A STUDY OF CARBONIFEROUS PALAEOECOLOGY

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I. INTRODUCTION

Previous palaeoecological researches have in large measure arisen as subsidiaries of stratigraphical and palaeontological studies. The conclusions drawn have necessarily bee confined to broad generalizations on the depositional environments, or to elucidation of the modes of life and the habitats of related groups of fossils. So far as had been ascertained at the commencement of this research, there had been no detaile palaeoecological study of a fossil assemblage from a limited marine horizon. Such a study seemed necessary and the researc described in this thesis is an endeavour to contribute towards the knowledge and understanding of fossil benthonic communities The objects of the research were twofold: to discover how the various fossils of a particular marine deposit had lived, and to reconstruct the physical and biological environments prevailing during the accumulation of that deposit.

The study has been confined to a detailed analysis of the fossil assemblage from a shale, two feet in thickness, of Lower Carboniferous age. The objects of the research have for the most part been achieved, and, in particular, the results ha shown that larval studies may be of greater importance in palaeontology than has hitherto been realised. The problems encountered have necessitated an approach based on recent ecolo gical studies of living animal communities.

II. HISTORICAL INTRODUCTION TO PALAEOECOLOGY

Palaeoecology, the study of fossils in relation to their environment, is a development of the gradual synthesis of palaeontology and ecology. To avoid ambiguity in subsequent discussion ecology is subdivided into Neoecology, ecology of th living, and Palaeoecology. Although the two ecological scienc have similar objectives - the understanding of life, past or pr sent, in relation to the environment - palaeoecology differs from neoecology in that the evidence is always fragmentary and incomplete. Consequently a reconstruction of a fossil environ ment must always be tentative, never dogmatic.

The origins of palaeoecology can be traced among the developments of biology and palaeontology during the nineteenth century, and the unification of palaeoecology as a science in the more co-ordinated activities of the twentieth century.

Forbes initiated the study of palaeoecology in a paper contributed to the British Association for the Advancement of Science in 1843, entitled "Report on the Mollusca and Radiata of the Aegean Sea, and on their distribution, considered as bearing on geology". In this pioneer contribution he tabulated the results of dredging operations carried out in the Aegean Sea and concluded that that sea-floor was divisible into eight depth zones /

zones, each characterised by its own fauna. His remark to geologists (p. 172) is particularly apposite:- "By carefully observing the mineral character of the stratum in order to ascertain the nature of the former sea-bottom, by noticing the associations of species and the relative abundance of the individuals of each in order to ascertain the depth, and by calculating the percentage of northern or southern forms separatel for each tribe, our conclusions as to former climate and distribution will doubtless approximate very nearly to the truth"

Four years later the Palaeontographical Society was instituted with the object of publishing descriptive monographs of British fossils. Monographs covering many of the vertebrat invertebrate, and botanical groups of palaeontology have been published annually since then, and form the most valuable singl source of information on British fossils. Although primarily descriptive, the early monographs are occasionally prefaced by an account of the zoology of the living representatives of the fossils described, thus showing an awareness of the relation between living animals and fossils.

Darwin's contribution of the "Origin of Species" and other works to the development of the biological sciences can scarcely be over-emphasised; and Darwin's contemporary, T.H. Huxley, championed his cause in many papers and notably, as regards /

regards palaeontology, those two provocative discourses, both on homotaxis and evolution of fossils, to the Geological Societ of London in 1862 and 1870. Darwin and Huxley, although since proved wrong in some of their views, acted as stimulators to the philosophical side of the Natural Sciences.

In 1869 Haeckel defined the term "Oekologie" in the sense in which it is now accepted as:- "comprising the relationship of the animal to its inorganic, as well as its organic environment, especially its friendly or hostile relations with those animals or plants with which it comes into contact".

The most important enterprise in the advancing growth of ecology - and with it palaeoecology - was the Challenger Expedition (1873-76), the results of which laid the foundations of the science of oceanography and included much new and valuable knowledge regarding the ecology and sediments of the sea-floor.

With the turn of the century two other lines of investigation came into prominence. Firstly, with the researches of Jukes-Brown, Buckman and others into the palaeogeograph of British formations, there was erected a very necessary back-cloth for subsequent work on palaeoecology. Watts adequately surveyed the situation in 1911 in his presidential address, "Geology /

"Geology as Geographical Evolution", to the Geological Society of London.

Secondly, there appeared within a period of eleven years, two papers - now considered classics of their kind - on the evolution of certain fossil gens. The earlier paper by Rowe (1899) dealt with the gradual evolution of successive communities of the heart-urchin Micraster under the almost unvarying conditions of deposition of the upper zones of the Chalk. The later paper by Carruthers (1910) recorded the stages in the evolution of the rugose coral Zaphrentis delanouei (s.l.) durin the very variable conditions of deposition of the sediments of the Scottish Lower Carboniferous. Both authors demonstrated the gradualness of evolution, the former gens under almost uniform, the latter under variable conditions of sedimentation, and the palaeoecological importance of their contributions lies in the fact that they both placed emphasis on the study of the community rather than the individual.

Thus the multiple origins of palaeoecology can be observed among the necessary developments of morphology, philosophical palaeontology, oceanography, natural history and palaeogeography. The unification and expansion of palaeoecology is properly a part of the history of science in the twentieth century.

The /

The basis of modern palaeoecology is to be found in the papers of Louis Dollo, at one time Professor of Palaeontology at Brussels University. In his dissertation of 1909 he sketched the development of European palaeontology as occurring in three epochs, Fableuse, Morphologique, and Transformiste, and from these expounded his main thesis on "La Paléontologie Ethologique", "qui recherche les moeurs des Organismes fossiles pour découvrir les Convergences et éviter les erreurs dans l'établissement des liens de Parenté" (p. 418). In illustration of this thesis he described the convergent adaptations among the Ostracodermi, Merostomata, and Trilobita.

In Britain, Vaughan's researches in Carboniferous palaeontology and stratigraphy, and in particular his joint paper with Dixon in 1911, show an appreciation of the relationship between the fossil and its environment.

However, it was not until 1921 that a purely palaeoecological study appeared in this country. Davies, the author, had collected plants systematically for some twenty-five years from the shales overlying coal seams of Westphalian and Staffordian age, which were worked in the mines of Clydach Vale and Gilfach Goch (East Glamorgan). From a statistical treatment of the 45,000 plants collected, he reconstructed the palaeoecology of that area during Upper Carboniferous times.

Four /

Four years later, an equally important paper by Marr (1925) on the conditions of deposition of the Stockdale Shales (Silurian) was published. Marr's paper, although not so detailed, is perhaps the more balanced of the two, since he examined both fossil and lithological evidence. His studies enabled him to distinguish between the fossil plankton and benthos and to relate their occurrence to the changing lithology. His conclusions make a valuable contribution to the knowledge of the conditions of deposition of black shales.

Elles (1923), in her presidential address to Section C of the British Association focussed attention on Petersen's concept of characteristic animal communities and its application to palaeontology, observing (p. 97) that the palaeontology of the future "must vitalise fossil organisms, and regard them as parts of once-living entities possessing definite ancestors and descendants". Two years later Stamp (1925) attacked Buckman's tenet of uniform wide distribution of fossils by enumerating the various physical factors controlling the distribution of living faunas. In the ensuing discussion Lang, while welcoming the paper, claimed that palaeontologists realised the importance of the environment in which fossils lived.

These three papers by Marr, Elles, and Stamp bear evidence of a growing interest in the study /

study of the environment of the animal and the importance of co-ordination between palaeontology and ecology. Nevertheless subsequent research in Britain, while maintaining an interest in the ecological approach, has been essentially stratigraphica

Contemporary and subsequent research can be but briefly outlined. Bather (1928) briefly reviewed the history of palaeoecology, or "Palethology" as he termed it, as the prelude to his main theme on environment and fossil Pelmatozoa, concluding with an analysis of evolutionary hypotheses and processes. Marr's book "Deposition of the sedimentary rocks" published in 1929, contains much palaeoecological information. The work of Arkell (1933) on the Jurassic, the papers by George (1933) and Hudson (1924) on the various facies of the Carboniferous Limestone, King (1928) and Whittard (1932) on the Ordovician sediments, and studies of a single horizon such as the Aymestry Limestone by Alexander (1936), although all primarily stratigraphical, contain examples of the treatment of fossils as entities in an active environment. More directly palaeoecological are the papers by Lamont (1934) on the modes of life of fossil brachiopods, and Nopsca (1934) on the factors controlling the evolution and distribution of certain Amphibia and Reptilia. Trueman (1940) reconstructed the modes of life of various ammonites by determining their centres of buoyancy and gravity /

gravity. Hawkins (1943) followed Bather's example by devoting his presidential address to "Evolution and habit among the Echinoidea".

In the immediate post-war years Eager (1947) in a detailed study dealt with the variation and evolution in relation to lithology, of the non-marine lamellibranch fauna of a thirty-foot succession in the Yorkshire Coal Measures. He continued along similar lines with a review (1948) of the effects of the environment on the shell-form of recent Unionidae and the comparable effects to be found among shells of the related Carboniferous Anthracosiidae.

In the U.S.A. the contrast in the development of the science is striking. In the 1920's the term "palaeoecology" was already being used, mainly by palaeobotanists. The scienc expanded rapidly and in 1933 a symposium on palaeoecology was held by the Paleontological Society. Four papers presented at that meeting were later published in the Journal of Paleontology (1935) and may be briefly noted. Fenton crisply defined the viewpoints and objects of palaeoecology; Ruedemann reviewed the conditions of deposition of graptolitic black shales Fish analysed some aspects of marine biology and their possible applications to palaeoecology; and Lucke described the bottom conditions of a tidal lagoon on the New Jersey coast.

In /

In 1936 and 1937 discussions on palaeoecology were organised by Twenhofel, and two mimeographed reports published.

Bucher (1938) drew the attention of American geologists to the valuable publications of the German Institute, Senckenberg-am-Meer, which (p. 726) "is devoted to the study of the sediments in modern shallow seas from the viewpoint of geology and paleontology", summarised some of the papers, and appended a complete list of the publications of the institute.

Reference may also be made to the symposium "Recent Marine Sediments" edited by Trask (1939), and the book on the same subject "Treatise on Sedimentation" by Twenhofel published as early as 1926. Both books contain an immense amount of information on sediments and deposition and are naturally of great value to the palaeoecologist.

In 1940 Vaughan, in his presidential address to the Geological Society of America, dealt with the "Ecology of modern marine organisms with reference to paleogeography", concluding (p. 466) with the remark that "there should be a continuous shuttling from studies of the modern to studies of the ancient and back again from the ancient to the modern".

It was largely due to Vaughan's efforts that a subcommittee on the ecology of marine organisms was formed in 1940 Since 1941 this committee has presented a yearly report to the Division /

Division of Geology and Geography of the National Research Council, Washington. These reports contain extensive bibliographies and summaries of papers on all subjects relating to palaeoecology and form, to date, the most valuable source of information on palaeoecology and kindred subjects. More recently the committee has been concerned with the preparation of a treatise on marine ecology as related to palaeontology.

In view of these multifarious developments in the U.S.A. it seems somewhat surprising that Allan (1948) should feel it necessary to write a brisk paper designed as a stimulant to stratigraphical philosophy; a paper in which he condemns the present static concepts of stratigraphy and urges that more attention should be paid to the study of evolving lineages and palaeoecology.

The rapid development of palaeoecology in the U.S.A. is in contrast to the more gradual expansion in Britain. The amount of palaeoecological research accomplished in this country is liable to be underestimated no doubt because of an apparent reluctance on the part of British geologists to use the term 'palaeoecology'. The term itself is cacophonous and, moreover, it implies a closer relationship to ecology than is perhaps justified. It has, however, such widespread usage in America that little purpose is served in opposing its adoption.

III. LOCALITY and STRATIGRAPHY

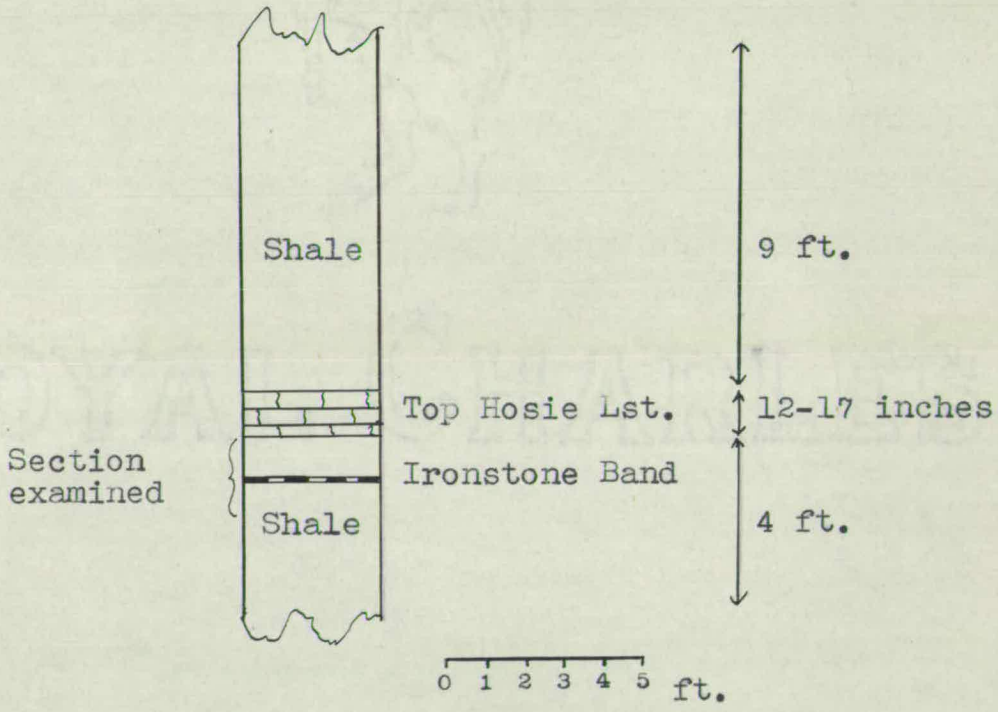
The present research was undertaken with the object of investigating the palaeoecology of the fossil assemblage of a Carboniferous marine horizon. No specific horizon was sough merely a well-exposed rock face containing fairly abundant fossils which could be extracted in a reasonable state of preservation. Nevertheless, several localities in the West of Scotland were examined and rejected before the final site was chose

The site (National Grid Reference 682781) is located in a small burn cutting, on the southern slopes of the Campsie Hills, some 200 yds. S.S.W. of Burnhead Farm, and lying within the area covered by the 6-inch Stirlingshire/Dumbartonshire Sheet XXVIII S.E. of the 1-inch geological Sheet 31.

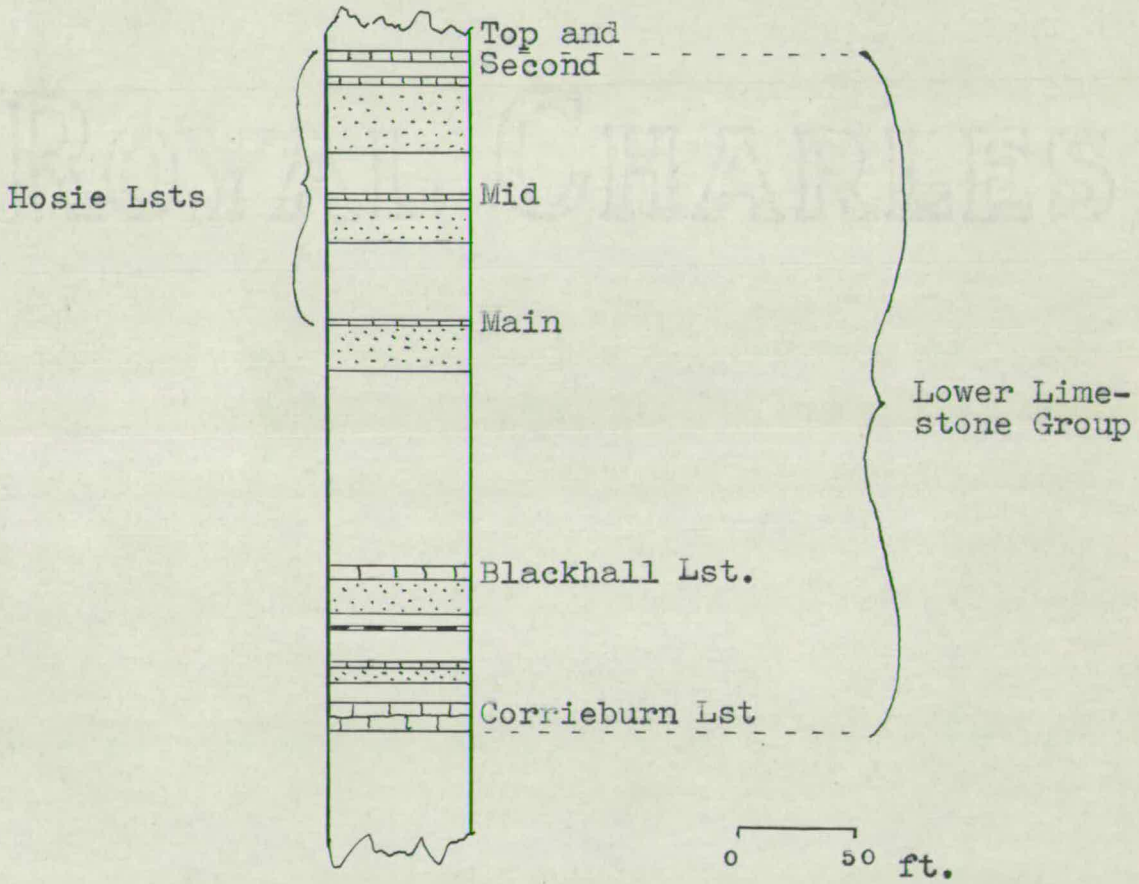
6-inch Sheet XXVIII S.E., surveyed by Peach and Jack was published in 1875, and a revised edition by Crampton and Carruthers in 1923. The strata within this area belong to the Lower Limestone and Limestone Coal Groups of the Scottish Lower Carboniferous formation, and form part of the easterly dipping westerly limb of the Central Coalfield syncline of the Midland Valley. The Geological Survey's publications of the "Explanation of Sheet 31" (1879) and the Memoir of the Glasgow District 1911 (2nd edition 1925), contain descriptions of the geology of the area.

The /

The face, some 14 feet high and 20 feet long, forms the southern bank of a small burn flowing into Wham Glen. The successions are as follows:-



TEXT-FIG. 1. Vertical section of strata on cliff face.
(Plate I, figs. 1 and 2)



TEXT-FIG.2. Vertical section of the Lower Limestone Group in the Corrie District.

(after The Geology of the Glasgow District, 1925, p.33, fig.2.)

IV. COLLECTING

The specimens were collected so that they could be located to within one inch vertically and two feet laterally. The upper surface of each specimen was marked. The face is not ideal for such collecting since it is oblique to the strike resulting in a small apparent dip. Moreover, the strata are locally disrupted by a small reversed fault.

Collecting was started in the shales immediately below the Top Hosie Limestone and as work proceeded it was decide to confine the scope of the thesis to the two feet of shale underlying the limestone.

In all some 2,000 macrofossils and 3,000 microfossils were collected and examined.

V. PETROLOGY

(i) Petrography

The stratum directly underlying the Top Hosie Limestone is a dark calcareous shale, flaggy[1] when fresh but becoming shaly[1] or fissile[1] on weathering. The dry shale varies in colour from dark grey (N3)[2] in fresh rock to olive grey (5Y 4/1)[2] on weathered surfaces. Small crystals of secondary gypsum are abundant on many of the bedding-planes.

The basal four inches of the two feet of shale is more fissile than the shale above due to the abundance of small valves of the lamellibranch Posidonia corrugata defining the bedding-planes. Above this Posidonia-band the shale is more calcareous, less fossiliferous, and contains occasional calcareous nodules. The shale sequence is interrupted six inches above the band by a nodular ironstone band about an inch thick. Thereafter nodules are absent and the shale remains uniform in lithology until it passes rapidly into the overlying Top Hosie Limestone, a massive[1] argillaceous limestone.

In /

[1] Fissile laminae less than 2 mm. in thickness
Shaly laminae 2-10 mm. in thickness
Flaggy strata 10-100 mm. in thickness
Massive strata more than 100 mm. in thickness after Pettijohn (1949, p.12

[2] Rock-Color Chart, 1948, distributed by the National Research Council, Washington.

In thin sections of the shale clear or grey-brown calcite is seen to be the most conspicuous mineral. The particles (.006->.12 mm. in length) mostly derived from broken shells, are fibrous or tabular in shape and orientated more or less parallel to the bedding-planes. Microfossils and debris of macrofossils, although abundant, tend to be concentrated in irregular bands and lenses, and the bands and wisps of carbonaceous matter emphasise the slight irregularity of the bedding. The groundmass consists of anhedral calcareous material, clay minerals, and amorphous carbonaceous matter. Iron pyrites occurs as finely disseminated granules (about .003 mm.) and irregular aggregates (< .05 mm.) in the matrix; it is also developed in shell fragments and microfossils (see p.18). Rarely minute flakes of muscovite can be distinguished in the groundmass. The bedding is occasionally traversed by irregular veinlets of calcite.

The ironstone band, coloured grey-brown in thin section, is composed of small equi-dimensional crystals of calcite and siderite ranging between .002 and .02 mm. Many of the crystals are sub-angular but a few show perfect rhombohedral form. Pyrites and carbonaceous matter are not common; fossils are rare. Veinlets of calcite traverse the band. The nodules, although similar in composition, contain calcareous fibres; fossils, pyrite, and carbonaceous matter are more /

more abundant than in the ironstone band.

(ii) Pyritization in shells

As previously noted pyrite occurs within the tests and shells of microfossils. Almost without exception, when it does not entirely fill the shell, the mineral occurs in the lower part (with regard to the sediment) of the shell and the remaining space is filled with interlocking crystals of calcite The pyrite filling the basal part of the shells is composed of an aggregate of granules, the upper surface of the layer - the pyrite/calcite interface - being more or less parallel to the bedding-planes. Occasionally a thin film of pyrite adheres to the top of the shell. Shale particles do not occur within the calcite and do not appear to be present in the pyrite layer. In addition to occurring inside microshells, pyrite fills the interstices of crinoid ossicles and so reveals the minute radiating network of canals. The mineral is also developed along growth planes of macroshell fragments.

The pyrite granules must have been precipitated inside the shells following the deaths of the animals. After the granules had settled on the floor of the shell, the remaining space was filled with calcite. Literature is cited in a succeeding section (p.) to show that one method by which pyrite /

pyrite may be precipitated in the tests of foraminifera is by the action of bacteria on the dead protoplasm of the animal producing hydrogen sulphide which reacts with soluble iron salts to precipitate iron pyrites inside the test.

Lately Zobell and Rittenberg (1949) have pointed out that sulphate-reducing bacteria are abundant and widely distributed at the present day in marine bottom deposits. These bacteria are physiologically active only in the absence of free oxygen, and produce hydrogen sulphide by the reduction of sulphates and other sulphur radicals. The authors list a wide variety of organic compounds, including chitin, which can be utilised by the bacteria as hydrogen donors for this reaction. They consider that sulphate-reducing bacteria may be responsibl for the formation of metallic sulphides in marine sediments.

Such bacteria may well have been responsible for the production of pyrite inside the microshells by utilising the dead protoplasmic contents. Similarly the organic content of the ossicles and the shell fragments may have provided material for bacterial activity with consequent pyritization in and around the shell fragments.

However it must be recorded that pyrite although undoubtedly a guide to the nature of the bottom conditions, does not necessarily indicate the existence of anaerobic conditions on /

on the surface of the muddy bottom. Bruce (1928) has shown that in a shore sand at Port Erin anaerobic conditions exist only in the subsurface, the topmost layers 3 - 20 cms. thick having sufficient oxygen to prevent the formation of ferrous sulphide.

(iii) Compaction of sediment

In order to estimate the original thickness of the mud now forming the two feet of shale, and to determine the possible variation in horizon of the vertical shells of Lingula squamiformis (see p. 28), an approximate compaction factor for the mud was calculated.

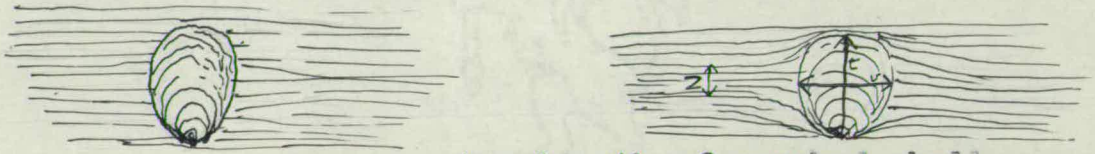
Lingula shells were chosen for this purpose on accoun of their vertical position in the sediment. Shells deposited on a sea-floor are eventually enclosed by curved laminae of sediment. The curved laminae under a shell are due to the deformation of horizontal laminae by the shell settling in the mud or silt, the curvature being modified by the subsequent compaction of the sediment. The laminae above the shell are initially curved as a result of sedimentation on a projection, the curvature of the laminae being later modified by compaction

It is probable that a burrowing Lingula caused little deformation /

deformation of the horizontal laminae, and that the curvature of the laminae found around the anterior and posterior ends of its shell is due mainly to compaction, since the laminae at both ends are equally distorted (Text-fig. 3). This equal distortion - or curvature - suggests that during the life of the animal the shell was more or less completely buried.

Before compaction

After compaction



t = length of crushed shell
v = breadth of crushed shell
z = thickness between bedding-planes enclosing shell taken at side of shell

TEXT-FIG.3. Effect of compaction on vertical Lingula

The following formula for obtaining the compaction factor is based on two assumptions, and in so far as these may not be wholly justified, two possible errors are involved:

(1) The area of the valves is assumed to be the same before and after compaction.

(2) The laminae are assumed to have remained in the same position with regard to the shell during compaction.

FORMULA /

FORMULA

Area of ellipse $= \pi ab$ where $a = \frac{1}{2}x$
$b = \frac{1}{2}y$

x = length
y = breadth

UNCRUSHED LINGULA

Area approximates to $\pi ab = \pi \frac{xy}{4}$

From data on flat Lingulas (Length / Breadth of L. squamiformis = 1.35)

$y = x/1.35$

Area $= \pi x/4 \times 1.35$

CRUSHED LINGULA

Area approximates to $\pi tv/4$ where

t = length of crushed specimen
v = breadth of " "

Area before crushing = Area after crushing

$\therefore \pi tv/4 = \pi x^2/4 \times 1.35$

$\therefore x^2 = tv \times 1.35$

$\therefore x = \pm\sqrt{\text{Area of crushed specimen } (tv) \times 1.35}$

COMPACTION FACTOR = $\frac{\text{Original Length}}{\text{Thickness between Bedding-planes enclosing specimen, taken at side of specimen. (z)}}$ (see Text-fig. 3)

The data are given in Table I.

TABLE I.

Specimen No.	t in mm.	v in mm.	x in mm.	z in mm.	COMPACTION FACTOR
94	8	9	9.9	5	2
95	4	6?	5.7	2.5	2.3
149	9	8.5	10.2	6	1.7
174	7	6·	7.5	4	1.9
211	2	2	2.3	1.5	1.5
233	8	6.25	8.2	4?	2.1
247	8?	7?	8.7	4?	2.2
455	13.5	12.5	15.1	7.5	2.1

Average = 1.97

Average Compaction Factor $\doteq$ 2.

The calculated compaction factor of 2 indicates that the two feet of shale were formed from some four feet of mud and that the vertical distance travelled by a burrowing Lingula in the mud is halved in the shale.

VI. SYSTEMATIC DESCRIPTIONS

(i) Introduction

List of fossils collected from the Top Hosie Shale:-

Girvanella? sp.

Glomospirella sp.
Hyperaminna sp.

Athyris sp.
Camarotoechia pleurodon (Phillips)
Lingula squamiformis Phillips
Orthotetid
Paeckelmannia [Tornquistia] polita (McCoy)
Productus (Productus) concinnus J. Sow.

Actinopteria persulcata (McCoy)
Aviculopecten sp. probably A. [Limatulina] scotica (Hind)
'Nucula' laevirostrum Portlock
Nuculopsis gibbosa (Fleming)
Posidonia corrugata (R. Etheridge)
Pseudamusium? aff. ellipticum (Phillips)
Sanguinolites costellatus (McCoy)
S. variabilis (McCoy)

Bucaniopsis striatus (Fleming)
Euphemites urei (Fleming)
Glabrocingulum armstrongi Thomas
Naticopsis sp.
Pleurotomariid?
Pseudozygopleura (s.l.) spp.
Soleniscus sp.

Cycloceras sp.
Loxoceras? sp.
Nautiloid
Pseudorthoceras aff. knoxense (McChesney)
Rugocyrtoceras cf. northumbriense J.S. Turner MS.

Coleolus aff. carbonarius Demanet

?Amphissites centronotus (Ulrich and Bassler)
Bairdia? sp.
Healdia cuneola (Jones and Kirkby)

Cavusgnathus /

Cavusgnathus sp. nov.
Gnathodus clavatus sp. nov.
Hindeodella spp.

Scolecodont

Crinoid ossicles

Fish teeth and scales

Plant fragments

The interest in the rich assemblage of fossils from the Top Hosie Shale lies not so much in the macrofossils as in the rich and varied microfossils and their relations to the macrofossils. The macrofossils (> 2 mm.) are dominantly molluscan, lamellibranchs being the most abundant class, followed by gastropods. Cephalopods are rare, but are of particular interest because of their variety. Brachiopods are common, and scaphopods, crinoid debris, fish fragments and plant remain are occasionally to be found. In defining the character of the assemblage it is worth noting that corals are absent.

The microfossils (< 2 mm.), estimated to be some 1500 times as numerous as the macrofossils, are extremely varied and include larval shells of lamellibranchs, gastropods and brachiopods, hitherto undescribed; algae, arenaceous foraminifers, ostracods, conodonts of which two are new species, Cavusgnathus sp. nov., and Gnathodus clavatus sp. nov., a scolecodont /

scolecodont, scaphopods, crinoid debris and macroshell fragments such as productid spines. Paradoxically, in contrast to the macrofossils, gastropods are by far the most abundant of the larval molluscs.

Posidonia corrugata, the most common lamellibranch, is characteristic of Hosie horizons as are also the bellerophontids Euphemites urei and Bucaniopsis striatus which at times are common enough in the Top Hosie Limestone to justify the name sometimes given to it of the Bellerophon Limestone. American forms previously unrecorded from the Scottish Carboniferous are Pseudozygopleura spp., a gastropod genus of Pennsylvanian age, and an orthoceracone closely related to Pseudorthoceras knoxense a species which ranges from the Pennsylvanian to the Lower Permian.

For the purpose of description the assemblage is divided into two groups: Macrofossils and Microfossils. The latter is considered in more detail since little is known about Carboniferous microfossil assemblages, particularly the earlier growth stages of macrofossils.

(ii) /

(ii) Macrofossils

The following macrofossils were collected from the shale:-

Camarotoechia pleurodon
Lingula squamiformis
Orthotetid
Paeckelmannia polita
Productus concinnus

Actinopteria persulcata
Aviculopecten sp. probably A. scotica
'Nucula' laevirostrum
Nuculopsis gibbosa
Posidonia corrugata
Pseudamusium? aff. ellipticum
Sanguinolites costellatus
S. variabilis

Bucaniopsis striatus
Euphemites urei
Glabrocingulum armstrongi
Naticopsis sp.
Soleniscus sp.

Cycloceras sp.
Loxoceras? sp.
Nautiloid
Pseudorthoceras aff. knoxense
Rugocyrtoceras cf. northumbriense

Coleolus aff. carbonarius

Fish teeth and scales

Plant fragments

Brachiopoda /

Brachiopoda

Genus LINGULA Brugière, 1797

Lingula squamiformis Phillips, 1836 Plate II, fig.1
Plate III, fig.2

Remarks Most of the shells of this species were found in a position vertical or nearly vertical to the bedding planes, all with the anterior end uppermost. This attitude, as evidenced by a study of the modern Lingula, is the normal position during life. All the vertical shells, with the exception of those few found in nodules, have been deformed by the compaction of the mud with a decrease in length and an increase in breadth (see p. 20). Often the shells have been fractured by the compacting pressure, but in some cases there has been deformation without breakage. In spite of crushing the shells are identifiable as L. squamiformis.

It was often impossible under field conditions to extract the whole shell so that many of the collected specimens of Lingula consist of only one valve vertical to the bedding-planes; but whenever both halves of a fragment of shale enclosing a vertical Lingula were collected, a complete shell was obtained. The position of a shell is often revealed by a low ridge on the surface of an otherwise smooth bedding-plane and the complete shell can be obtained by breaking the shale along the ridge.

Only /

Only two of the vertical Lingulas examined, showed what were probably the pyritized remains of pedicles. The first of these (No. 211) is 2 mm. long (crushed) (Plate III, fig. 2). Posterior to the umbo and 0.5 mm. displaced from it runs a vertical pyritized rod about 0.5 mm. in diameter and with a length of at least 3 mm. - the posterior end is broken.

In the second specimen (No. 550) a pyritized irregular rod of a similar thickness runs posteriorly for almost 4 mm. from the umbo of the vertical shell 7 mm. long (crushed). As in the previous specimen the rod does not connect with the umbo but is about 0.5 mm. distant.

Compaction would account for the slight displacement of these rods from the umbos.

Genus PAECKELMANNIA Licharev, 1934

Paeckelmannia [Tornquistia] polita (McCoy, 1855) PlateII, figs. 2 and 3

Description Concavo-convex, transversely hemicircular shells with a straight hinge-line. Small median umbo with a shallow sulcus which disappears rapidly anteriorly; umbonal slopes distinct. Two or three small, curved, hollow spines (sometime represented by spine-bases) about 1 mm. in length occur on the hinge-margin /

hinge-margin of the ventral valve on either side of the umbo. The ornament consists of concentric lamellae of growth.

Specimen No. 412b is a cast of the convex ventral valve with the dorsally directed interior of a palintrope extending two-thirds of the distance from the umbo to the cardinal extremities. Opposite this ventral cast occurs an anteriorly directed area - the internal cast of the dorsal palintrope. Both areas are interrupted by obscure casts of median processes.

Another cast (P.1) clearly shows the impressions of the internal processes. A short median septum extending anteriorly from the umbo of the ventral valve is flanked by two short plates diverging anteriorly at an angle of about 90°. In the dorsal valve two septa diverge anteriorly at an angle of 25° for about three-quarters of the height of the valve. Flanking these septa are radiating rows of elongated pustules. The area between the septa is smooth except for a faint median row of pustules.

Dimensions

	Height	Width
412a (shell)	1.2 mm.	1.6 mm.
412b (cast)	1.9 mm.	2.5 mm.
511 (shell)	0.5 mm.	0.6 mm.

Remarks /

Remarks No specimen has been extracted with all the spines complete. This defect is thought to be due rather to the method of collecting than to any original imperfections of the fossils.

It is difficult to recognise the ontogenetic stage of these shells. They possess many of the adult characters of Chonetes, although they are only half the size of the shells of Chonetes polita described by Davidson (1858-63, vol. 2, p. 190) and do not show the characters usually associated with maturity and old age - coarsening of growth-lines and shell-thickening. Paeckelmann (1930) tabled measurements of some individuals of Chonetes (Tornquistia) politus ranging from 2.5 mm. - 13 mm. in width.

The smaller shells appear to be in the late nepionic or early neanic stages and the larger in the neanic stages.

Genus PRODUCTUS J. Sowerby, 1814

Subgenus Productus, J. Sowerby, 1814, emend. H.M. Muir-Wood, 1930

Productus (Productus) concinnus J. Sowerby, 1821 Plate II, fig. 4

Remarks Fragments of valves and shells of Productus (s.l.) occur in the shale but in only a few specimens have the subgeneric and specific /

specific characters been observed. Specimen No. 126 shows the interior of a dorsal valve, 21 mm. in width and 17 mm. in height. A small bilobed cardinal process extends downwards as a median septum to the anterior end of the visceral disc which is rimmed by a diaphragm some 2 mm. in width. Other internal characters could not be observed since the innermost shell layers are missing. Costae number 15 in 10 mm., at a distance of 15 mm. vertically below the cardinal process.

Lamellibranchia

Genus AVICULOPECTEN McCoy, 1851, emend. Newell, 1937

Aviculopecten sp. probably A. [Limatulina] scotica (Hind), 1903

Remarks Specimen No. 437, a broken left valve, is comparable with A. scotica.

Genus /

Genus NUCULOPSIS Girty, 1911, emend. Schenk, 1934

Nuculopsis gibbosa (Fleming, 1828)

Remarks The specimens accord, in general, with Hind's description (vol. 1, p. 178, 1896-1905), except for his confusion of anterior with posterior. Three specimens were immersed in weak hydrochloric acid in order to obtain internal casts. These casts showed that the shells were dimyarian and integripalliate; the anterior teeth large at the umbo, decreasing in size anteriorly, numbering 13-15 in each valve; posterior teeth poorly developed, numbering 2-4 in each valve. The dentition is interrupted immediately posterior to the umbones - the position of the ligament pit. Neither the external nor the internal ventral margin is denticulate. These facts confirm Schenk's opinion that Nucula gibbosa Fleming belongs to the genus Nuculopsis.

Dimensions

	293a Shell	Cast	293b Shell	Cast
Length	13.5 mm.	11 mm.	14 mm.	11 mm.
Height	8 mm.	6 mm.	8 mm.	4.5 mm.
Thickness	7.5 mm.	6 mm.	8 mm.	5 mm.

	207 Shell	Cast (crushed laterally)
Length	16 mm.	13 mm.
Height	11 mm.	8.5 mm.
Thickness	7.5 mm.	6 mm.

Note on the genus Nuculopsis

The genus Nuculopsis was erected by Girty (1911) for the reception of those palaeozoic Nuculids with a continuous series of taxodont teeth, uninterrupted by a chondrophore; short side anterior; external ligament present. Schenk (1934 criticised the schematic figures of the geno-type, Nucula ventricosa Hall (Geol. Survey Iowa, vol. 1, pt. 11, Palaeontology, p. 716, pl. 29, figs. 4, 5a, 5b, 1858) which pictured a shell without a chondrophore, since hypotype No. 5646[1] possesses a chondrophore. Schenk compared the type of Nuculopsis with a number of Recent specimens of similar shell structure (especially the lunular areas) and suggested that the ligament of Nuculopsis was internal and that the short side was posterior. Thus although Girty's diagnosis is inaccurate, the name has value since it is the earliest one to be applied to palaeozoic Nuculids with a smooth ventral margin and without definite concentric ribs. For this reason Schenk retained the name with an emended diagnosis.

Nucula /

[1] Stanford Univ. Pal. Type Coll.

Nucula ventricosa Hall, 1858, however, is a homonym of Nucula ventricosa Hinds, 1843, and so Schenk changed the name of the former to Nuculopsis girtyi Schenk, 1934, nom. nov. for Nucula ventricosa Hall, 1858, non Hinds, 1843, non Pøchelintsev, 1927.

Schenk in his classification of the Nuculidae considered Nuculopsis Girty, 1911 to be a valid genus which included the subgenera Nuculopsis (s.s.) and Palaeonucula Quenstedt, 1930. These two subgenera differ merely in matter of degree - the opisthogyrate nature of the umbos being stronger in Nuculopsis than in Palaeonucula.

Genus PSEUDAMUSIUM Klein, 1853

Pseudamusium? aff. ellipticum (Phillips, 1836)

Remarks The valves collected are rather variable in outline and ornament and are similar to P. anisotum except for the absence of ribs on the ears. Newell (1937) doubtfully referred anisotum to his new genus Streblochondria but left Pseudamusium ellipticum as 'unresolved'.

Genus /

Genus SANGUINOLITES McCoy, 1844

Sanguinolites costellatus (McCoy, 1851) Plate III, fig. 8

Description Shell very thin, sub-ovate to elongate sub-rectangular, the longer axis coinciding with the antero-posterior axis; umbones anterior, incurved; anterior end short; ventral margin gently convex; posterior end truncated but sometimes gently rounded; lunule defined by two sharp ridges running posteriorly from the umbones to the postero-dorsal angle; carina curves dorsally from the umbone to the postero-ventral angle delimiting the convex anterior and ventral area from the flat to slightly concave poster~~ior~~-dorsal area; a poorly defined groove curves similarly from the umbone to the mid-posterior margin. Ornament consists of strong concentric ribs and sulci passing abruptly into fine striae posteriorly to the carina. Interior unknown.

Remarks Hind (1896-1900, vol. 1, p. 374) considered that the three species omalianus, costellatus, and variabilis formed one group within the genus Sanguinolites, differing from each other in width, and in strength and number of ribs. Examination of Hind's dimensions and figures shows these differences to be slight and overlapping. The range of variation shown /

shown in the figures suggests that the three species form only part of a species group within which there may well be several distinct morphological species. It is felt that Hind's delimitation of the species is unsatisfactory, but no attempt is made here to erect new species since the specimens collected are incomplete. The following characters are considered to be of value in determining the variants within the group:

(1) Curvature and direction of the carina.

(2) Postero-dorsal angle.

(3) Degree of truncation of the posterior margin.

(4) Nature of the ribbing.

The degree of gibbosity is unreliable since the shell is very thin and therefore often crushed.

All the specimens in the author's collection possess a distinct carina which curves towards the postero-ventral angle Hind's figured specimens show a carina fading to the posterior margin, a more rounded postero-ventral angle, and a smaller postero-dorsal area.

Sanguinolites variabilis (McCoy, 1851)

Remarks Specimen No. 517 shows close affinities with the type of the ovate species, S. variabilis, as figured by Hind. The posterior end is broken but would appear to have the straight hinge-line of this species. Bifurcation of the ribbing is not prominent in the author's specimen.

Gastropoda

Genus GLABROCINGULUM Thomas, 1939

Glabrocingulum armstrongi Thomas, 1939

Remarks Specimen No. 317 accords with Thomas's description of this species. Thomas stated (1939, p. 43) that the range of G. armstrongi was from the Upper Limestone Group to the Millstone Grit, yet in her table of ranges (p. 67) the species is shown as occurring in the Lower Limestone Group. The uncrushed specimens in the writer's collection undoubtedly possess the more quadrate outline of the aperture and the relatively shorter height which distinguish G. armstrongi from G. atomarium.

Cephalopoda

Genus CYCLOCERAS McCoy, 1844, emend. Bassler, 1915

Cycloceras sp. Plate IV, fig. 7

Description Only a few fragments referable to this genus have been found. The fragments are straight, elongate, sub-cylindrical cones always slightly flattened. Externally they are ornamented /

ornamented with strong transverse annulations numbering 2 in 11 mm. at 20 mm. mean diameter (No. C.1) and 3 in 13 mm. at 17 mm. mean diameter (No. 162). The annulations are separated by grooves some 3 mm. in width. Superimposed on the annulations and intervening grooves are fine transverse striae numbering about 10 in 1 mm. Internal structure unknown.

Note on the genus Cycloceras and related genera

McCoy in 1844 erected the genus Cycloceras for the reception of (p. 6) "those conical species marked with prominent concentric rings, and having the surface frequently sculptured with transverse scaly laminae, and often decussated; siphuncle dorsal". Three species were listed:- C. annulare (Fleming), laevigatum McCoy, and lineolatum (Phillips), but the genotype was not indicated. Hyatt (1900) limited Cycloceras to those forms with discontinuous longitudinal ridges. Foerst (1924) observed that Hyatt's emendation of Cycloceras McCoy left without generic designation those forms possessing only transverse striae and no longitudinal markings, and to receive these forms he erected the genus Perigrammoceras, designating as genotype O. laevigatum McCoy as figured by Foord (1897, pl. 5, figs. 1d, 1e). At the same time he nominated Orthoceras rugosum Fleming as represented by Phillips (1836, pl. 21, fig. /

fig. 16) genotype of Cycloceras McCoy, emend. Hyatt, 1900, since McCoy's figure and description of the genus were much closer to that species than the three species McCoy had listed under the name of Cycloceras.

Subsequently Croneis (1926) reinterpreted Cycloceras McCoy as follows (p. 192):- "Annulated orthoceracones and cyrtoceracones with or without vertical striae or ribs. Siphuncle small. Type C. laevigatum McCoy. Carboniferous". Croneis rejected Perigrammoceras Foerste as a synonym of Cycloceras McCoy, emend. Croneis.

Foerste (1932) pointed out that Bassler as early as 1915 had selected Orthoceras annulare Fleming as the genotype of Cycloceras McCoy, and so he now adopted this species as the genotype. Foerste's description of Cycloceras McCoy (genotype O. annulare Fleming) now read (1932, p. 83):- "Annulated conchs, with transverse striae, but without vertical markings of any kind". O. annulare has priority as genotype (Article 30g, Rules of Zoological Nomenclature) and is therefore not subject to change. As Miller, Dunbar, and Condra (1933) pointed out, on the basis of Foerste's (1932) description of Cycloceras Perigrammoceras Foerste becomes a synonym of Cycloceras McCoy unless the nature of the siphuncle of O. laevigatum (genotype of /

of Perigrammoceras) should prove to be different from that of O. annulare (genotype of Cycloceras). The siphuncles of those two species were then unknown. Foerste (1932) did not refer to Perigrammoceras in his acceptance of O. annulare as genotype of Cycloceras McCoy.

The matter has unfortunately been resurrected by Demanet (1941) who wrongly upheld O. rugosa to be genotype of Cycloceras, as erected by Foerste in his earlier paper (1924). Demanet described O. rugosa under the generic name of Cycloceras

O. rugosa, consequent on the emendation of Cycloceras McCoy by Foerste (1932) is left without generic designation since Orthoceras is no longer valid as a nautiloid genus (Teichert and Miller, 1936). The species appears to fall within the family Kionoceratidae Hyatt. No genus, however, within that family is suitable. Spyroceras, as noted by Shimer and Shrock (1944) is a 'form-genus' ranging from ?Ord.-Dev. (Hyatt (1900) gave the range as Ord.-Carb), and Thoracoceras Fischer de Waldheim non Eichwald, to which O. rugosa was assigned by Demanet (1938) was later noted by that author (1941, p. 106) to be without the transverse annulations attributed to it by Hyatt (1900).

Fortunately some of Fleming's holotypes are housed in the Royal Scottish Museum. During investigation of Fleming's specimen /

specimen of O. rugosa the author discovered that Mr Selwyn Turner of Leeds University had examined the collection in 1949 and had erected a new genus, Rugorthoceras for O. rugosa Fleming. Turner considers Orthoceras rugosum Phillips to be generically distinct from Orthocera rugosa Fleming, the former of which he renames Rugocyrtoceras northumbriense since it is a homonym of O. rugosa Fleming. Rugocyrtoceras is a cyrtocone, Rugorthoceras an orthocone.

The species Rugocyrtoceras northumbriense is here adopted with the permission of Mr Turner, whose work is still unpublished.

Genus LOXOCERAS McCoy, 1844

Loxoceras? sp. Plate V, fig.4, and PlateVIII,fig.1

Description Conch small, slender, straight, almost cylindrical adapically, flattened adorally; shell very thin; surface of conch smooth; sutures somewhat sinuous and oblique, being directed adorally from the marginal siphuncle; septa subcircular in outline, convex adapically; about two camerae occupy a length equal to their mean diameter; siphuncle marginal, small at its passage through the septa; septal necks appear to be short.

Adorally /

Adorally the conchs are flattened and no internal structures can be seen. Adapically, however, the camerae have been filled with pyrite which can be exposed by dissolving the outer shell with dilute hydrochloric acid. The greatest diameter of the pyritized part of the conchs is about 1 mm.

The specimens are doubtfully referred to the genus Loxoceras, since only the characters of the extreme adapical part of the conch are known.

Dimension Length of Specimen No. 606g = 30 mm.

Nautiloid

Remarks One generically indeterminable fragment of a globose, involute nautiloid was collected. The shell substance of the fragment is thick and ornamented with growth lines. The nautiloid outline is revealed by an imperfect internal cast.

Dimension Diameter of Specimen No. 153 = 72 mm.

Genus /

Genus PSEUDORTHOCERAS Girty, 1911

Pseudorthoceras aff. knoxense (McChesney, 1860) Plate V, figs.1 and 2

Pseudorthoceras knoxense Miller and Youngquist, 1949, pp. 18-22, Pl. 2, figs. 1-7; Pl. 3, figs. 2-8; Pl. 55, figs. 15-17.

Remarks Only one conch was sufficiently well-preserved to permit of sectioning. The sectioned conch distinctly shows the lamellar deposits within the camerae, the short, strongly recurved, septal necks, and the fusiform shape of the adapical segments of the siphuncle. The conch differs from P. knoxense in possessing broader septal necks (about $\frac{1}{8}$ of the diameter as against about 1/12 in P. knoxense), and a less spherical shape of the segments of the siphuncle adorally.

Genus RUGOCYRTOCERAS J.S. Turner (MS)

Rugocyrtoceras cf. northumbriense J.S. Turner (MS) Plate V, fig. 3

Orthoceras rugosum J. Phillips, 1836, p. 239, Pl. XXI, fig. 16.

Description Conch slightly curved, crushed. Ornament of transverse annulations and fine irregular transverse ribbing, crossed /

crossed by 23-24 tuberculated longitudinal ribbs and exceedingly fine longitudinal sigmoidal striae. Siphuncle unknown in author's specimens. The annulations are much closer together than in Phillips type specimen - 4 in 20 mm. as opposed to 2-3 in 20 mm. at a mean width of 20 mm.

(iii) /

(iii) Microfossils

The following microfossils were extracted from the shale:-

Girvanella? sp.

Glomospirella sp.
Hyperaminna sp.

Athyris sp.

Nuculopsis gibbosa
Posidonia corrugata
Sanguinolites costellatus, s.l.

Cf. Bucaniopsis striatus
Cf. Euphemites urei
Glabrocingulum sp. probably G. armstrongi
Naticopsis? sp.
Pleurotomariid?
Pseudozygopleura(s.l.) spp.
Soleniscus sp.

Coleolus aff. carbonarius

?Amphissites centronotus
Bairdia? sp.
Healdia cuneola

Cavusgnathus sp. nov.
Gnathodus clavatus sp. nov.
Hindeodella spp.

Scolecodont

Crinoid ossicles

Macrofossil fragments

Method /

Method of Extraction of Microfossils from the shale

A weighed amount of shale (app. 10 grams) was mechanically disintegrated into mud by alternate boiling and cooling in a saturated solution of sodium sulphate. Two other methods tried - namely alternate boiling and cooling in a saturated solution of sodium carbonate, and boiling and freezing in water - were less effective.

According to its condition the resistance of the shale to the sulphate varied greatly. Unweathered black shale, with poorly defined bedding-planes, was only partly disintegrated after some ten to fifteen treatments, whereas weathered grey shale was reduced to sludge after half-a-dozen operations. The sludge was washed through 30-, 100- and 200-mesh sieves and the three fractions dried and weighed.

Irregular shale pellets constituted the greater part of the three fractions and the fossils were picked out under a binocular microscope with a fine, moistened, camel-hair brush. There is no method of complete separation since the shells are filled with the shale matrix and/or pyrite. A thin film of each fraction was spread over a quarter-plate glass slide to the underside of which had been glued 7 mm. lined paper (i.e. the field of the binocular), and the picked microfossils were then transferred to and classified in a Perspex tray with forty countersunk /

countersunk compartments. Only a portion of the 200 fraction was extracted, the total 'on 200' microfossils being estimated by weighing. The microfossils were mounted on a 100-compartment tray-slide, using gum tragacanth to which formaldehyde had been added to prevent the formation of mildew.

Complete extraction of the microfossils in any one shale sample is impossible, since some of the more fragile shell are destroyed during the operation. Ostracod shells, for instance, sometimes break down into their two component valves, fragments of the valves occurring in the 200 fraction. Further, there is always a crop of shale pellets which may envelop microfossils. Nevertheless, a sufficiently close estimate of the relative proportions of the various species composing the microfossils can be made.

Latterly, a new method, used by the D.V.O.A.G. laboratory in Germany to break down Coal-Measure shales and suggested to the author by Mr F.D.S. Richardson of the Anglo-Iranian Oil Co., proved to be extremely efficient. The shale is wrapped in a piece of tin and crushed in a vice - a process that does not seem to damage the microfossils. The fragments are placed in a porcelain basin, damped and then covered with a 30 per /

per cent. solution of hydrogen peroxide. In about a week the shale is sufficiently broken down to permit the microfossils to be washed free from the sludge. The hydrogen peroxide reacts with the finely disseminated pyrite, so common in black shales, to form iron sulphate.

The D.V.O.A.G. laboratory used 50 per cent. hydrogen peroxide on Coal-Measure shales, apparently disintegrating the fragments in a few minutes with a violent spontaneous reaction.

The only disadvantage of this otherwise excellent method is that some of the microfossils with adherent pyrite are partly broken by the reaction.

An attempt was made to clean microfossils with adherent shale particles by boiling them in a weak solution of potassium hydroxide. The results were unsatisfactory.

Algae /

Algae

Genus GIRVANELLA Nicholson and Etheridge, 1878

Girvanella? sp. PlateVII,fig.1

Description Stumpy calcareous tubes, colonial in habit and either free or adherent to shell surfaces; tubes separate or touching but never quite polygonal in cross-section. Walls of tubes thick (up to ¾ of external tube diameter) but thinner where in contact with each other. Dichotomous branching appears to take place in a few tubes. External diameter of tubes ranges from 0.1 mm. down to about 0.03 mm.

Only a few fragments of these colonies have been found among the extracted microfossils. Their stumpy habit and thick walls make reference to Girvanella doubtful.

Foraminifera /

Foraminifera

Genus GLOMOSPIRELLA Plummer, 1945

Glomospirella sp. Plate VII, figs. 2 and 3

Description Test free, disc-shaped, with the earliest whorls (about two) coiled irregularly, and followed by up to three tubular whorls coiled in a planospiral; whorls unchambered and slightly embracing. The wall material of succeeding whorls fills the umbilici of the test obscuring the sutures and imparting a biconvex cross-section to the test. Wall finely arenaceous with much yellowish-brown cement.

Remarks The nature of the coiling can be observed only in thin sections of shale containing Glomospirella, and in one pyritized internal cast.

Dimension Diameter app. 0.15 mm.

Genus HYPERAMMINA H.B. Brady, 1878

Hyperammina sp. Plate VII, fig. 4

Description Test consists of an irregular arenaceous tube, usually flattened. Diameter of tube fairly constant. Test unaffected by dilute hydrochloric acid.

Remarks /

Remarks All specimens found are open at both ends and are probably broken. The species is rare except in the Posidonia-band.

Dimensions Length < 0.6 mm. Diameter 0.15 - 0.3 mm.

Brachiopoda

Genus ATHYRIS. McCoy, 1844

Athyris sp. Plate III, fig. 1

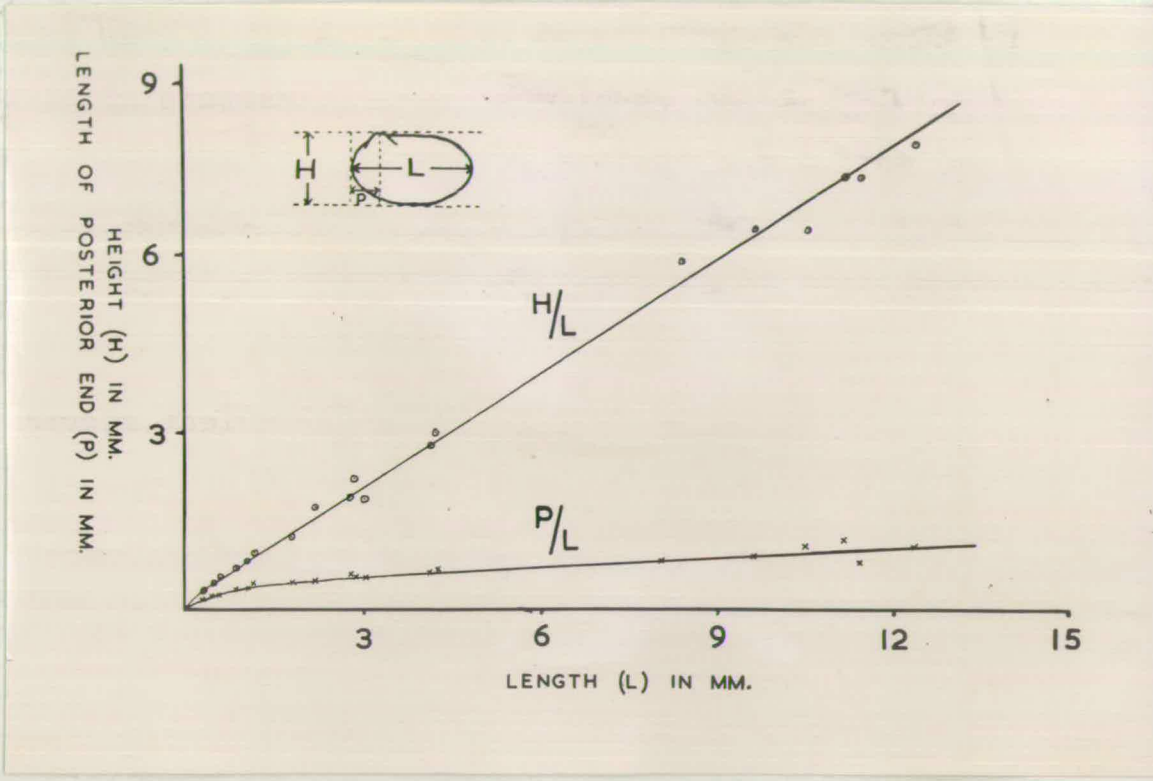
Description The figured specimen No. 388.7 is a well-preserve internal cast, biconvex and sub-circular in shape, being pointe posteriorly and slightly concave anteriorly. The ventral valv is almost flat with two strong dental plates at the apex diver-ging anteriorly at an angle of about 32°. The dorsal view shows the more convex dorsal valve flattening anteriorly. The hinge-line is approximately one-third of the width of the cast and curved; the crural bases flank the hollow underlying the dorsal umbo, their outer lateral margins forming the inner wall of the dental sockets. The teeth rise from the antero-dorsal extremities of the dental plates and curve inwards to the denta sockets /

sockets. A small dorsal median groove widens out anteriorly and probably represents a sulcus of the dorsal valve. Both the ventral and dorsal casts are ornamented with fine grooves running antero-posteriorly.

Dimensions Length = 1.1 mm.

Width = 1.1 mm.

Thickness not measured since cast is slightly crushed.



TEXT-FIG.4. Graphs illustrating the changing ratios of H/L and P/L during the ontogeny of Nuculopsis gibbosa.

Lamellibranchia

Nuculopsis gibbosa PlateIII, figs.3-7

Remarks The microfauna includes a few shells regarded as the nepionic and neanic forms of Nuculopsis gibbosa, since they grade into typical adults as is shown by the accompanying graphs of overall length (L), plotted against height (H), and length of the posterior end (P); for data see Table II, p.56.

The ratio H/L, after the earliest stages of growth, is almost constant and can be represented by a straight-line graph (Text-fig. 4). The ratio P/L decreases appreciably until the shell attains a length of about 1 mm. Thereafter the ratio remains fairly constant.

The smallest shells are sub-circular with small central umbones and ornament of growth-lines. As growth proceeds the shells lose their sub-circular outline and become elongated antero-posteriorly, with attendant decrease in curvature of the ventral margin; the umbones evolve from orthogyrate to opisthogyrate, become more pronounced and move posteriorly, due to the relative decrease of shell addition on the posterior margin.

Specimen No. 388.49.4 (PlateIII,fig.5), a broken right valve approximately 0.6 mm. in height, has a taxodont dentition /

dentition consisting of four anterior teeth and two posterior teeth separated by the ligament pit underneath the umbo. This dentition makes an interesting comparison with the previously described adult dentition of N. gibbosa (p.33) which has from 13-15 anterior teeth and 2-4 posterior teeth in each valve. The valve, less than 1 mm. in length, has thus nearly all the posterior teeth but only one-quarter to one-third of the anterior teeth present.

TABLE II

Measurements of Height (H), Length (L), and Length of Posterior End (P) of 27 specimens of Nuculopsis gibbosa

Specimen Nos.	H (in mm.)	L (in mm.)	P (in mm.)
106.1/2 (crushed)	1.75	2.2	.46
" 35	.84	1.05	.35
312.40.1.C	.3-	.35	.15
" 40.2.C	.27	.3	.15
388.5.1	1.2	1.8	.42
" 5.2 (crushed)	.9	1.23	.38
" 49.1.C	.35	.35	.15
" " 2.	.53	.6	.2
" " 3. /			

TABLE II (Contd.)

Specimen Nos.	H (in mm.)	L (in mm.)	P (in mm.)
388.49.3.	.23	.3	.15
" " 5.	.42	.5	.15?
" " 6.	.5	.57	.2
" " 7.	.5	.57 (broken)	.2
" " 8.	.27	.3	.15
560.66.1.	.46	.53	.15+
" " 2.	.23	.3-	.12
" " 3.	.7	.81	.3
157	6.6	9.6	.9
162	1.9	2.7	.53-.6
238	1.9	3	.46-.53
258	6	8.4	.75-.9
267	7.5	11.4	.75?
380	6.6?	10.5	1.05
399	2.25	2.85	.53
425	8.1	12.3	1.05
467	2.8	4.05	.6
495	7.5	11.1	1.2
614a	3.1	4.2	.6-.68

$\frac{+}{?}$ indicates uncertain increase or decrease
? is an estimated value
C is a cast

For the sake of clearness in the graph, the measurements of eight of the smaller specimens were not plotted.

Posidonia corrugata Plate IV, fig.6

Remarks Larval shells of Posidonia corrugata are abundant in the Posidonia-band. The smallest shells, about 0.25 mm. in height, are subcircular in outline with small pointed umbones situated centrally. Growth-lines are regular and fine. Shells of this size are similar to the smallest shells of Nuculopsis gibbosa which can be distinguished from the former by their thicker shell substance. The straight hinge-margin of Posidonia becomes apparent in shells of about 0.4 mm. in height. At this stage the shells are edentulous and a twisted 'cardinal area' occurs along the length of the hinge-margin. Larger shells of Posidonia corrugata, because of their fragility do not occur among the extracted microfossils.

Sanguinolites costellatus, s.l. Plate III, fig. 9

Remarks A few poorly preserved, pyritized casts have been found with the general outline of species of the S. costellatus group so common in the microfauna. The impressions of the concentric ribs are strong ventrally and fade dorsally. The postero-dorsal margin of the best-preserved specimen is broken, but the cast is only slightly crushed and shows the biconvex nature of the shell. The impressions of the right valve only, could be observed.

Dimensions No. 312.32/33 Length 2.6 mm. Height 1.9 mm.

Gastropoda

Gastropod nuclei are common in the microfauna. The absence of both coarse growth lines and shell thickening suggests that most of the shells are immature, although a few, especially among the glabrocingulid group, are the nuclear whorls of larger shells probably broken during the process of extraction. A gradation *in situ* between nuclei and adult shells implies some degree of genetic relationship among the individuals of the gradation and is evidence of immaturity of the nuclei. Such gradations are shown to exist among the individuals of *Euphemites*, of *Glabrocingulum*, and of *Soleniscus*.

Even although nuclei bear close similarities to the nuclear whorls of adult gastropods, it does not necessarily follow that, had the nuclei reached the ephebic stage, they would have developed the characters of those adult shells. Knight (1930) demonstrated divergence among species of the Pseudozygopleurinae in which sub-family individuals with similar nuclear whorls developed different generic characters in the ephebic stage. This paper was the first of a series of detailed papers in the Journal of Paleontology 1930-34 in which Knight described a number of new genera and many new species of small gastropods from the St. Louis Pennsylvanian outlier.

In /

In some respects the fauna he described is comparable with the abundant although less varied assemblage of microscopic gastropods from the Top Hosie shale.

It is perhaps advisable to note the lithology of the beds in which the American gastropods were found. Most of them occurred in the upper part of the Labette shale and the lower part of the Pawnee Limestone, a total of six feet of strata occurring immediately above a carbonaceous streak which was interpreted as a weathered soil capped by humus (1930, p. 24). The strata are part of a rhythmic unit with the calcareous red and green Labette shale representing a marine incursion. The fauna thus occurs in sediment laid down under shallow-water conditions.

Wherever possible the nuclei have been assigned to their respective species or genera. It is possible that some of the nuclei are new species but the author does not feel justified in erecting new species on immature shells.

The writer has adopted Knight's (1941) terminology for gastropods and to avoid misunderstanding wishes to define the more important terms used in the following descriptions.

Anomphalous /

Anomphalous ..... without an umbilicus

Apical angle ..... angle at the apex of the shell

Nucleus ..... shell up to four whorls (used without inference of ontogenetic stage - unlike Knight)

Phaneromphalous ..... with an open umbilicus

Pleural angle ..... angle between lines drawn to touch last two whorls of a shell on opposite sides

Protoconch ..... first-formed part of a shell - usually cap- or bulb-shaped

Selenizone ..... band formed by secretion of shell material in the slit (if present)

Steinkern ..... cast of the interior of the shell

Genus EUPHEMITES Warthin, 1930

Cf. Euphemites urei (Fleming, 1828) Plate IV, fig. 5

Description Planospiral, phaneromphalous, unchambered nuclei consisting of from one to two whorls; whorls rounded and smooth the second whorl embracing the protoconch; dorsum slightly flattened; apertural wall flaring postero-laterally. All the nuclei are smooth with the exception of the two largest specimens, one of which (No. 560.86.1) shows the commencement of spiral /

spiral ribbing on the outside whorl continuing to the aperture which appears to be broken. The dorsum of this nucleus is broken but the lirae probably numbered from 15-20 near the aperture. The ribs of the other nucleus (No. 312.46.1) fade out before the aperture.

Dimensions Specimen No. 560.86.1

Greatest diameter of nucleus 0,9 mm.

Length of longer apertural axis 0.9 mm. (crushed)
(i.e. the axis transverse to plane of coiling)

Remarks A thin section was made of a nucleus, parallel to the plane of coiling, to determine the number of whorls composing the nucleus and the nature of the protoconch. The section of Specimen No. 388.21.5 (Plate IV, fig. 4) is of a limonitised and pyritized nucleus, diameter 0.5 mm., of one and one-quarter whorls. The protoconch is vermicular and coils from its inception, leaving a small central perforation filled with sediment.

The relationship of the larger bellerophontid shells (Euphemites and Bucaniopsis) to these nuclei was examined. Four small shells, 2-3 mm. in diameter, of Bucaniopsis sp. were broken down towards the protoconch. The reticulate ornament became finer as the whorls were traced back towards the origin but whether or not the ornament disappeared and the shel became /

became smooth could not be determined since the partly pyritize nuclei, diameter 1-2 mm., either broke or disintegrated on further dissection. The shell substance of these larger nuclei was much thicker than that of the smaller nuclei and the umbilical slopes were partly filled with the shell substance of later whorls flaring over the earlier.

The lirae of a dissected anomphalous shell of Euphemites urei, diameter 9 mm., continued back, gradually convergin At a shell diameter of 2 mm. the umbilici were completely fille with shell substance forming a solid axis. Further dissection broke the shell.

Genus BUCANIOPSIS Warthin, 1930

Cf. B. striatus (Fleming, 1828)

Remarks The evidence presented does not exclude the possibility of the occurrence of larval shells of B. striatus and the author considers that they may be represented among the bellerophontid nuclei.

Bellerophontid nuclei of the size collected appear to be unrecorded, although Weir (1931, p. 823) notes that the young of Bucaniopsis decussatus, about 1 mm. across the inner lip /

lip, have widely spaced ribs. In his description of Euphemus urei (p. 845) he states that "Lirae appear at an early stage of growth, being strongly developed in specimens about 1 mm. wide at the axis; at this stage the shell is umbilicated with circular whorl section".

Knight (1941) states that the nuclei are unknown in his descriptions of twenty-one genera of the Bellerophontacea.

Genus GLABROCINGULUM Thomas, 1939

Glabrocingulum sp. probably G. armstrongi Plate IV, fig. 1

Description Phaneromphalous, turbinate nuclei of 2-4 whorls, pleural angle almost a right angle. Protoconch and first whorl flatly coiled, rounded and smooth. The ornament of fine spiral threads commences on the second whorl and numbers about 18 on the third whorl from the suture to the base (No. 388.8.2). Towards the end of the third whorl the threads coarsen, are reduced in number by the increase and decrease in strength of alternate threads and give an angled profile to the whorl. On the fourth whorl the two threads on the lateral face define a spiral groove (probably the selenizone although growth lines could not be seen) broader than the other grooves.

The /

The bases of the larger specimens are broken and the detail of the ornament obscured by adherent shale, but Specimen No. 560.81.1, cleaned with acid, showed reticulate ornament on the third whorl between the suture and the lateral face.

Dimensions	No. 388.8.2 ($2\frac{1}{2}$ whorls) (broken)	No. 560.81 (4 whorls
Height	0.75 mm. (estimated)	1 mm.
Width	0.5 mm. (estimated)	1.5 mm.

Remarks These nuclei are very similar in both shape and ornament to the apical whorls of the adult Carboniferous pleurotomariid shells described by Thomas (1939). Synthesis of her specific descriptions shows that the Carboniferous pleurotomariid nuclei are in general characterised by a smooth protoconch and one to two rounded whorls followed by whorls with spiral, transverse, or reticulate ornament. The shape of these early whorls is turbinate. The selenizone does not become evident until the third or the fourth whorl.

The nuclei can be assigned to the genus Glabrocingulum common in the Lower Limestone Group. Thomas (1939, p. 41) describes the ontogeny of G. atomarium, typical of the Glabrocingulum atomarium-armstrongi group:-

> "The nepionic stage is characterised by a smooth protoconch and one smooth turn, then two to two and half rounded whorls carrying five or six spiral lines, band not discernable (sic discernible). In the neanic stage /

stage the spirals fade, leaving two of their number, which strengthen and form the bounding keels of the band, which occupies about half the width of the fourth whorl, thereafter becoming relatively smaller until the adult proportions are attained. The ornament on the first neanic whorl consists of a single nodular spiral thread immediately below the suture. In later whorls others appear but the initial one remains prominent for some time. In the adult the beading is weaker, the resulting ornament being rather a delicate reticulation of the growth lines and spirals".

This description accords in most respects with that of the nuclei, except that the ornament between the posterior suture and selenizone in the nuclei consists of two spirals not one, on the third whorl, that one adjacent to the suture being slightly beaded (No. 560.82.1).

Thomas's suggestion (1939, p. 40) that the spirals in the nepionic stage continue below (i.e. anterior to) the band and are developed on the base, is confirmed.

Genus PSEUDOZYGOPLEURA Knight, 1930

Pseudozygopleura (s.l.) spp. Plate IV, figs. 2 and 3

Description High-spired, anomphalous nuclei of 2-3 whorls; whorls evenly convex, sutures depressed; protoconch smooth, second and third whorls ornamented with strong, transverse, sigmoidal costae numbering about 20 on the third whorl; the outer apertural lip appears to run parallel to the costae.

The /

The costae curve slightly backwards from the posteric suture towards the anterior suture. Midway between the two sutures they become strongly geniculated aperturally for about a third of their suture-to-suture length (in the most extreme forms becoming sub-parallel to the sutures), finally curving down in a near transverse direction to the anterior suture. In the most extreme forms the costae coalesce at the geniculation to form a revolving lira. On the third whorl the costae continue on to the flattened base as weak threads where they become directed abaperturally.

The second whorl does not show the anterior part of the ornament because of the adpression of the third whorl. In Specimen No. 312.5.7, the adpression is sufficiently strong to partly obscure the geniculation of the costae of the second whorl so giving the appearance of a whorl ornamented solely with simple curved costae.

Remarks Knight (1930, p. 11) erected the sub-family Pseudozygopleurinae for the reception of those loxonematoid gastropods possessing a smooth protoconch and transverse, sigmoidal costae on the succeeding nuclear whorls. The present author desires to use Pseudozygopleura (s.l.) as being indicative of any form within the family. Judging from Knight's photograph (1930, Pl. 5, fig. 13), the nepionic shell of an undetermined genus /

genus of the Pseudozygopleurinae is almost identical with some specimens from the Top Hosie shale.

Longstaff (1933), in a revision of the British Carboniferous Loxonematidae, re-examined in the light of Knight's paper the British species and also the numerous representative of several species of Zygopleura Koken from St. Cassian, but was unable to find on any of their nuclear whorls the sigmoidal ornament so characteristic of Pseudozygopleura Knight. On all the nuclear whorls were fine curved ribs, similar in character to, but not so strong as those of the later whorls. Longstaff figured the simple, costate, nuclear whorls of adult shells, but neither figured nor described any isolated loxonematoid nuclei.

The wide variation in the type and coarseness of ornament shown by the nuclei suggests that the Pseudozygopleura from the Top Hosie shale represent more than one species group. The nuclei belong to different communities in time, and, had they reached the ephebic stage, might well have been divisible into several distinctive morphological species or even genera. Still more important is the fact that several nuclei (e.g. No. 312.5.7) have the sigmoidal curvature of the costae concealed by the adpression of subsequent whorls on all but the last whorl. Had these nuclei become adults it is probable that /

that they would have been classified as Zygopleuras since the critical character, that of the sigmoidal ribbing of the nuclear whorls, would have been concealed.

Attention is drawn to these nuclear Pseudozygopleuras in view of the abundance of Zygopleuras in the Lower Limestone Group of Scotland. The former have hitherto been unrecorded from the Scottish Carboniferous.

Genus SOLENISCUS Meek and Worthen, 1860, emend. Knight, 1931

Soleniscus sp.

Description Moderately high-spired, anomphalous nuclei of from 3-5 whorls, with a pleural angle of about 50°; protoconch globular, whorls smooth with gently arched profile; sutures slightly impressed. The aperture appears to possess a small anterior canal.

The nuclei are poorly preserved, many occurring as uncrushed steinkerns of pyrite but with the internal shell material still present. Section 106.24.3 is of such a nucleus with a slightly sinuous columella.

Remarks The nuclei resemble the much larger species of Soleniscus /

Soleniscus described by Knight (1931) but, as in other instance the incomplete nature of the nucleus prevents satisfactory determination. Knight noted that the few distinctive characters developed in the group made accurate discrimination of the species difficult.

Unidentified gastropods

The smallest nuclei ranging in size from $1\frac{1}{2}$ to $2\frac{1}{2}$ whorls are mostly unornamented. A few are well-preserved but the majority are compressed and broken, with adherent sedimentary particles. It has been found impossible to assign them to any particular genus since so few critical morphological characters are developed, but they can be divided into two distinct groups:-

Naticiform nuclei

Turbinate nuclei

which can be compared with identified shells in the sediment.

Naticiform Nuclei

Description Smooth, globular, phaneromphalous nuclei of $1\frac{1}{2}$ - $2\frac{1}{2}$ whorls. The coiling of the protoconch and first whorl is discoidal /

discoidal and the increase in whorl diameter rapid. Two sectioned nuclei have apical angles of 140° and 116° respectively.

Remarks Many of these shells have been filled with pyrite. In some cases the outer shell material has been removed, probably during the treatment of the shale, since the casts are clean, while those with calcareous shells have adhering sedimentary particles.

The nuclei were at first thought to belong to the genus Naticopsis which occurs in the sediment in adult form. Section No. 239 of an adult Naticopsis has an apical angle of approximately 120°.

However, two of the largest nuclei show the commencement of faint spiral threads near the aperture and are probably the smaller shells of the genus Glabrocingulum (312.44.1 and 3) But this fact does not necessitate the inclusion of all the smaller unornamented nuclei in the genus Glabrocingulum and the author considers that the group is probably heterogeneous.

Turbinate Nuclei

Description Turbinate, phaneromphalous nuclei of $1\frac{1}{2}$ - $2\frac{1}{2}$ whorls. Protoconch globular, followed by one smooth rounded turn. On the centre of second whorl a faint spiral thread can be seen in well-preserved specimens, e.g. Nos. 312.15.4 and 388.38.5). These nuclei may be young pleurotomariids but are very similar to the early whorls of Soleniscus.

Scaphopoda

Genus COLEOLUS Hall, 1879

Coleolus aff. carbonarius Demanet, 1938 Plate VII, fig.6

Description Gently curved, greatly elongated cone, circular in cross-section although sometimes crushed; shell thick; ornament consists of fine ribbing obliquely transverse to the axis of the cone. The ribs number about 24 to 1 mm. length at a diameter of 0.5 mm.

Remarks Fragments of these cone-shaped tubes, ranging in length from less than 1 mm. to about 3 mm., constitute a small part of the microfauna.

One shell only was found complete (No. 606e). It is 31 mm. in length and has a width of almost 3 mm. at the posterior end which is crushed. The ribs number 14 to 1 mm. at 1 mm. breadth. The cone does not expand so rapidly as C. carbonarius and the ribs number 14 - not 12 as in carbonarius - to 1 mm. It is on the evidence of this cone that the microfossil fragments are assigned to the species carbonarius.

Ostracoda

Genus AMPHISSITES Girty, 1910, emend. Cooper, 1941

?Amphissites centronotus (Ulrich and Bassler, 1906)

Description Valve sub-rectangular; dorsal margin long and straight with cardinal angles obtuse, ventral margin almost straight and curving into the rounded ends. Both ventral and dorsal margins are overlapped by flanges. Two prominent concentric carinae originate from the dorsal flange and run subparallel to the margin of the valve. The rest of the exterior of the valve and the whole of the interior are obscured by adherent shale matrix.

Dimensions (No. 560.64)

Length = 0.8 mm. Height = 0.45 mm.

Genus BAIRDIA McCoy, 1844

Bairdia? sp.

Remarks A few poorly-preserved carapaces of some 2 mm. in length have been found in the shale immediately below the Top Hosie Limestone. The carapaces are oval and biconvex, and the valves /

valves appear to be unequal in size. The exteriors are obscured by shale matrix except in one instance, Specimen No. 106.18, which is covered with adherent tubes of Girvanella? sp

Genus HEALDIA Roundy, 1926

Healdia cuneola (Jones and Kirkby, 1867) Plate VI, figs. 7 and 8

Cythere cuneola Jones and Kirkby, 1867, p. 223; 1871, p. 27. (Name only)

Bythocypris? cuneola Jones and Kirkby, 1886, p. 250, Pl. VI, figs. 3-7.

Healdia cuneola Latham, 1932, p. 381, Text-fig. 24.

Description Carapace small, inequivalve, sub-oblong in outline; ventral margin straight or slightly concave, rarely convex; anterior margin evenly rounded; dorsal margin convex and variable in outline, but usually possessing a slight median geniculation; posterior margin oblique and truncated. The carapace is thickest posteriorly and tapers anteriorly. Both valves are swollen in the postero-ventral region which generally possesses a small tubercle often extended on the right valve into a short, posteriorly-directed, spine. The left valve overlaps the right valve conspicuously on all sides. Interior

ly /

Interiorly the left valve is provided with a shallow groove running completely round the margins into which groove the edges of the right valve fit. Shell thin, surface finely punctate (especially No. 560.40.6).

Dimensions	No. 560.1.2	No. 560.1.7
Length	0.6 mm.	0.68 mm.
Height	0.3 mm.	0.34 mm.
Thickness	0.23 mm.	0.23 mm.

Remarks Healdia cuneola is the most abundant species in the microfauna and shows wide variation in shape. The earlier moults carry larger spines than the later moults in the ontogenetic series (see pp. 131—138).

Jones and Kirkby (1886) first described and figured the species under the genus Bythocypris?. Their specimens (1886, Pl. VI, fig. 4 and 5) are identical with some specimens in the writer's collection and exhibit a feature described neither by Jones and Kirkby, nor by Latham (1932) - that of a spine occurring only on the right valve.

H. cuneola (B374d) figured by Latham from the collection of the Geological Survey, Edinburgh, was examined by the writer in an attempt to ascertain whether or not the spine occurred in this specimen. B374d is a slide containing 11 shell none of which possesses the spine. None of the shells tallies with /

with either the figure or dimensions given by Latham. Indeed not all of them belong to the species cuneola and one carapace is referable to the genus Bairdia.

Coryell and Billings, in the same year (1932) that Latham transferred Bythocypris? cuneola to the genus Healdia, used the trivial name of cuneata for another species of Healdia Apart from the orthographical similarities of the trivial names H. cuneata Coryell and Billings is nearly identical to H. cuneola (Jones and Kirkby) from which the former may be distinguished in dorsal aspect by the more truncate posterior.

Kellett (1935) described and figured five species of Healdia, two of them new. H. parallela Kellett is comparable with some carapaces in the writer's collection.

The authorities of the British Museum (Natural History) have informed the author that they have been unable to trace the holotype of Bythocypris? cuneola J. and K. although they have some specimens of that species.

Conodonts

The name'Conodonts' was given by Pander in 1856 to certain microscopic toothlike fossils. Their affinities are doubtful, since they are confined to Palaeozoic strata, and they have been assigned to such diverse groups as Gastropoda, Cephalopoda, Annelida, Crustacea, and Vertebrata; however, it is now generally accepted that they belong to an extinct group of fish.

The study of conodonts has been almost completely neglected in Britain, although Harley (1861) described forms from the Ludlow Bone Bed, and Hinde recorded the occurrence of conodonts in the rocks of the Scottish Carboniferous as early as 1879. It has been left to American palaeontologists to describe and classify the numerous genera and species abundant in the Palaeozoic rocks, and to use them for stratigraphical correlation. In this country their application to stratigraphy presents a virgin field for research.

Genus /

Genus CAVUSGNATHUS Harris and Hollingsworth, 1933

Cavusgnathus sp. nov. Plate VI, figs. 5 and 6

Description R.H.[1] dental platform broken anteriorly; platform convex orally, concave aborally: posterior end flared adorally. Oral surface narrow, ornamented with transverse tuberculated ridges interrupted by an antero-posterior groove open at both ends. The groove is smooth anteriorly but is tuberculated in the posterior quarter of its length. The outer parapet is produced abruptly into three large denticles in the anterior third of the platform. These denticles project well above the surface of the platform, the posterior denticle being much larger than the other two. The area between the three denticles and the inner crenulate parapet is smooth. The aboral surface is broadly excavated and asymmetrical, being produced on the inner side into a laterally directed wing. A deep groove runs along the length of the excavation.

Dimensions Length of Specimen No. 654.70.1 = 1.2 mm.

Remarks /

[1] The specimen has been orientated with the oral surface uppermost top and the anterior (blade) remote. Then curvature of the specimen convex to the right hand - R.H.
left hand - L.H.
The terms 'outer' and 'inner' are applied to the convex and concave lateral sides of the specimen respectively.

Remarks The specimen is most closely related to Cavusgnathus navicula (Hinde). Unfortunately the holotype of this species is lost although the tray (JS22184) which contained the specimen has been kept in the Geological Survey Collection, Edinburgh. There is a pencil drawing on the tray of the specimen differing somewhat from the figure of the holotype in Smith, 1900, Pl. ix, fig. 5. The figure is reversed and has more transverse ridges than the drawing. Moreover, it suggests that the blade arises medianly, whereas the drawing on the tray shows the blade originating from the outer parapet. The figur probably led Youngquist and Miller (1949) to record their doubt as to whether Polygnathus navicula Hinde should be assigned to the genus Cavusgnathus or Taphrognathus, since Hinde's description of the species is vague. The accuracy of Smith's figure may be questioned but the loss of the holotype prevents further enquiry.

The author's specimen differs from both figure and drawing in (a) the presence of tuberculated ridges and (b) the absence of ornament on the area opposite the denticles. The specimen is a new species but the author would prefer to leave the specimen unnamed until more complete material is obtained.

Genus GNATHODUS Pander, 1856

Gnathodus clavatus sp. nov. Plate VI, figs. 1-3

Description Complete L.H. dental unit broken between blade and platform. Platform convex orally, concave aborally; oral surface narrow in outline, hollowed (but partly obscured by shale) and bounded by crenulate margins diverging slightly anteriorly; carina nodose, weak, apparently not continuing to the posterior end of the platform. The aboral surface, smooth asymmetrical, leaflike, is broadly excavated and has a postero-anterior groove terminating at the beginning of the blade. The aboral excavation is flanked by two smooth ridges, the outer being extended into a prominent, laterally directed wing, the inner ridge being smaller and aborally directed.

The blade consists of some fifteen irregular denticles concave orally, geniculate convex aborally. The strongest denticles are situated at the anterior and posterior ends of the blade. The antero-aboral angle is obtuse, the anterior sharp and straight.

Specimen No. 145.21.1 appears to be within the same species group as the holotype just described (No. 312.21.5) but differs in the following respects:- R.H., oral platform relatively broader, carina more prominent and runs the full length /

length of the platform to the posterior end, denticles of blade form a more even concave edge.

Dimensions Length of holotype (No. 312.21.5) = 1.6 mm.

Remarks Several specimens of this species were sent to Dr. Youngquist of the University of Idaho for comment. Dr. Youngquist agreed with the author that the specimens appear to fall close to, or within, the limits of the definition of Gnathodus, although confessing that no one knows for certain what Gnathodus is. Gnathodus clavatus is quite distinct from all previously described species of the genus, and from the variation shown by the carina, appears to be intermediate in its characters between Gnathodus and Streptognathodus.

Note on the genus Gnathodus and related genera

The genus Gnathodus was erected by Pander in 1856. A translation of the original description and a reproduction of the figures were given by Roundy in 1926. His translation (p. 12) is as follows:- "In the marls of the lowest shales of the Mountain limestone in Tula [Russia] and the higher Governments of Mosca well-preserved jawlike fossils are found, which by their configuration and by their base are distinguished from those as yet described, but which are closely joined to them /

them by their microscopic structure. From a high, narrow, compressed base, constructed of double walls, arise in a row minute teeth, giving it the appearance of being bordered with a denticulate margin. Below, these walls diverge strongly from one another and build a cavity, while at the opposite end they remain close together. This cavity, which represents the pulp cavity, lengthens out laterally and, as would be expected, affords for each denticle an ascending continuation".

Pander's reproduced figures show the lateral (2) and aboral views, and also a greatly enlarged fragment of the cone-in-cone structure of denticles. The figures were of the species G. mosquensis, the generic description evidently applying to that species, the only one figured.

Hinde (1879) erected the genus Polygnathus for the reception of a number of very variable forms which he had found crowded together in a small patch of shale in the Genesee Shale considering that they formed the remains of one individual.

In an appendix to Smith's (1900) paper, Hinde described (and Smith figured) a number of conodonts from the Carboniferous limestone of the West of Scotland, among them Polygnathus (Gnathodus) mosquensis Pander. The oral surface is both described and figured.

Bryant /

Bryant (1921, pp. 22-23) discussed the affinities of Gnathodus and described a new species of the genus:- "This genus, [Gnathodus] transitional between the narrow-based pectinate forms like Prioniodus and the broad-based tuberculated tritoral plates of Polygnathus, has hitherto been known by a solitary species described by Pander from the marl in the vicinity of Moscow. It illustrates the progressive adaptation of the basal portion of the plate into a grinding tritor. In Polygnathus this transformation is complete, the pectinate ridg either disappearing or being confined to a crest projecting beyond the tritor.

"A form very close to Gnathodus mosquensis occurs in Conodont bed [the Conodont bed of Hinde - Genundewah limestone of Genesee age] and I propose to name this species, the first to be discovered in this country, Gnathodus americanus.

"For about one-half of its length the base expands and curls upward like a withered leaf. Its upper surface bear a number of prominent tubercules. Surmounting the base is a long, thin ridge of flat coalesced teeth unequal in height. The cavity beneath the base is centrally located, of the usual lozenge shape and much smaller than that in Gnathodus mosquensis Bryant's figure (Plate VII, fig. 5) of G. americanus is a lateral view.

Further /

Further, Bryant considered that the genus Polygnathus Hinde, should be restricted so as to include only those tuberculated and rugose tritoral plates discovered in the type specimen, since he believed that Hinde's specimen of teeth consisted of several different genera, not one species. The diagnosis of Polygnathus Hinde, emend. Bryant, is as follows:- Leaf-shaped plates with a central rib or ridge which is produced beyond the tritoral margin into a stem-like flattened crest of pectinate teeth.

While Ulrich and Bassler (1926) were unable to arrive at a satisfactory definition of Gnathodus and figured a lateral view of ?Gnathodus sp. which on more careful examination they decided was Polygnathus sp., Roundy (1926) stated that the genus was one of the most common conodonts in the Barnett shale (Mississippian) and described a new species G. texanus, and a variety G. texanus var. bicuspidus, from that shale.

Currie (1937, pp. 432-3, Pl. III, fig. 4) described and figured Gnathodus cf. Mosquensis Pander from Skipsey's Marine Band (Carboniferous Coal Measures). The specimens were embedded in the matrix and only a lateral view was obtained.

Ellison (1941, p. 127) stated that Gnathodus differs from Streptognathodus in that the carina of the former is commonly prominent for the full length of the platform and no accessory /

accessory lobes (laterally directed, nodose processes on the platform) are developed on the platform. Gnathodus may acquir a distinctly radial ornamentation on the platform and in this way become sub-circular in platform outline.

Youngquist and Downs (1949, pp. 163-5) in a discussio of Gnathodus interpret the genus as having a posterior continua tion of the blade as a nodose or ridge-like carina to the pos- terior end of the platform or beyond. The platform is broadly excavated aborally, and asymmetrical with one winglike exten- sion of the aboral-lateral margin. They consider that an oral view is necessary in distinguishing between Streptognathodus, Idiognathodus and Gnathodus.

From examination of the literature it becomes evident that the original definition of Gnathodus is equally applicable to two other genera, namely Streptognathodus and Idiognathodus. The genus Gnathodus has been interpreted and restricted by Youngquist and Downs, and in their definition the oral surface is critical for generic determination.

The oral view of Polygnathodus (Gnathodus) mosquensis was first figured by Smith (1900), and the platform consists of a carina surmounting an asymmetrical tuberculated base. Un- fortunately the specimen is lost and the only tray (JS21971, Geological /

Geological Survey Collection, Edinburgh) labelled Polygnathus mosquensis contains fragmentary specimens not even referable to the genus Gnathodus. Roundy (1926) figured an oral view of a new species G. texanus (Pl. II, fig. 8b) which also shows a carina as the posterior continuation of the blade surmounting the asymmetrical leaf-like flanges of the aboral surface. The carina is not flanked by ridges but by a single cusp on the inner side (G. texanus) or two cusps, one on either side (G. texanus var. bicuspidus, Pl. II, fig. 9a). G. websteri Youngquist and Downs (Pl. 31, figs. 4 and 5) is the first figured Gnathodus to show well-formed ridges arising orally from a symmetrical leaf-like flanged base.

The conception of the genus by different authors is varied, and it is thought advisable to accept the definition of Youngquist and Downs, which is the most comprehensive, until further evidence is forthcoming.

Genus HINDEODELLA Ulrich and Bassler, 1926

Hindeodella spp. Plate VI, fig. 4

Remarks Specifically indeterminable fragments of Hindeodella occur among the microfossils. They are characterised by a bar with closely set recumbent denticles, alternating in size.

Scolecodont /

Scolecodont

? gen.

Remarks Only one fragment of a scolecodont jaw was found. The fragment (No. 312.51.6) is a shiny-black, compressed bar with small recumbent denticles. The fragment, unlike conodont teeth, is insoluble in dilute hydrochloric acid.

Dimension Length = 0.3 mm.

VII. ECOLOGY

(i) Palaeoecological Principles

Animals or plants continuously populating an area with a certain environment are adjusted to that environment. It is this balance in neoecology which enables such ecological aspects as morphological development, population changes, behaviour, &c., to be correlated with the physical or biological conditions prevailing. The living animal or plant and its environment are observed simultaneously and in this way the causes of the effects observed in the individual or community can be ascertained. This situation cannot exist in palaeoecology. The once-living animal or plant is now represented by the fossil; the original environment of the once-living animal or plant may now be represented by the surrounding sediment and its contained fossils, although the environment of the fossil is not necessarily the fossilised environment of the once-living animal or plant. There are in fact three environments to be considered: the environment in which the animal or plant lived; the environment in which the fossil was buried; the environment in which the fossil is found.

In water-laid deposits five different faunal and floral elements may be represented on one bedding-plane, namely the /

the single element of the benthos native to that biotope[1], the four foreign elements of plankton, nekton, benthos from other marine biotopes, and terrigenous matter. Only one of these elements is in its original geographical environment, the native benthos all the others have been introduced from various depths and different geographical localities by such environmental factors as gravity, currents, winds, &c.

It is therefore necessary in palaeoecology to analyse the assemblage of fossils in order, if possible, to distinguish the various elements of which the assemblage may be composed, especially the native benthos; also to examine the lithology in order to reconstruct so far as possible the original environment of the native benthos, that environment into which the other elements were brought.

Comparison between the neoecology of the living descendants of a fossil and the palaeoecology of that fossil emphasises the similarity of, or reveals the contrast between, the modes of life of the individuals of the group during its phylogeny, and in some instances enables additions to be made to the palaeoecological data of a fossil from the neoecological data of its descendant. These comparisons are most useful when dealing /

1 'Biotope', according to Hesse, Allee, and Schmidt (1937, p. 135) is "an area in which the principal habitat conditions and the living forms adapted to them are uniform".

dealing with the fauna or flora of Quaternary and Tertiary strata, less so with Mesozoic and Palaeozoic.

In the following sub-section, the autoecology of the more abundant species is investigated. Finally, the synecology of the animals populating the mud - now part of the Top Hosie shale - is considered.

(ii) Autoecology of the fossils and related living forms

Foraminifera

Norton (1930) observed that members of the Ammodiscidae (to which family Glomospirella is referred) are most often found in the cooler and deeper oceanic waters. Species of the Hyperaminnidae are also deep-water forms. Cushman (1935, p. 286), however, considered that "Arenaceous faunas are usually most abundant and most varied in species and genera in relatively shallow water" and that the occurrence of arenaceous forams in deep water environments is due to their ability to persist in such habitats rather than to any preference for such conditions. Glaessner (1945) recorded that at two stations in the Mediterranean abundant arenaceous foraminifera had been found in warm water. These occurrences he considered to be exceptional, since arenaceous assemblages normally indicate /

indicate cold-water conditions. Temperature and not depth, is the most important factor controlling the distribution of living foraminifera.

Glomospirella and Hyperammina, like the great majority of living foraminifers, were probably benthonic animals living on the surface of the mud. In the present state of knowledge, surmises concerning the depth and temperature ranges within which these palaeozoic foraminifera lived, are not attempted.

Brachiopoda

Camarotoechia pleurodon

This species occurs in the shale as scattered valves and fragments. No complete, either micro- or macro-shells, have been found and so their original habitat cannot be satisfactorily determined.

Living rhynchonellids are attached by the pedicle to the sea-floor. Apart from their bathymetrical and geographical distribution, little is known of their habits, since they are fairly deep water forms. Schuchert (1911) has shown that living genera extend from 90 feet to over 200 fathoms and concludes that rhynchonellids at the present day are deep-water animals. He points out, however, that this was not the case during the Palaeozoic and considers that the living rhynchonellids give no satisfactory guidance concerning the bathymetrical distribution of extinct forms.

Lingula

The first comprehensive study of the development of Lingula was undertaken by Yatsu (1902a) although Brooks (1878) had /

had described some of the later stages of development of the related genus Glottidia.

Yatsu, in his paper on the development of L. anatina, divided the free-swimming larvae into different stages dependent upon the number of pairs of cirri developed. The larvae result from sexual reproduction and their free-swimming existence appears to last for about one month. They occurred abundantly in the plankton in the inlet of Moroiso, Japan, and were caught offshore between the surface and depths of a few feet. The sedentary habit began immediately after the protusion of the pedicle from the shell. At this stage the shell was approximately 1 mm. long (adult 35 mm. long (Yatsu, 1902b)). The larvae lived on diatoms and other unicellular algae.

Ashworth (1915) found in the south part of the Red Sea larvae of L. anatina in sea-water pumped aboard ship from a depth of 18 feet. The sea at the locality concerned was between 16 and 40 fathoms in depth. Larvae of the same species were found by the same method 4°S. of Colombo in water of about 2200 fathoms, some 200 miles away from the nearest coast (Ceylon). The largest larvae measured 1.6 mm.

In a short paper on the ecology of Lingula, Yatsu (1902b) stated:- "Lingula occurs only along the coast of southern /

southern Japan but in that part one may expect to find it in every suitable mud flat. It is not found in deep water at all ..... in the neighbourhood of the Station (Misaki) every mud flat yields specimens of Lingula. Such flats are exposed at low tide and are covered at high water to the depth of 3-4'; of these the most favourable for Lingula are composed of sandy mud, blackened and ill-smelling from the decomposition of organic matter. Over such a black mud a layer of dirty brown mud 2-3 mm. thick is found which is probably formed by the excrements of Annelids, Lingula, &c. The flats of clean sand do not seem fit for the animal".

He observed that specimens were found about a foot below the surface. The tip of the pedicle was either fixed to the hard sandy mud or to shell fragments. The burrow was not always vertical, at times being oblique or almost horizontal. The shell could be extruded partly above the surface of the mud but was withdrawn when the animal was alarmed.

Tolerance of varying conditions was shown by Lingula existing for a considerable time in aquaria even after the water had become spoiled and fetid. An interesting case was cited of an inlet, Matsubase, forming part of the Bay of Ariake largely covered by a sandy flat inhabited by abundant Lingulas, Tapes /

Tapes, Cythereas, &c. exposed at low tide. After twenty days of heavy rain the flat was covered by a thick layer of muddy sediment brought down by a brook running into the creek. All the lamellibranchs were killed and had putrified but the Lingulas were quite unaffected. This example shows that Lingula can exist under conditions of reduced salinity.

Davidson (1888) found Glottidia palmeri at the head of the Gulf of California, on the Lower Californian shore, opposite the mouth of the Colorado River. Here also is evidence of a species of the Lingulidae surviving in brackish water at the mouth of the Colorado River.

Johnston and Hirschfield (1920), in their description of a new Queensland species, L. bancrofti, gave the locality as Burnett Head which is on the south side of the estuary of the Burnett River. The salinity of the water at this locality was not recorded.

Morse (1902) found great numbers of Glottidia pyramidata on the Bird Shoals, Beaufort Harbour, N. Carolina. These shoals were exposed at low tide and were evidently sandy although not specifically stated to be so. Some individuals placed on sand under laboratory conditions, started burrowing using the anterior portion of the shell with a shovelling movement /

movement. This observation would explain the upside-down position of any fossil Lingula so found. Others penetrated the sand by means of the pedicle dragging the shell downwards. When at rest the shell was half out of its burrow and the valves partly open with the lateral setae erect and meeting at their tips - the normal living condition. On the death of the animal the body protruded from the burrow, lay on the sand, and gradually turned black as a result of decomposition. The slightest jar of the vessel containing the animal caused the body to separate from the buried pedicle and shell, and float away. No young were found in the examination of a hundred individuals and there was little variation in size.

Recently Cloud (1948) recorded that Morse's specimens were spilled en route, and were carried for part of the journey (700 miles by train) in fresh water before they were transferred to sea-water again. They showed no apparent ill-effects from this treatment.

There is general agreement among writers that individual species of Lingula or Glottidia are gregarious and live in shoals, banks, or mud-flats exposed at low tide. Unfortunately in some instances the nature of the sea- and shore-bottoms is not described, but in general the sediment varies from /

from a fetid mud to a clean sand, the majority of species living in the muddy environment. Lithological terms include:- mud, soft mud, sandy mud, sandy shelly mud, sandy clay, fine coral sand, coarse sand. The banks and shoals are found in inlets, bays, river estuaries, and in an inland sea, Asaki, Japan.

The deeper-water limits of Lingula and Glottidia are difficult to define since dredging is the only feasible method of investigating the problem. Hence records of deeper water habitats are fewer than those of the more accessible littoral zone. References to depths of 7-10 fathoms are frequent, but records of deeper water - 16, 17, 50, 60 fathoms - are rarer. It is beyond question that they are essentially shallow-water animals, but their tolerance of deeper water and thei mode of life therein are difficult to ascertain.

The geographical distribution of the Lingulidae is wide (Schaeffer, 1926), ranging from the Indian and Pacific Oceans (coasts of Hawaii, Samoa, Viti, Java, Moluccas, Phillipines, N. and N.E. Australia, China, Korea, Japan, California to the Atlantic (Florida, Ecuador, Guineas). These localities cover a belt of latitude between approximately 40°N and 30°S. Temperatures of the sea, 0-100 fathoms, in this belt vary within /

within the extremes of 5° and 28°C. (Sverdup, 1942). Shore temperature extremes, however, are greater than these.

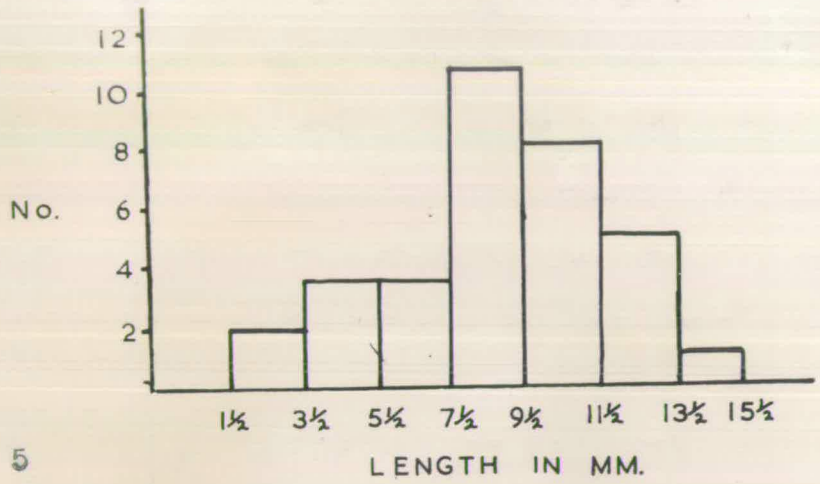
Summary

(1) Distribution of Lingula is effected during the free-swimming planktonic larval stages.

(2) Lingula possesses a wide tolerance of matrix, temperature, and salinity.

(3) Depths in which Lingula has been found vary from the shore-line to 60 fathoms, but most often the former

As Morse (1902) observed:- "One cannot help associating this remarkable vitality in these genera [Lingula and Glottidia] with their persistence through geological horizons from the Cambrian to the present day almost unchanged in character. Living as they do in shallow seas, the gradual elevation or subsidence of the coast-line would in no way affect their condition. Temperature alone has probably caused their disappearance from the more northern regions, but otherwise, they have survived all the mutations of geological times unchanged, and with the persistence of this vitality, they may be the last forms of life to survive on the earth as they were amongst the earliest preserved".



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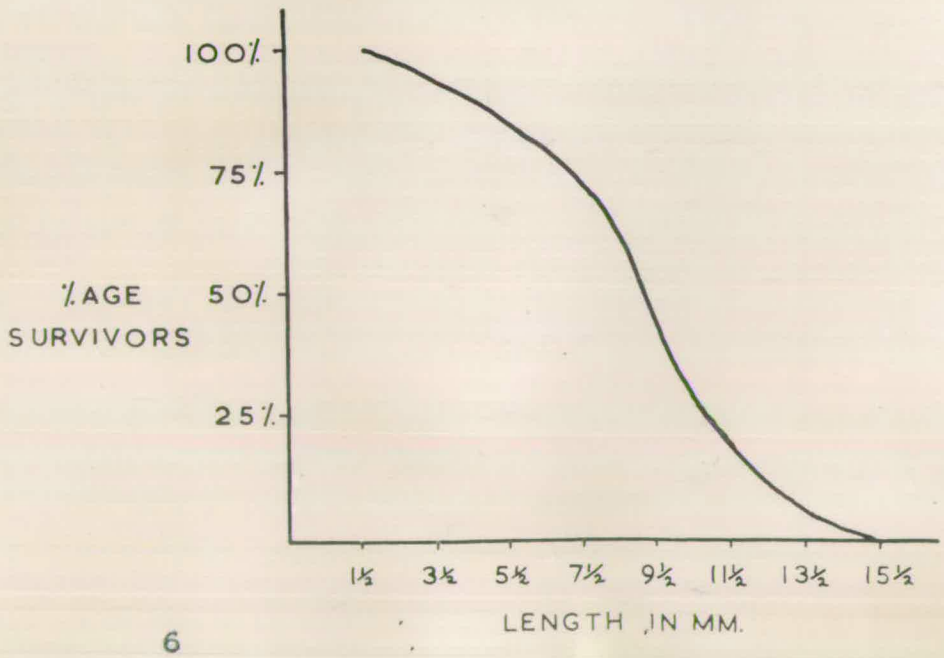


6

TEXT-FIG. 5. Histogram of frequency distribution of vertical shells of Lingula squamiformis according to length (crushed).

TEXT-FIG. 6. Graph of percentage of survivors of L. squamiformis according to length (crushed).

The neoecology of Lingulids has been reviewed in some detail since shells of Lingula squamiformis are the only fossils in the shale which can be proved conclusively to have lived in the sediment in the positions in which they are now found. Therefore, in so far as neoecology can aid palaeoecology, these shells are most valuable indicators of the conditions prevailing during the deposition of the mud now forming the shale underlying the Top Hosie Limestone.

97 specimens of Lingula squamiformis were collected, including 68 vertical shells and valves all with the anterior end uppermost and 29 horizontal shells, valves and fragments. Estimating each vertical valve as one-half of a shell, and each fragment as one-third of a shell, then 84 per cent. of all the shells found are vertical to the bedding-planes of the shale. 43 vertical specimens (24 shells, 19 valves) from different horizons in the shale, are suitable for statistical treatment. The histogram (fig. 5, p. 99) illustrates the distribution in length of shell (crushed) of the 33.1/2 shells. It shows firstly, that, although different time communities are included there is an approach to a normal distribution; secondly, that L. aquamiformis occurs in every class grouping from the smallest vertical shell collected (2.3 mm. uncrushed) to the largest (15.1 mm. uncrushed), i.e. L. squamiformis was a burrower from an /

an early stage onwards to at least 15 mm. in length.

The same data, differently expressed in the second graph, illustrate the percentage of survivors according to shell length. It will be observed that although three-quarters of the Lingulas attain a length of 8 mm. (7.5 mm. crushed) only one-fifth survive beyond a length of 12.5 mm. (11.5 mm. crushed). No shells greater than 15 mm. in length (crushed) have been found.

Davidson (1858-63, p. 205) recorded the dimensions of two individuals of L. squamiformis, the larger 40 mm., the smaller 19 mm. in length. The holotype, Pl. XLIX, fig. 1, measures 20 mm. in length. The Top Hosie specimens are therefore either a dwarfed variety of this species or are immature. Dwarfing and immaturity is discussed on page 153 .

From neoecological data it has been shown that the young Lingula after a planktonic existence adopts a burrowing mode of life in the sediment of the sea floor. There is no evidence to suggest that the Carboniferous Lingulas behaved otherwise. There are two hypotheses to account for their presence in the shale; either the vertical shells grew in situ from introduced larvae, or were swept in as larger forms which then commenced to burrow. An objection to this latter hypothesis is that the larger animals would have been derived from eroded /

eroded Lingula-mud-flats and would be associated with dead animals leaving horizontal shells as their record. The Carboniferous Lingula-bands - finely-bedded, dark shales crowded with detached valves of Lingula, parallel to the bedding planes - are excellent examples of the products of the erosion of Lingula-mud-flats. The proportion of horizontal valves and fragments in the Top Hosie shale is insufficient to support the hypothesis that live animals were introduced from an eroded flat.

The former hypothesis - that of introduction of larval forms and growth in situ - is more acceptable, considering the high percentage of vertical shells collected. But the paucity of small shells is puzzling. Apart from six vertical shells of less than 6 mm. in length (uncrushed), only one small specimen (No. 402) - a horizontal valve 2 mm. in length and parallel to the bedding - was found. A larval bottom waste, greater than that found, was expected. It would appear that nearly all the larvae encountering the muddy substratum were able to burrow and grow.

From a consideration of both neoecological and palaeoecological data it is concluded that the vertical shells of Lingula squamiformis were introduced into the area as larvae smaller than 2 mm. in length, which descended from the plankton and /

and were able to burrow into the mud and grow. The environment, although supporting life, was such that the animals were unable to develop to the normal adult size and thus are dwarfed and perhaps immature. The few horizontal valves and associated fragments were swept in and deposited with the sediment.

Paeckelmannia

The shells of Paeckelmannia (a sub-genus of Chonetes) are well-preserved and are concentrated on certain bedding-planes in the shale. The smallest is 0.6 mm., the largest about 3 mm. in width. Their position in the sediment is either with the dorsal or ventral valve to the bottom with the delicate spines of the hinge-margin still attached. On the surface (four square inches) of one specimen (No. 511) there are 10 shells with the ventral valve beneath and 6 with the ventral valve uppermost.

Lamont (1934) discussed the position of life of certain Palaeozoic brachiopods from the Girvan district and considered that the Strophomenacea in general - mentioning Chonete among other genera - lived with the convex ventral valve downwards. Swinnerton (1947) on the other hand indicated that Chonetes lived in a vertical position supported by the posterio spines with the posterior margins downward.

It is difficult to ascribe a 'normal' position of life to the shells of Chonetes (s.l.). A distinction should be drawn between passive, sedentary animals incapable of movement, and those active animals which, although normally sedentary, are able if disturbed from the position of life to regain that position by their own efforts. In the latter case there is a 'normal' position of life: in the former, the position is dependent upon the environment and the animal is either forced to adapt itself to the position which is imposed on it by the environment, or die.

The pedicle in members of the Strophomenacea was small and was often atrophied in the adult (Lamont, 1934, p. 165; Swinnerton, 1947, p. 85). A pedicle functional in the early stages of ontogeny would erect the shell which, on atrophy of the pedicle, would fall over on to one of the valves or stay erected on its posterior spines which may be an adaptation consequent to the atrophy of the pedicle.

The majority of the shells of Paeckelmannia in the Top Hosie shale have the dorsal valve uppermost. It is of course possible that the pedicle was functional in these immature animals but there is no evidence to support this suggestion. The obvious immaturity of the shells again indicates an unfavourable bottom environment into which young animals were /

were introduced, but nevertheless an environment which was able to support limited growth. The majority of shells of Paeckelmannia polita are located in the sediment with the dorsal valves uppermost but it does not necessarily follow that this was the position most favoured by the animal for life.

Productus

55 shells, valves and fragments of Productus were collected from the shale, comprising 29 dorsal valves, 13 ventral valves, 9 shells and 4 unassigned fragments. As has been previously noted, it has not been possible in all cases to assign the specimens to their species but the more complete specimens can be referred to Productus (Productus) concinnus. The presence of valves and fragments indicates currents sufficiently strong to separate the valves of the shells. The selective nature of these currents is indicated by dorsal valves occurring much more frequently than ventral valves (cf. Nuculopsis gibbosa).

6 of the 9 shells are located in the sediment with the ventral valve below, 2 with the dorsal valve below. The position of the remaining shell is unknown. Neither of the 2 shells (width about 20 mm.) with the dorsal valve below have spines longer than 2 mm., but of the 6 shells, dorsal valve uppermost /

uppermost, one (No. 375) estimated to be 24 mm. in width has spines at least 28 mm. in length and 2 have spines at least 8 mm. in length. The spines of the other 3 shells with the ventral valve below were not seen. The conclusion drawn is that those shells with the long spines attached are in the position of growth of the animal (i.e. ventral valve below). Those shells without spines have been moved into their present position, the long fragile spines being broken off near the spine-bases during movement.

Muir-Wood (1928) discussed in some detail the mode of life of Productus and observed that the general opinion with regard to the orientation of a shell of Productus during life has been that the dorsal valve, the smaller valve, was uppermost. She noted, however, that in specimens of the semireticulatus group, to which P. concinnus belongs, the ventral valve with projecting spines is usually uppermost. If there had been a free-swimming distribution of productid larvae as is usual among living brachiopods (Helmcke, 1939, pp. 209-211), then the young shells would have descended eventually on to the sea-floor with the convex ventral valve downwards. If the pedicle were functional during the early stages of growth, as Muir-Wood stated (1928, p. 24), it would have erected the shell but when the pedicle atrophied in the later stages of growth, the /

the shell - depending on such factors as weight, shape, currents &c. - would have fallen over and rested on one of the valves. The animal without power of movement, remained in the new position unless shifted by currents. Survival and further growth depended on the ability of the animal to adapt itself to its environment.

Long complete spines attached to a productid shell must surely indicate that the position in which the shell is found was the position during growth of the spines (i.e. position of life of the animal), since the possibility of a shell after the death of the animal being swept into that position without the fragile spines being unbroken, is most unlikely. Both positions are known to occur with complete spines attached to the shell and there is no reason why, under appropriate conditions, the animal could not live in either position.

Lamellibranchia

Nuculopsis

Drew (1901) in his study of the life-history of Nucula delphinodonta, stated (pp. 313-314): "N. delphinodonta is a small form, seldom growing to be more than 4 mm. in length, and ..... lives below low-tide mark. Individuals may be found living under very different conditions; in inlets and protected places, and exposed to the open sea, and from near low-tide mark to a depth of several fathoms. The principal habitat, however, is in the shallow inlets and near the heads of sounds, where the bottom is composed of fine mud, mixed with some sand, broken shells, and some vegetable matter ..... in water which at low tide is from one to three fathoms deep ..... The average tide of about ten feet ..... keeps the water very pure over a comparatively foul bottom".

The food consisted mainly of diatoms, but individuals of algae, ostracods, foraminifers, small lamellibranchs and gastropods, were occasionally found in the stomachs of preserved specimens.

The embryos are contained in an external brood-sac attached to the posterior end of the shell. In N. delphinodonta there is no free-swimming existence, the embryos transferring /

transferring directly from the protected sac to the bottom environment. Drew observed, however, that the embryos of N. proxima are free-swimming and have no brood-sac and he considered that the embryos of the ancestors of N. delphinodonta were free-swimming.

Contrary to the observations of earlier authors, Drew noted that the foot is used for burrowing, not creeping (i.e. in position of life the dorsi-ventral plane of the shell is near vertical to the bedding-plane of the sediment, with the dorsal edge uppermost). This view has since been confirmed by both Hirasaka (1927) and Yonge (1939).

Hirasaka investigated the feeding habits of three species of Nucula, namely N. nucleus, N. radiata, and N. nitida The specimens were dredged from a depth of 20 to 30 fathoms, in mud, off Plymouth, England. All three species burrowed immediately when put in a glass dish with mud on the bottom.

Yonge's description of the habits of Nucula may be quoted (p. 81): "Three species of Nucula were examined at Plymouth, N. hanleyi, N. nucleus, and N. turgida. Of these the first and largest occurs on shell gravel, the second on a bottom of thick muddy sand mixed with gravel, and the last and smallest on fine muddy sand or silt ..... The habits of N. nucleus were studied, an adequate supply of bottom material being /

being available. When placed on this the animal quickly extruded the foot which first appears ventrally, then extends outwards and forwards [anteriorly] ..... At the same time the two halves of the sole open out widely and are finally withdrawn between the anterior margins of the shell valves, when they come together again. Usually after a few ineffective attempts the foot succeeds in extending under the mud. This is gripped by the two halves of the sole when these open out and the animal is able to erect itself and is pulled down and forward. In some cases burrowing follows immediately, in others the animal moves about on the surface for some time, forming a groove in the mud. But burrowing, ~~however~~, always eventually occurs. The foot is repeatedly extended obliquely downwards and, with the co-operation of the pedal retractors, the animal is pulled under the mud. The hinder margin of the shell remains visible when the umbo is buried, but finally mud falls in and obliterates the pit behind the shell. When completely buried the animals cease moving. They then lie with the anterior [antero-dorsal] margin of the shell parallel to the surface of the sub-stratum and covered to a depth of about 1 mm. An opening to the exterior is then remade at the posterior end, in the first place by the sudden contraction of the adductors which forces water out through the posterior end of /

of the mantle aperture. The opening so made is about 0.5 mm. in diameter, rounded if edged with mud, irregular if with gravel. A mound composed largely of faecal pellets is gradually built up around the margin. There are no siphons and no portion of the palps was ever observed. The statement of Drew (1901) that Nucula feeds below the surface was confirmed".

The animal feeds by extracting nutriment from the bottom sediment.

Moore (1931) described the faecal pellets in the British species of Nucula (N. nitida, tenuis, nucleus, radiata) as being voided in the form of a long rod of compact mud which broke into lengths of 0.2 mm. to 1.0 mm. or more, the breadth being about 0.15 mm. The intestine showed thickened longitudinal ridges which formed grooves on the smooth surface of the pellet, their number and position varying according to the species. The pellets were sufficiently firm to allow identification in muds laid down on the bottom for over 50 years. These pellets may possibly be preserved in older strata.

162 specimens of Nuculopsis gibbosa were collected from the Top Hosie shale comprising 66 shells and 96 valves. No fragments were found. Estimating a valve as one-half of a /

a shell, 58 per cent. are complete shells. 87 (91 per cent.) valves and 50 (76 per cent.) shells are parallel to the bedding-planes (i.e. dorsi-ventral plane parallel to the bedding-planes) and the remaining 9 per cent. of the valves and 24 per cent. of the shells are oblique or vertical to the bedding-planes.

The individual valves of the shells have been disarticulated by currents. There has been no preferential selection of either the right or left valves since there are approximately equal numbers of both (49 right, 47 left). This is to be expected since Nuculopsis is equivalve.

Convex valves settle in still water concave upwards. Bottom currents, however, if sufficiently strong, will overturn the valves into the more stable position of convex upwards (see Shrock, 1948, p. 316). Valves of Nuculopsis are distributed throughout the 20 inches of shale above the Posidonia-band, 47 in the position of convex upwards and 35 concave upwards. Both positions occur throughout the 20 inches of shale and both positions can occur on one bedding-plane. It is suggested that the valves were transported to the area by being swept along the sea-floor by currents. The variable currents were not completely selective in the orientation of the /

the valves with the result that more valves are in the position of convex upwards. Further evidence to support the presence of bottom currents is found in the parallel orientation of minute calcareous fibres on certain bedding-planes.

Only two shells were found with their valves gaping. The rest (97 per cent) of the shells have closed valves. There are three possible explanations, taken either singly or in combination, to account for the very high percentage of closed shells. Firstly, the taxodont hinge combined with the weak internal ligament hindered easy opening (the ligament of the modern Nucula is very weak); secondly, the shells may have been surrounded by sediment which prevented an outwards movement of the valves, while the ligament was still capable of opening the valves; thirdly, a slight gape of a shell lying parallel to the sediment would be closed by the pressure of the compacting sediment. In fact many of the closed bivalves are crushed in spite of the strength of the thick shelly material.

Shells, vertical or oblique to the bedding-planes, are proportionately almost three times as numerous as the valves in the same position (24 per cent/9 per cent). This difference may be accounted for by the different shapes of a shell and a valve; a biconvex shell because of its sub-ovoid form /

form being less prone to lie parallel to the bedding-plane than a curved plate of a valve. There is, however, another possible explanation. Because the umbonal region is the heaviest part of a valve it is to be expected that more vertical valves will lie with the umbonal region to the bottom than to the top. There are 9 valves, vertical or oblique to the bedding-planes of the sediment, 6 (67 per cent) with the umbonal region to the bottom and 3 (33 per cent) with the umbonal region uppermost. A somewhat similar proportion might be expected with regard to the shells but, of the 16 oblique or vertical shells, 6 (38 per cent) lie with the umbones to the bottom and 8 (50 per cent) with the umbones uppermost. Of the remaining two shells one has the posterior end uppermost, and the position of the other with respect to the sediment is unknown. The figures show an unduly high percentage of shells with the umbones uppermost and suggest that, in addition to shells of dead animals washed into a vertical position with the umbones either to the bottom or top, there were animals living in a vertical position with the umbonal region uppermost. These shells remained undisturbed in this position after the deaths of the animals contained therein. The vertical shells may thus consist of both shells swept into a vertical position after /

after death, and shells unaffected by currents, preserved in position of life (i.e. umbones and dorsal edge uppermost).

The shells, parallel to the bedding-planes of the shale, are (a) the remains of dead animals falling or being swept over on to one side from a vertical nestling position in the mud, or (b) shells transported some distance before burial.

Neo- and palaeo-ecological data indicate that Nuculopsis gibbosa lived on the sea-floor in a vertical position perhaps best described as nestling. There may have been a free-swimming larval stage during which distribution was effected. The area examined is considered to lie within a much larger area which was populated by Nuculopsis and swept by variable bottom currents, at times sufficiently strong to separate some shells into their component valves and to transport both shells and valves from their habitat. Only 5 per cent of the shells can be considered to be in their original position of life. The absence of fragments is a reflection both of the strength of the valves and the amount of movement. Larval shells and intermediate forms are abundant and are to be expected in a normal population.

Posidonia /

Posidonia and Pseudamussium

Yonge (1936) noted that the swimming habit among the lamellibranchs is confined to members of the Pectinacea, the Pectinidae, Amussiidae and Limidae, except for the genus Solenomya. Swimming is carried out by movements of the shell valves and has been made possible by comparatively minor modifications of the mantle, shell and adductor muscle.

Yonge considered that the monomyarian condition had evolved from byssally attached lamellibranchs in clear water near the surface - perhaps in the surf region of moving water. The assumption of the monomyarian condition necessitated an improvement in the cleansing mechanism to deal with sediment. After this improvement the animals extended their vertical range into deeper water where muddier conditions prevailed. Loss of the byssus followed, and with minor adjustments free-swimming forms evolved.

Dakin (1909) observed that Pecten had a world-wide distribution and that the habitat ranged from the littoral zone to about the 450 fathoms. P. maximus and operculatis (to the study of which the Memoir was devoted) are gregarious. Both species prefer a sand or gravel bottom but sometimes occur on mud. The most favourable conditions for the formation of a Pecten bed are a shelly bottom with a little mud at depths from

5 /

5-20 fathoms, although species occur sporadically in deeper water but not as communities.

After a free-swimming larval stage (shells about 0.2-0.3 mm. long (Jørgensen, 1946)) Pecten descends to the sea-floor and crawls by means of the foot. Subsequently some species (e.g. opercularis and irradians from the American coast) are attached by the byssus before assuming a free existence. It has been observed by various authors that Pecten normally lies on its right valve and if disturbed from that position will make efforts to return to it.

Pecten, according to Dakin, feeds largely on vegetable matter such as diatoms, fragments and spores of algae, together with the smaller micro-crustacea. Very often the shells are bored by a sponge and where the tubes enter the interior of the shell the mantle secretes nodules of a dark colour. The outer surface of the upper valve provides a good platform for such sessile animals as Balanus, Zoophytes, Serpula, &c.

Pecten, unlike Mytilus or Ostrea, lives only a short time when exposed to the air, since sea-water cannot be retained in the pallial cavity.

Valves /

Valves of Posidonia corrugata occur in great abundance in the bottom four inches of the two feet of shale. Nearly all the specimens are separate but unbroken valves, and only very occasionally does a shell occur. Most of the valves are less than 10 mm. in breadth although one specimen 24 mm. in breadth was found. Young valves about 1 mm. broad are abundant and occur associated with the larger valves. The valves lie parallel to the bedding-planes and the shales containing them are more fissile than the shales above.

The pectiniform valves and the edentulous hinge suggest a mode of life akin to that of living species of the Pectinacea. Posidonia corrugata was probably an active benthonic lamellibranch, the animals living as a gregarious community or communities during the period of deposition of the Posidonia-band. The animals lived on a substratum subject to currents capable of disarticulating the bivalved shells. The limited occurrence of shell fragments, however, suggests that the valves were not carried for any great distance.

90 per cent of the specimens of Pseudamusium? aff. ellipticum are single valves in a fair state of preservation. Only three specimens (shells) can be interpreted as having died where they are /

are now found. A mode of life for Pseudamusium? similar to that of living Pectens is postulated.

Sanguinolites

Sanguinolites is confined to Carboniferous strata. Its closest living comparable form is Solenomya which has been shown by various authorities (Pelseneer 1891, Stempell 1900) to be a primitive lamellibranch.

Morse (1913) noted that the genus Solenomya, represented by a few species, is widely distributed throughout the world at the present day. He examined living specimens of S. velum which had been found buried in 6-9 inches of sandy mud composing Round Flat, Duxbury Bay, Mass. The animal burrows by lying on its dorsal side, thrusting out its foot anteriorly and dorsally, thus lifting the anterior end and depressing the posterior end downwards into the mud. In this respect Morse observed that it differed from all other burrowing lamellibranchs, by burrowing posterior end downwards. S. borealis, collected from mud dredgings in 6-7 fathoms of water in Portland Harbour, Maine, was believed to behave in the same way, although Morse was not convinced of the fact that Solenomya burrowed posterior end downwards. Solenomya is also capable /

capable of swimming by opening and shutting its valves.

Yonge (1939) examined specimens of S. togata at Naples and observed that the animal occurs in shallow water in a bottom of fine muddy sand containing much flocculent organic matter. The animal erects itself by protuding its foot anteriorly into the mud, and then burrows into the mud diagonally with the anterior end downwards. He found difficulty in understanding Morse's statement that S. velum burrows posterior end downwards. Yonge observed that conditions in Solenomya are certainly very different from those in any other protobranch, or indeed any other lamellibranch. The genus appears to be unique in its ability to live for a great part of, if not all the time, without direct contact with the water above the substratum in which it burrows. On p. 132 he noted:- "All species of the Protobranchia are specialised for burrowing into and moving through a soft substratum. Different species are adapted for life in different types of bottom material. In Yoldia alone is burrowing habitually vertical and horizontal movement absent".

Yonge considered that the edentulous hinge is correlated with the need for swift closing movements of the valves, in order to remove the sediment from the mantle cavity, and that these movements cause Solenomya to swim.

Valves /

Valves and shells of Sanguinolites costellatus occur frequently in the 20 inches of shale above the Posidonia-band. 83 per cent of the 168 specimens found are fragments of valves. 24 complete shells (34 per cent)[1] were collected, all of which are closed and crushed. Only a few young forms of approximately 2 mm. in length were found.

The extreme fragility of the shell and the edentulous nature of the hinge explain the high proportion of fragments and the low proportion of shells. The shells and valves would be easily transported because of their low weight/area ratio.

Since most of the specimens are fragmentary, it is difficult to investigate the mode of life of Sanguinolites. Five of the 24 shells are vertical to the bedding-planes with the dorsum uppermost; one is in a reversed position, venter uppermost; the orientation of the shale fragments containing two vertical shells is unknown; the remainder (16) are parallel to the bedding-planes of the sediment. There are no large fragments of valves vertical to the sediment, yet eight shells are so placed, five with the dorsum uppermost and only one with /

[1] 34 per cent estimating a fragment of a valve as 1/3 of a shell. Fragments totalling between 1/2 valve and one valve in area were recorded as one fragment.

with the venter uppermost. These five shells are regarded as being in position of life. The inverted shell was probably swept into that position by currents (cf. Nuculopsis gibbosa, p. 114).

The burrowing habit is universal amongst the Protobranchia at the present day and there is little reason to doubt that Sanguinolites, like its present day descendant Solenomya, was a mud-burrower. Most of the shells of Sanguinolites were swept from their habitat and broken during transportation to their present position in the shale.

Gastropoda

The ratio of gastropod microshells to their macroshells is high. With the exception of Pseudozygopleura and possibly the Pleurotomariid? included in the Turbinate group, gradations between the smaller and larger shells occur. None of the genera present in the shale are in existence to-day and the available neoecological information concerning the living representatives of their families can be taken only as a possible indication of the mode of life of these Carboniferous gastropods.

Pseudozygopleura

The Pseudozygopleuras are unique among the gastropod microfauna since their range of variation in size, measured in terms of number of whorls developed, is only one whorl. Most of the other species of gastropods present in the microfauna show gradations, with a range of variation in size of several whorls, from the nuclei to the larger shells of the macrofauna.

General reasons for regarding the gastropod nuclei as immature have already been discussed (p. 59). Further evidence /

evidence to support the conclusion that the nuclei of Pseudozygopleura are larvae is, firstly, that the nuclei (2-3 whorls) are almost identical with the nuclear whorls of adult gastropods of some ten whorls in size; secondly, the size of the nuclei corresponds with that of larvae of living species of the Pyramidellidae to which family Zygopleura is referred (Zittel, 1913), if doubtfully.

Thorson (1946) has written a detailed report on the reproduction and larval development of marine-bottom invertebrates. He observes (p. 243) that members of the Pyramidellidae spawn egg-ribbons or cocoons normally attached to a substratum. After hatching from the egg-masses, the larvae either remain on the bottom or assume a pelagic existence for a variable period - a matter of some weeks, but figures for Pyramidellidae are not given - before metamorphosis to a bottom habitat. It is interesting to note that shell size at hatching (p. 430) may be either constant or variable, depending on the type of development, and that metamorphosis from plankton to benthos takes place at a shell size of some two whorls.

Granted that the nuclei are larvae and incapable of reproduction, then the absence of adults, the absence of intermediate forms, and the small variation in size require explanation. /

explanation. No adult Pseudozygopleuras are present in the shale. Therefore, the breeding-ground must have been elsewhere and the nuclei were transported into the area from the breeding-grounds. A probable explanation for the absence of intermediate forms is that the nuclei were transported sufficiently far from the breeding-ground to separate them from all larger forms. The most effective method of wide distribution is as plankton. On metamorphosis the larvae encountered a lethal bottom environment and died.

Other Gastropods

Yonge (1947), from a consideration of the structures of the pallial organs in the gastropods, postulates that the fossil planospiral shells with a median slit (Bellerophontids) were confined to a hard substratum since they had no mechanism capable of dealing with the quantities of fine sediment that would have been encountered had their environment been mud. It is difficult to reconcile this deduction with the continued presence of the two bellerophontids Euphemites urei and Bucaniopsis striatus in the shale as young and adults. Yonge's theory would necessitate the occurrence of a ledge or other /

other suitable substratum tolerably free from muddy sediment and at no great distance from the locality where the shells are now found; a ledge which must have been swept by currents strong enough to transport the shells to their present position.

Further, Yonge observes (p. 444) that all living aspidobranchs crawl on a hard substratum. All the species of gastropods in the shale are classified in this group and the question immediately arises:- Did the fossil aspidobranchs have a mode of life comparable with their living descendants? On the one hand, there is the presence of the fossils in what was a muddy environment and on the other hand, the statement that all modern aspidobranchs are confined to a hard substratum.

Admittedly the dead gastropods probably underwent transportation by currents since there is ample evidence from separated bivalves and fragments of other fossils that currents swept the area during the deposition of the mud.

Acceptance of the concept of a mud-free bottom habitat for the fossil aspidobranchs necessitates the presence of a hard substratum which might well have been an erosion surface towards a shore-line, swept by variable currents necessary to transport shells of different sizes to the same locality. The breeding-ground of Pseudozygopleura, however, must have been remote /

remote from the main gastropod colonies in an ecological niche where the agents of transportation were unable to bring adult shells into the area examined.

Distribution of the larval shells could have been effected during a pelagic larval life. Thorson (1946, p. 431) states that about 66 per cent of the prosobranchs (to which group the aspidobranchs belong) he had examined have a pelagic larval life. The small shells (including Bellerophontids, Glabrocingulum, Soleniscus, ?Naticopsis) however, show such a wide variation in size above the Posidonia-band that it is evident that further growth took place after the shells had acquired bottom habitat. Did this growth take place on a hard or soft (i.e. muddy) bottom?

The neo- and palaeo-ecological evidence is conflicting, but the abundance of gastropod shells indicates that if they were not natives of the muddy bottom, their breeding-grounds were not far distant.

Nautiloids

Divergent views have been and still are held as to the mode of life of nautiloids. Ruedemann (1921) advanced evidence to show that Orthoceras and Cyrtoceras were benthonic forms crawling on the sea-floor. Trueman (1940) suggested that the straight nautiloids were tilted up by their buoyant early chambers so that the aperture was pointed downwards. Flower (1942, p. 40) concluded from detailed observations that the nautiloids "were facies organisms, benthonic to a very great extent, and that they were much more restricted by environmental conditions than their potentially nektonic gas-filled shells would lead a casual observer to believe". Orthoceracones frequently rested and crawled along the bottom, yet he noted that certain shells have been found resting in a vertical position with the apex elevated, indicating that they had contained gas in their camerae and may have floated. Miller and Youngquist (1949) observed that nautiloids were almost certainly quite buoyant and may have floated a considerable distance before coming to rest.

Perhaps the most interesting point about the nautiloids in the shale is the relatively high proportion of genera to individuals. No other group of fossils is relatively so diversiform. /

diversiform. With the exception of Loxoceras? which occurs in fair abundance in, and is confined to, the Posidonia-band, the specimens were distributed throughout the two feet of shale spasmodically, mostly as fragments but occasionally as complete shells, parallel to the bedding-planes.

Transportation of the fragments undoubtedly took place, and the occurrence of few but varied specimens suggests that these nautiloids did not exist as small gregarious communities but lived dispersed over a wide area. The facts support a pelagic mode of life, with the one exception of Pseudorthoceras. The weight and thickness of the cameral deposits in Pseudorthoceras would seem to preclude a floating existence and indicate rather, a bottom habitat. Loxoceras? on the other hand has such a thin shell and such relatively large camerae that there seems to be little doubt that the animal was capable of buoyancy.

Scaphopoda

Coleolus

At the present day the Scaphopoda comprise only three genera. Yonge (1937) described the mode of life of one species - Dentalium entalis. This animal occurs in vast numbers on muddy gravel bottoms at moderate depths, in the sea near Bergen Fjord. The animal burrows by means of a tri-lobed foot and rests in an oblique position in the sediment with some two-thirds of the shell buried. The posterior aperture of the mantle communicates with the exterior, through the posterior terminal opening of the shell. In some cases when the posterior aperture is blocked, a lateral opening occurs about 1 mm from the posterior end. This opening was presumed to be due to the mantle dissolving the calcium carbonate of the shell.

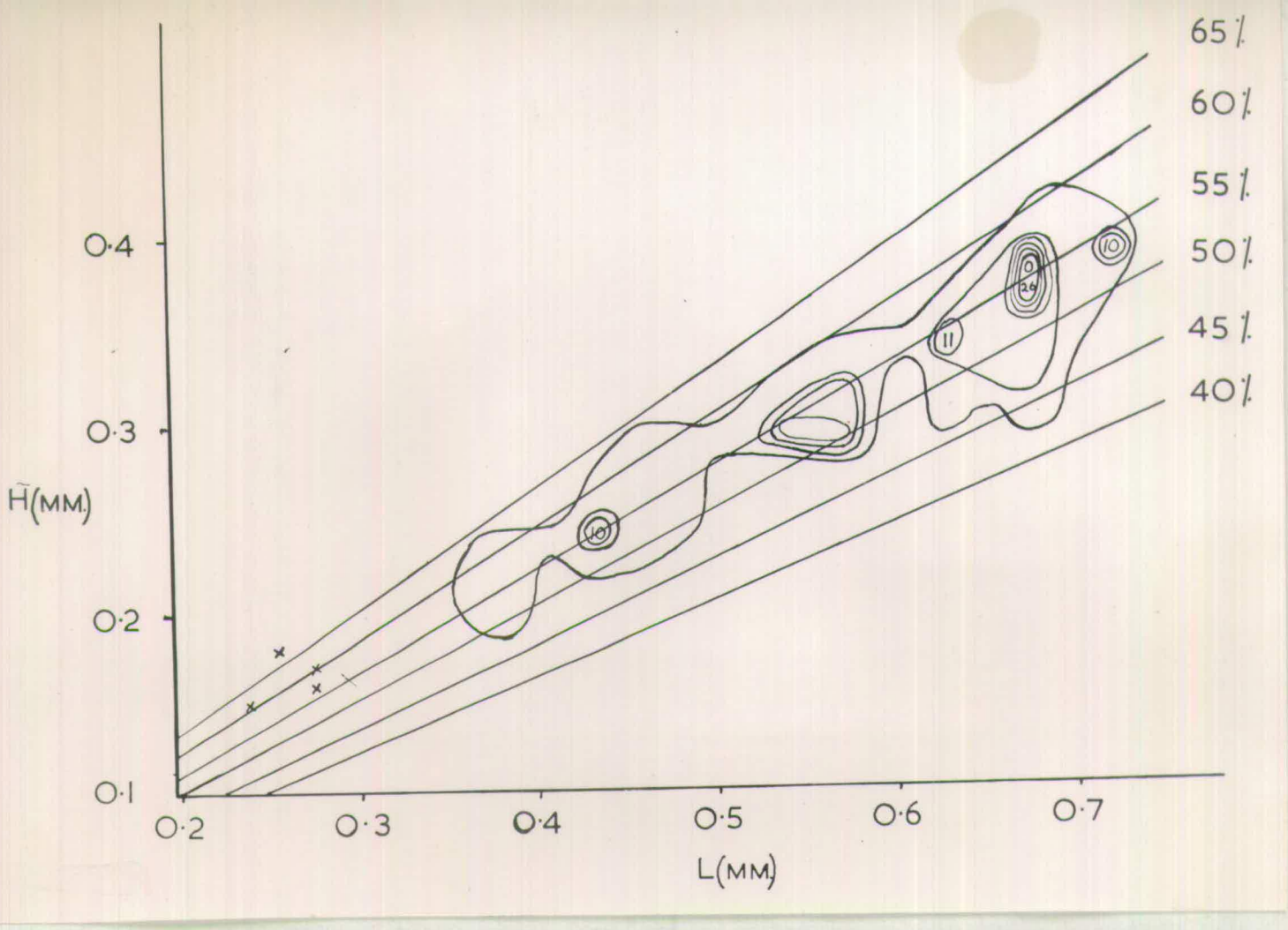
Only one complete shell of Coleolus was found. This shell 31 mm. long lies parallel to the bedding-plane. All the other specimens of Coleolus occur among the extracted microfossils. The clean sharp edges of many of the fragments indicate that many of the tubes were broken during the separation of the microfossils and not during the original deposition, so that it is possible that Coleolus lived in the area where it is now found. Neo-ecological data suggest that Coleolus was a benthonic form, burrowing in the mud.

Ostracoda

Healdia

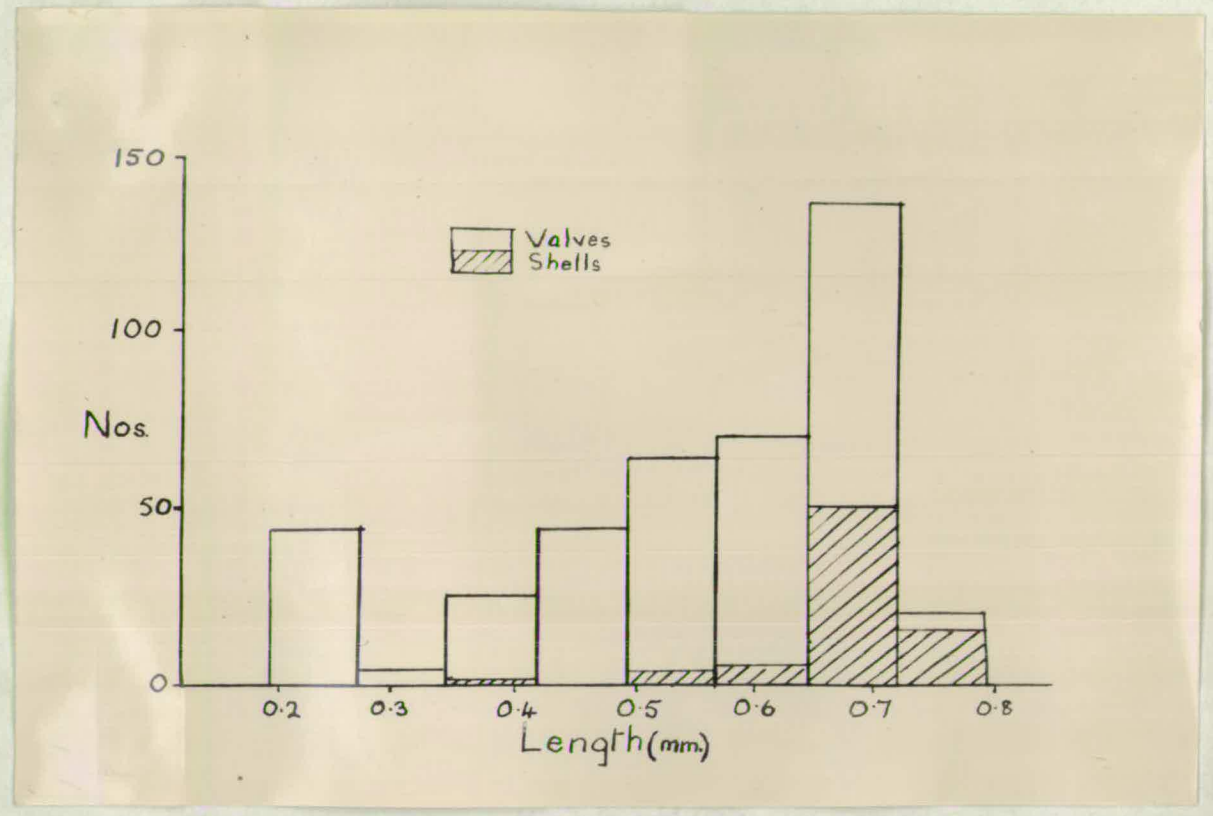
Healdia cuneola next to Glomospirella is the most abundant microfossil in the shale. However, by reason of each ostracod secreting several carapaces during its ontogeny, the number of animals producing the carapaces and valves is considerably less than the number of specimens, and at a rough estimate is $\frac{1}{8}$ of the number of specimens recorded.

LeRoy (1945) observed that there had been little systematic investigation of moult-stages in ostracods. He traced the development of various characters in what he considered to be seven moult-stages of Cythereis simiensis, a Pliocene species, and recorded that the sixth and seventh moults were the same length. Cooper, later in the same year, noted that nine moult-stages are known to occur in living ostracods. By means of a statistical analysis of 43 specimens of the Pennsylvanian species Ectodemites plummeri, he discovered nine moult-stages, observing that the difference in size (length and height) between successive moults increased at each moult with only one exception. He also found several paired carapaces - carapaces with the previous, moulted carapace attached dorsally, hinge upon hinge.



TEXT-FIG. 7. Density distribution of dots representing the H/L ratio of the valves and shells of H. cuneola. Contours bound areas with a density distribution of dots equal to or greater than 3, 7, 10, 15, 20, 25 and 30, per 50 sq. mm.

N.B. The four specimens represented by crosses in this graph were picked from a sample of the 200-mesh fraction. In the histogram (Text-fig. 8) the estimate of the total (4 x 12 = 48) has been used.



TEXT-FIG. 8. Histogram showing the distribution of the shells and valves of H. cuneola according to length.

331 specimens (40 carapaces - bivalved shells - and 291 valves) of Healdia cuneola from Slide No. 560 proved suitable for the measurement of height (H) and length (L). The graph[1] (Text-fig. 7, p. 132) illustrating the relation between H and L shows four distinct clusters enclosed by the outermost contour. These four clusters are considered to represent successive moult-stages of H. cuneola. Smaller moults also occur, necessarily limited in minimum size by the size of the nauplius.

The frequency distribution of length (L) is illustrated by Text-fig. 8, p. 133.

Provided that the ontogeny of an ostracod consists of a series of moults, then in a community of ostracods there should be a maximum number of valves from the first moult, the numbers decreasing throughout successive moults to a minimum in the last moult, since not all of the ostracods will reach maturity. The specimens of H. cuneola measured do not show this mathematical distribution, rather the reverse with the greater number of individuals among the larger not the smaller valves. There are three reasons which when taken in conjunction give a probable explanation of this anomaly.

Firstly /

[1]This density-distribution diagram has been devised to enable two variables and the quantitative distribution of the dots in the resultant scatter-diagram to be plotted on one graph, instead of employing a histogram or frequency polygon with one variable only plotted against frequency.

Firstly, the paucity of specimens of about 0.3 mm. L, 0.2 mm. H, is at least partly due to the breakage of specimens during passage through the 100-mesh sieve; secondly, the relative infrequency of the smaller valves may be due to a scattering action by currents or movement by the animals themselves The third explanation is directly concerned with the occurrence of the large number of valves and carapaces of about 0.68 mm. L In the last four class groupings (between 0.5 mm. and 0.8 mm. L of the histogram, the carapaces (estimated as two valves) constitute 6, 8, 38, and 76 per cent in that order, of the total number of valves in each group. The author considers that these carapaces are mostly the remains of dead ostracods whereas the valves are chiefly the remains of moulted carapaces

Ostracod valves are attached dorsally by a ligament and centrally by adductor muscles. The two valves cast off during moulting are held together by the ligament only. The two valves containing a dead animal are joined by both the ligament and the body until the decomposition or removal of the soft parts. The latter union is thus stronger than the former. A priori, carapaces which contained dead animals are more likely to be found intact than moulted carapaces. Apropos of ostracod ligaments it may be noted that Sohn (1949) observed that the hinge-structures of Palaeozoic ostracods did not /

not always dovetail, and he postulated that the groove and flange elements [present in Healdia] composing the hinge-structures of many Palaeozoic ostracods served partly as a fulcrum and partly to strengthen the attachment of the ligament to the valve.

Further evidence to support the view that the bivalved carapaces are the remains of dead ostracods is, firstly, the development of pyrite in the carapaces and not in the valves. Myers (1942) discussed the occurrence of pyrite in the tests of foraminifera from Plymouth Sound, England. He showed that the foraminifera had been buried by sediment so deeply that they had been unable to escape. The animals died and the protoplasmic contents were removed by bacterial decomposition, producing hydrogen sulphide which reacted with soluble iron salts in the water to produce pyrite inside the tests. A similar process is considered to have occurred in the dead ostracods: hence the occurrence of pyrite in the carapaces and not in the valves. Secondly, all the carapaces are closed, not gaping, and moulted carapaces must, originally at least, have gaped to allow the exist of the animals.

In Text-fig. 7 the largest cluster of specimens, 0.62 - 0.73 mm. L, contains some 35 carapaces and 120 separate valves. If, as has been indicated, the valves are chiefly the /

the remains of moulted carapaces and the bivalved carapaces mostly the remains of dead ostracods, then associated in one cluster are some 60 moulted carapaces (120 valves) and 35 dead animals. It is considered that this association is the consequence of the ostracods moulting and then secreting a carapace of about the same size as the moult. Most of the animals then died without further moulting.

The presence of the mode at the last cluster is thus interpreted as being due to the association of moults with dead ostracods which had grown carapaces about the same size as their last moult.

The ecology of living ostracods related to Healdia may be briefly discussed. Sars (1922) noted that the antennae of ostracods belonging to the sub-family Bairdiinae are not adapted for swimming [but used for crawling?]. Tressler (1941) in an account of ostracods obtained from North Atlantic deep-sea cores, outlined the ecology of ostracods. He observed that the great majority are strictly bottom-dwellers and that many are quite incapable of swimming. In some genera the females are confined to the bottom but the males are active swimmers. Bairdia - to which Healdia is closely related - is a bottom-dwelling form, widely distributed at the present time in tropical and southern waters. Tressler found shells referable /

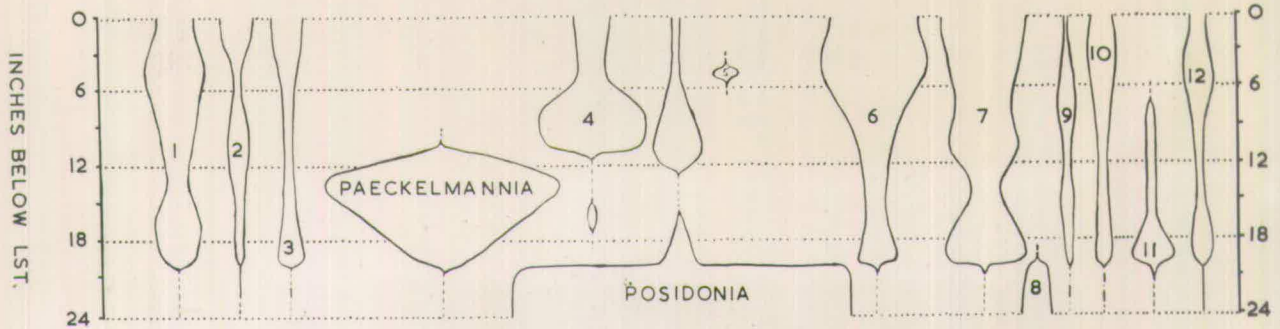
referable to this genus in cores taken from the sea-floor at depths of 1280-3230 metres.

It is concluded from the evidence presented that Healdia cuneola was a benthonic form probably crawling in the mud. Moreover, the presence of six, perhaps seven moult-stages, suggests that the species was indigenous to the area, in spite of the sorting that has taken place. After the last moult stage the ostracod almost ceased to grow, merely secreting a carapace of about the same size as the previous moult. This retardation of growth may indicate the onset of maturity.

Conodonts

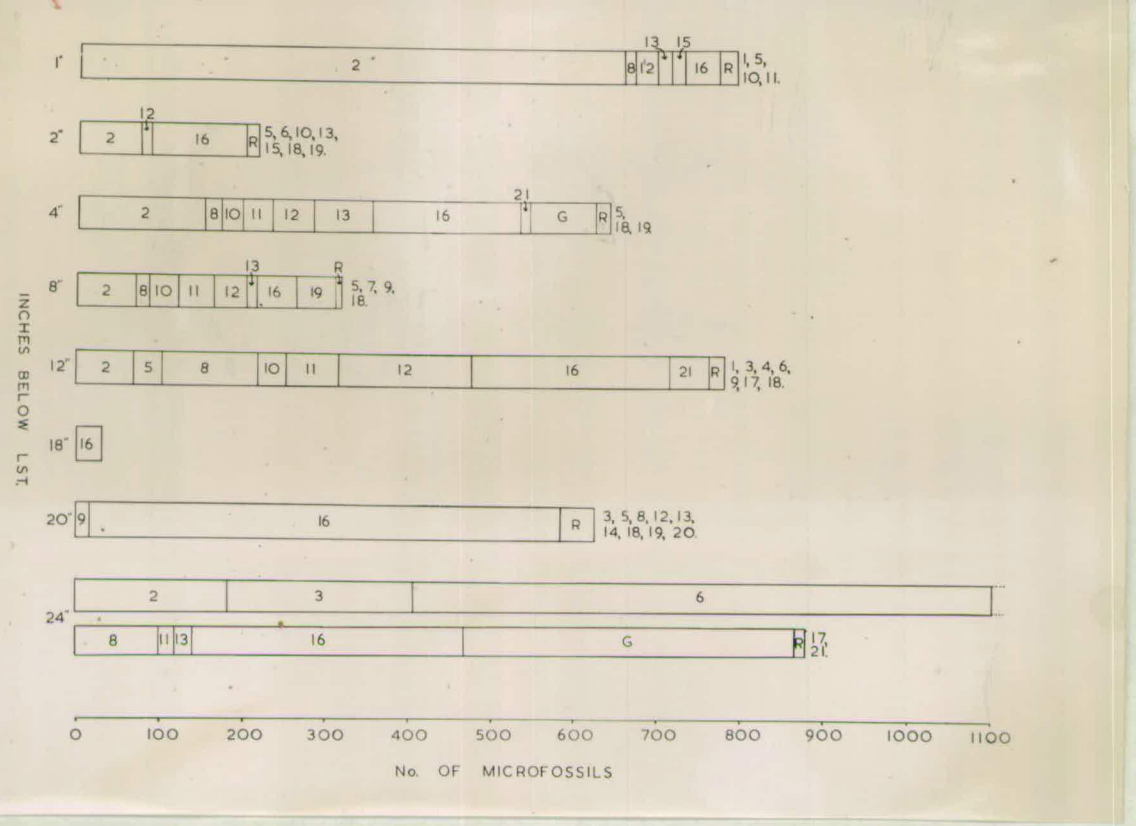
Conflicting views are held as to the affinities and mode of life of conodonts. Schmidt (1935) for instance considered that conodont teeth were related to the branchial apparatus of Gemuendina-like fish. DuBois (1943) related conodonts to the Annelida. Specimens he collected seemed to represent pharyngeal and buccal structures and he deduced that the animal which bore these teeth was an elongate worm, seldom more than 3 mm. in width, with a length of 3 cms. and probably 5 cms. or more. Ellison (1944) reviewed the literature on the palaeoecology of conodonts. The occurrence of conodonts in all kinds of sediments suggested to him that the animals were free swimmers and possibly pelagic.

The occurrence of conodonts in the Top Hosie shale, apart from the value of associations, throws no further light on the problem.



TEXT-FIG. 9. The relative abundance and distribution of macrofossils in the two feet of shale below the Top Hosie Limestone, in three-inch groupings.

(1) Lingula
(2) Productus
(3) Camarotoechia
(4) Pseudamusium?
(5) Actinopteria
(6) Nuculopsis
(7) Sanguinolites
(8) Loxoceras?
(9) Nautiloids
(10) Bucaniopsis and Euphemites
(11) Glabrocingulum
(12) Other macrofossils



TEXT-FIG. 10. The abundance and distribution of microfossils in eight 10 gram samples of shale.

(1) Girvanella?
(2) Glomospirella
(3) Hyperaminna
(4) Athyris
(5) Nuculopsis
(6) Posidonia
(7) Sanguinolites
(8) Bellerophontids
(9) Glabrocingulum
(10) Naticopsis?
(11) Pseudozygopleura
(12) Soleniscus
(13) Coleolus
(14) Amphissites?
(15) Bairdia?
(16) Healdia
(17) Cavusgnathus
(18) Gnathodus
(19) Hindeodella
(20) Scolecodont
(21) Crinoid ossicles
G Unidentified gastropods
R Remainder

(iii) Synecology of the fossils

Text-figs. 9 and 10 respectively illustrate the variation in the relative abundance of the major macrofossils occurring in the two feet of shale, and the numbers of, and the variation in, the microfossils from 10 gram samples of the shale, taken at selected horizons. The assemblage has been divided into macrofossils and microfossils as a result of the different methods employed in collecting. In the ensuing discussion the two groups, wherever possible, are treated together.

The Posidonia-band, at least four inches in thickness forms the base of the two feet of shale and is crowded with small valves of Posidonia corrugata. The only other common macrofossil is Loxoceras? sp., although towards the top of the band the pleurotomariid Glabrocingulum armstrongi makes its first appearance. Microfauna is abundant and includes larvae of Posidonia corrugata, Bellerophontids, Pseudozygopleura, and indeterminable gastropods; the ostracod Healdia cuneola, the foraminifers Glomospirella and Hyperaminna, fragments of the scaphopod Coleolus aff. carbonarius, and a few conodonts.

The macrofossils undergo a remarkable change at about 20 inches[1]. At this horizon Loxoceras? sp. disappears and P. corrugata /

[1]Distance below the Top Hosie Limestone.

corrugata wanes rapidly. These two species are succeeded by a much more varied although less abundant fauna including amongst others the following species:- the brachiopods Lingula squamiformis, Productus concinnus, Camarotoechia pleurodon and Paeckelmannia polita, the lamellibranchs Nuculopsis gibbosa and Sanguinolites costellatus, and the bellerophontids Euphemites urei and Bucaniopsis striatus. Despite the almost complete change in the composition of the macrofossils, the composition of the microfossils is little affected. As might be expected, larvae of Posidonia corrugata become rare, but Healdia cuneola, Glomospirella, larvae of bellerophontids, Pseudozygopleura and Glabrocingulum armstrongi, fragments of Coleolus aff. carbonarius and conodonts remain. Common larval shells recognisable for the first time are Nuculopsis gibbosa and Soleniscus sp. Larval shells of certain other species occur infrequently. The qualitative composition of this assemblage of micro- and macrofossils remains fairly constant throughout the remaining twenty inches of shale with some variations in the relative abundance of certain species and minor additions to and subtractions from the composition of the assemblage.

Among the more prominent invasions are those of Healdia cuneola (20 inches), Paeckelmannia polita (18-12 inches) Posidonia corrugata closely followed by Pseudamusium? aff. ellipticum /

ellipticum (12-8 inches), Actinopteria persulcata (4 inches), and Glomospirella sp. immediately below the Top Hosie Limestone

Such is the distribution of the more abundant fossils in the shale. It is not the distribution of the communities of animals which lived on that floor of sedimentation, for as has previously been shown, many of the macrofossils were introduced into the area as fragments and incomplete shells, not as living animals.

Before proceeding with the discussion on communities, it may be advisable to restate collectively the various criteria used in this thesis to determine whether or not any given fossil once lived in the environment as now represented by the sediment in which it is entombed. In a marine environment populated by invertebrates these criteria are:-

In general (1) The ability of a species to invade an ecological niche (biotope), to thrive there, and to successively populate that niche (biotope).

In particular (2) Presence within a species of gradations from larval shells to adults.

(3) Position of fossils with regard to the sediment.

(4) Occurrence of whole shells or fragments.

Considered singly these criteria are rarely sufficient to prove whether or not a species was an indigene, but taken collectively they can often do so.

The /

The communities of animals can best be considered in two well-defined and contrasted sections, namely the communities of the Posidonia-band, and the communities in the stratum between that band and the limestone. It must be emphasised that the assemblages collected are only samples of successive communities determined by successive biotopes probably of wide areal extent, embracing within their boundaries the area examined.

McNair and Conacher (1913) observed that P. corrugata at certain horizons spread over large areas in great numbers. The Posidonia-band at the base of the two feet of shale must have been a shell-bed for a number of years, added to by the shells and valves of the dead animals which had lived on its surface. The occurrence of gradations from larvae to adults, and the unworn state and large number of fossils, lead to the conclusion that Posidonia corrugata was an indigene. Evidence from the successive moults of Healdia cuneola points to the same conclusion for this species. Neoecological data previously discussed (p. 138) suggest that Healdia was a bottom crawling form. Glomospirella too may have been an inhabitant of this biotope although there is no evidence, apart from numerical abundance, to support this hypothesis.

Undoubtedly the most singular associate of this bottom /

bottom community is the orthoceracone Loxoceras? sp. The occurrence of unbroken conchs in varying stages of growth strongly suggest that this animal was part of the community. The animal was probably capable of floating (p. 129) but may well have spent much of its life on the sea-floor. The species recurs under similar conditions in a Posidonia-band some four feet above the Top Hosie Limestone, although it should be recorded that Loxoceras? does not reappear with the small invasion of Posidonia corrugata at 12 inches. Apparently similar but not identical environmental conditions favoured both species.

It is significant that the larval shells from the Posidonia-band are smaller and exhibit less variation than at any other horizon in the shale, with the exception of those of Posidonia corrugata and the moults of Healdia cuneola. Bellerophontids and Pseudozygopleura are recognisable but there is a large crop of indeterminable gastropod larvae, some of which may belong to the genus Glabrocingulum; there are also turbinate nuclei perhaps referable to Soleniscus. Few or no adults of these species occur in the band and it is apparent that these small shells had a greater freedom of movement than their parent communities which lived outside the area examined and probably outside the biotope. These small shells probably drifted as pelagic larvae or as plankton since in general they correspond /

correspond with related, living, planktonic larvae. The larvae at the end of their pelagic existence encountered an unfavourable bottom environment and died. That environment, nevertheless, permitted the existence of Posidonia, Loxoceras?, Healdia, Glomospirella, and perhaps Hyperaminna and Coleolus. There is here clear evidence of a biotope determining and controlling its biocoenosis by selecting and eliminating the constituent species of the spatfall.

Very occasionally among the valves of Posidonia corrugata are to be found shells and fragments of a few of the species which were later to establish themselves in or nearer to the area. A fragment of Productus, four bellerophontids, a Cycloceras fragment, and a small Camarotoechia compose the total of other invertebrate specimens found among the nine hundred or so specimens of P. corrugata collected.

Within a vertical distance of half-an-inch of shale the character of the macrofauna changes completely. The shale becomes less fissile and there is a slight decrease in the amount of pyrite, which changes may be a direct result of the disappearance of Posidonia corrugata and can be correlated respectively with a reduction of platy material - valves - and of decaying protoplasm. The effects are evident, but the underlying causes of the disappearance of the Posidonia-community /

community are not apparent. These underlying causes, almost certainly environmental, resulting in the disappearance of the Posidonia-community, were not of a widespread catastrophic nature, since the composition of the microfossils is little affected. However, in the shale above the Posidonia-band, the adults of these microfossils are much more abundant, some appearing for the first time; the average size of the microfossils is increased, and more species grade from larvae to adults. Whatever conditions caused the disappearance of the Posidonia-community, these same conditions enabled bottom-dwelling forms from neighbouring biotopes to establish themselves in a previously uninhabitable ecological niche.

The new biotope was invaded by mud-burrowers including Lingula squamiformis, Nuculopsis gibbosa, Sanguinolites costellatus, and Coleolus aff. carbonarius, this last species occurring also in the Posidonia-band. Accompanying these burrowers are sessile and crawling animals living on the surface of the mud, such as Productus concinnus, Paeckelmannia polita, Camarotoechia pleurodon, and Healdia cuneola and Glomospirella sp.

In the twenty inches of shale between the Posidonia-band and the limestone, complete or partial gradations from spat to adults have been found in the following species:- Lingula squamiformis /

squamiformis, Paeckelmannia polita, Nuculopsis gibbosa, Pseudamusium? aff. ellipticum, Glabrocingulum armstrongi, Soleniscus, Healdia cuneola, and probably Euphemites urei and Bucaniopsis striatus.

Only one species can be proved conclusively to have lived in the mud. That species is Lingula squamiformis. It can therefore furnish valuable evidence as to the conditions obtaining during the deposition of the mud. Text-fig. 9 indicates a seemingly continuous distribution of Lingula from immediately above the P.-band to the limestone. This, however, is not necessarily so. The animal was capable of vertical movement in the mud by means of the pedicle. The range of movement was probably about four inches allowing for a vertical extension of the pedicle nine times the length of a shell 12 mm. long. Subsequent compaction halved the distance. It is therefore possible that there was a break in the continuity of Lingula-communities especially at the ironstone band (14-13 inches) where no shells of Lingula have been found; equally there is no evidence to disprove the continuity of Lingula-communities above the Posidonia-band.

The evidence that Nuculopsis gibbosa was indigenous to the area is satisfactory, but that of the other burrowers less so. Sanguinolites costellatus is to be found in position of /

of life only in one narrow band (20-18 inches) where shells of this species occur in a vertical position. Elsewhere in the shale, valves and fragments are common but shells are rare. This evidence, coupled with the paucity of larvae and smaller shells, becomes most conflicting when considered along with the abundance of the species and the ecological conclusions. The balance of evidence tends to support the view that S. costellatus was an indigene. Conclusions about Coleolus aff. carbonarius have already been drawn (p. 130).

Only occasionally among the animals believed to be sessile or crawling, can the actual mode of life be ascertained The specimens of Productus clearly show the effects of selection by currents, although a few shells found in position of life prove that an occasional individual survived in situ. Paeckelmannia polita is interesting because the shells are complete, although in most cases - if not all - immature. Indeed, some specimens appear to have been the shells of larvae and the indications are that during successive larval distributions the animals were brought into the area where they encountered an environment which, although not lethal, discouraged optimum development and perhaps reproduction. Eventually, larvae of Paeckelmannia polita failed to reach the area. There is no lithological change that can be correlated with the disappearance of this species.

With /

With the wane and disappearance of Paeckelmannia polita two other species came into prominence, namely, Posidonia corrugata and Pseudamusium? aff. ellipticum. Both occurrences are almost entirely of valves, not shells, the former species having smaller valves and being much less common than in the Posidonia-band. A modification in the environment, still favourable to certain basic species, encouraged the burst of Posidonia and Pseudamusium? - an instance of similar species occurring under similar conditions.

Actinopteria persulcata likewise is found only as scattered valves and fragments. The mode of occurrence of these three last mentioned species is in contrast to that of Paeckelmannia polita since they were introduced as valves and fragments and not as living animals.

Reference has already been made in the previous section (pp. 125-127) to the unsatisfactory state of knowledge regarding the habits of the fossil gastropods. Basing conclusions solely on palaeoecological evidence, most of the species would be accepted as natives, and yet neoecological evidence denies the possibility that those species lived in a muddy habitat. Pseudozygopleura spp. are the only species of gastropods which can be reasonably considered as foreign to the mud. The changed conditions which permitted the establishment of a new /

new fauna, including gastropods, above the Posidonia-band still proved lethal to species of this genus. As was noted on p. 127, if the gastropods "were not natives of the muddy bottom, their breeding-grounds were not far distant". It is worth while reflecting on the fact that the fauna of a rocky area will rarely be preserved in situ in geological formations. A common present day example is that of empty shells of Littorina and Purpura washed from rocky shore habitats on to sandy beaches and mud flats (e.g. Solway Firth).

The cephalopods, with the exception of Pseudorthoceras, cannot strictly be considered as part of the communities if they are accepted as being pelagic, but since they are so small a unit of the assemblage, their inclusion or exclusion does not fundamentally alter the characteristics of the communities.

Crinoids were not part of the communities examined, since the only fragments found are stem columnals whose microscopic size and porous nature would enable them to be carried far from their parent communities. Healdia cuneola excepted, there is no evidence for the inclusion of the true microfauna, the foraminifers and the conodonts, in the communities, apart from their abundance and continued presence in the shale.

(iv) Summary of Synecology

The fauna in the shale is dwarfed, that is to say that the largest shells of the various species are smaller than previously described shells of those species. It may be dangerous to consider as dwarfed those shells which are smaller than previously described specimens, which may not be typical of the species concerned; but since in almost every instance the shells from the shale are smaller, it is to be concluded that environmental conditions were unfavourable. It may be argued that sorting by currents alone was responsible. Sortin may explain some but by no means all of the dwarfed shells (e.g. Lingula). Shimer (1908) has discussed the various conditions which may result in dwarfing or immaturity. Among the more important factors listed are:- kind of sediment, chemical content of water (salinity, hydrogen sulphide, iron salts, &c.), temperature, and depth.

The macrofossils tend to be concentrated on certain bedding-planes in the shale with intervening unfossiliferous or poorly fossiliferous laminae. Such concentrations of fossils, many of which are fragmentary, are due to the winnowing action of scouring currents. The alternative explanation of the accumulation of shells through a lack of sedimentation is not acceptable in view of the fragmentary nature of the fossils

on /

on these planes. Some of the fossiliferous bedding-planes, however, are due simply to spatfall. Such examples are confined to the chonetid Paeckelmannia polita, fossils of which are complete, immature shells in varying stages of growth, lying on bedding-planes which infrequently contain other fossils. A theory of scouring is not tenable in such instances.

The analysis of the Posidonia-biotope is necessarily incomplete. The surface of the mud was swept by currents, and subsurface conditions were certainly anaerobic and conducive to the formation of hydrogen sulphide; but it is a matter of conjecture whether the surface of the mud, and the water immediately above, were also anaerobic, in view of the presence of bottom currents. Authigenic organic matter derived chiefly from the decay of the protoplasmic contents of the lamellibranchs, and allogenic organic matter at least in the form of a few plant fragments were contributed to the sediment. On the fringes of the Posidonia-biotope other biotopes supported animals many of whose young - but very occasionally, adults - were transported into the Posidonia-biotope.

The appearance of a new macrofauna above the Posidoni band is accompanied by slight changes in the lithology, pyrite decreasing and the shale becoming less fissile. Both changes are considered to be the direct consequences of the very marked decline /

decline in the abundance of Posidonia corrugata. The replacement of the thin-shelled Posidonia and Loxoceras? by thicker-shelled animals suggests that stronger currents may have been partly instrumental in the faunal change. It is emphasised that the change in the character of the macrofauna is not accompanied by an equivalent change in the microfauna. The active surface animals of the Posidonia-band were replaced by other surface species, both sessile and active. More fundamental to the character of the new communities is the appearance of burrowing invertebrates. Most of these species, both surface and burrowing, were washed out of the mud, perhaps during periodic storms, and redeposited, often as fragments. Blended with these fragments during periods of intense current activity, were fragments of shells apparently not indigenous to the biotope existing.

It is an interesting commentary on the habits of Lingula that this animal escaped from much of the denudation which removed other burrowers. Its ability to contract its pedicle, thereby effecting a rapid vertical descent, was undoubtedly a most important factor in its ability to survive. The other burrowers - Nuculopsis, Sanguinolites, Coleolus - were able to move downwards only by laborious digging with the foot, so that most of these animals could not escape from the frequent scouring of the sea-floor.

Throughout /

Throughout deposition numerous larvae descended on to the muddy substratum and many of them were probably redeposited after storms during which the surface layers of the sediment were scoured by strong currents. Larval waste, especially among gastropods, was high. Above the Posidonia-band the average size of the microshells increases and more species show complete or partial gradations from larval shells to adults. Environmental conditions were more favourable to these species than in the Posidonia-band, which had a highly selective environment. Larvae, although most important for the understanding of a community, are not so significant for the definition of the community as those species which survive to maturity. Larvae are not necessarily in harmony with the environment, whereas those animals in one biotope which survive to maturity, are.

Anaerobic conditions prevailed in the bottom waters during periods of quiescence. The ironstone nodules and iron pyrites suggest penecontemporaneous bacterial activity during deposition. Life on the site with the exception of bacteria, was almost non-existent during the formation of the ironstone band (14-13 inches).

The /

The shale is a consolidated mud-flat probably of subtidal[1] (low tide - 50 metres) or perhaps of sublittoral[1] (50 metres - 200 metres) origin. This mud-flat during its formation supported a limited infauna which consisted principally of burrowers but also included sessile and motile animals The relative proportions of these three groups varied with the varying environmental controls so that in the basal four inches of shale, for example, only the fossils of motile animals occur. The surface of the flat was periodically scoured by strong currents concentrating shells previously entombed and introducing fragments of species believed to be foreign to that habitat.

(v)

[1] After the classification of marine environments adopted by the Committee on a treatise on Marine Ecology and Paleoecology, Rep. No. 9, 1949, Nat. Res. Council, Wash.

(v) The Concept of Communities

Petersen (1918) firmly established the concept of marine bottom communities. These communities consist of certain commonly recurring combinations of animals which are confined to certain areas of the sea-floor. Although his concept of communities was apparently not intended to be synonymous with that of the more ecological term 'biocoenosis', his work has been criticised on this count.

Jones (1950) has shown that, basically, there are two lines of approach to the subject - the first considers control of the community by the physical environment, the second contro by biological factors. The two approaches are not so antagonistic as might appear at first sight. The former is the more fundamental, since life is ultimately dependent on the physical factors of the environment, yet the latter recognises the importance of the biological factors which, after all, constitute an important part of most environments. Jones has advocated that the physical environments of zoogeographical regions should first be investigated, and then followed by a description of the communities capable of living in such environments.

Fossil communities and their environments have often been /

been described under the general heading of 'facies'. Recently, in the U.S.A., a number of new geological terms have been proposed to deal with the ever widening field of research on facies. These terms could be used in palaeoecology and therefore merit discussion. From the simple word 'facies' - commonly used to denote the sum of the lithological and palaeontological characters of a rock unit - there have arisen such words defined by Moore (1949, p. 32) as 'lithofacies'.- the rock record of any sedimentary environment, including both physical and organic characters; 'physiofacies' (p. 17) - the total inorganic characteristics of a sedimentary rock; 'biofacies' (p. 17) - the total biological characteristics of a sedimentary deposit. This last term is considered by Moore (p. 17) "to have a matching ecological term, 'biotope', which signifies organic environment". This definition of 'biotope' is contrary to common ecological usage (see Footnote p. 89).

Wells (1947, p. 119) defines by implication the terminology he uses in one sentence. "..... an attempt will be made to point out some of the significant environments (biotopes) and their organic communities (biocoenoses) as they are revealed by the rock records of their environments (lithotopes) and their fossil contents (thanatocoenoses)". Yet Moore (1949) interprets Wells' lithotope as referring to the environment itself /

itself, not the record of it. Lastly, the ecological use of the word 'facies' is for " ... particular modifications of a biotope, differing from the typical conditions in recurrent minor aspects" (Hesse, Allee and Schmidt, 1937, p. 136).

These few examples are recorded in order to illustrate the present confusion created by these new terms and to emphasise the necessity for standardization of geological and ecological terminology wherever the two sciences overlap.

Valuable work has been contributed towards the elucidation of the many facies of the British Carboniferous particularly by Vaughan (1911) on the Carboniferous Limestone of the South of England, Hudson (1924 &c.) on the Yoredale sequence and other Lower Carboniferous horizons in the North of England, and more recently Eager (1948) on the non-marine lamellibranch communities of the Coal Measures. Hudson (1924) used assemblage and community synonymously, but the present author would prefer to distinguish between these two terms, by confining assemblage to the fossil content of a rock unit, and community to those animals /fossils characteristic of the biotope/facies examined.

In this research two communities have been recognised. Eventually it should be possible to synthesise the more /

more local communities and define the major biological communities of the Carboniferous system. The diagnosis of these two communities is as follows:-

I. Posidonia-community. A dark pyritous shale containing abundant shells and valves of the motile lamellibranch Posidonia. Other species sparse. Microfauna may or may not be abundant. Browsing ostracods and arenaceous forams may be present. A shallow sublittoral deposit near marine end of rhythm.

II. Lingula-Nuculopsis-community. A dark calcareous shale with some pyrite. Defined by a burrowing fauna consisting of Lingula and burrowing molluscs including Nuculopsis. Surface fauna variable. Microfauna may include browsing ostracods and arenaceous forams. A shallow sublittoral deposit near marine end of rhythm.

VIII. SUMMARY

1. The history of the development of palaeoecology is traced.
2. The assemblage of some 5000 fossils collected from two feet of shale underlying an outcrop of the Top Hosie Lst. (Lower Carboniferous) near Kilsyth, is described.
3. The petrology of the shale is investigated and conclusions reached concerning the pyritization of the shale and the compaction of the sediment.
4. The assemblage consists of at least 40 species of fossils. The microfossils, estimated to be some 1500 times as abundant as the macrofossils, are varied and include previously undescribed shells of molluscs. Two new species of conodonts, Cavusgnathus sp nov. and Gnathodus clavatus sp. nov., are described.
5. The larval shell development of the following forms is described:- Nuculopsis gibbosa, Posidonia corrugata, Bellerophontids, Glabrocingulum armstrongi, and Healdia cuneola.
6. Relevant ecological literature is reviewed which, together with the palaeoecological evidence, has enabled conclusions to be drawn concerning the modes of life of most of the fossils.
7. Criteria to distinguish between the animals/fossils native to/

to the mud/shale and the shells introduced, are defined. Application of these criteria has enabled separation of the assemblage into native and influent species.

8. The conditions of deposition are considered and the control of the environment on the fauna emphasised.

9. Environmental control is well shown in the basal four inches of the shale where, out of a total of some 20 species, only four or five survive to maturity.

10. The change in the environmental conditions leading to the disappearance of the dominant species in the basal four inches of shale, enabled larvae previously unable to survive in the old ecological niche to inhabit successfully the new niche, thereby establishing a new fauna.

11. The community concept in ecology and the facies concept in geology are briefly reviewed.

12. Two animal communities in the shale are recognised:-

i. Posidonia-community.
ii. Lingula-Nuculopsis community.

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ROYAL CHARLES

PLATES

PLATE I.

Fig.

1. View of burn cutting.

2. Close-up of face showing the Top Hosie Limestone and the underlying two feet of shale.

PLATE I

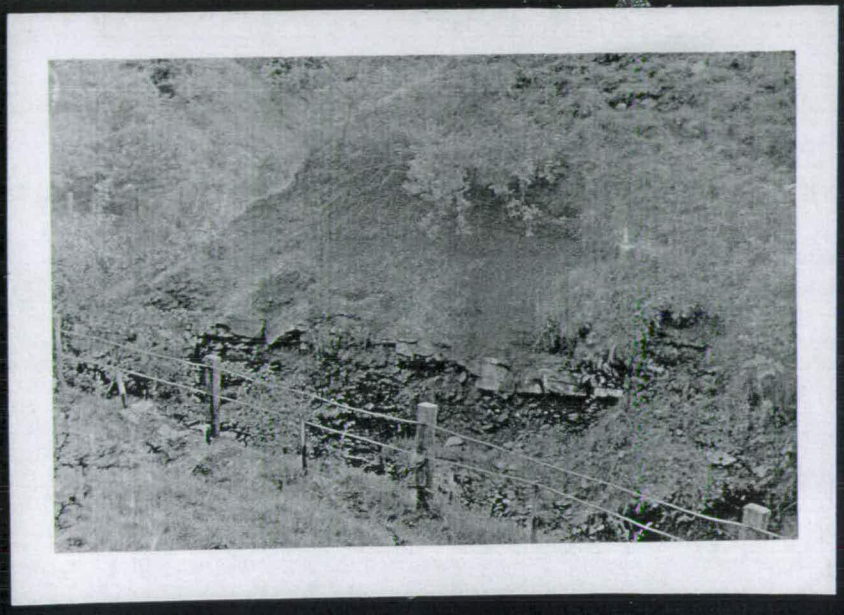

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PLATE II.

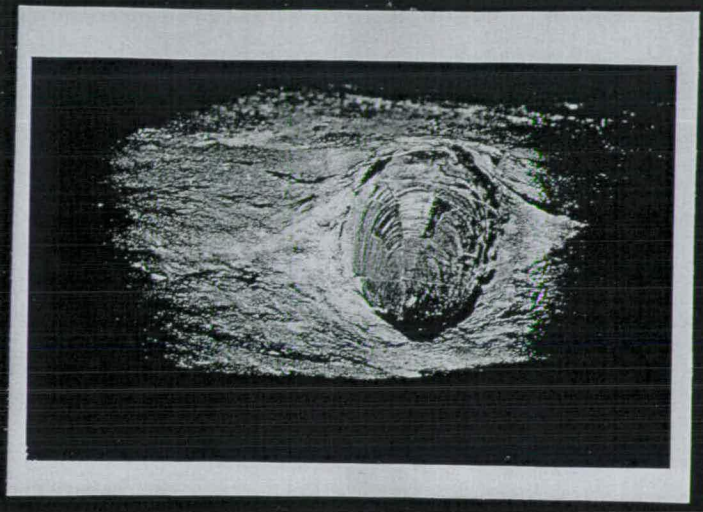
Fig.

1. Lingula squamiformis Phillips; shell vertical to bedding-planes of shale; No. 511b; xl.5.

2-3. Paeckelmannia polita (McCoy); fig.2, No. 412a, x7; fig.3, internal cast, dorsal view, No.P1, x10.

4. Productus concinnus?; external cast of ventral valve with spines, No. 375, xl app.

PLATE II



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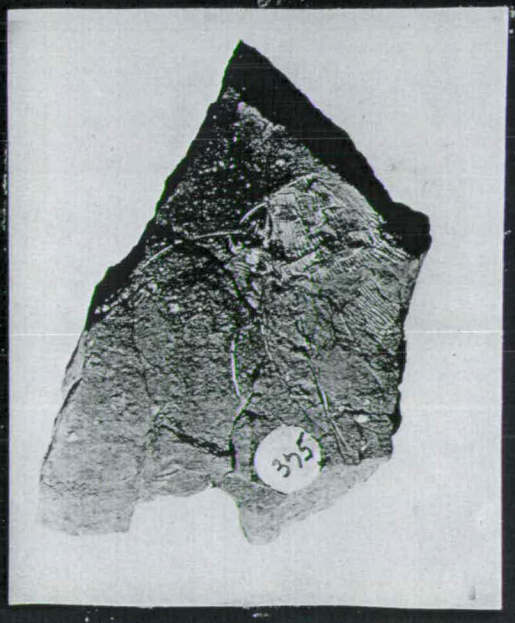

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PLATE III.

Fig.

1. *Athyris* sp.; internal cast, dorsal view, No. 388.7, x23.

2. *Lingula* with pyritized pedicle (?); No. 211, x6.

3-7. Growth-stages of *Nuculopsis gibbosa* (Fleming);
fig. 3, No. 388.5.1
4, 388.5.2
5, 388.49.4 showing dentition
6, 388.49.5
7, 388.49.1

All x20.

8-9. *Sanguinolites costellatus* (McCoy);
fig. 8, No. L1, x1.
9, 312.32/33, x10
(*S. costellatus*, s.l.)

PLATE III

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PLATE IV.

Fig.

1. *Glabrocingulum* sp. probably *G. armstrongi* Thomas;
No. 388.8.2, x20.

2-3. *Pseudozygopleura* (s.l.) spp.;
fig. 2, fine-ribbed variety,
No. 388.28.8, x30.
3, coarse-ribbed variety,
No. 312,5.7, x30.

4-5. Bellerophontid nuclei;
fig.4, thin section parallel to plane of coiling,
No. 388.21.5, x30.
5, apertural view,
No. 560.86.1, x20.

6. *Posidonia corrugata* (R. Etheridge);
No. 654.76.1,2,3, x30.

7. *Cycloceras* sp.; No. C1, x2.

PLATE IV

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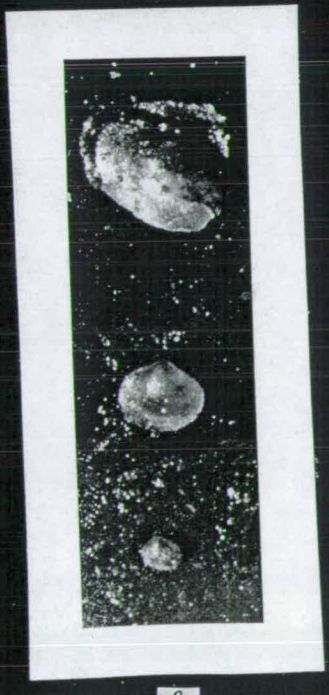

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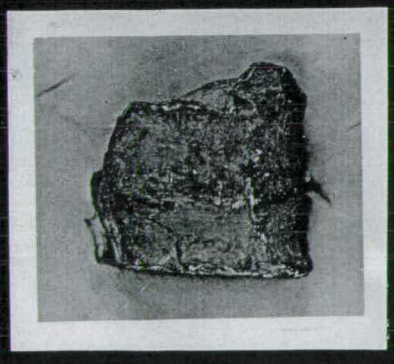

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PLATE V.

Fig.

1-2. Pseudorthoceras aff. knoxense (McChesney, 1860); fig.1, No.407, x1; fig.2, same specimen x2, to show cameral deposits, recurved septal necks, and nature of siphuncle.

3. Rugocyrtoceras cf. northumbriense J.S. Turner (MS); No.241, x1.

4. Loxoceras? sp.; No.643, x17. Two fragments showing oblique sutures, and centre fragment showing marginal siphuncle.

PLATE V

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PLATE VI.

Fig.

1-3. Gnathodus clavatus sp. nov.;
fig. 1, lateral view of holotype, No. 312.21.5, x20.
2, oral view of platform, No. 312.21.5, x20.
3, oral view of platform and lateral view of blade (specimen broken), No. 145.21.1, x20.

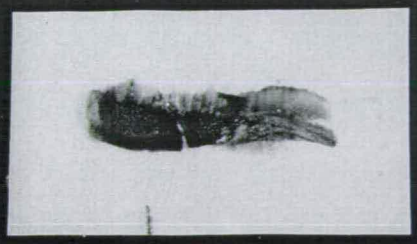
4. Hindeodella sp.; No. 654.70.2, x30.

5-6. Cavusgnathus sp. nov.;
fig. 5, lateral view, No. 654.70.1, x20.
6, oral view, No. 654.70.1, x20.

7. Healdia cuneola (Jones and Kirkby); moult stages,
No. 560.76.1,.. .66mm.
2,.. .56mm.
3,.. .4mm
4,.. .23mm.
All x30.

8. Healdia cuneola; interior of left valve showing groove, No. 654.23.7, x40.

PLATE VI



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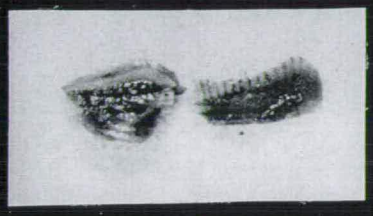

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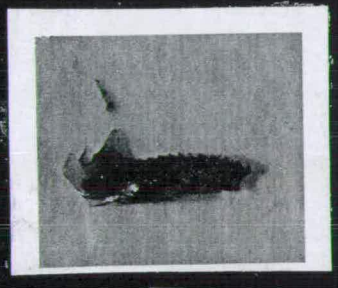

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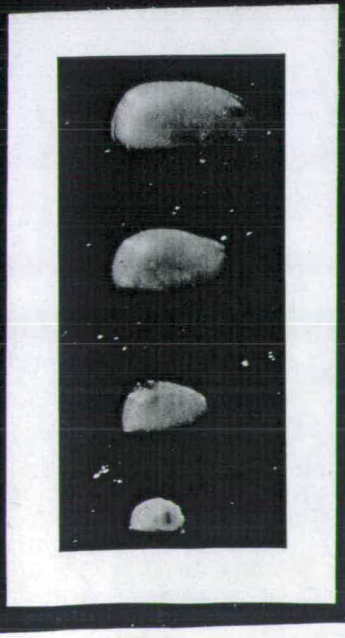

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PLATE VII.

Fig.

1. Girvanella? sp.; No. 106.16, x35.

2-3. Glomospirella sp.; fig.2, No.312.51.4, x50app.
3, cross-section,
Slide 662, x80app.

4. Hyperammina sp.; No. 654.66.6, x20.

5. Thin section of the shale with pyrite developed in the lower part of a shell of Healdia cuneola, Slide 388, x60 app.

6. Coleolus aff. carbonarius Demanet;
No. 312.24.5, x20.

PLATE VII

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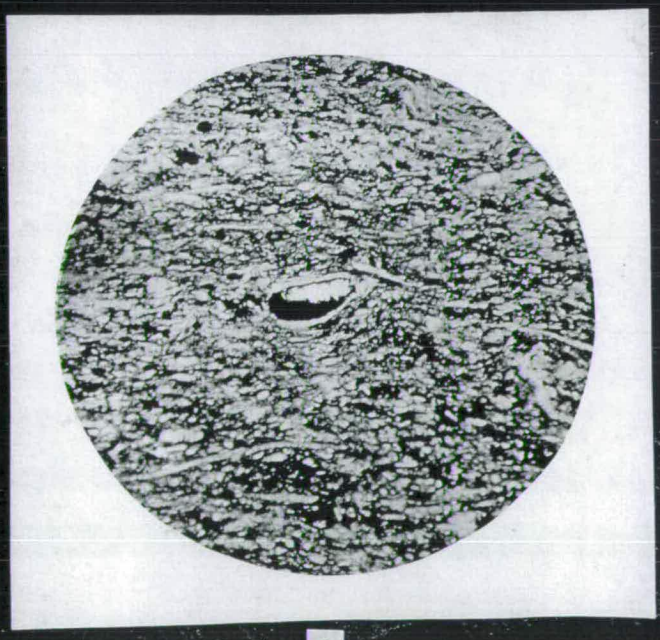

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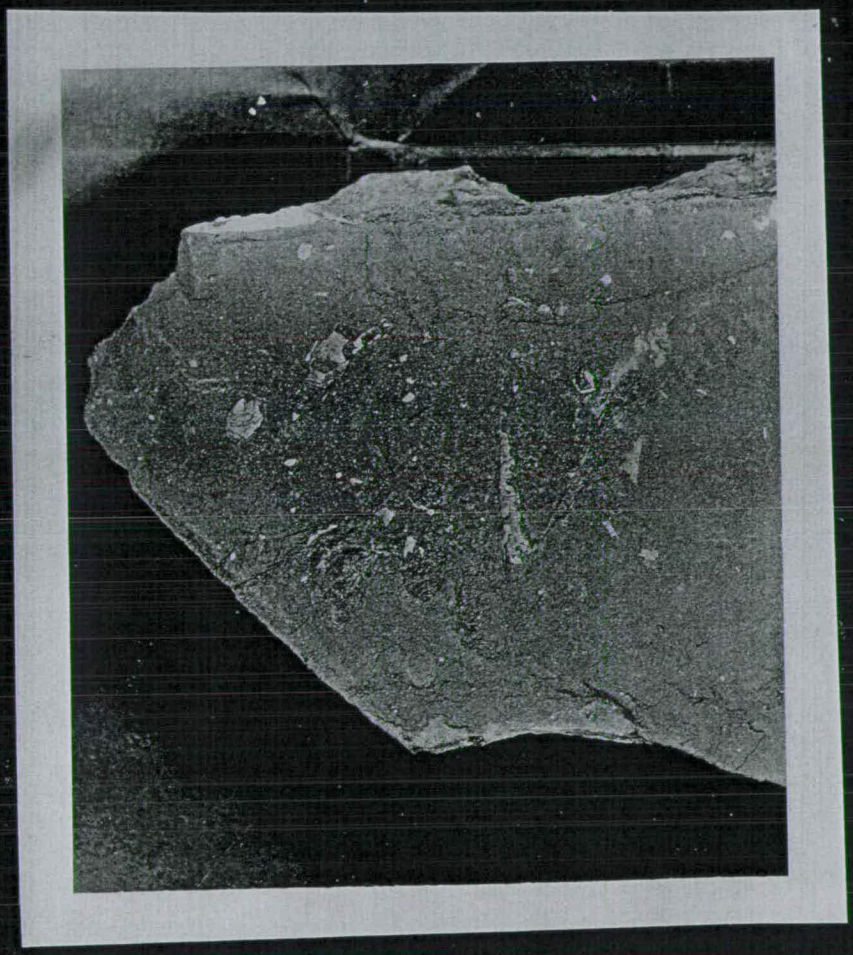
PLATE VIII.

Fig.

1. Specimen showing the association of valves of *Posidonia corrugata* with conchs of *Loxoceras?* sp. No. 606g, xl.

PLATE VIII.



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