, 31 (1979) M1—M4

Letter Section

AUTHIGENIC GYPSUM IN MARINE SEDIMENTS — A COMMENT

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Dept. Geology, Glasgow University, Glasgow, Scotland (U.K.)

(Received August 15, 1978; accepted January 8, 1978)

In a recent paper, Briskin and Schreiber (1978) noted the occurrence of authigenic tabular gypsum crystals in marine sediments. Their model for its formation suggested that it formed on a relatively stagnant seafloor during a short period in which oxygen-rich bottom waters undersaturated with respect to Ca^{2+} and CO_3^{2-} swept the sea bottom.

They suggest that initially the ($CaCO_3$ saturated) seafloor accumulated calcareous shell material (mainly planktonic and benthic foraminifera) on its surface and SO_4^{2-} ions (formed as a result of normal post-mortem decomposition processes) in the sediment; and that the influx of oxygen-enriched, calcium-carbonate-depleted bottom waters to this seafloor would result in (1) a calcium-carbonate depletion of the sediments and (2) gypsum precipitation in the sediment (resulting from an oversaturation of the sediment porewaters with respect to Ca^{2+} and SO_4^{2-} ions).

If this oxygen-rich bottom water persists for any length of time, a higher primary and secondary planktonic production and hence a higher organic contribution to the sediment should result. This increased organic input may alter the sediment microenvironments to produce an anoxic environment a few centimetres below the aerobic sediment/water interface (cf. Baturin, 1971; Burnett, 1974). Within this anoxic, organic-rich environment it is probable that organophosphates will form (cf. Summerhayes, 1973; Emsley and Hall, 1976) and that these organosphates will bind with and eventually replace the adjacent clays (Antia and Whitaker, 1978) and form soft phosphatic nodules which can be excavated and concentrated in the sediment (Baturin, 1969, 1971). Also as a result of the higher plankton concentrations, the fish population should increase in size and may leave abundant remains in the sediment (cf. Malz, 1978).

Although Briskin and Schreiber (1978) do not describe this latter phosphatic extension of their model, there is some evidence for it in the geological column.

Near Birmingham in the Dudley Canal section at Netherton (British National Grid Reference SO 936874) there is an Upper Silurian (Whitcliffe Beds, Ludlow Series) sequence which may be described from base to top as follows:

2^{+}m Olive green silts with rippled layers of commutated shell fragments rich in foraminifera (about 2 per g of sediment).
5 cm Gypsum-rich black clays.
35 cm Silts, clays and sands enriched in phosphatic nodules and fish scales. The basal 10 cm also contains some gypsum.

The occurrence of the gypsum-rich layer marks three important changes in the faunas and mineralogy of the section (Table I).

(1) Below the gypsum layer the sediment is enriched in calcite, while in the layer and above, clays, quartz and phosphate dominate the sediment and calcite is absent.

(2) The fish fauna and phosphatic nodules become abundant above the gypsum layer.

TABLE I

The Netherton section

	1	2	3
Mineralogy			
Calcite	A	—	—
Quartz	C	C	VC
Chlorite (+ other clays)	—	A	VC
Gypsum	—	FC	R
Phosphate	—	—	VC
Macrofossils			
Fuchsella amygdalina	C*	—	—
Protochonetes ludloviensis	C*	—	—
Salopina lunata	VC*	—	—
Ceratiocaris sp.	—	—	P
Loxonema gregaria	—	—	A
Hyolites forbesi	—	—	FC
Orbiculoidea rugata	—	—	P
Microfossils			
Foraminifera	A	—	—
Ostracods	R	—	—
Vertebrates			
Thelodus spp.	—	VC*	A
Logania ludlowiensis	—	C*	FC—P
Acanthodian scales and spines	—	R*	R
Algae			
Pachytheca sp.	—	—	P
organic debris	—	A	C

1 = olive-green carbonate sediment; *2* = gypsum layer; *3* = phosphatic clays, silts and sands; only the major elements are listed here. *A* = Abundant (>50%); *VC* = Very Common (30—50%); *C* = Common (20—30%); *FC* = Fairly Common (10—20%); *P* = Present (4—10); *R* = Rare (< 4%); * = low density.

(3) The calcareous macroinvertebrate fauna above (as determined from phosphatic casts and moulds) the gypsum layer differs from that below (Table I).

If the expanded Briskin and Schreiber (1978) model is used to interpret these sediments, it could be suggested that:

(1) The olive-green carbonate sediments containing a *Salopina* community fauna (Calef and Hancock, 1974) and a high-density foraminifera assemblage represent a quiet, soft-bottom environment (Fursich and Hurst, 1974) in which the bottom waters were saturated or supersaturated with respect to calcium carbonate.

(2) The gypsum-rich clays contain a rare fauna of fish scales and abundant tabular gypsum crystals in an organic-debris-rich clay. Thin sections show the sediment to be draped over the crystals, suggesting either early in-situ diagenetic growth or predepositional crystal growth. The absence of calcite and presence of gypsum crystals in organic-rich clays may result from a change in the chemistry of the depositional bottom waters to an oxygen-rich, and calcium-carbonate-depleted bottom water; resulting in the solution of calcium carbonate and combination of Ca^{2+} ions (from $CaCO_3$ breakdown) and SO_4^{2-} ions (from the breakdown of biogenic organic debris) to form gypsum. The high concentration of organic debris in the sediment may indicate an increased plankton population and/or a change in chemistry of the sediment porewaters.

(3) The phosphatic sediments contain gypsum and phosphatic nodules in their clay layers and large quantities of fish scales. This sediment might have arisen from a prolonged period of calcium-carbonate-depleted, oxygen-rich waters sweeping the seafloor and removing calcareous debris (by solution). The phosphatic nodules might have formed by the processes already outlined and the fish debris might result from the mortality of fish schools feeding on the plankton (cf. Antia, 1979; Malz, 1978).

If, as has been suggested here, the Briskin and Schreiber (1978) model can result in a marine phosphorite deposit overlying a gypsum deposit, then it may provide an alternative explanation for the genesis of some phosphorites and phosphatic bonebeds to the traditional explanation of formation in regions of upwelling currents (cf. McKelvey, 1967).

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REFERENCES

Antia, D.D.J., 1979. Bone-beds: a review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering and microbiotas. Mercian Geol., 7(2): 93–174.

Antia, D.D.J. and Whitaker, J.H.McD., 1978. A scanning electron microscope study of the genesis of the Upper Silurian Ludlow Bonebed. In: B. Whalley (Editor), Scanning Electron Microscopy in the Study of Sediments. Geobooks, Norwich.

Baturin, G.N., 1969. Authigenic phosphate concretions in recent sediments of the South West African Shelf. Dokl. Earth Sci. Sections, 189: 227—230.

Baturin, G.N., 1971. Stages of phosphorite formation on the seafloor. Nat. Phys. Sci., 232: 61—62.

Briskin, M. and Schreiber, B.C., 1978. Authigenic gypsum in marine sediments. Mar. Geol. 28: 37—49.

Burnett, W.C., 1974. Phosphorite Deposits from the Seafloor off Peru and Chile. Radiochemical and Geochemical Observations Concerning their Origin. Thesis, University of Hawaii, 164 pp. (unpublished).

Calef, C.E. and Hancock, N.J., 1974. Wenlock and Ludlow marine communities in Wales and the Welsh Borderlands. Palaeontology, 17: 779—810.

Emsley, J. and Hall, D., 1976. The chemistry of phosphorous. Harper and Row, London, 563 pp.

Fürsich, F.T. and Hurst, J.M., 1974. Environmental factors determining the distribution of brachiopods. Palaeontology, 17: 879—900.

Malz, H., 1978. Aquitance Otolithen-Horizonte im Untergrund von Frankfurt am Main. Senckenbergiana Lethaea, 58: 451—471.

Summerhayes, C.P., 1973. Distribution, origin and economic potential of phosphatic sediments from the Agulas Bank, South Africa. Trans. Geol. Soc. Afr., pp. 271—277.

McKelvey, V.E., 1967. Phosphate deposits. U.S. Geol. Surv. Bull., 1252-D: 1—21.

Paleobiology. 1977. vol. 3, pp. 404–414.

A comparison of diversity and trophic nuclei of live and dead molluscan faunas from the Essex Chenier Plain, England

David D. J. Antia

Abstract.—The rarefaction graphs and trophic nuclei of dead molluscan shell cumulates and their associated live molluscan fauna from seven 'ecological' habitats in the Essex Chenier Plain facies are examined and compared. The results show that while the trophic nuclei of the live and dead faunas tend to be dissimilar, the rarefaction graphs indicate that the dead fauna will be more diverse than the live, though changes in the diversity of the live fauna tend to be mirrored in the dead fauna.

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Introduction

In many recent palaeoecological studies much has been made of the statistical methods used by modern marine ecologists. Yet little has been done to determine the validity of these methods in the analysis of recurrent fossil assemblages (Scott and West 1976). The two statistical methods which will be examined here are the rarefaction graph (a measure of ecological diversity) and the trophic nucleus.

The rarefaction graph was conceived by Sanders (1968) as a means of comparing the diversities of similar ecological habitats at varying depths and latitudes. Its advantage over previous diversity measurements is that it takes account of sample size and allows the diversity of different sized collections to be compared graphically at a collection size common to each. Sanders (1968) showed that while individuals are added to a collection at an arithmetic rate, species are added at a logarithmic rate. Furthermore, he showed that diversity can best be described as a species abundance curve, rather than the absolute number of specimens in a sample and that each particular environment has its own characteristic rate of species increment, with its rarefaction curves lying within particular fields.

Since the rarefaction method was originally proposed, it has received heavy theoretical criticism in some statistical studies (Fager 1972; Simberloff 1972; Heck et al. 1975; Clifford and Stephenson 1975; Antia and Wood 1977), while at the same time gaining increasing usage in palaeoecological (Calef 1972; Stanton and Evans 1972; Calef and Hancock 1974; Duff 1975; Antia and Wood 1977; Fursich 1977; Watkins 1978), evolutionary (Raup 1975), and ecological studies (Sanders 1968; Sanders and Hessler 1969; Boesch 1971; Young and Rhodes 1971; Stout and Vandermeer 1975). Hurlbert (1971), Fager (1972), Simberloff (1972) and Clifford and Stephenson (1975) following a re-analysis of Sanders' (1968) data suggest that the rarefaction method is wrong since it tends to overestimate true species richness (diversity) of the fauna. However, since species richness ($E(s)$) can be calculated directly (Hurlbert 1971; Heck et al. 1975) a modified rarefaction graph based on explicit $E(s)$ values will be used here to provide a correct rarefaction plot. The formulae by which the graphs (Fig. 2) were calculated are given as follows:

$$E(s) = s - \sum_{i=1}^{s} (1 - N_i/N)^n \qquad (1)$$

$$\begin{aligned} E(v) = {} & \sum_{i=1}^{s} [(1 - N_i/N)^n 1 - (1 - N_i/N)^n] \\ & + 2 \sum_{j=2}^{s} [(1 - N_i/N - N_j/N)^n \\ & - (1 - N_i/N)^n (1 - N_j/N)^n], \qquad (2) \end{aligned}$$

Where $E(s)$ = species richness; $E(v)$ = species richness variance; N_i = species population size for $i = 1 \ldots S$; N = total number of individuals; S = number of species; n = required sample size.

The formulae for calculating $E(s)$ and

$E(v)$ given here (after Harris 1959; Heck et al. 1975) were used in preference to other formulae given in Heck et al. (1975) and Calef (1972) since when computing the rarefaction plots, the vast majority of calculated points occurred in situations where (n) was so much smaller than N. that drawing n individuals randomly approximated to sampling with replacement (cf. Heck et al. 1975).

Although marine ecological diversity is dependent on a large number of variables which include temperature, local evolution rates, predation rates, nutrient availability, salinity, latitude, depth of water and habitat area (Sanders 1968; Sanders and Hessler 1969; Slobodkin and Sanders 1969; Schopf 1972; Porter 1972; Valentine 1973; Barbour and Brown 1973), some palaeoecologists, when using the rarefaction graph, have assumed that one or more of these variables is more important than the rest; for example Duff (1975) assumed that latitude and temperature are the primary controls on ecological diversity when he used the graph to suggest that the Oxford clay of Central England was deposited in the Boreal Province; in contrast Calef and Hancock (1974) assumed depth to be the primary control on ecological diversity when they used the graph to investigate depth relationships between different Wenlockian and Ludlovian benthonic communities. However, though the validity of the latter usage has been questioned (Lawson 1975) on sedimentological and palaeontological grounds, little has been published illustrating the relationship between actively forming shell deposits and the local ecology.

In any fossil assemblage or ecological community it is usual for a small number of species numerically to dominate the fauna. These species have been variously defined as the prevalent species (Curtis 1959; Calef and Hancock 1974) or the trophic nucleus (Turpaeva 1948; Neyman 1967; Walker 1972; Rhodes et al. 1972; Duff 1975; Fursich 1977). The prevalent species comprise the 'top species' in a faunal assemblage and are determined with respect to their proportional abundance and ubiquity by methods outlined elsewhere (Calef and Hancock 1974). The trophic nucleus is defined as the numerically dominant species which comprise 80% of the fauna (Neyman 1967 p. 151). Both indices are useful in ecological studies; the former shows how widespread a species is in a community, while the latter illustrates the relative abundance of the species and the importance of the various trophic groups.

The facies chosen for this study was that of the Essex Chenier Plain, since the results will be directly applicable to the author's current palaeoecological study of the intertidal (chenier?) Downtonian (Upper Silurian) sediments of the Welsh Borderlands, England.

The chenier plain facies was originally defined by Price (1955) as a number of 'shallow based, perched sandy ridges resting on clay along a marshy or seaward facing tidal shore with other beach ridges stranded in the the marsh behind' but was later modified by Greensmith and Tucker (1967, 1975) to include perched gravel ridges.

The taphonic nature of the dead shell assemblages is considered here only to the extent of determining a shell's completeness since in many recent palaeoecological analyses the amount of abrasion undergone by fossil shells is either indeterminable, as in some rottenstone faunas, or not considered (cf. Watkins, in press; Pickerill 1976; Lawson 1975; Calef and Hancock 1974). Also since many recent statistical palaeoecological studies (e.g. Watkins, in press) do not consider whether or not the faunal 'community' examined at a particular locality is in situ, this aspect has been ignored in sampling.

Methods

Three cheniers within the Blackwater Estuary were examined (Fig. 1). They were the Gore Spit Chenier (TL928082), the Mersea Stone Chenier (TM075154) and the Sales Point Chenier (TM032087) of Greensmith and Tucker (1975). At each chenier the main habitats were examined. These habitats have been partially defined by Davis (1964, 1965 a, b, c, 1967), Davis and Milligan (1964), Greensmith and Tucker (1967), and Greensmith et al. (1973 and will be described in detail by the author in a separate publication.

At each habitat the molluscan fauna was sampled by taking a random area (usually between one and three square metres) and sieving all the sediment in the area down to a depth of 50 cm with a one millimetre mesh sieve. In practice sieving was continued till the number of live molluscan shells in each

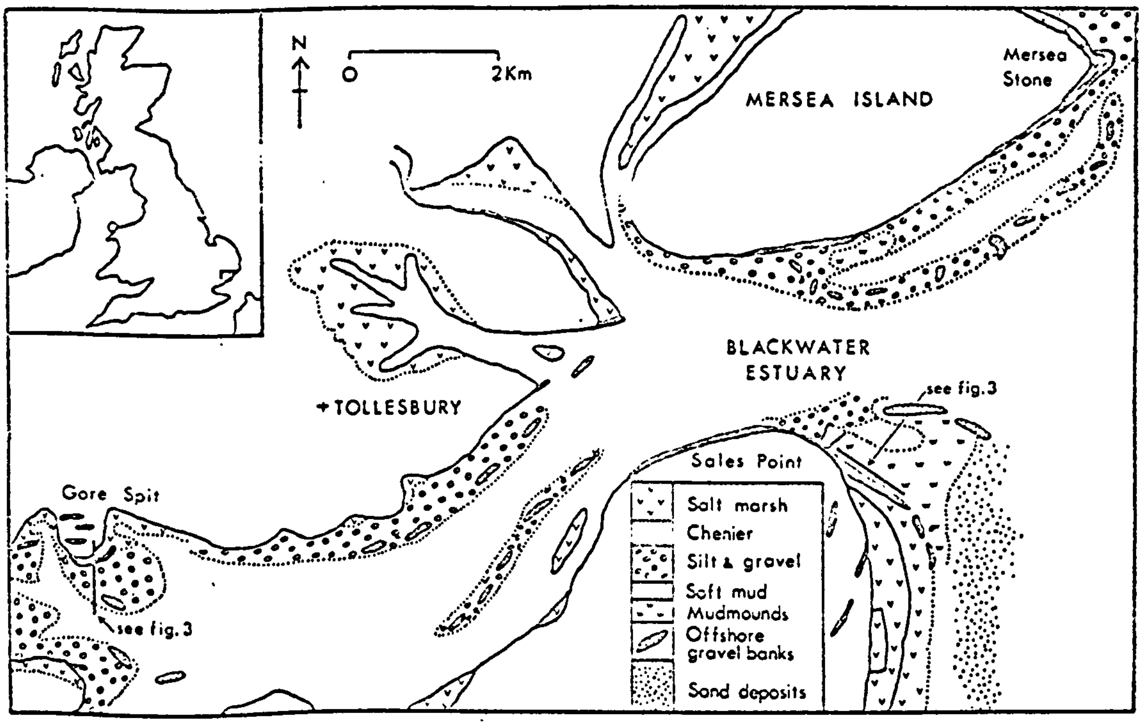

FIGURE 1. Sketch map of the Blackwater Estuary showing sediment distribution. (Inset map shows the relative position of the Blackwater Estuary within the British Isles.)

sample exceeded 500 individuals. A similar number of entire dead molluscan shells were also sampled at each sampling point. The trophic nuclei and rarefaction graphs for each sample were then determined and the results are presented in Table 1 and Fig. 2.

A sample size of 500 individuals was chosen in this instance in order to minimise sampling error (Clifford and Stephenson 1975) and to allow comparison with smaller samples obtained in palaeoecological studies from similar ancient environments.

The Trophic Nucleus of the Fauna

After examination of the data in Table 1, six points of interest are immediately apparent.

(1) The facies can be divided on the bases of morphology and sedimentology into seven ecological habitats labelled A–G in Table 1.

(2) The cheniers themselves contain no live molluscan fauna.

(3) The trophic nucleus of the live fauna bears little relationship in composition to that of its associated shell cumulate, except in the ripple drifted mud habitats where there is no molluscan epifauna and the dead shells are in life position.

(4) The trophic nuclei all contain less than 6 species.

(5) In the majority of habitats, species of the gastropod *Littorina* comprise a dominant part of the trophic nucleus of the live fauna, while in the associated dead shell cumulates the bivalve *Cerastoderma edule* is the dominant member.

(6) Species occurring in the trophic nucleus of the live fauna may be completely unrepresented in the trophic nucleus of the shell cumulate and vice versa.

The abundance of *Cerastoderma edule* in the shell cumulates is an enigma, since the species is not abundant in the live fauna of any of the habitats studied (except in the offshore mudmound habitat—G.R. TM0420SS). However, in disagreement with Greensmith (1977) who suggests an intertidal origin for the shell cumulates, the faunal evi-

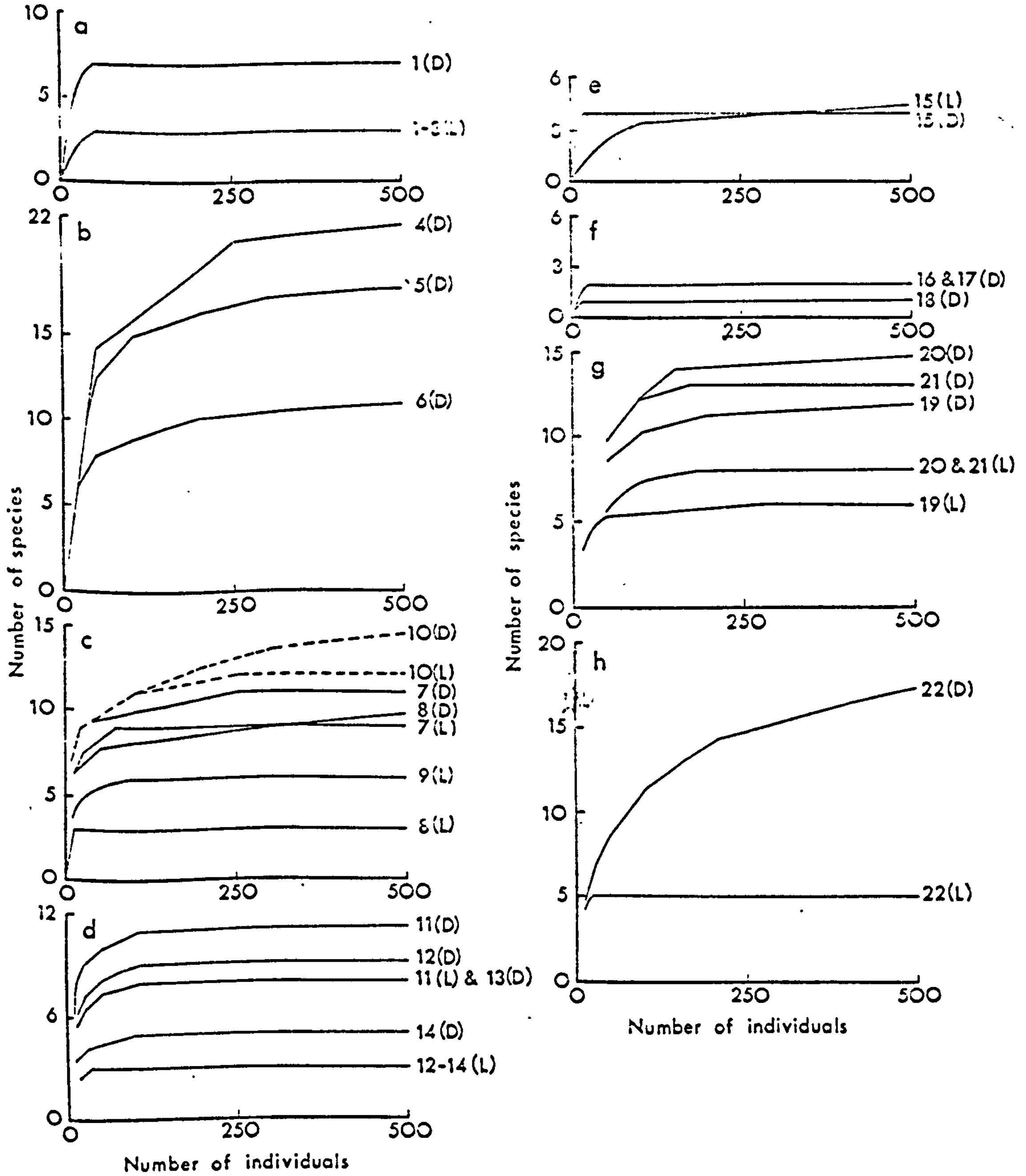

Figure 2. Rarefaction graphs for each sample. Broken line indicates that the sample was sublittoral. L = live molluscan fauna; D = molluscan fauna of associated shell cumulate. (a) Salt marsh habitat grid references 1 = TL928083; 2 = TM072155; 3 = TM036079. (b) Chenier habitat grid references: 4 = TM032087; 5 = TM073151; 6 = TL915082. (c) Silt and gravel habitat grid references: 7 = TL930080; 8 = TM074155; 9 = TL921088; 10 = TL928073. (d) Shell pebble and muddy sand habitat grid references: 11 = TM032088 12 = TM035090; 13 = TM033086; 14 = TM037087. (e) Ripple drifted mud habitat grid references 15 = TM037086. (f) Mudmound habitat grid references. 1. Fauna from the mounds: 16 = TM034087; 17 = TM042088. 18 = TM034085. (g) 2. Fauna from the channels: 19 = TM034085; 20 = TM042088; 21 = TM034087 (h) Offshore shell bank habitat grid reference: 22 = TM039091.

535

TABLE 1. Molluscan species present in the trophic nucleus of each habitat examined (based in part on Greensmith and Tucker 1975). Results expressed where possible as percentage of total population. Note the differences in composition of the trophic nuclei of the live and dead faunas. – = absence of species from the trophic nucleus, + = species present in the trophic nucleus, where the exact abundance is uncertain, * = after Greensmith & Tucker (1967).

HABITATS		FAUNA IN THE TROPHIC NUCLEUS											
		Buccinum undatum (Linn.)	*Cerastoderma edule* (Linn.)	*Crassostrea angulata* (Lamarck)	*Crepidula fornicata* (Linn.)	*Hydrobia* spp.	*Lepidochitona cinereus* (Linn.)	*Littorina* spp.	*Macoma balthica* (Linn.)	*Mytilus edulis* (Linn.)	*Ostrea edulis* (Linn.)	*Scrobicularia plana* (da Costa)	Height of station above M.L.W.M. in metres
A. *Salt Marsh*													
1. Gore Marsh	(Live)	–	–	–	–	+	–	–	+	–	–	+	1.7
(TL928083)	(Dead)	–	+	–	–	–	–	–	–	+	+	–	
2. Sales Point	(Live)	–	–	–	–	–	–	91	–	–	–	–	1.8
(TM036079)	(Dead)	NOT RECORDED											
3. Mersea Stone	(Live)	–	–	–	–	–	–	100	–	–	–	–	1.8
(TM072155)	(Dead)	NOT RECORDED											
B. *Chenier* (No live observed)													
1. Gore Spit (TL915082)	(Dead)	–	46	7	–	–	–	–	–	23	7	–	2.1
2. Sales Point (TM032087)	*(Dead)	–	70	–	–	–	–	10	–	–	–	–	2.8
3. Mersea Stone (TM073154)	(Dead)	–	46	–	–	23	–	–	–	11	–	–	2.9
C. *Silt and Gravel*													
1. Gore Spit													
TL924088	(Live)	–	–	–	–	–	–	92	–	–	–	–	1.5
TL928073	(Live)	–	–	–	78	–	6	–	–	–	–	–	1.4
	(Dead)	22	–	–	61	–	–	–	–	–	–	–	
TL930080	(Live)	–	11	–	18	–	–	31	–	23	–	–	0.9
	(Dead)	–	22	–	11	–	–	–	13	15	–	19	
2. Mersea Stone													
TM074155	(Live)	–	–	–	–	–	–	+	+	–	–	+	1.4
	(Dead)	–	+	–	–	+	–	–	–	–	–	+	
D. *Shell, pebble and muddy sand*													
TM035090	(Live)	–	–	–	–	–	–	81	–	–	–	–	1.3
	(Dead)	–	53	–	–	–	–	17	–	21	–	–	
TM037087	(Live)	–	–	–	–	–	–	92	–	–	–	–	1.2
	(Dead)	–	63	–	–	–	–	27	–	–	–	–	
TM033086	(Live)	–	–	–	–	–	–	91	–	–	–	–	1.3
	(Dead)	–	45	–	–	–	–	21	–	14	–	–	
TM032088	(Live)	–	–	–	11	–	–	57	–	15	–	–	1.2
	(Dead)	–	28	–	17	–	–	13	–	19	–	8	
E. *Ripple drifted mud*													
TM037086	(Live)	–	–	–	–	–	–	–	–	–	–	92	0.8
	(Dead)	–	–	–	–	–	–	–	–	–	–	96	

TABLE 1.—(Continued).

HABITATS		*Buccinum undatum* (Linn.)	*Cerastoderma edule* (Linn.)	*Crassostrea angulata* (Lamarck)	*Crepidula fornicata* (Linn.)	*Hydrobia* spp.	*Lepidochitona cinereus* (Linn.)	*Littorina* spp.	*Macoma balthica* (Linn.)	*Mytilus edulis* (Linn.)	*Ostrea edulis* (Linn.)	*Scrobicularia plana* (Da Costa)	Height of station above M.L.W.M. in metres
		FAUNA IN THE TROPHIC NUCLEUS											
F. *Mudmounds*													
1. Dead fauna from mounds													
TM042088		–	–	–	–	–	–	–	–	–	–	95	0.4
TM034087		–	–	–	–	–	–	–	–	–	–	85	1.1
TM034085		–	–	–	–	–	–	–	–	–	–	100	1.4
2. Fauna from channels													
TM042088	(Live)	–	18	–	14	–	–	20	16	23	–	–	
	(Dead)	–	42	–	–	–	–	12	–	18	–	8	
TM034087	(Live)	–	–	–	–	–	–	83	–	–	–	–	
	(Dead)	–	41	–	–	–	–	14	8	16	–	7	
TM034085	(Live)	–	–	–	–	–	–	87	–	–	–	–	
	(Dead)	–	46	–	–	–	–	22	–	8	–	11	
G. *Offshore shell bank*													
TM039091	(Live)	–	–	–	–	–	–	66	–	17	–	–	0.4
	(Dead)	–	40	–	8	–	–	14	–	18	–	–	

dence presented here (Tables 1 and 2) suggests that much of the fauna in the shell cumulates may have a subtidal origin (also Tucker, pers. com., 1977) having been swept onshore primarily by wave action and secondarily by tidal currents, as in the Solway Chenier Plain (Farrow, pers. com., 1977), from two main sources; (1) the Blackwater Estuary itself, as can be inferred from the presence of *Crassostrea angulata* and *Ostrea edulis* in the trophic nucleus of the Gore Spit Chenier (Table 1)—see Davis (1965a, 1967) and Barnes and Coughlan (1971) for details regarding the numerical distribution of these species in the Blackwater Estuary; and (2) the open sea benthos as is indicated by the presence of the marine species *Neptunea antiqua* (Linn.) and *Glycimeris glycimeris* (Linn.) in the shell cumulates of the offshore shell bank at Sales Point, Bradwell (TM039091).

The Rarefaction Graphs of the Fauna

The rarefaction graphs for the different habitats (Fig. 2) consistently show a higher diversity dead molluscan fauna associated with a less diverse live molluscan fauna at each sample locality (Table 3), except in the ripple-drifted mud habitat, where both live and dead molluscan shells are only found infaunally in life position and hence have the same faunal diversity. Two other trends were also observed (1) lateral changes in diversity can occur within a habitat, for example the shell, pebble and muddy sand habitat of the Sales Point region (Figs. 2 & 3a), and (2) diversity decreases as the fauna proceeds up the littoral zone as at Gore Spit (Fig. 2 & 3b). However, general diversity gradients may contain a superimposed varietal component since diversity also appears to decrease with decreasing topographic complexity of the

TABLE 2. Rank order distribution of species in corresponding live and dead faunas, for samples of 500 individuals. A key to localities is given in Fig. 2. * Indicates species usually confined to a subtidal habitat in life. Note the differences in species rank orderings presented by the live and dead faunas; also note the high percentages of subtidal species in the dead shell faunas.

	LOCALITIES																									
SPECIES	1L	1D	7L	7D	8L	8D	10L	10D	11L	11D	12L	12D	13L	13D	14L	14D	15L	15D	19L	19D	20L	20D	21L	21D	22L	22D
Abra alba (Wood)*	–	–	–	–	–	–	3	4	–	–	–	–	–	–	–	–	–	–	–	–	–	15	–	–	–	12
Acanthodoris pilosa (Muller)*	–	–	–	–	–	–	10	13	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Barnea candida (L.)	–	–	–	7	–	–	–	–	8	10	–	9	–	–	–	–	3	3	–	9	–	11	–	7	–	8
Buccinum undatum L.*	–	–	–	10	–	10	8	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10
Cardium exiguum L.*	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	–	–	–	7
Cerastoderma edule (L.)	–	3	4	1	–	1	12	–	5	1	–	1	–	1	–	1	4	4	6	1	2	1	6	1	–	1
Chlamys varia (Muller)*	–	–	–	8	–	–	–	8	–	9	–	–	–	–	–	–	–	–	–	–	–	–	–	9	–	–
Crassostrea angulata (Lamarck)*	–	4	–	9	–	–	9	11	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Crepidula fornicata (L.)	–	5	3	5	–	4	1	1	4	3	–	–	–	–	–	–	–	–	–	6	5	6	–	11	4	4
Ensis sp.*	–	–	–	–	–	–	–	–	–	11	–	–	–	–	–	–	–	–	–	–	–	10	–	13	–	–
Gibbula cineraria L.	–	–	–	–	–	–	6	12	–	–	–	–	–	–	–	–	–	–	–	–	–	12	–	–	–	17
Hydrobia ulvae (Penn.)	2	–	9	–	–	3	–	–	–	8	–	–	–	7	–	–	–	–	–	10	–	7	–	6	–	–
H. ventrosa (Mont.)	–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lepidochitona cinereus (L.)	–	–	–	–	–	–	2	–	6	–	3	–	–	–	–	–	–	–	3	–	6	–	5	–	5	–
Littorina littorea (L.)	–	6	1	–	1	6	5	6	1	4	1	3	1	2	1	2	1	1	1	2	4	3	1	3	1	3
L. littoralis (L.)	–	–	–	–	–	–	–	14	–	–	–	–	–	–	–	–	–	–	–	–	7	–	4	–	2	5
L. saxatilis (Olivi)	–	7	6	–	–	–	–	–	3	–	–	8	3	6	3	4	–	–	2	7	–	–	–	–	–	–
Macoma balthica (L.)	1	–	7	4	2	5	–	10	–	5	–	–	–	4	–	–	–	–	5	5	3	4	3	4	–	9
Modiolus modiolus (L.)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9	–	–	–	–
Mya arenaria L.	–	–	5	–	–	9	–	3	–	–	–	–	–	–	–	–	–	–	–	–	8	8	–	–	–	13
M. truncata L.	–	–	–	–	–	–	–	15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mytilus edulis L.	–	1	2	3	–	–	–	–	2	2	2	2	2	3	2	3	–	–	4	4	1	2	2	2	3	2
Nassarius reticulatus L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11
Nucula nucleus (L.)*	–	–	–	–	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ostrea edulis (L.)*	–	2	–	6	–	7	7	–	–	7	–	6	–	8	–	–	–	–	–	8	–	13	–	8	–	6
Petricola pholadiformis (Lamarck)*	–	–	–	–	–	–	–	5	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Scrobicularia plana (da Costa)	3	–	8	2	3	2	–	–	7	6	–	5	–	5	–	–	2	2	–	3	–	5	7	5	–	14
Teredo navilis L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–	–	–
Urosalpinx cinerea (Say)*	–	–	–	–	–	–	11	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	–	15
Venerupis aurea (Gmelin)*	–	–	–	–	–	–	–	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
% species designated by*	0	29	0	40	0	20	50	60	0	27	0	38	0	13	0	0	0	0	0	10	0	27	0	31	0	41

TABLE 3. Species richness variances $E(v)$ and absolute values where $n = 100\,E(d)$ and $n = 500\,E(s)$, and the difference between live and dead fauna expressed in the form (EsL-D) and (EsL-D)/s where s = total number of species present. Key to samples given in Fig. 2. Note (1) that the species richness variance (col. 2) tends to be higher in the dead faunas than in the corresponding live. (2) Less than 50% of the samples showed no increase in the number of species present (col. 6) when the sample size was increased from 100 individuals (col. 4) to 500 individuals (col. 3). (3) The number of species in the live and dead faunas (col. 3) are different (col. 5); these differences tend to be most marked with respect to the total number of species present in a sample (col. 7) which is taken from a habitat low in the intertidal zone (22).

(1) Sample	(2) E(v)	(3) E(s)	(4) E(d)	(5) EsL-D	(6) (Es-Ed)	(7) EsL-D/s
1L	0.634	3.000	3.000		0.000	
1D	0.751	7.000	7.000	4.000	0.000	0.4
2D	0.481	3.000	3.000		0.000	
3D	0.577	3.000	3.000		0.000	
4D	0.459	20.558	14.296		6.262	
5D	0.733	16.902	12.739		4.163	
6D	0.646	10.568	7.908		2.660	
7L	0.822	9.000	9.000		0.000	
7D	0.853	11.000	10.008	3.000	0.992	0.2
8L	0.654	3.000	3.000		0.000	
8D	0.770	9.634	8.327	6.634	1.307	0.7
9L	0.689	6.000	5.914		0.086	
10L	0.459	12.000	10.949		1.051	
10D	0.578	14.488	10.653	2.288	3.835	0.1
11L	0.744	8.000	8.000		0.000	
11D	0.828	11.000	11.000	3.000	0.000	0.2
12L	0.486	3.000	3.000		0.000	
12D	0.715	9.000	8.833	6.000	0.167	0.6
13L	0.297	3.000	3.000		0.000	
13D	0.735	8.000	8.000	5.000	0.000	0.6
14L	0.233	3.000	3.000		0.000	
14D	0.547	5.000	5.000	2.000	0.000	0.5
15L	0.086	4.496	3.389		1.107	
15D	0.646	4.055	4.011	0.441	0.044	0.1
16D	0.254	2.000	2.000		0.000	
17D	0.095	2.000	2.000		0.000	
18D	0.000	1.000	1.000		0.000	
19L	0.393	6.000	5.394		0.606	
19D	0.731	11.994	10.386	5.994	1.608	0.5
20L	0.840	8.000	8.000		0.000	
20D	0.744	15.000	12.949	7.000	2.451	0.4
21L	0.369	8.000	7.156		0.844	
21D	0.772	13.000	12.400	5.000	0.600	0.3
22L	0.718	5.000	5.000		0.000	
22D	0.737	17.272	11.125	12.272	6.147	0.7

environment. For instance the topographically complex inner mudmounds of Sales Point (TM034085 Fig. 2) are more diverse than the less complex ripple drifted muds slightly further offshore (TM037086 Fig. 2). A similar effect has been observed by Kohn (1968) in the Indian Ocean among gastropods of the genus *Conus* in both inter and subtidal habitats and by MacArthur (1964, 1968) among woodland birds.

Conclusions

The chenier plain deposits of the River Blackwater are divided into seven ecological habitats, each of which contain a low diversity molluscan fauna, associated with a slightly higher diversity actively forming shell cumulate. This environment was used to test the validity of two statistical indices which are gaining increasing popularity in palaeoecological studies (the concept of the trophic nucleus and the rarefaction curve) by comparing the local molluscan fauna with its associated shell cumulates. From this comparison a number of points relevant to the palaeoecologist arise.

(1) Rarefaction graphs tend to give a higher diversity value for the associated

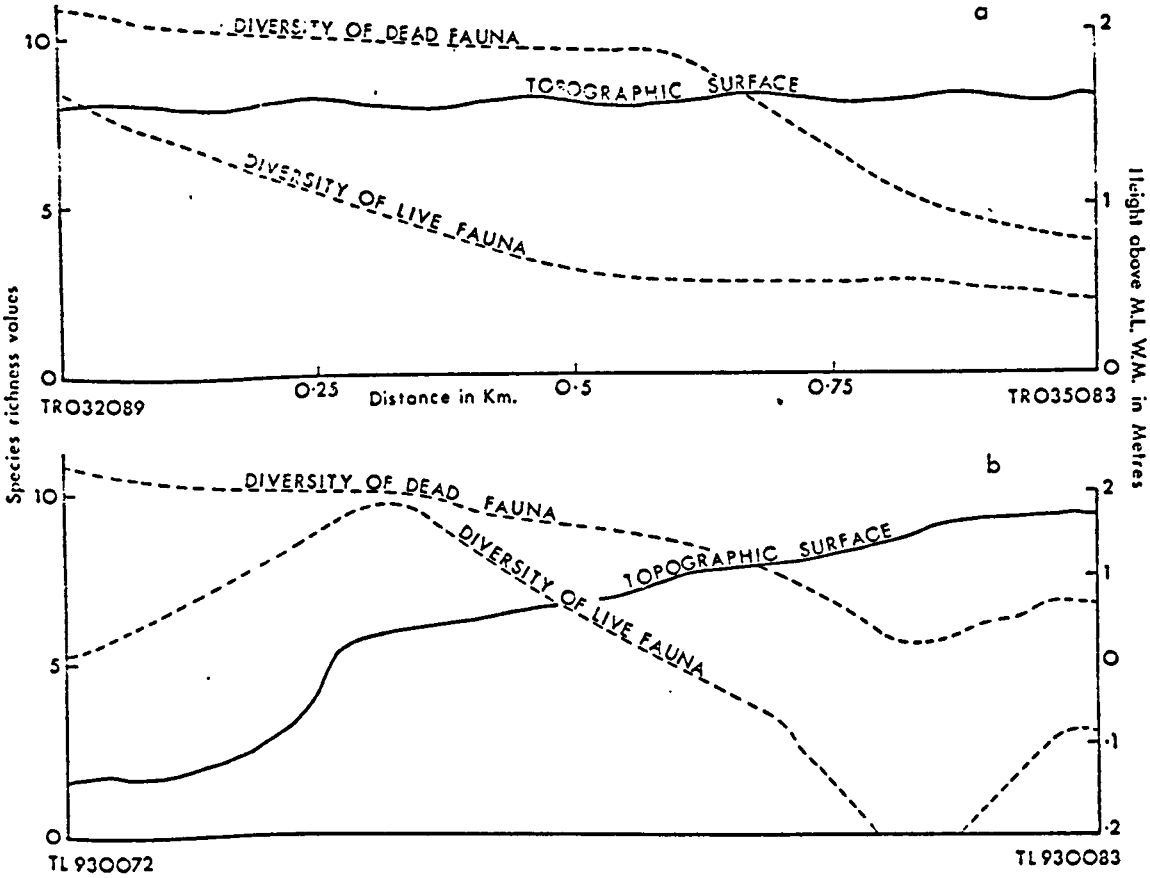

FIGURE 3. The relationship of diversity (species richness) to topography in two areas (where species richness is defined in terms of the number of species per 500 individuals); illustrating (a) variations in diversity within the shell pebble and muddy sand habitat of Sales Point and (b) variations in diversity across the littoral zone at Gore Spit. TR numbers should read as TM.

shell cumulate than they do for the live molluscan fauna. Thus, diversity values produced by the rarefaction method in palaeoecology will tend to overestimate, rather than underestimate, the original diversity of the fauna.

(2) Changes in molluscan diversity of the local fauna, recorded by rarefaction methods, tend to mirror similar diversity changes in the associated shell cumulates.

(3) The composition of the trophic nucleus of the indigenous fauna is often very different from that suggested by the associated shell cumulates.

Thus it would appear from this study that the palaeoecologist studying a fossil chenier could be reasonably confident in interpreting diversity changes but not so in interpreting the trophic nuclei of the fauna.

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Literature Cited

ANTIA, D. D. J. AND B. A. WOOD. 1977. Some aspects of the palaeoecology of the Eb zone of the Edale Shales (Namurian) in the Edale Valley. Derbyshire. Mercian Geol. *6*(3):In Press.
BARBOUR, D. S. AND J. H. BROWN. 1974. F species diversity in lakes. Am. Nat. *108*:473–

Barnes, R. S. K. and J. Coughlan. 1971. A survey of the bottom fauna of the Blackwater Estuary: 1970. Essex Nat. 32:263–276.

Boesch, D. F. 1971. Distribution and structure of benthic communities in a gradient estuary. Ph.D. Dissertation. Virginia Institute of Marine Science; Virginia.

Calef, C. E. 1972. Palaeoecological and stratigraphical studies of the Ludlow in Wales and the Welsh Borderlands. Ph.D. Thesis. Oxford University; Oxford.

Calef, C. E. and N. J. Hancock. 1974. Wenlock and Ludlow marine communities in Wales and the Welsh Borderland. Palaeontology. *17*:779–810.

Clifford, H. T. and W. Stephenson. 1975. An Introduction to Numerical Classification. 229 pp. Academic Press; London.

Curtis, J. T. 1959. The Vegetation of Wisconsin. 657 pp. University of Wisconsin Press; Madison, Wisconsin.

Davis, D. S. 1964. The physical and biological features of the Mersea flats. Central Electricity Research Lab. Note No. RD/L/N131/164. 14 pp.

Davis, D. S. 1965a. A study of the bottom fauna of the Blackwater Estuary: 1960–1963. Central Electricity Research Lab. Report No. RD/L/R 1300. 54 pp.

Davis, D. S. 1965b. Biology of the Bradwell shore. Central Electricity Research Lab. Note No. RD/L/N 3/65. 24 pp.

Davis, D. S. 1965c. The biological effects of Bradwell power station: precommissioning studies on the fauna of Bradwell Creek. Central Electricity Research Lab. Note No. RD/L/N 2/65. 18 pp.

Davis, D. S. 1967. The marine fauna of the Blackwater Estuary and adjacent waters, Essex. Essex Nat. 32:2–61.

Davis, D. S. and G. M. Milligan. 1964. Bradwell biological investigations: seaweeds of the Blackwater Estuary. Central Electricity Research Lab. Note No. RD/L/N 41/64. 20 pp.

Duff, K. L. 1975. Palaeoecology of a bituminous shale—the Lower Oxford Clay of central England. Palaeontology. *18*:443–482.

Fager, E. W. 1972. Diversity, a sampling study. Am. Nat. *106*:293–310.

Fursich, F. T. 1977. Corallian (Upper Jurassic) marine benthic associations from England and Normandy. Palaeontology. *20*:337–386.

Greensmith, J. T. 1977. Carbonate bodies in Essex marshlands. Geol. Soc. London. News Letter. *6*(2):22.

Greensmith, J. T. and E. V. Tucker. 1967. Morphology and evolution of inshore shell ridges and mudmounds on modern intertidal flats, near Bradwell, Essex. Proc. Geol. Assoc. 77:329–346.

Greensmith, J. T. and E. V. Tucker. 1975. Dynamic structures in the Holocene chenier plain setting of Essex, England. Pp. 251–272. In: Hails, J. and A. Carr, eds. Nearshore Sediment Dynamic and Sedimentation.

Greensmith, J. T., R. G. Blezard, C. R. Bristow, R. Markham, and E. V. Tucker. 1973. The Estuarine Region of Suffolk and Essex. Geol. Assoc. Guide No. 12, 41 pp.

Harris, B. 1959. Determining bounds on integrals with application to cataloguing problems. Ann. Math. Stat. *30*:521–548.

Heck, K. L., G. V. Belle, and D. Simberloff. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. Ecology. 56:1459–61.

Hurlbert, S. H. 1971. The non-concept of species diversity: A critique and alternative parameters. Ecology. *52*:557–586.

Kohn, A. J. 1968. Microhabitats abundance and food of *Conus* on atoll reefs in the Maldive and Chagos Islands. Ecology. *49*:1046–1062.

Lawson, J. D. 1975. Ludlow Benthonic Assemblages. Palaeontology. *18*:509–525.

MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. Am. Nat. 98:387–397.

MacArthur, R. H. 1968. The theory of the niche. In: Lewontin, R. C., ed. Population Biology and Evolution. Syracuse Univ. Press; Syracuse, New York.

Neyman, A. A. 1967. Limits to the application of the Trophic group concept in benthonic studies. Oceanol. Acad. Sci. U.S.S.R., *7*:149–155.

Pickerill, R. R. 1976. Significance of a new fossil locality containing a Salopina community in the Waweig Formation (Silurian-uppermost Ludlow/Pridoli) of South West New Brunswick. Can. J. Earth Sci. *13*:1328–31.

Porter, J. W. 1972. Predation by *Acanthaster* and its effect on coral species diversity. Am. Nat. *106*:487–492.

Price, W. A. 1955. Environment and formation of the chenier plain. Quaternaria. 2:75–86.

Raup, D. M. 1975. Taxonomic diversity estimation using rarefaction. Paleobiology. *1*:333–342.

Rhodes, D. C., I. G. Speden, and K. M. Waage. 1972. Trophic group analysis of Upper Cretaceous (Maestrichtian) bivalve assemblages from South Dakota. Bull. Am. Assoc. Petrol. Geol. *56*:1100–1113.

Sanders, H. L. 1968. Marine Benthic diversity: a comparative study. Am. Nat. *102*:243–282.

Sanders, H. L. and R. R. Hessler. 1969. Ecology of the deep sea benthos. Science. *163*:1419–1424.

Schopf, T. J. M., ed. 1972. Models in Paleobiology. 250 pp. W. H. Freeman and Co.; San Francisco.

Scott, R. W. and R. R. West. 1976. The structure and classification of paleocommunities. Hutchinson & Ross; Stroudsburg, Pennsylvania.

Simberloff, D. 1972. Properties of the rarefaction diversity measurement. Am. Nat. *106*:414–418.

Slobodkin, L. B. and H. L. Sanders. 1969. On the contribution of environment predictability to species diversity. Pp. 71–81. In: Woodwell, G. M. and H. H. Smith, eds. Diversity and Stability in Ecological Systems. Brookhaven Sympos. Biol. 22; Upton, New York.

Stanton, R. J. and I. Evans. 1972. Community structure and sampling requirement in paleoecology. J. Paleontol. *46*:845–858.

Stout, J. and J. Vandermeer. 1975. Comparison of species richness for stream inhabiting insects in tropical and mid latitude streams. Am. Nat. *107*: 295–302.

Turpaeva, E. P. 1948. The feeding of some benthic invertebrates of the Barents Sea. Zool. Zh. Ukr. 27.

Valentine, J. W. 1973. Evolutionary palaeoecology of the marine biosphere. 510 pp. Prentice-Hall; New Jersey.

Walker, K. R. 1972. Trophic analysis: a method for studying the function of ancient communities. J. Paleontol. *46*:82–93.

Watkins, R. 1978. Benthic community organisation in the Ludlow series of the Welsh Borderland. Bull. Brit. Mus. In Press.

Young, D. K. and D. C. Rhoads. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. I. A transect study. Mar. Biol. *11*:242–254.

542.

Paleobiology. 1977. vol. 3, pp. 404–414.

A comparison of diversity and trophic nuclei of live and dead molluscan faunas from the Essex Chenier Plain, England

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Abstract.—The rarefaction graphs and trophic nuclei of dead molluscan shell cumulates and their associated live molluscan fauna from seven 'ecological' habitats in the Essex Chenier Plain facies are examined and compared. The results show that while the trophic nuclei of the live and dead faunas tend to be dissimilar, the rarefaction graphs indicate that the dead fauna will be more diverse than the live, though changes in the diversity of the live fauna tend to be mirrored in the dead fauna.

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Introduction

In many recent palaeoecological studies much has been made of the statistical methods used by modern marine ecologists. Yet little has been done to determine the validity of these methods in the analysis of recurrent fossil assemblages (Scott and West 1976). The two statistical methods which will be examined here are the rarefaction graph (a measure of ecological diversity) and the trophic nucleus.

The rarefaction graph was conceived by Sanders (1968) as a means of comparing the diversities of similar ecological habitats at varying depths and latitudes. Its advantage over previous diversity measurements is that it takes account of sample size and allows the diversity of different sized collections to be compared graphically at a collection size common to each. Sanders (1968) showed that while individuals are added to a collection at an arithmetic rate, species are added at a logarithmic rate. Furthermore, he showed that diversity can best be described as a species abundance curve, rather than the absolute number of specimens in a sample and that each particular environment has its own characteristic rate of species increment, with its rarefaction curves lying within particular fields.

Since the rarefaction method was originally proposed, it has received heavy theoretical criticism in some statistical studies (Fager 1972; Simberloff 1972; Heck et al. 1975; Clifford and Stephenson 1975; Antia and Wood 1977), while at the same time gaining increasing usage in palaeoecological (Calef 1972; Stanton and Evans 1972; Calef and Hancock 1974; Duff 1975; Antia and Wood 1977; Fursich 1977; Watkins 1978), evolutionary (Raup 1975), and ecological studies (Sanders 1968; Sanders and Hessler 1969; Boesch 1971; Young and Rhodes 1971; Stout and Vandermeer 1975). Hurlbert (1971), Fager (1972), Simberloff (1972) and Clifford and Stephenson (1975) following a re-analysis of Sanders' (1968) data suggest that the rarefaction method is wrong since it tends to overestimate true species richness (diversity) of the fauna. However, since species richness ($E(s)$) can be calculated directly (Hurlbert 1971; Heck et al. 1975) a modified rarefaction graph based on explicit $E(s)$ values will be used here to provide a correct rarefaction plot. The formulae by which the graphs (Fig. 2) were calculated are given as follows:

$$E(s) = s - \sum_{i=1}^{s} (1 - N_i/N)^n \qquad (1)$$

$$\begin{aligned} E(v) = {} & \sum_{i=1}^{s} [(1 - N_i/N)^n 1 - (1 - N_i/N)^n] \\ & + 2 \sum_{j=2}^{s} [(1 - N_i/N - N_j/N)^n \\ & - (1 - N_i/N)^n (1 - N_j/N)^n], \qquad (2) \end{aligned}$$

Where $E(s)$ = species richness; $E(v)$ = species richness variance; N_i = species population size for i = 1...S; N = total number of individuals; S = number of species; n = required sample size.

The formulae for calculating $E(s)$ and

$E(v)$ given here (after Harris 1959; Heck et al. 1975) were used in preference to other formulae given in Heck et al. (1975) and Calef (1972) since when computing the rarefaction plots, the vast majority of calculated points occurred in situations where (n) was so much smaller than N, that drawing n individuals randomly approximated to sampling with replacement (cf. Heck et al. 1975).

Although marine ecological diversity is dependent on a large number of variables which include temperature, local evolution rates, predation rates, nutrient availability, salinity, latitude, depth of water and habitat area (Sanders 1968; Sanders and Hessler 1969; Slobodkin and Sanders 1969; Schopf 1972; Porter 1972; Valentine 1973; Barbour and Brown 1973), some palaeoecologists, when using the rarefaction graph, have assumed that one or more of these variables is more important than the rest; for example Duff (1975) assumed that latitude and temperature are the primary controls on ecological diversity when he used the graph to suggest that the Oxford clay of Central England was deposited in the Boreal Province; in contrast Calef and Hancock (1974) assumed depth to be the primary control on ecological diversity when they used the graph to investigate depth relationships between different Wenlockian and Ludlovian benthonic communities. However, though the validity of the latter usage has been questioned (Lawson 1975) on sedimentological and palaeontological grounds, little has been published illustrating the relationship between actively forming shell deposits and the local ecology.

In any fossil assemblage or ecological community it is usual for a small number of species numerically to dominate the fauna. These species have been variously defined as the prevalent species (Curtis 1959; Calef and Hancock 1974) or the trophic nucleus (Turpaeva 1948; Neyman 1967; Walker 1972; Rhodes et al. 1972; Duff 1975; Fursich 1977). The prevalent species comprise the 'top species' in a faunal assemblage and are determined with respect to their proportional abundance and ubiquity by methods outlined elsewhere (Calef and Hancock 1974). The trophic nucleus is defined as the numerically dominant species which comprise 80% of the fauna (Neyman 1967 p. 151). Both indices are useful in ecological studies; the former shows how widespread a species is in a community, while the latter illustrates the relative abundance of the species and the importance of the various trophic groups.

The facies chosen for this study was that of the Essex Chenier Plain, since the results will be directly applicable to the author's current palaeoecological study of the intertidal (chenier?) Downtonian (Upper Silurian) sediments of the Welsh Borderlands, England.

The chenier plain facies was originally defined by Price (1955) as a number of 'shallow based, perched sandy ridges resting on clay along a marshy or seaward facing tidal shore with other beach ridges stranded in the the marsh behind' but was later modified by Greensmith and Tucker (1967, 1975) to include perched gravel ridges.

The taphonic nature of the dead shell assemblages is considered here only to the extent of determining a shell's completeness since in many recent palaeoecological analyses the amount of abrasion undergone by fossil shells is either indeterminable, as in some rottenstone faunas, or not considered (cf. Watkins, in press; Pickerill 1976; Lawson 1975; Calef and Hancock 1974). Also since many recent statistical palaeoecological studies (e.g. Watkins, in press) do not consider whether or not the faunal 'community' examined at a particular locality is in situ, this aspect has been ignored in sampling.

Methods

Three cheniers within the Blackwater Estuary were examined (Fig. 1). They were the Gore Spit Chenier (TL928082), the Mersea Stone Chenier (TM075154) and the Sales Point Chenier (TM032087) of Greensmith and Tucker (1975). At each chenier the main habitats were examined. These habitats have been partially defined by Davis (1964, 1965 a, b, c, 1967), Davis and Milligan (1964), Greensmith and Tucker (1967), and Greensmith et al. (1973 and will be described in detail by the author in a separate publication.

At each habitat the molluscan fauna was sampled by taking a random area (usually between one and three square metres) and sieving all the sediment in the area down to a depth of 50 cm with a one millimetre mesh sieve. In practice sieving was continued till the number of live molluscan shells in each

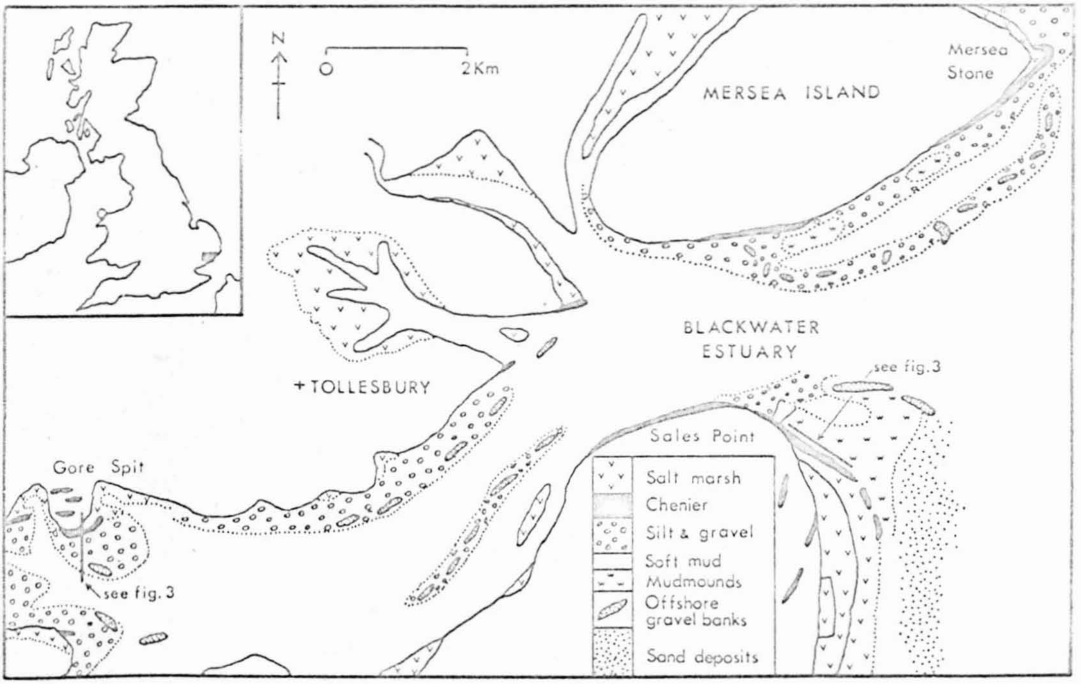

FIGURE 1. Sketch map of the Blackwater Estuary showing sediment distribution. (Inset map shows the relative position of the Blackwater Estuary within the British Isles.)

sample exceeded 500 individuals. A similar number of entire dead molluscan shells were also sampled at each sampling point. The trophic nuclei and rarefaction graphs for each sample were then determined and the results are presented in Table 1 and Fig. 2.

A sample size of 500 individuals was chosen in this instance in order to minimise sampling error (Clifford and Stephenson 1975) and to allow comparison with smaller samples obtained in palaeoecological studies from similar ancient environments.

The Trophic Nucleus of the Fauna

After examination of the data in Table 1, six points of interest are immediately apparent.

(1) The facies can be divided on the bases of morphology and sedimentology into seven ecological habitats labelled A–G in Table 1.

(2) The cheniers themselves contain no live molluscan fauna.

(3) The trophic nucleus of the live fauna bears little relationship in composition to that of its associated shell cumulate, except in the ripple drifted mud habitats where there is no molluscan epifauna and the dead shells are in life position.

(4) The trophic nuclei all contain less than 6 species.

(5) In the majority of habitats, species of the gastropod *Littorina* comprise a dominant part of the trophic nucleus of the live fauna, while in the associated dead shell cumulates the bivalve *Cerastoderma edule* is the dominant member.

(6) Species occurring in the trophic nucleus of the live fauna may be completely unrepresented in the trophic nucleus of the shell cumulate and vice versa.

The abundance of *Cerastoderma edule* in the shell cumulates is an enigma, since the species is not abundant in the live fauna of any of the habitats studied (except in the offshore mudmound habitat—G.R. TM042088). However, in disagreement with Greensmith (1977) who suggests an intertidal origin for the shell cumulates, the faunal evi-

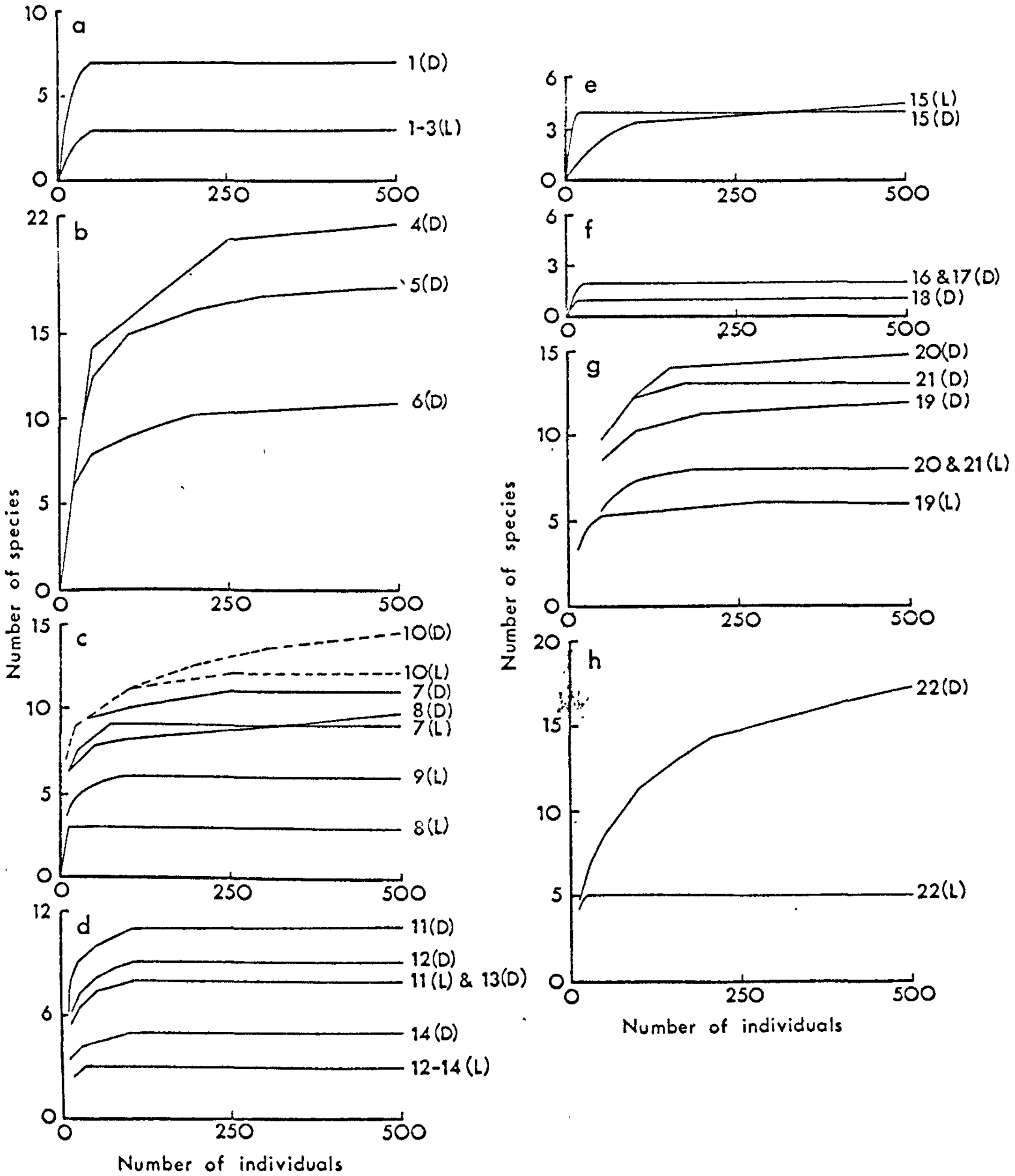

FIGURE 2. Rarefaction graphs for each sample. Broken line indicates that the sample was sublittoral. L = live molluscan fauna; D = molluscan fauna of associated shell cumulate. (a) Salt marsh habitat grid references 1 = TL928083; 2 = TM072155; 3 = TM036079. (b) Chenier habitat grid references: 4 = TM032087; 5 = TM073151; 6 = TL915082. (c) Silt and gravel habitat grid references: 7 = TL930080; 8 = TM074155; 9 = TL921088; 10 = TL928073. (d) Shell pebble and muddy sand habitat grid references: 11 = TM 032088. 12 = TM035090; 13 = TM033086; 14 = TM037087. (e) Ripple drifted mud habitat grid references 15 = TM037086. (f) Mudmound habitat grid references. 1. Fauna from the mounds: 16 = TM034087; 17 = TM042088. 18 = TM034085. (g) 2. Fauna from the channels: 19 = TM034085; 20 = TM042088; 21 = TM034087(h) Offshore shell bank habitat grid reference: 22 = TM039091.

Table 1. Molluscan species present in the trophic nucleus of each habitat examined (based in part on Greensmith and Tucker 1975). Results expressed where possible as percentage of total population. Note the differences in composition of the trophic nuclei of the live and dead faunas. – = absence of species from the trophic nucleus, + = species present in the trophic nucleus, where the exact abundance is uncertain, * = after Greensmith & Tucker (1967).

		FAUNA IN THE TROPHIC NUCLEUS											
HABITATS		*Buccinum undatum* (Linn.)	*Cerastoderma edule* (Linn.)	*Crassostrea angulata* (Lamarck)	*Crepidula fornicata* (Linn.)	*Hydrobia* spp.	*Lepidochitona cinereus* (Linn.)	*Littorina* spp.	*Macoma balthica* (Linn.)	*Mytilus edulis* (Linn.)	*Ostrea edulis* (Linn.)	*Scrobicularia plana* (da Costa)	Height of station above M.L.W.M. in metres
A. *Salt Marsh*													
1. Gore Marsh	(Live)	–	–	–	–	+	–	–	+	–	–	+	1.7
(TL928083)	(Dead)	–	+	–	–	–	–	–	–	+	+	–	
2. Sales Point	(Live)	–	–	–	–	–	–	91	–	–	–	–	1.8
(TM036079)	(Dead)					NOT RECORDED							
3. Mersea Stone	(Live)	–	–	–	–	–	–	100	–	–	–	–	1.8
(TM072155)	(Dead)					NOT RECORDED							
B. *Chenier*													
(No live observed)													
1. Gore Spit (TL915082)	(Dead)	–	46	7	–	–	–	–	–	23	7	–	2.1
2. Sales Point (TM032087)	*(Dead)	–	70	–	–	–	–	10	–	–	–	–	2.8
3. Mersea Stone (TM073154)	(Dead)	–	46	–	–	23	–	–	–	11	–	–	2.9
C. *Silt and Gravel*													
1. Gore Spit													
TL924088	(Live)	–	–	–	–	–	–	92	–	–	–	–	1.5
TL928073	(Live)	–	–	–	78	–	6	–	–	–	–	–	1.4
	(Dead)	22	–	–	61	–	–	–	–	–	–	–	
TL930080	(Live)	–	11	–	18	–	–	31	–	23	–	–	0.9
	(Dead)	–	22	–	11	–	–	–	13	15	–	19	
2. Mersea Stone													
TM074155	(Live)	–	–	–	–	–	–	+	+	–	–	+	1.4
	(Dead)	–	+	–	–	+	–	–	–	–	–	+	
D. *Shell, pebble and muddy sand*													
TM035090	(Live)	–	–	–	–	–	–	81	–	–	–	–	1.3
	(Dead)	–	53	–	–	–	–	17	–	21	–	–	
TM037087	(Live)	–	–	–	–	–	–	92	–	–	–	–	1.2
	(Dead)	–	63	–	–	–	–	27	–	–	–	–	
TM033086	(Live)	–	–	–	–	–	–	91	–	–	–	–	1.3
	(Dead)	–	45	–	–	–	–	21	–	14	–	–	
TM032088	(Live)	–	–	–	11	–	–	57	–	15	–	–	1.2
	(Dead)	–	28	–	17	–	–	13	–	19	–	8	
E. *Ripple drifted mud*													
TM037086	(Live)	–	–	–	–	–	–	–	–	–	–	92	0.8
	(Dead)	–	–	–	–	–	–	–	–	–	–	96	

TABLE 1.—(Continued).

		FAUNA IN THE TROPHIC NUCLEUS											
HABITATS		*Buccinum undatum* (Linn.)	*Cerastoderma edule* (Linn.)	*Crassostrea angulata* (Lamarck)	*Crepidula fornicata* (Linn.)	*Hydrobia* spp.	*Lepidochitona cinereus* (Linn.)	*Littorina* spp.	*Macoma balthica* (Linn.)	*Mytilus edulis* (Linn.)	*Ostrea edulis* (Linn.)	*Scrobicularia plana* (Da Costa)	Height of station above M.L.W.M. in metres
F. *Mudmounds*													
1. Dead fauna from mounds													
TM042088		–	–	–	–	–	–	–	–	–	–	95	0.4
TM034087		–	–	–	–	–	–	–	–	–	–	85	1.1
TM034085		–	–	–	–	–	–	–	–	–	–	100	1.4
2. Fauna from channels													
TM042088	(Live)	–	18	–	14	–	–	20	16	23	–	–	
	(Dead)	–	42	–	–	–	–	12	–	18	–	8	
TM034087	(Live)	–	–	–	–	–	–	83	–	–	–	–	
	(Dead)	–	41	–	–	–	–	14	8	16	–	7	
TM034085	(Live)	–	–	–	–	–	–	87	–	–	–	–	
	(Dead)	–	46	–	–	–	–	22	–	8	–	11	
G. *Offshore shell bank*													
TM039091	(Live)	–	–	–	–	–	–	66	–	17	–	–	0.4
	(Dead)	–	40	–	8	–	–	14	–	18	–	–	

dence presented here (Tables 1 and 2) suggests that much of the fauna in the shell cumulates may have a subtidal origin (also Tucker, pers. com., 1977) having been swept onshore primarily by wave action and secondarily by tidal currents, as in the Solway Chenier Plain (Farrow, pers. com., 1977), from two main sources; (1) the Blackwater Estuary itself, as can be inferred from the presence of *Crassostrea angulata* and *Ostrea edulis* in the trophic nucleus of the Gore Spit Chenier (Table 1)—see Davis (1965a, 1967) and Barnes and Coughlan (1971) for details regarding the numerical distribution of these species in the Blackwater Estuary; and (2) the open sea benthos as is indicated by the presence of the marine species *Neptunea antiqua* (Linn.) and *Glycimeris glycimeris* (Linn.) in the shell cumulates of the offshore shell bank at Sales Point, Bradwell (TM039091).

The Rarefaction Graphs of the Fauna

The rarefaction graphs for the different habitats (Fig. 2) consistently show a higher diversity dead molluscan fauna associated with a less diverse live molluscan fauna at each sample locality (Table 3), except in the ripple-drifted mud habitat, where both live and dead molluscan shells are only found infaunally in life position and hence have the same faunal diversity. Two other trends were also observed (1) lateral changes in diversity can occur within a habitat, for example the shell, pebble and muddy sand habitat of the Sales Point region (Figs. 2 & 3a), and (2) diversity decreases as the fauna proceeds up the littoral zone as at Gore Spit (Fig. 2 & 3b). However, general diversity gradients may contain a superimposed varietal component since diversity also appears to decrease with decreasing topographic complexity of the

TABLE 2. Rank order distribution of species in corresponding live and dead faunas, for samples of 500 individuals. A key to localities is given in Fig. 2. * Indicates species usually confined to a subtidal habitat in life. Note the differences in species rank orderings presented by the live and dead faunas; also note the high percentages of subtidal species in the dead shell faunas.

	LOCALITIES																									
SPECIES	1L	1D	7L	7D	8L	8D	10L	10D	11L	11D	12L	12D	13L	13D	14L	14D	15L	15D	19L	19D	20L	20D	21L	21D	22L	22D
Abra alba (Wood)*	–	–	–	–	–	–	3	4	–	–	–	–	–	–	–	–	–	–	–	–	–	15	–	–	–	12
Acanthodoris pilosa (Muller)*	–	–	–	–	–	–	10	13	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Barnea candida (L.)	–	–	–	7	–	–	–	–	8	10	–	9	–	–	–	–	3	3	–	9	–	11	–	7	–	8
Buccinum undatum L.*	–	–	–	10	–	10	8	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10
Cardium exiguum L.*	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	–	–	–	7
Cerastoderma edule (L.)	–	3	4	1	–	1	12	–	5	1	–	1	–	1	–	1	4	4	6	1	2	1	6	1	–	1
Chlamys varia (Muller)*	–	–	–	8	–	–	–	8	–	9	–	–	–	–	–	–	–	–	–	–	–	–	–	9	–	–
Crassostrea angulata (Lamarck)*	–	4	–	9	–	–	9	11	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Crepidula fornicata (L.)	–	5	3	5	–	4	1	1	4	3	–	–	–	–	–	–	–	–	–	6	5	6	–	11	4	4
Ensis sp.*	–	–	–	–	–	–	–	–	–	11	–	–	–	–	–	–	–	–	–	–	–	10	–	13	–	–
Gibbula cineraria L.	–	–	–	–	–	–	6	12	–	–	–	–	–	–	–	–	–	–	–	–	–	12	–	–	–	17
Hydrobia ulvae (Penn.)	2	–	9	–	–	3	–	–	–	8	–	–	–	7	–	–	–	–	–	10	–	7	–	6	–	–
H. ventrosa (Mont.)	–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lepidochitona cinereus (L.)	–	–	–	–	–	–	2	–	6	–	3	–	–	–	–	–	–	–	3	–	6	–	5	–	5	–
Littorina littorea (L.)	–	6	1	–	1	6	5	6	1	4	1	3	1	2	1	2	1	1	1	2	4	3	1	3	1	3
L. littoralis (L.)	–	–	–	–	–	–	–	14	–	–	–	–	–	–	–	–	–	–	–	–	7	–	4	–	2	5
L. saxatilis (Olivi)	–	7	6	–	–	–	–	–	3	–	–	8	3	6	3	4	–	–	2	7	–	–	–	–	–	–
Macoma balthica (L.)	1	–	7	4	2	5	–	10	–	5	–	–	–	4	–	–	–	–	5	5	3	4	3	4	–	9
Modiolus modiolus (L.)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9	–	–	–	–
Mya arenaria L.	–	–	5	–	–	9	–	3	–	–	–	–	–	–	–	–	–	–	–	–	8	8	–	–	–	13
M. truncata L.	–	–	–	–	–	–	–	15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Mytilus edulis L.	–	1	2	3	–	–	–	–	2	2	2	2	2	3	2	3	–	–	4	4	1	2	2	2	3	2
Nassarius reticulatus L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11
Nucula nucleus (L.)*	–	–	–	–	–	–	–	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ostrea edulis (L.)*	–	2	–	6	–	7	7	–	–	7	–	6	–	8	–	–	–	–	–	8	–	13	–	8	–	6
Petricola pholadiformis (Lamarck)*	–	–	–	–	–	–	–	5	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Scrobicularia plana (da Costa)	3	–	8	2	3	2	–	–	7	6	–	5	–	5	–	–	2	2	–	3	–	5	7	5	–	14
Teredo navilis L.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–	–	–
Urosalpinx cinerea (Say)*	–	–	–	–	–	–	11	10	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	–	15
Venerupis aurea (Gmelin)*	–	–	–	–	–	–	–	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
% species designated by*	0	29	0	40	0	20	50	60	0	27	0	38	0	13	0	0	0	0	0	10	0	27	0	31	0	41

TABLE 3. Species richness variances $E(v)$ and absolute values where $n = 100\,E(d)$ and $n = 500\,E(s)$, and the difference between live and dead fauna expressed in the form (EsL-D) and (EsL-D)/s where s = total number of species present. Key to samples given in Fig. 2. Note (1) that the species richness variance (col. 2) tends to be higher in the dead faunas than in the corresponding live. (2) Less than 50% of the samples showed no increase in the number of species present (col. 6) when the sample size was increased from 100 individuals (col. 4) to 500 individuals (col. 3). (3) The number of species in the live and dead faunas (col. 3) are different (col. 5); these differences tend to be most marked with respect to the total number of species present in a sample (col. 7) which is taken from a habitat low in the intertidal zone (22).

(1) Sample	(2) E(v)	(3) E(s)	(4) E(d)	(5) EsL-D	(6) (Es-Ed)	(7) EsL-D/s
1L	0.634	3.000	3.000		0.000	
1D	0.751	7.000	7.000	4.000	0.000	0.4
2D	0.481	3.000	3.000		0.000	
3D	0.577	3.000	3.000		0.000	
4D	0.459	20.558	14.296		6.262	
5D	0.733	16.902	12.739		4.163	
6D	0.646	10.568	7.908		2.660	
7L	0.822	9.000	9.000		0.000	
7D	0.853	11.000	10.008	3.000	0.992	0.2
8L	0.654	3.000	3.000		0.000	
8D	0.770	9.634	8.327	6.634	1.307	0.7
9L	0.689	6.000	5.914		0.086	
10L	0.459	12.000	10.949		1.051	
10D	0.578	14.488	10.653	2.288	3.835	0.1
11L	0.744	8.000	8.000		0.000	
11D	0.828	11.000	11.000	3.000	0.000	0.2
12L	0.486	3.000	3.000		0.000	
12D	0.715	9.000	8.833	6.000	0.167	0.6
13L	0.297	3.000	3.000		0.000	
13D	0.735	8.000	8.000	5.000	0.000	0.6
14L	0.233	3.000	3.000		0.000	
14D	0.547	5.000	5.000	2.000	0.000	0.5
15L	0.086	4.496	3.389		1.107	
15D	0.646	4.055	4.011	0.441	0.044	0.1
16D	0.254	2.000	2.000		0.000	
17D	0.095	2.000	2.000		0.000	
18D	0.000	1.000	1.000		0.000	
19L	0.393	6.000	5.394		0.606	
19D	0.731	11.994	10.386	5.994	1.608	0.5
20L	0.840	8.000	8.000		0.000	
20D	0.744	15.000	12.949	7.000	2.451	0.4
21L	0.369	8.000	7.156		0.844	
21D	0.772	13.000	12.400	5.000	0.600	0.3
22L	0.718	5.000	5.000		0.000	
22D	0.737	17.272	11.125	12.272	6.147	0.7

environment. For instance the topographically complex inner mudmounds of Sales Point (TM034085 Fig. 2) are more diverse than the less complex ripple drifted muds slightly further offshore (TM037086 Fig. 2). A similar effect has been observed by Kohn (1968) in the Indian Ocean among gastropods of the genus *Conus* in both inter and subtidal habitats and by MacArthur (1964, 1968) among woodland birds.

Conclusions

The chenier plain deposits of the River Blackwater are divided into seven ecological habitats, each of which contain a low diversity molluscan fauna, associated with a slightly higher diversity actively forming shell cumulate. This environment was used to test the validity of two statistical indices which are gaining increasing popularity in palaeoecological studies (the concept of the trophic nucleus and the rarefaction curve) by comparing the local molluscan fauna with its associated shell cumulates. From this comparison a number of points relevant to the palaeoecologist arise.

(1) Rarefaction graphs tend to give a higher diversity value for the associated

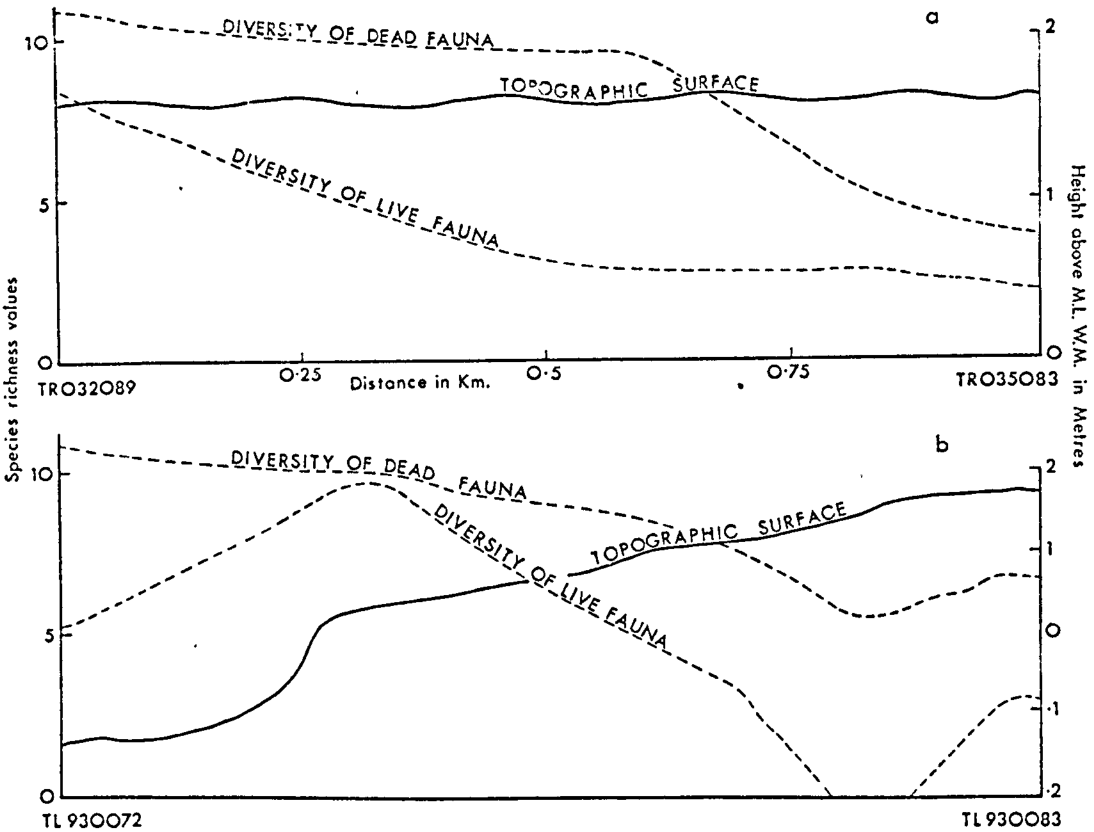

FIGURE 3. The relationship of diversity (species richness) to topography in two areas (where species richness is defined in terms of the number of species per 500 individuals); illustrating (a) variations in diversity within the shell pebble and muddy sand habitat of Sales Point and (b) variations in diversity across the littoral zone at Gore Spit. TR numbers should read as TM.

shell cumulate than they do for the live molluscan fauna. Thus, diversity values produced by the rarefaction method in palaeoecology will tend to overestimate, rather than underestimate, the original diversity of the fauna.

(2) Changes in molluscan diversity of the local fauna, recorded by rarefaction methods, tend to mirror similar diversity changes in the associated shell cumulates.

(3) The composition of the trophic nucleus of the indigenous fauna is often very different from that suggested by the associated shell cumulates.

Thus it would appear from this study that the palaeoecologist studying a fossil chenier could be reasonably confident in interpreting diversity changes but not so in interpreting the trophic nuclei of the fauna.

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Literature Cited

ANTIA, D. D. J. AND B. A. WOOD. 1977. Some aspects of the palaeoecology of the E_1b zone of the Edale Shales (Namurian) in the Edale Valley. Derbyshire. Mercian Geol. *6*(3):In Press.

BARBOUR, D. S. AND J. H. BROWN. 1974. Fish species diversity in lakes. Am. Nat. *108*:473–489.

Barnes, R. S. K. and J. Coughlan. 1971. A survey of the bottom fauna of the Blackwater Estuary: 1970. Essex Nat. *32*:263–276.

Boesch, D. F. 1971. Distribution and structure of benthic communities in a gradient estuary. Ph.D. Dissertation. Virginia Institute of Marine Science; Virginia.

Calef, C. E. 1972. Palaeoecological and stratigraphical studies of the Ludlow in Wales and the Welsh Borderlands. Ph.D. Thesis. Oxford University; Oxford.

Calef, C. E. and N. J. Hancock. 1974. Wenlock and Ludlow marine communities in Wales and the Welsh Borderland. Palaeontology. *17*:779–810.

Clifford, H. T. and W. Stephenson. 1975. An Introduction to Numerical Classification. 229 pp. Academic Press; London.

Curtis, J. T. 1959. The Vegetation of Wisconsin. 657 pp. University of Wisconsin Press; Madison, Wisconsin.

Davis, D. S. 1964. The physical and biological features of the Mersea flats. Central Electricity Research Lab. Note No. RD/L/N131/164. 14 pp.

Davis, D. S. 1965a. A study of the bottom fauna of the Blackwater Estuary: 1960–1963. Central Electricity Research Lab. Report No. RD/L/R 1300. 54 pp.

Davis, D. S. 1965b. Biology of the Bradwell shore. Central Electricity Research Lab. Note No. RD/L/N 3/65. 24 pp.

Davis, D. S. 1965c. The biological effects of Bradwell power station: precommissioning studies on the fauna of Bradwell Creek. Central Electricity Research Lab. Note No. RD/L/N 2/65. 18 pp.

Davis, D. S. 1967. The marine fauna of the Blackwater Estuary and adjacent waters, Essex. Essex Nat. *32*:2–61.

Davis, D. S. and G. M. Milligan. 1964. Bradwell biological investigations: seaweeds of the Blackwater Estuary. Central Electricity Research Lab. Note No. RD/L/N 41/64. 20 pp.

Duff, K. L. 1975. Palaeoecology of a bituminous shale—the Lower Oxford Clay of central England. Palaeontology. *18*:443–482.

Fager, E. W. 1972. Diversity, a sampling study. Am. Nat. *106*:293–310.

Fursich, F. T. 1977. Corallian (Upper Jurassic) marine benthic associations from England and Normandy. Palaeontology. *20*:337–386.

Greensmith, J. T. 1977. Carbonate bodies in Essex marshlands. Geol. Soc. London. News Letter. *6*(2):22.

Greensmith, J. T. and E. V. Tucker. 1967. Morphology and evolution of inshore shell ridges and mudmounds on modern intertidal flats, near Bradwell, Essex. Proc. Geol. Assoc. *77*:329–346.

Greensmith, J. T. and E. V. Tucker. 1975. Dynamic structures in the Holocene chenier plain setting of Essex, England. Pp. 251–272. In: Hails, J. and A. Carr, eds. Nearshore Sediment Dynamic and Sedimentation.

Greensmith, J. T., R. G. Blezard, C. R. Bristow, R. Markham, and E. V. Tucker. 1973. The Estuarine Region of Suffolk and Essex. Geol. Assoc. Guide No. 12, 41 pp.

Harris, B. 1959. Determining bounds on integrals with application to cataloguing problems. Ann. Math. Stat. *30*:521–548.

Heck, K. L., G. V. Belle, and D. Simberloff. 1975. Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. Ecology. *56*:1459–61.

Hurlbert, S. H. 1971. The non-concept of species diversity: A critique and alternative parameters. Ecology. 52:557–586.

Kohn, A. J. 1968. Microhabitats abundance and food of *Conus* on atoll reefs in the Maldive and Chagos Islands. Ecology. *49*:1046–1062.

Lawson, J. D. 1975. Ludlow Benthonic Assemblages. Palaeontology. *18*:509–525.

MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. Am. Nat. *98*:387–397.

MacArthur, R. H. 1968. The theory of the niche. In: Lewontin, R. C., ed. Population Biology and Evolution. Syracuse Univ. Press; Syracuse, New York.

Neyman, A. A. 1967. Limits to the application of the Trophic group concept in benthonic studies. Oceanol. Acad. Sci. U.S.S.R., *7*:149–155.

Pickerill, R. R. 1976. Significance of a new fossil locality containing a Salopina community in the Waweig Formation (Silurian-uppermost Ludlow/Pridoli) of South West New Brunswick. Can. J. Earth Sci. *13*:1328–31.

Porter, J. W. 1972. Predation by *Acanthaster* and its effect on coral species diversity. Am. Nat. *106*: 487–492.

Price, W. A. 1955. Environment and formation of the chenier plain. Quaternaria. *2*:75–86.

Raup, D. M. 1975. Taxonomic diversity estimation using rarefaction. Paleobiology. *1*:333–342.

Rhodes, D. C., I. G. Speden, and K. M. Waage. 1972. Trophic group analysis of Upper Cretaceous (Maestrichtian) bivalve assemblages from South Dakota. Bull. Am. Assoc. Petrol. Geol. *56*:1100–1113.

Sanders, H. L. 1968. Marine Benthic diversity: a comparative study. Am. Nat. *102*:243–282.

Sanders, H. L. and R. R. Hessler. 1969. Ecology of the deep sea benthos. Science. *163*:1419–1424.

Schopf, T. J. M., ed. 1972. Models in Paleobiology. 250 pp. W. H. Freeman and Co.; San Francisco.

Scott, R. W. and R. R. West. 1976. The structure and classification of palaeocommunities. Hutchinson & Ross; Stroudsburg, Pennsylvania.

Simberloff, D. 1972. Properties of the rarefaction diversity measurement. Am. Nat. *106*:414–418.

Slobodkin, L. B. and H. L. Sanders. 1969. On the contribution of environment predictability to species diversity. Pp. 71–81. In: Woodwell, G. M. and H. H. Smith, eds. Diversity and Stability in Ecological Systems. Brookhaven Sympos. Biol. 22; Upton, New York.

Stanton, R. J. and I. Evans. 1972. Community structure and sampling requirement in paleoecology. J. Paleontol. *46*:845–858.

Stout, J. and J. Vandermeer. 1975. Comparison of species richness for stream inhabiting insects in tropical and mid latitude streams. Am. Nat. *107*: 295–302.

Turpaeva, E. P. 1948. The feeding of some benthic invertebrates of the Barents Sea. Zool. Zh. Ukr. 27.

Valentine, J. W. 1973. Evolutionary palaeoecology of the marine biosphere. 510 pp. Prentice-Hall; New Jersey.

Walker, K. R. 1972. Trophic analysis: a method for studying the function of ancient communities. J. Paleontol. *46*:82–93.

Watkins, R. 1978. Benthic community organisation in the Ludlow series of the Welsh Borderland. Bull. Brit. Mus. In Press.

Young, D. K. and D. C. Rhodes. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. I. A transect study. Mar. Biol. *11*:242–254.

Table 1. Faunas in the Brookend Borehold. Note the distinct faunal break at the Junction of the Whitcliffe Beds (Ludlovian) and the Downton Castle Formation (Downtonian).

A = Abundant; VC = Very common; C = Common; P = Present; R = Rare

	Depth in Borehole (m)																																	
	Downton Castle Formation									Whitcliffe Beds (undifferentiated)																						Leintwardine Beds	
SPECIES	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116
BRACHIOPODS																																		
Atrypa recticularis (Linnaeus)		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
Craniops implicata (J. de C. Sowerby)		-	-	-	-	-	-	-	-	2	-	-	-	-	12	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Howellella elegans (Muir Wood)		-	-	-	-	-	-	-	-	2	-	1	-	-	-	-	-	1	-	-	-	-	4	-	-	-	-	-	-	-	1	-	6	2
Isorthis sp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9	1	-	56	23
Lingula cf. *lata* J. de C. Sowerby		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lingula cf. *minima* J. de C. Sowerby		-	-	105	23	-	-	6	36	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Microsphaeridiorhynchia nucula (J. de C. Sowerby)		-	-	-	-	-	-	-	-	-	1	2	-	-	3	-	1	-	10	-	3	15	40	33	24	14	6	1	6	4	11	28	16	30
Orbiculoidea rugata (J. de C. Sowerby)		-	-	-	-	-	-	-	6	-	-	1	-	-	3	-	-	-	-	1	-	-	-	16	2	3	5	-	-	-	-	-	-	3
Protochonetes ludloviensis Muir Wood		-	-	-	-	-	-	-	-	25	47	40	13	90	9	-	1	-	18	107	74	712	240	278	186	127	130	-	1	-	-	142	45	6
Salopina lunata (J. de C. Sowerby)		-	-	-	-	-	-	-	-	52	167	151	13	153	226	14	8	-	107	6	15	2	3	-	2	26	3	-	-	-	-	11	4	-
Schizocrania striata (J. de C. Sowerby)		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Shagamella ludloviensis Boucot & Harper		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	-	-
Sphaerirhynchia wilsoni (J. de C. Sowerby)		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Hyattidina canalis (J. de C. Sowerby)		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Leptaena depressa (J. de C. Sowerby)		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	4
BIVALVES																																		
Leptodesma sp.		-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fuchsella amygdalina (J. de C. Sowerby)		-	-	-	-	-	-	-	-	1	4	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	10	5	-	-	-	-
Coniophora cymbaeformis (J. de C. Sowerby)		-	-	-	-	-	-	-	-	-	-	-	-	11	2	-	3	-	41	-	3	5	5	-	-	-	-	-	4	-	-	-	-	-
Grammysia sp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2	-	-	-	-	-	2	-	-	-	-	-	-
Modiolopsis complanata (J. de C. Sowerby)		-	-	-	-	-	24	6	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nuculites antiquas (J. de C. Sowerby)		-	-	-	-	-	-	-	-	1	-	19	6	14	20	-	6	12	23	12	6	17	23	-	20	14	32	-	-	-	-	-	-	-
Pteronitella inexpecta		-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pteronitella retroflexa (Wahlenberg)		-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	-	-
"Pterinea" tenuistriata (McCoy)		-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ptilodictya sp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Solenamya sp.		-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GASTROPODS																																		
Cyclonema corallii (J. de C. Sowerby)		-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Loxonema obsoletum (J. de C. Sowerby)		-	-	-	-	-	-	-	-	1	-	-	-	3	-	-	-	-	-	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Murchisonia sp.		-	-	-	-	-	-	-	-	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	2	-	-
Naticopsis sp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Turbocheilus helicites (J. de C. Sowerby)		-	-	-	-	-	-	-	64	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CEPHALOPODS																																		
Orthoceras sp.		-	-	-	-	-	-	-	-	-	1	-	-	-	1	1	1	-	2	1	-	8	-	-	-	1	-	-	8	-	-	-	-	-
'Litulites' ibex (J. de C. Sowerby)		-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	3	-	3	1	-	-	-	-	-	-	-	-	-
Kionoceras angulatum (Wahlenberg)		-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	4	1	-	-	1	-
Leurocycloceras sp.		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	1	1	4	2	-	-	-	-	-	-
OTHER MOLLUSCS																																		
Bucanopsis expansus (J. de C. Sowerby)		-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	2	-	-	-	-	-
Hyolithes forbesi (Sharpe)		-	-	-	-	-	-	-	-	-	-	1	1	-	1	-	2	-	-	-	-	1	-	-	-	1	3	-	-	-	-	-	-	-
OSTRACODS																																		
Cytherellina siliqua Jones		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	5	4	-
Calcaribeyrichia torosa (Jones)		-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hebellum cf. *tetragonum* (Krause)		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	8	1	-
Kuressaria circulata (Nejacka)		-	-	-	-	-	-	-	-	1	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scandiella cf. *simplex* (Krause)		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	6	5	-	-	-	-	-	4	-
ANNELIDS																																		
'Serpulites' longissimus J. de C. Sowerby		-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	14	32	-	-	-	-	-	-	-
Spirobis sp.		-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
CONODONTS																																		
Ozarkodina cf. *confluens* (Branson & Mehl)		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	3	-	-	-	-	-	-	-
BRYOZOANS																																		
Ceramopora sp.		-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leioclema sp.		-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
TRILOBITES																																		
Calymene sp.		-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ECHINOIDS																																		
Crinoid columnals		-	-	-	-	-	-	-	-	6	43	27	-	61	32	-	-	-	-	-	-	-	1	-	21	-	15	-	-	-	-	-	-	1
FISH																																		
Thelodont scales		-	C	VC	-	P	P	P	A	A	P	R	P	P	R	P	P	P	P	P	P	P	P	P	P	-	-	-	-	-	-	-	-	-
Acanthodian scales		-	-	P	-	-	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Climatius sp.		-	-	26	-	-	4	-	4	-	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gomphonchus sp.		-	-	-	-	-	-	-	P	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EURYPTERIDS AND PLANTS																																		
Eurypterids		-	-	-	-	1	-	3	-	-	1	-	-	-	2	-	-	1	2	-	-	1	1	1	-	2	-	-	-	-	-	-	-	-
Pachytheca sp.		-	-	-	2	11	145	27	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plant debris		-	-	-	-	C	C	P	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total No. of invertebrate fossils		0	-	105	23	-	24	12	108	94	267	248	35	341	318	21	23	14	207	132	102	767	316	337	263	212	240	5	36	20	13	196	145	71

	UPPER LEINTWARDINE BEDS																																
Sample Position	128	114	94	72	40	37	6	0	96	152	200	[illegible]	310	326	340	400	430	450	465	480	495	510	525	530	555	596	617	673	679	690	726	728	748
BRACHIOPODS																																	
Aegeria grayi (Davidson)	5.0	2.7	-	1.6	-	-	0.4	-	-	-	-	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Craniops implicatus (J. de C. Sowerby)	25.3	13.6	-	7.6	9.6	0.6	10.9	1.7	-	-	-	[illegible]	-	-	-	-	-	0.2	-	-	1.2	1.5	-	-	-	-	0.6	4.0	1.5	-	-	1.3	-
Dayia navicula (J. de C. Sowerby)	1.2	-	-	0.2	-	0.9	0.1	3.4	-	50.0	-	4.3	3.8	72.5	35.7	1.9	0.1	1.1	-	-	2.5	-	-	0.6	-	-	0.5	-	-	-	-	-	-
Isorthis sp.	-	-	-	-	-	0.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Howellella sp.	-	-	-	-	1.9	-	-	1.7	-	-	-	-	-	-	-	-	0.1	-	-	-	-	-	-	-	0.8	-	-	-	-	-	-	-	-
Lingula lewisi J. de C. Sowerby	-	-	-	0.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lingula lata J. de C. Sowerby	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Microsphaeridiorhynchia nucula (J. de C. Sowerby)	6.3	15.7	31.2	10.9	26.9	64.9	16.0	5.2	8.7	-	14.3	5.3	11.5	-	-	10.3	6.3	6.5	-	-	-	-	-	9.1	-	-	0.7	1.2	10.8	3.0	5.7	-	11.5
Orbiculoidea rugata (J. de C. Sowerby)	-	-	-	-	-	-	0.1	-	-	-	-	-	-	-	-	0.9	-	-	-	-	-	-	-	0.6	-	-	-	-	-	-	-	-	-
Protochonetes ludloviensis Muir Wood	3.7	-	-	-	-	4.8	0.1	-	-	-	50.0	62.6	50.0	11.3	3.5	6.6	67.3	78.9	69.4	80.7	92.5	61.5	44.4	76.9	71.1	96.1	90.9	70.2	76.9	93.9	92.9	-	78.8
Salopina lunata (J. de C. Sowerby)	10.1	26.0	37.5	14.5	5.7	5.1	15.6	12.0	41.7	-	8.5	10.2	23.1	-	-	24.5	8.3	4.9	10.3	-	0.8	-	-	3.0	16.6	3.8	1.8	1.2	6.1	1.5	-	90.5	-
Shagamella ludloviensis Boucot & Harper	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Shaleria ornatella (Davidson)	-	0.6	-	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BIVALVES																																	
Cardiola interrupta (Sowerby)	-	-	-	-	-	-	-	1.72	-	-	-	0.5	-	-	-	0.9	-	-	-	-	-	-	-	0.6	-	-	-	-	-	-	-	-	-
Fuchsella amygdalina (J. de C. Sowerby)	-	-	6.2	-	-	-	-	-	19.8	16.6	[illegible]	5.3	-	8.0	25.0	15.1	0.1	0.4	-	-	1.6	-	22.2	0.6	2.4	-	0.7	1.5	1.5	2.1	-	1.9	-
Goniophora cymbaeformis (J. de C. Sowerby)	-	-	-	-	-	-	-	-	-	-	-	0.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Grammysia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.3	-
Modiolopsis sp.	-	-	-	-	-	-	-	-	1.0	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nuculites antiquas (J. de C. Sowerby)	-	-	-	-	-	-	-	5.2	1.0	-	-	-	-	-	-	0.9	-	-	-	-	-	3.1	-	-	0.8	-	-	-	-	-	-	-	-
Nuculites ovata (J. de C. Sowerby)	-	-	6.2	-	-	-	-	-	2.2	-	-	0.5	-	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pterinea lineata (J. de C. Sowerby)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pterinea tennistriata (McCoy)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7.5	0.3	-	-	-	-	-	-	1.8	-	-	-	-	-	-	-	-	-
Pteronitella retroflexa (Wahlenberg)	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	0.9	-	-	-	-	-	-	-	-	0.8	-	-	-	-	-	-	-	-
Solenomya sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GASTROPODS																																	
Cyclonema corallii (J. de C. Sowerby)	-	-	-	-	-	-	-	-	2.2	-	-	-	-	3.3	-	2.8	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-
?*Liospira* sp.	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Loxonema gregarium (J. de C. Sowerby)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Loxonema obsoletum (J. de C. Sowerby)	-	-	-	-	-	-	-	-	4.4	-	-	-	-	-	-	1.9	-	-	-	-	-	1.5	-	-	-	-	-	-	-	-	-	-	1.9
Murchisonia sp.	-	-	-	0.3	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Naticopsis cf. *treverpatriciorum* Peel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kionoceras angulatum (Wahlenberg)	-	2.0	-	-	-	-	-	-	-	-	-	-	-	1.6	-	-	0.2	-	-	-	-	-	5.5	-	-	-	-	-	-	-	-	-	-
Michelinoceras bullatum (J. de C. Sowerby)	-	-	-	0.3	-	0.3	-	-	2.2	-	2.8	1.5	3.8	-	17.8	0.9	1.4	1.7	12.8	-	-	-	11.1	1.2	1.6	-	0.5	-	-	-	1.4	-	-
'Orthoceras' sp.	-	-	-	1.0	1.9	0.9	0.3	-	-	33.3	-	0.5	-	-	-	2.8	-	-	-	-	-	-	-	0.6	-	-	0.2	-	-	-	-	-	-
Paraphragmites ibex (J. de C. Sowerby)	-	-	-	-	-	-	-	-	-	-	-	-	7.7	-	-	0.9	-	-	-	-	-	-	-	0.6	-	-	-	-	-	-	-	-	-
OTHER MOLLUSCS																																	
Bucanopsis expansus (J. de C. Sowerby)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.6	-	-	-	-	-	-	-	-
Hyolithes forbesi (Sharpe)	-	-	-	-	-	-	-	-	1.0	-	5.7	0.5	-	-	7.1	-	0.5	0.2	-	-	-	-	-	-	0.8	-	-	-	-	-	-	-	-
TRILOBITES																																	
Calymene sp.	2.5	0.6	6.2	1.8	-	2.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Encrinurus sp.	-	2.7	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BRYOZOAN COLONIES																																	
Ceramopora sp.	-	-	-	-	-	-	0.4	-	-	-	-	1.9	-	3.3	-	6.6	-	-	2.5	1.2	-	-	16.7	-	-	-	0.5	-	-	-	-	2.5	1.9
Leioclema sp.	1.2	2.7	-	0.3	-	-	5.3	5.1	12.0	-	-	0.9	-	-	-	6.6	-	0.6	-	15.6	-	27.7	-	-	-	-	0.2	0.5	-	-	-	-	-
Rhopalonaria sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2	-	-	-	-	-
OSTRACODS																																	
Amygdalina sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
'*Beyrichia*' sp.	-	0.6	-	-	-	0.3	-	15.5	1.0	-	-	0.5	-	-	3.5	0.9	3.3	1.4	2.5	1.2	-	1.5	-	3.0	0.8	-	-	9.8	1.5	-	-	-	-
Calcaribeyrichia tegula Siveter	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cavellina cf. *primaria* Sarv	-	0.6	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cytherellina siliqua Jones	12.6	-	-	1.0	-	0.9	2.6	-	-	-	-	-	-	-	-	1.9	1.1	0.4	2.5	-	1.2	-	-	-	-	-	-	3.2	-	-	-	-	-
Hebellum cf. *tetragonum* (Krause)	1.2	12.3	-	5.4	28.4	-	19.9	10.4	-	-	-	-	-	-	-	-	3.5	0.2	-	-	-	-	-	-	0.8	-	0.9	0.5	-	-	-	-	1.9
Hebellum cf. *triviale* Gailite	-	-	-	-	-	-	0.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Neobeyrichia lauensis (Kiesow)	12.6	16.4	12.5	19.7	-	12.2	0.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Neobeyrichia sissica Martinsson	-	0.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nyhamnella sp.	-	-	-	0.3	-	-	0.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scaldiana simplex (Krause)	17.7	2.7	-	27.7	25.0	4.2	25.1	36.2	-	-	-	0.5	-	-	-	0.9	6.8	1.4	-	1.2	-	1.5	-	-	0.8	-	-	7.2	1.5	-	-	-	-
ANNELIDS																																	
Keilorites sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.8	-	-	-	-	-	-	-	-
Spirobis lewisi J. de C. Sowerby	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	0.2	-	-	-	-	1.5	-	-	-	-	-	-	-	-	-	-	-
'*Serpulites*' *longissimus* J. de C. Sowerby	-	-	-	1.0	1.9	0.9	0.3	-	2.2	-	-	1.9	-	-	3.5	2.8	-	0.6	-	-	-	-	-	-	-	-	0.2	-	-	-	-	-	-
OTHER FOSSILS																																	
Ozarkodina sp.	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-
Solitary coral	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ischnacanthus kingi Woodward	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sample size from 2-10 kg sediment	172	239	13	652	52	322	1347	371	321	6	35	397	66	60	28	560	794	811	39	83	121	65	80	164	108	26	554	542	64	66	138	63	51

Sample Position	[illegible]	[illegible]	864	914	973	1014	1067	1077	1097	1112	1120	1138	1161	1245	1290	1316	1339	1355	1388	1432	1446	1458	1459	[illegible]	[illegible]	1562	1580	1615	1637	1660	1676	1715
BRACHIOPODS																																
Aegeria grayi (Davidson)	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Craniops implicatus (J. de C. Sowerby)	[illegible]	1.2	-	-	0.1	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	0.7	[illegible]	[illegible]	-	-	-	-	-	-	-
Dayia navicula (J. de C. Sowerby)	[illegible]	-	-	-	-	0.3	-	-	-	-	-	-	0.8	-	-	-	-	-	0.3	-	-	-	0.1	[illegible]	[illegible]	0.7	-	9.1	6.7	-	-	-
Isorthis sp.	[illegible]	1.2	0.7	0.5	0.4	0.3	-	1.4	1.7	-	-	-	-	1.1	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Howellella sp.	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Lingula lewisi J. de C. Sowerby	[illegible]	-	-	-	-	-	2.9	-	-	-	-	-	-	0.8	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	0.3	-	-	-	-
Lingula lata J. de C. Sowerby	[illegible]	-	-	-	-	-	-	-	0.4	-	-	-	0.3	0.5	-	-	-	1.6	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Microsphaeridiorhynchia nucula (J. de C. Sowerby)	[illegible]	[illegible]	5.5	5.5	17.2	7.2	17.1	53.6	15.3	49.8	25.5	-	7.4	63.3	28.5	29.1	26.7	16.8	2.2	-	-	14.3	11.8	[illegible]	[illegible]	14.2	42.9	22.5	20.2	12.5	42.5	62.0
Orbiculoidea rugata (J. de C. Sowerby)	[illegible]	-	-	-	-	-	-	-	-	-	9.8	-	-	-	-	-	-	1.6	0.6	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Protochonetes ludloviensis Muir Wood	[illegible]	80.2	88.2	93.5	76.2	88.3	57.1	28.9	47.7	64.6	48.9	60.4	54.5	28.4	29.7	28.4	28.3	33.6	77.9	80.0	33.3	57.1	74.9	[illegible]	[illegible]	77.0	-	51.3	51.9	62.5	15.0	-
Salopina lunata (J. de C. Sowerby)	[illegible]	1.2	-	-	1.8	1.4	11.4	13.0	13.2	-	0.6	34.9	8.2	-	32.3	30.1	20.0	27.2	2.2	-	-	14.3	2.5	[illegible]	[illegible]	0.2	-	12.6	10.1	-	2.5	38.0
Shagamella ludloviensis Boucot & Harper	[illegible]	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Shaleria ornatella (Davidson)	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
BIVALVES																																
Cardiola interrupta (Sowerby)	[illegible]	-	-	-	-	-	-	-	-	-	0.6	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Fuchsella amygdalina (J. de C. Sowerby)	[illegible]	-	-	-	0.1	1.0	5.7	1.4	9.4	29.4	7.9	4.7	23.8	3.8	-	3.8	5.0	8.8	6.3	13.3	66.6	-	7.9	[illegible]	[illegible]	2.4	57.9	1.3	1.3	12.5	25.0	-
Goniophora cymbaeformis (J. de C. Sowerby)	[illegible]	-	-	-	-	-	-	-	0.4	-	-	-	0.2	-	-	-	-	0.8	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Grammysia sp.	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Modiolopsis sp.	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Nuculites antiquas (J. de C. Sowerby)	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.8	0.3	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Nuculites ovata (J. de C. Sowerby)	[illegible]	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	0.7	-	-	-
Pterinea lineata (J. de C. Sowerby)	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Pterinea tennistriata (McCoy)	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Pteronitella retroflexa (Wahlenberg)	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Solenomya sp.	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
GASTROPODS																																
Cyclonema corallii (J. de C. Sowerby)	[illegible]	-	-	-	-	-	2.9	-	-	-	-	-	0.3	-	-	-	-	-	0.3	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
?*Liospira* sp.	[illegible]	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Loxonema gregarium (J. de C. Sowerby)	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Loxonema obsoletum (J. de C. Sowerby)	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	1.7	-	0.3	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Murchisonia sp.	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Naticopsis cf. *treverpatriciorum* Peel	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Kionoceras angulatum (Wahlenberg)	[illegible]	[illegible]	-	-	-	-	-	-	0.4	-	0.6	-	-	-	-	-	-	0.3	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Michelinoceras bullatum (J. de C. Sowerby)	[illegible]	[illegible]	-	-	0.6	-	-	-	7.7	-	3.7	-	-	-	4.4	1.7	1.7	-	-	-	-	-	-	[illegible]	[illegible]	0.5	-	-	2.7	-	5.0	-
'Orthoceras' sp.	[illegible]	[illegible]	-	-	0.2	-	-	0.4	-	-	-	-	0.3	-	-	1.0	-	0.3	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	10.0	-
Paraphragmites ibex (J. de C. Sowerby)	[illegible]	[illegible]	-	-	-	-	-	-	1.2	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4	[illegible]	[illegible]	-	-	-	0.3	12.5	-	-
OTHER MOLLUSCS																																
Bucanopsis expansus (J. de C. Sowerby)	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Hyolithes forbesi (Sharpe)	[illegible]	[illegible]	-	-	0.3	-	-	-	0.4	-	0.6	-	1.6	-	1.3	0.7	-	0.8	0.3	6.2	-	-	-	[illegible]	[illegible]	0.2	-	-	-	-	-	-
TRILOBITES																																
Calymene sp.	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Encrinurus sp.	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
BRYOZOAN COLONIES																																
Ceramopora sp.	[illegible]	[illegible]	-	-	0.1	-	-	-	1.3	0.3	0.6	-	0.3	1.1	0.6	-	-	2.4	0.9	-	-	-	-	[illegible]	[illegible]	0.5	-	-	-	-	-	-
Leioclema sp.	[illegible]	[illegible]	4.9	-	0.3	0.5	2.9	-	-	0.8	-	-	-	0.5	1.3	4.2	16.7	3.2	2.5	-	-	-	-	[illegible]	[illegible]	0.7	-	-	-	-	-	-
Rhopalonaria sp.	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
OSTRACODS																																
Amygdalina sp.	[illegible]	[illegible]	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
'*Beyrichia*' sp.	[illegible]	[illegible]	-	-	-	-	-	1.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Calcaribeyrichia tegula Siveter	[illegible]	[illegible]	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Cavellina cf. *primaria* Sarv	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Cytherellina siliqua Jones	[illegible]	[illegible]	0.7	-	1.5	-	-	-	0.4	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4	[illegible]	[illegible]	-	-	0.5	0.4	-	-	-
Hebellum cf. *tetragonum* (Krause)	6.3	[illegible]	-	-	0.6	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	1.7	-	-	-
Hebellum cf. *triviale* Gailite	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Neobeyrichia lauensis (Kiesow)	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Neobeyrichia sissica Martinsson	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Nyhamnella sp.	2.1	[illegible]	-	-	0.1	-	-	-	-	-	1.8	-	0.8	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Scaldiana simplex (Krause)	[illegible]	[illegible]	-	-	0.1	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4	[illegible]	[illegible]	-	-	-	0.3	-	-	-
ANNELIDS																																
Keilorites sp.	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Spirobis lewisi J. de C. Sowerby	[illegible]	[illegible]	-	-	-	-	-	-	0.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
'*Serpulites*' *longissimus* J. de C. Sowerby	[illegible]	[illegible]	-	-	0.1	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
OTHER FOSSILS																																
Ozarkodina sp.	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Solitary coral	[illegible]	[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14.3	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Ischnacanthus kingi Woodward	[illegible]	[illegible]	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	[illegible]	[illegible]	-	-	-	-	-	-	-
Sample size from 2-10 kg sediment	60	[illegible]	141	204	852	759	35	74	571	139	282	34	1291	348	138	1473	402	117	568	15	15	7	387	[illegible]	[illegible]	607	7	297	471	9	40	10

Palaeontology of the Deer Park Road Section, Mortimer Forest, Ludlow with respect to the Leintwardinian - Whitcliffian boundary. (Total sample size = 18,047 fossils). Sample positions (in cm).

1. Upper Leintwardine Beds in Track below Quarry

3 m break in section

Sample Position	204	199	173	172	150	118	105	75	38	32	0	0	36	49	55	90	129	140	228	296	337	342	352	361	365	489	518	530	598	630	637	651	662	691	858	892	941
BRACHIOPODS																																					
Aeyeria grayi (Davidson)	-	-	5.1	-	-	-	4.4	8.3	1.5	2.8			-	-	-	-	3.8	-	-	-	4.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Atrypa recticularis (Linnaeus)	1.4	-	-	-	-	1.5	5.8	-	-	2.8			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Craniops implicata (J. de C. Sowerby)	-	0.3	2.0	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dayia navicula (J. de C. Sowerby)	-	1.7	-	-	10.5	-	-	-	-	5.6			-	9.0	-	5.4	-	-	-	-	1.1	-	-	-	2.4	-	-	0.8	0.6	-	-	-	-	-	-	-	-
Howellella elegans (Muir Wood)	-	-	5.1	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptaena depressa (J. de C. Sowerby)	2.8	-	-	-	-	-	-	-	-	1.4			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lingula lata (J. de C. Sowerby)	-	-	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	33.3	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lingula lewisi (J. de C. Sowerby)	-	-	-	16.6	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Microsphaeridiorhynchia nucula (J. de C. Sowerby)	25.3	11.2	25.5	50.0	26.3	53.9	10.0	8.3	14.0	15.8			3.4	12.6	-	-	15.4	29.4	17.6	33.3	5.6	20.8	10.3	20.8	11.9	1.6	3.7	6.1	3.7	4.4	2.6	9.4	0.4	9.1	19.9	78.7	28.7
Orbiculoidea rugata (J. de C. Sowerby)	-	0.3	-	-	-	-	-	-	-	0.7			-	2.7	-	-	-	5.9	-	-	1.2	-	-	-	2.4	-	-	-	-	-	-	-	-	-	-	-	-
Protochonetes ludloviensis Muir Wood	17.9	30.6	2.0	-	-	6.3	41.1	-	-	-			[illegible]	67.6	-	25.0	-	17.6	-	-	61.2	15.1	85.3	36.0	52.4	96.1	87.0	86.0	91.9	89.6	92.1	81.2	98.4	79.5	1.9	7.1	65.2
Salopina lunata (J. de C. Sowerby)	16.3	17.8	43.8	33.3	52.6	23.8	17.7	75.0	53.1	50.3			13.6	5.4	9.1	42.4	27.3	2.9	-	-	24.2	-	-	1.8	2.4	0.8	8.1	5.3	2.5	5.5	5.3	2.1	-	6.8	68.9	7.1	3.4
Shagamella ludloviensis Boucet & Harper	-	-	-	-	-	-	2.2	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Shaleria ornatella (Davidson)	-	-	-	-	-	-	-	-	-	9.3			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sphaerirhynchia wilsoni (J. Sowerby)	-	-	-	-	-	-	-	1.1	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BIVALVES																																					
Cardiola interrupta (Sowerby)	-	-	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	1.2	-	-	39.6	14.3	-	1.2	1.8	-	-	-	-	-	-	-	-	-
Fuchsella amygdalina (J. de C. Sowerby)	-	9.5	-	-	5.2	3.1	-	-	-	1.4			6.8	0.9	9.1	-	3.8	-	11.8	33.3	-	-	1.9	-	-	-	-	-	-	-	-	6.8	0.4	4.5	2.9	-	-
Goniophora cymbaeformis (J. de C. Sowerby)	-	-	-	-	-	-	-	-	-	-			1.1	-	27.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nuculites antiquas (J. de C. Sowerby)	-	-	-	-	-	-	-	-	-	-			-	-	-	-	7.7	-	-	-	-	-	-	-	-	-	-	-	-	0.6	-	-	-	-	-	-	-
Nuculites ovata (J. de C. Sowerby)	-	-	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pterinea tennistriata (McCoy)	-	-	-	-	-	-	-	-	-	-			-	-	-	2.2	3.8	-	17.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pteronitella retroflexa (Wahlenberg)	-	-	-	-	-	-	-	-	1.5	-			-	-	-	-	3.8	2.9	5.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
GASTROPODS																																					
Cyclonema corallii (J. de C. Sowerby)	-	-	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	2.4	-	-	-	-	-	-	-	-	-	-	-	-
Loxonema obsoletum (J. de C. Sowerby)	-	-	-	-	-	-	-	-	-	-			-	-	18.2	-	-	2.9	11.8	-	0.6	1.9	-	-	-	-	-	-	-	-	-	-	-	-	2.9	7.1	-
Naticopsis cf. trevorpatriciorum Peel	-	-	-	-	-	-	-	-	-	-			-	-	-	-	3.8	5.9	5.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CEPHALOPODS																																					
Kionoceras angulatum (Wahlenberg)	-	-	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	9.4	1.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-
'Orthoceras' sp.	-	-	-	-	-	-	-	-	-	2.8			1.1	-	-	16.3	11.5	8.8	-	-	-	20.7	-	-	2.4	-	-	-	-	-	-	0.7	0.4	-	-	-	-
Paraphragmites ibex (J. de C. Sowerby)	-	0.3	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	0.8	-	-	0.8	-	-	-	-	-	-	-	-	-	-	-
OTHER MOLLUSCS																																					
Bucanopsis expansus (J. de C. Sowerby)	-	-	-	-	-	-	-	-	-	-			-	-	-	2.2	7.7	2.9	-	-	0.3	-	-	-	-	-	-	-	-	-	-	0.7	0.4	-	-	-	-
Hyolithes forbesi (Sharpe)	-	7.3	-	-	-	-	2.2	-	-	0.7			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BRYOZOAN COLONIES																																					
Coramopora sp.	7.4	1.7	-	-	5.2	-	-	-	-	-			-	-	27.3	2.2	-	5.9	17.6	-	0.3	-	-	-	-	-	-	-	-	-	-	0.7	0.4	-	-	-	-
Loioclema sp.	5.9	5.0	-	-	-	11.1	-	-	21.8	-			1.1	-	-	-	-	5.9	-	-	2.1	32.1	-	1.8	4.8	-	-	-	-	-	-	-	-	-	-	-	1.1
OSTRACODS																																					
Calcaribeyrichia tegula Siveter	-	-	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cavellina sp.	-	1.0	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-
Cytherellina siliqua Jones	-	7.3	-	-	-	-	2.2	-	-	0.7			-	-	-	-	-	-	-	-	1.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hebellum cf. tetragonum (Krause)	7.4	0.7	5.1	-	-	-	2.2	-	-	-			-	-	-	-	3.8	-	5.9	-	3.8	-	-	-	0.6	-	-	-	1.2	-	-	-	-	-	-	-	-
Kuresaaria circulata (Neckaja)	20.9	-	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Neobeyrichia lauensis (Kiesow)	-	-	-	-	-	-	3.3	-	-	6.4			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scaldianella cf. simplex (Krause)	5.9	4.2	12.2	-	-	-	3.3	-	-	0.7			-	-	-	-	-	-	-	-	2.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ANNELIDS																																					
Arabellites sp.	-	0.7	-	-	-	-	-	-	-	-			-	-	-	-	3.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
'Serpulites' longissimus J. de C. Sowerby	1.4	7.3	-	-	-	-	3.3	-	-	-			1.1	1.8	9.1	3.3	3.8	5.9	5.9	-	0.3	-	-	-	2.4	-	-	-	-	-	-	-	-	-	-	-	0.6
TRILOBITES																																					
Calymene sp.	1.4	-	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Encrinurus sp.	-	-	-	-	-	-	-	7.8	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
OTHER FOSSILS																																					
Crinoid columnals	-	-	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cornulites sp.	1.4	-	-	-	-	-	-	-	-	1.4			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ischnacanthus kingi Woodward	-	0.3	-	-	-	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
'Onchus' sp.	-	-	-	-	-	-	-	-	-	-			[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ozarkodina sp.	-	-	1.0	-	-	-	-	-	-	-			[illegible]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sample size per 2-10 kg sediment	67	303	98	6	19	63	90	12	64	139			[illegible]	111	11	92	26	34	17	9	339	53	68	53	42	126	162	122	161	164	38	138	245	44	206	14	178

Faunal list for Overton Quarry and adjacent track sections in Mortimer Forest (n = 6161).
Sample positions are given as follows:- 1. Distance from top of Upper Leintwardine Beds track section.
2. Distance from base of Overton Quarry section. 3. Distance from base of track section above Overton Quarry.
All distances are in centimetres. British National Grid Reference for the section is SO 496 726

3. Lower Whitcliffe Beds in the track above Overton Quarry

4	0	29	37	47	63	72	80	103	130	142	165	196	206	226
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	8.8	2.6	3.5	5.8	5.9	4.5	4.6	-	14.6	20.9	5.2	5.5	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	26.4	2.6	8.8	6.3	24.9	4.5	22.6	22.2	12.4	7.2	17.6	5.9	10.0	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	59.2	93.5	78.9	74.4	61.2	90.9	66.2	75.0	63.9	66.5	73.2	59.1	85.0	
	-	1.3	7.0	2.3	7.5	-	2.6	-	6.2	4.2	-	28.7	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	1.6	-	1.8	-	-	-	0.5	-	0.8	-	-	0.8	5.0	
	0.8	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	0.5	-	-	-	
	-	-	-	0.1	-	-	-	-	-	-	0.7	-	-	
	-	-	-	-	-	-	0.5	-	-	-	-	-	-	
350 cm Gap	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	0.1	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	0.2	-	-	1.5	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	0.6	-	-	-	-	
	2.4	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	8.9	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	0.3	-	-	-	-	-	
	-	-	-	1.5	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	0.8	-	-	0.6	-	-	0.5	2.8	1.1	1.1	3.2	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	-	-	-	-	-	-	0.5	-	-	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	-	-	-	
	125	77	57	833	67	22	195	36	355	279	153	492	40	