The morphology, ethology and palaeoecology of certain trace fossils from the Jurassic rocks of England

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THE MORPHOLOGY, ETHOLOGY AND PALAEOECOLOGY OF CERTAIN TRACE FOSSILS FROM THE JURASSIC ROCKS OF ENGLAND.

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ABSTRACT.

In the present state of knowledge, thirty-one trace-fossil 'species' are known from the English Jurassic: seventeen (55%) are feeding burrows; eleven (36%) are dwelling burrows; two (6%) are crawling trails; one (3%) is a resting impression. No meandering grazing trails occur.

Six new 'species' are described:-

Arenicolites skeltonensis - basal Upper Lias, Yorkshire
Diplocraterion arkelli - widespread
Diplocraterion statheri - Bajocian, Yorkshire
Glossifungites lymensis - Ellerbeck Bed, Yorkshire

Asterosoma fosteri - Dogger, Yorkshire
Asterosoma multilobatum - Scarborough Beds, Yorkshire.

Bathymetric zones for the Jurassic sea may be defined in terms of commonly occuring assemblages of trace fossils. Littoral zones consist of monotypic banks of *Thalassinoides*; *Arenicolites* spp. or *Corophioides* spp.; or *Ophiomorpha*. *Gyrochorte* from the littoral zone show strong orientation and U-turns are common. In sublittoral zones monotypic banks of *Rhizocorallium* occur inshore; more varied assemblages, with *Teichichnus*, *Asterosoma* and *Chondrites*,

offshore. Zoophycos, diagnostic of still-water neritic zones, is absent.

Different trace-fossil 'species' are recognised from ironstone, calcareous and well-sorted sandstone "regimes" of sedimentation, though 'genera' may be identical. Rhizocorallium jenense and Rhizocorallium cicatricosus occur in ferruginous environments; Rhizocorallium commune in impure calcareous environments.

The Stomatopoda are considered likely producers of Rhizocorallium commune.

On the basis of comparative ecological categories of trace fossils, the system which most strongly resembles the English Jurassic is the Bohemian Ordovician.

The Middle Jurassic of Yorkshire does not compare closely with either the German Middle Jurassic or the Northumbrian Namurian.

The Jurassic trace-fossil fauna of England is the richest in dwelling and feeding burrows of any system so far described. In the total number of trace-fossil 'species' it is exceeded only by the Swiss Flysch.

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CHAPTER ONE . INTRODUCTION

(i) The status of Trace Fossils

A measure of the current palaeontological status of trace fossils may be obtained from the fact that not one standard English or American text-book contains a single chapter on them .

Part of the problem is undoubtedly nomenclatural , since the naming of trace fossils is not subject to ICZN rules as are body fossils . This has not , however , prohibited the inclusion of such enigmatic fossils as the conodonts in some text-books .

To ignore trace fossils on this basis is as absurd as to label their study unscientific and vague since it does not conform to orthodox systematics . Up to the present published work by the majority of British geologists involving trace fossils has indeed been both unscientific and vague , as it always will be when every type of problematic marking is dismissed as either a "fucoid" or a "concretion" .

It is a sad reflection that over 80 years have elapsed since NATHORST (1886) finally demonstrated conclusively that the majority of so-called "fucoids" were not seaweed casts at all . Why then do we still encounter such terms in the geological literature ?

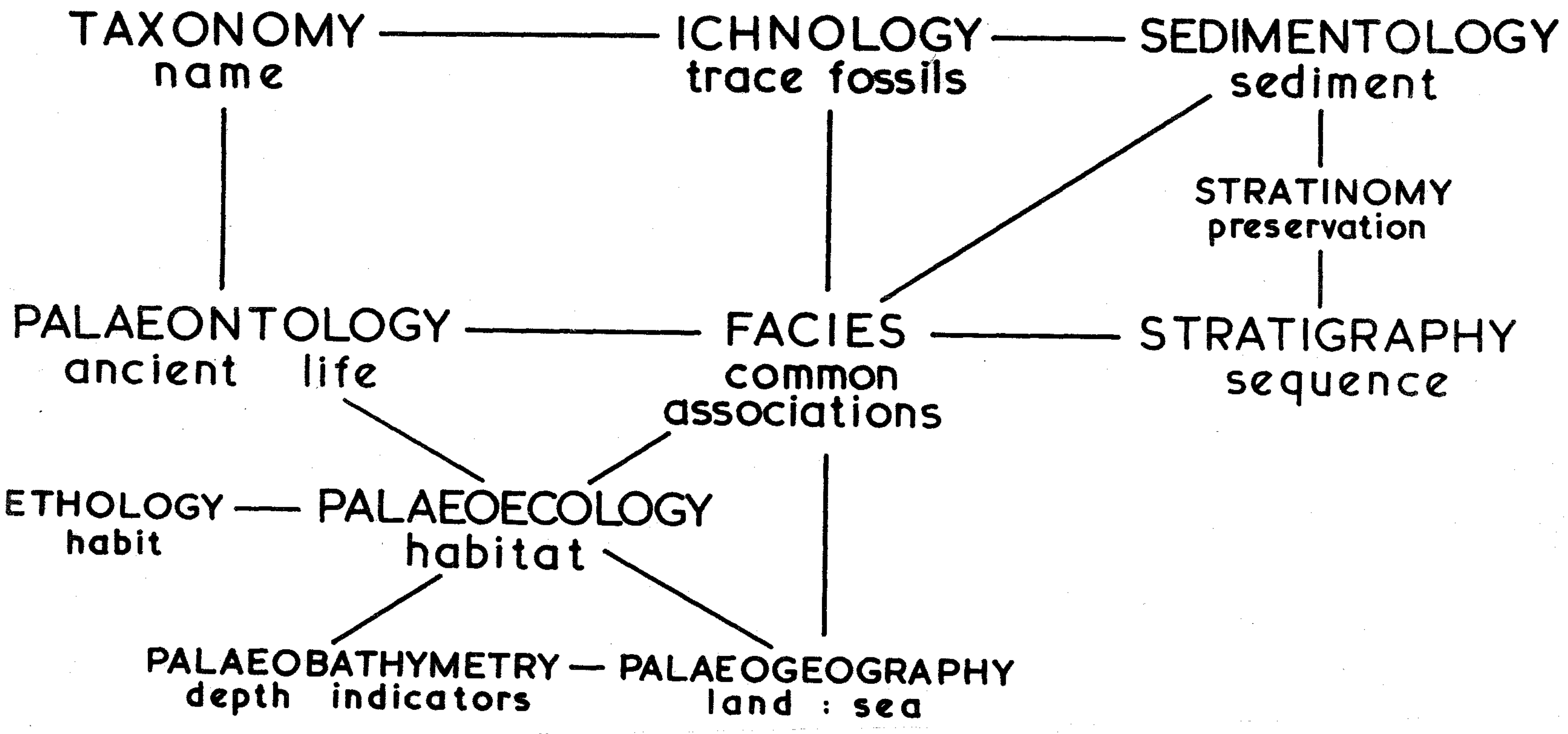
There are probably two main reasons . First , a reticence to consult and translate the foreign literature , which is monumental : second , an aversion towards studying any 'fringe-science' which does not fall neatly into the "Palaeontology" or "Stratigraphy" pigeon-holes .

Since trace fossils are only recognisable as distortions of , and rearrangements of , sedimentary laminations it is clear that the other major discipline with which their study is concerned is that of Sedimentology . In fact a study of any definition of the term 'trace fossil' reveals that the science is essentially concerned with the confluence of the two major disciplines Palaeontology and Sedimentology . Whether this hybrid science merits separate designation is debatable . However , if it is felt that a name is required it is as well to recall that one has been available since 1827 , when the term "Ichnology" was introduced by DEAN BUCKLAND in his studies on crocodilian tracks . According to Laws of Priority , it stands much higher on the list than many newer branches of Geology such as Palaeoecology .

The various aspects of the study of trace fossils are shown in Text-fig.1 . It is designed to place in perspective the various minor sub-disciplines upon which trace-fossil study impinges .

Text-figure 1.

Diagram illustrating the relationship of the science of trace-fossil study to the major disciplines of Geology.


TAXONOMY
name
ICHNOLOGY
trace fossils
SEDIMENTOLOGY
sediment
STRATINOMY
preservation
PALAEONTOLOGY
ancient life
FACIES
common associations
STRATIGRAPHY
sequence
ETHOLOGY
habit
PALAEOECOLOGY
habitat
PALAEOBATHYMETRY
depth indicators
PALAEOGEOGRAPHY
land : sea

(ii) The scope of Trace Fossils

The English term 'trace fossil' , through lack of usage , never received a formal definition until 1957 , when SCOTT SIMPSON defined it as a :-

> " sedimentary structure resulting from the activity of an animal moving on or in the sediment at the time of its accumulation " .

The corresponding German term 'lebensspuren' has been in existence since 1912 , when ABEL used it to refer to Recent tracks and burrows , and pathological phenomena , in addition to trace fossils sensu stricto . SEILACHER (1955) defined 'lebensspuren' as :-

> " structures in the sediment left by living organisms " .

Although it may appear that the latter definition is merely a more concise version of the former , there is an important difference . SCOTT SIMPSON specifically states that the structures must be produced in the sediment " at the time of its accumulation " . In fact very few trace fossils which can be observed in process of formation fulfil this requirement , though most structures are produced very shortly after the sediment has been deposited . But this is probably splitting hairs .

What is more serious is the fact that borings into hardgrounds (e.g. VOIGT 1959) are quite obviously excluded . Here the borings may not even belong to the same Era as the sediment penetrated . For example the unconformity of the Vesulian transgression across the Mendip Island of Carboniferous Limestone is extensively bored at Vallis Vale .

It would appear preferable therefore to follow SEILACHER's broader definition , within which the following structures are included :-

1) Vertebrate Tracks
2) Invertebrate Trails & Burrows
3) Vertebrate Coprolites
4) Invertebrate Faecal Pellets
5) Invertebrate borings into rocks and shells .

The distinction between vertebrate and invertebrate trace fossils is immediately apparent , as is the distinction between structures produced in soft sediment (1-4) and hard rocks and shells (5) .

The difference in character between vertebrate tracks and invertebrate trails is greater than is generally appreciated . Although both are the product of animals moving " on the surface of the sediment " the actual footprint of a walking or running tetrapod , relative to the sedimentary surface , is a stationary or 'static' record (unless the foot was skidding or being dragged across the surface). The vertebrate track is thus the sum of successive footprints each of which reveals an impression of the sole of the foot , often in great detail . Thus by comparative pedal morphology it is frequently possible to approach an identification of the producer : in the case of dinosaur tracks often the genus , and certainly the order , can be determined (e.g. BAIRD 1954) .

With invertebrate trails however , the producer nearly always drags itself across the surface , and the resulting structure , though it may be well-preserved , is never a true impression of the producer's morphology but a blurr .

This thesis is concerned solely with invertebrate trace fossils . Consideration of the fascinating vertebrate tracks from the Yorkshire Jurassic strata are out of context here and will be documented elsewhere ata later date .

(iii) Historical Perspective

A comprehensive review of the history of trace-fossil study remains to be written , in any language . This is scarcely surprising , since it would require a battery of translators if the reviewer himself were not a brilliant linguist .

A magnificent summary of the development of the science is presented by HANTZSCHEL (1962) in the Treatise account .

The most recent extensive bibliographies are to be found in HANTZSCHEL (1965 , 1966) " Vestigia Invertebratorum et Problematicum " and the Supplement to the Treatise : the former is noteworthy for complete references to type species and for giving full synonymies ; LESSERTISSEUR (1955) " Traces fossiles d'activité animale " and WILCKENS (1947) .

Much of the confusion concerning trace fossils originated in the earliest days of Palaeontology when tubular burrows were considered to be the casts of seaweeds . Many names remain in the literature to remind us of this , names like Chondrites and Fucoides , and a host with the suffix '-phycos'. The isolated works of scientists like HANCOCK (1858) on the Recent amphipod trails of the Durham coast , and DAWSON (1862) on limulid trails were largely unheeded , and it was left to NATHORST (1873 , 1886) and James (1884) to finally challenge , independently , the plant origin of these fossils on the basis of more complete studies of present-day forms .

This initiated a somewhat voluble discussion between two rival factions , with NATHORST finding the majority of palaeontologists against him , including most notably DE SAPORTA (1879 , 1884) . There are still apparently some Canadian and Indian author's adhering to the algal school , and even as late as 1938 FUCINI published his " Problematica Verrucana " , in which many inorganic markings were said to be of plant origin . This , in spite of a very detailed examination of European trace fossils by FUCHS (1895) which reinforced NATHORST's argument , and a fine work by ABEL (1935) , not to mention papers which were just beginning to appear from the Aktuopalaontological Institute of Senckenberg in Germany under the guidance of RUDOLF RICHTER (1924 , 1926) .

These studies continue to the present day . They involve work on the extensive North Sea tidal flats , recently increased in scope to include sublittoral regions (e.g. HERTWECK & REINECK 1966) , and provide much needed data on Recent trails and burrows . The work of the Aktuopalaontological Institute , perhaps , more than anything else , has placed the study of trace fossils on a truly scientific basis , though if any one contemporary palaeontologist deserves especial mention it is SEILACHER , for ingeniously devising the classification (1953) which is now in general use , and for pioneering extensive facies studies involving trace fossils (e.g. 1958) .

The debt we in Britain owe to the progressive approach of the Continentals should be readily apparent from this brief historical review . It is indeed remarkable that one hundred years should have elapsed between HANCOCK's (1858) article and the next significant British contribution on trace fossils , a study of Chondrites by SCOTT SIMPSON (1957) . The lone star throughout this period was BATHER (1910 , 1925) : though his papers were seldom of undue length he was one of the few to place British trace fossils on record and recognise their environmental significance .

In published work on the trace fossils then we have many areas of the world , and many parts of the stratigraphic column , represented in great detail in the foreign literature . Examples which immediately spring to mind are the Cambrian of the Salt Range Pakistan (SEILACHER 1955) , the Wurttemberg Jurassic (RIETH 1932) , the Westphalian Cretaceous (HANTZSCHEL 1964) and the Alpine Flysch and Molasse (SEILACHER 1958) . There is , however , very little British material adequately described in the literature , with the exception of early work on the Carboniferous of Northern England (M'COY 1851 , HANCOCK 1858 and TATE 1859) ; the Mesozoic (BATHER 1910 , 1911 , 1925) and more recent work on the Lias (SCOTT SIMPSON 1957 , HALLAM 1960) and on the Devonian (GOLDRING 1962) .

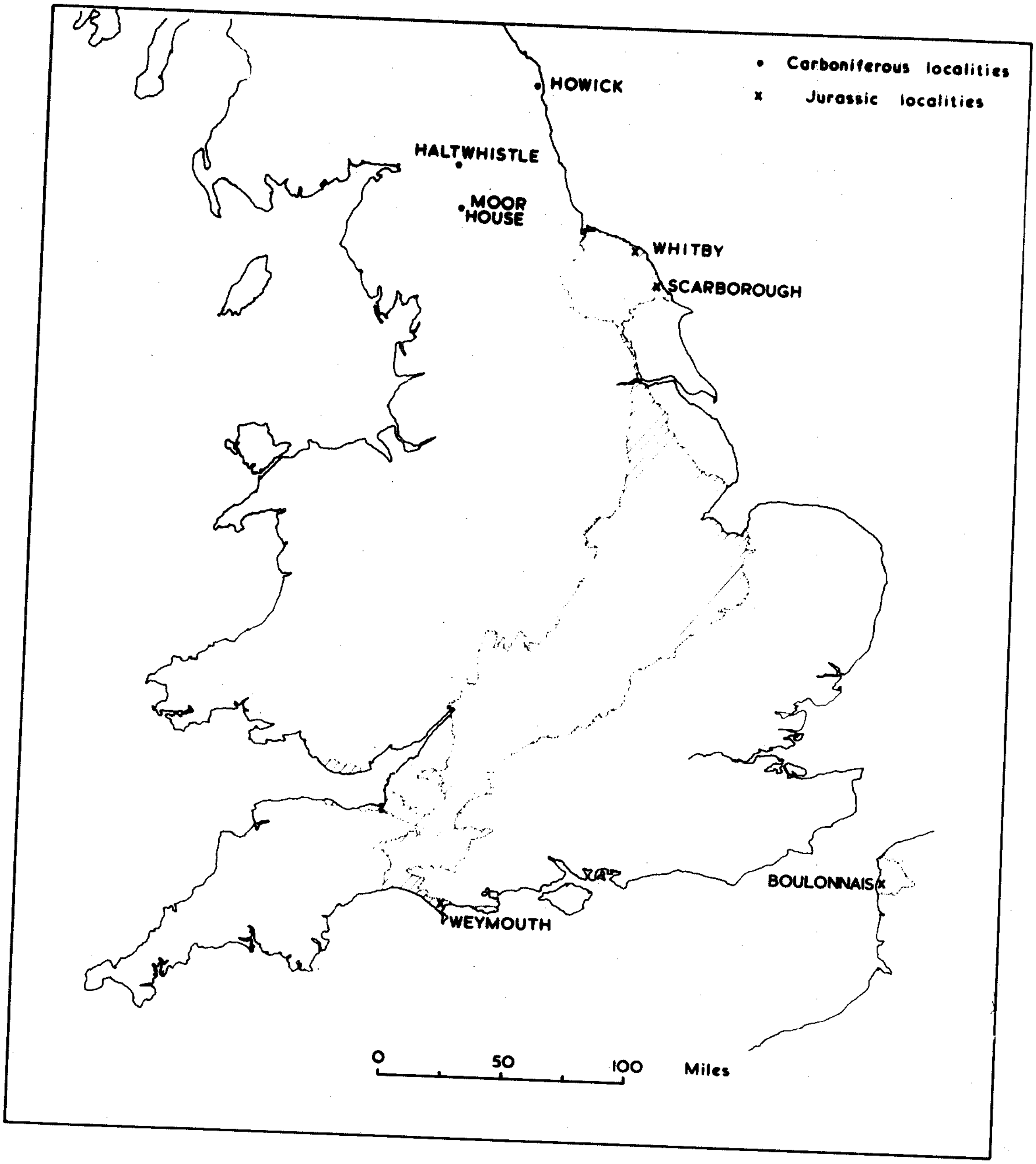
Compared with the inland areas just mentioned , often of limited exposure and indifferent preservation , the abundant coastal sections in the British Isles with their masses of beautifully-etched material present wonderful possibilities for enlarging the field of study of trace fossils in this country .

With so little written about so many different kinds of problematical trace fossils in the English Jurassic , and with the supreme exposures in the cliffs of East Yorkshire and Dorset , this System appeared eminently suitable for commencing a detailed examination of trace fossils in this country . A refined zonal stratigraphy , better perhaps than that of any other System , enabled bed-by-bed precision to be maintained in widely-spaced localities , and the meticulous studies of ARKELL (1933 , 1947) , HOWARTH (1955 , 1962) and WILSON (1949) facilitated the accurate application of lateral variation studies involving trace fossils .

The writer's primary objective throughout the period of study has been to investigate those ecological parameters to which trace fossils seem peculiarly susceptible : particular emphasis has been given to the possibility that they may be used as relative indicators of depth in shallow epicontinental seas .
Detailed fieldwork was generally restricted to coastal regions with good exposure and was begun on the Yorkshire coast (Text-fig.2) with a study of the Bajocian Scarborough Beds ,

Text-figure 2.

Map showing the major areas of study.


• Carboniferous localities
x Jurassic localities
HOWICK
HALTWHISTLE
MOOR HOUSE
WHITBY
SCARBOROUGH
BOULONNAIS
WEYMOUTH
0
50
100
Miles

and later extended to the Middle Lias Ironstone Series , Blea Wyke Beds and Dogger . Later field studies concentrated on the Corallian , where a study of the Dorset coastal successions was undertaken chiefly as a means of testing hypotheses formulated in Yorkshire .

Since comparisons between the deltaic environment in Yorkshire during Namurian and Bajocian times were at one time very popular , it was decided to see how far this was true for the trace fossils . Therefore a subordinate amount of fieldwork was undertaken on the Namurian rocks of Northumberland (Text-fig.2) .

The thesis is in three parts , dealing respectively with Techniques , Systematics and Palaeoecological syntheses . It is hoped that complicated terminology has been kept to the absolute minimum : a glossary of essential terms will be found in the Appendix , together with Tables of strata , experimental details and petrographic data .

PART ONE : TECHNIQUES OF STUDY

CHAPTER TWO . FIELD PROCEDURE

(i) Cliff Stratigraphy

In any detailed stratigraphic study there is always an element of " getting one's eye in " with the local bed-by-bed succession . This is particularly important in areas where the rocks all appear to be of one type , as in the Jurassic of the Ledonian Jura where at first glance there appears to be simply thousands of feet of limestone . Only after close examination does it become apparent that every grade from breccia to mudstone is present . A similar problem exists in the Pennine Yoredale cyclothems , where repetitions of limestone , shale , sandstone through thousands of feet of strata necessitate an intimate local knowledge of each part of the succession before reliable correlations can be established .

The magnitude of the problem in the British Jurassic lies somewhere between these two extremes . It is especially acute in the Middle Jurassic of Yorkshire where , within the Bajocian Scarborough Beds , there are several bands of limestone which are superficially similar , and many sandstones , any of which might easily be confused with Lower and Middle Deltaic sandstones which lie beneath them in the succession .

The sine qua non for any study involving material accumulated on the backshore at the base of lofty cliffs is therefore complete acquaintance with the in situ cliff stratigraphy . Since most trace fossils are best preserved in this vicinity , and only infrequently in situ , the importance of " getting one's eye in " can hardly be overstated .

(ii) Loose Blocks

The study of loose material by palaeontologists has never been popular , especially in view of the errors of S.S. Buckman during the later years of his life . However , a palaeontologist has to use what material is available , he cannot lay down the conditions of study , which are determined by Nature .

Thus , in the case of trace fossils , the area of greatest abundance and best preservation is the one that must be studied in the greatest detail . This area is the "spray-zone" immediately above high-water mark (Plate 1) , where the excellent etching effect of saline spray renders this narrow strip most suitable .

Before beginning to study any individual loose block some attempt should be made to ascertain its 'way-up' , since many of the blocks from high in the cliffs will have overturned before coming to rest on the backshore .

In most cases this is reasonably simple , using standard cross-bedding and ripple-mark criteria , as well as vertical 'U'-shaped burrows which are often abundant .

(iii) Methodological Sequence : Quadrat Technique

Since many fallen blocks are of tabular form (Plate 2) they lend themselves admirably to a standard observational procedure . This avoids any errors of omission , and provides a basis for comparison between blocks . The technique used was a modification of the Quadrat Method described in AGER (1963 , pp.221-223) , incorporating additional observations involving mode of preservation and sedimentology of the enclosing rock . The individual steps taken in each instance were as follows :-

1) Determination of 'way-up' :
2) Demarkation of unit square metre on horizontal surface :
3) Scale field-sketch of area to show :-
    a/ number of different trace-fossil types present;
    b/ approximate percentage abundance of each;
    c/ characteristic ethological pattern of each;
    d/ preferred orientation of certain traces , if present :

A field photograph of each unit area seldom portrays the total assemblage of forms accurately , since some are more obscure and lacking in relief than others .

4) Mode of preservation of each trace fossil to show if it is
 a/ a surface trail or burrow;
 b/ stuffed with faecal pellets or lined with debris;
 c/ more or less resistant than matrix :

5) Rock type of enclosing sediment :

6) Associated sedimentary structures to show whether rock is
 a/ massive (original or due to excessive bioturbation);
 b/ laminated (thickness of laminae);
 c/ cross-bedded (type and dimensions);
 d/ rippled (type, wavelength and orientation in relation to trace fossils);

7) Associated shelly remains to show :-
 a/ whether present;
 b/ dominant species (and probable mode of life);
 c/ indigenous or exotic;
 d/ degree of fragmentation, size sorting by currents;
 e/ any forms in suspected life position .

Large tabular fallen blocks possess one significant feature which renders them far more suitable for studying trace fossils than a simple vertical or sloping cliff-section . That is the simultaneous exposure of both vertical and horizontal aspects of the material being examined . A three-dimensional picture can thus be readily established and trace fossils with a dominantly horizontal trend , like <u>Rhizocorallium</u> , which would be very difficult to recognise in a near-vertical cliff face , are seen to perfection .

CHAPTER THREE. LABORATORY TECHNIQUES.

Natural weathering effects are generally sufficient for the direct examination of the majority of trace fossils, but for photography the simple expedient of smearing ink over the surface of the specimen, then washing it off, frequently leaves good contrast (e.g. plate 32; specimen of Rhizocorallium commune, where details of the Spreite are very much enhanced).

Of more sophisticated techniques, sand-blasting achieves good results where the initial relief is low, while etching with warm dilute hydrochloric acid takes longer but is nevertheless effective on limestones with a high detrital quartz fraction, such as are commonly found in the Scarborough Beds of the Yorkshire coast.

The best staining technique is that which involves Alizarin Red added to a ten per-cent solution of potassium hydroxide. It is effective when applied to slightly etched freshly-cut surfaces of limestones.

In recent years there has been an increased awareness of the possibility that the apparent absence of sedimentary structures, biogenic or otherwise, from certain lithologies may be due to unfavourable preservation, resulting in many homogeneous sandstones. HAMBLIN (1962, figs.1 & 2) revealed strikingly, by X-ray radiography, the presence of many minor structures in sandstones which, to the naked eye appeared featureless. In a later work (1965) he showed that in fact only 8% of a very large representative sample of apparently homogeneous sandstones were truly massive.

X-ray radiography was therefore undertaken on a number of 'suspect' Jurassic lithologies, including some vertical rootlet casts from the Middle Deltaic Series of Yorkshire which very much resembled burrows. These are very easily distinguished from X-ray photographs, since the carbonaceous sheath surrounding the plant cast gives a completely different picture from vertical burrows, where this is absent, and there is more disturbance of the sedimentary laminae.

Good discussions of experimental procedure will be found in HAMBLIN (1962) and ZANGERL (1965).

Through the co-operation of Dr. Holroyd of Dryburn hospital, Durham, it was possible to examine many slabs of bioturbated sediment. Since exposure factors vary with rock type and slab thickness no satisfactory mean values can really be given : details for various lithologies will be found in the Appendix.

Certain experimental details are common to all specimens. These chiefly concern the preparation of the specimen, where the following requirements must be fulfilled:-

1. The slab should be of uniform thickness;
2. All saw marks must be removed;
3. Particles of grinding powder must not become embedded in the slab;
4. Porous samples should not be cut on an oil-lubricated saw.

The thickness of slab chosen depends on:-

a. Cohesiveness of the sample;
b. Burrow density;
c. Kilovoltage of X-ray unit.

In general terms, a one inch slab of ripple-marked Deltaic sandstone containing isolated root casts is satisfactory, though a slab 3 mm. thick was required in a sample from the highly bioturbated Nothe Grits in order to resolve burrow detail.

In practice, there were found to be very few lithologies which still appeared massive after being cut and polished, and the detailed study of trace fossils was mostly carried out by the serial grinding of polished sections. Grinding in two directions at right angles proved essential in the study of internal detail in the limbs of *Rhizocorallium cicatricosus*, and of *Chondrites*.

PART TWO . MORPHOLOGY & ETHOLOGY

CHAPTER FOUR . PRESERVATION AND ITS SIGNIFICANCE IN TRACE-FOSSIL TAXONOMY

It may be thought that trace fossils , possessing no skeletal parts , stand little chance of being preserved in the sedimentary record . Yet their abundance is quite staggering , for they occur not only in every System from the Pre-Cambrian to the Holocene , but in deposits of many different environments : from the deep sea , through epicontinental seas , to the intertidal zone ; from 'brackish' and freshwater regions , and even from continental deposits .

(i) The need for an inhomogeneous medium

Generally , a prerequisite for the preservation of any trace fossil is some degree of inhomogeneity in the enclosing sediment so that the organism effectively re-sorts the sediment . This need not always be necessary , however , since merely by compacting material within its burrow an animal may induce a slightly greater resistance to weathering than is found in the matrix , and the structure may be etched out satisfactorily . Similarly , a surface-formed trail does not depend on any inhomogeneity of the sediment in which it is impressed , for it is recognisable simply as a distortion of a single bedding plane . Thus in apparently homogeneous Westphalian shale sinoid trails like Belorhaphe kochi may be visible , even in totally unweathered core material , so long as the shale is fissile .

Burrows constructed in very fine-grained sediments are often difficult to discern because of the uniform grain-size . Thus the apparent absence of bioturbation in some Liassic shales may be due simply to a lack of lithological contrast ; or the distinction may be on such a fine scale as to be incapable of resolution by the human eye . In such instances techniques utilising slight changes in the absorptive characters of the sediment particles , such as infra-red photography or X-Ray radiography , may reveal bioturbation structures . Therefore , it may be misleading to state , on the basis of field evidence alone , that bioturbation is absent from certain fine-grained rock types : supplementary observations may be necessary to prove its existence .

Not all fine-grained sediments present this problem , however , for KENNEDY (personal communication) has experienced no difficulty in observing Chalk burrows in sawn hand-specimens , and considers that the problem is generally overstated . This may possibly be explained by the fact that the Chalk , though very fine-grained is not homogeneous , but composed of varying proportions of clay , foraminifera , coccoliths and shell fragments which are re-sorted by burrowing organisms . GOLDRING (1966) has , however , demonstrated that staining with methylene blue considerably enhances structural detail in Chalk . This is due to changes in porosity caused by the organic reconstitution of the sediment , and the stain becomes preferentially absorbed by the more porous regions . In this manner many traces are shown up which are only discernible with difficulty from untreated sawn surfaces . Anomalous trace-fossil distributions may result from random use of the stain .

(ii) Degree of re-working in relation to the recognition of trace-fossil genera

The recognition of any trace-fossil genus usually depends on its characteristic geometric outline being preserved . Generally this means that it must be preserved in isolation from its neighbours in a comparatively unobliterated state . The amount of re-working of a unit volume of sediment will therefore influence to a high degree the adequate recognition of different sorts of trace fossil . Thus in strata which have been burrowed only slightly it should be possible to identify with ease all the genera present . In strata which have been 'churned' , however , the degree of interference between adjacent burrows is such that in most cases individual trace-fossil genera cannot be distinguished , and evidence of organic activity may be evident only in vertical section , and recorded simply as "bioturbation" (Plate 3) .

This results in a dangerous situation , where the greater taxonomic diversity may be (subconsciously) equated with greater abundance of individuals , especially when reading descriptions of trace fossils in the literature . Experience shows that the simple reference to "bioturbation" is frequently overlooked , or misunderstood as a 'sack' term , though MIDDLEMISS (1962) has done something towards rectifying the position .

(iii) The importance of diagenesis and weathering

The transition from sediments with even lamination , rarely disrupted by burrowing organisms , through 'mottled' sands to apparently homogeneous massive sand has been reported from the Mississippi Delta region by MOORE & SCRUTON (1957 , p.2743) and shown to be related to increased benthonic activity . We must therefore beware of apparently homogeneous sandstones in the sedimentary record , and if possible check by means of X-Ray radiography their internal structure . HAMBLIN (1965) , aware of this , X-rayed over one hundred sandstones , but found that only 8% appeared massive due to complete organic re-working .

It is probable that although the Recent samples from the Mississippi Delta region appear , in their unconsolidated state , to be homogeneous , they would in fact after diagenesis and subsequent weathering as a hard rock not appear so . This is because the process of diagenesis is invariably helpful , as are the agents of weathering , in enhancing any slight differences in structural detail . Thus the comparable state in the fossil record should be recognisable on account of clay stringers and discordant wisps of sandstone which will have been differentiated in the process of fossilization (Plate 3) .

Although diagenesis and weathering may hinder the geochemist they are helpful to the sedimentologist . It is highly probable that the Liassic bioturbation shown in Plate 4 would not have been visible when the rock was unconsolidated , but preferential diagenetic enrichment of calcite in the burrows has given the rock a distinctive mottled appearance .

(iv) Confused preservation and rate of sedimentation

The varied degree of "churning" exhibited by fossil sediments has often been used as an indication of the rate of accumulation (e.g. MIDDLEMISS 1962), presumably because the amount of re-working caused by a unit number of animals is dependent upon time. However it is also dependent upon the number of animals, and equally, the same degree of re-working can be achieved by greater numbers of animals working for the same time. This is a facile statement, but a brief review of factors influencing the distribution of burrowing creatures at the present day should demonstrate its validity.

Most creatures have very narrowly defined ecological limits within which they tend to be very abundant, and outside which they are generally very scarce. Moreover, even in their optimum zone organisms are distinctly gregarious in habit, so that in one layer of sediment, all deposited at a uniform rate, population density may vary greatly. The burrowing decapod crustacean order Thalassinidea (Text-fig.3) provides a good illustration of the fastidious ecological requirements of one group of Recent burrowers. They are considered here since their characteristic burrows can be more easily recognised in the fossil state than those of other burrowers.

GUSTAFSON (1935) has shown that the depth distribution of Upogebia deltura in the fjords of the Swedish west coast is very restricted (Table 1). The main restricting factor is the occurrence of suitable substrata,

TABLE ONE . THE DISTRIBUTION OF THE BURROWING DECAPOD
Upogebia deltura IN THE GULLMAR FJORD SWEDEN
(Data from GUSTAFSON 1935)

DEPTH IN METRES	Gasevik	Klubbau	Essvik	Finsbo	Garvik
0	-	-	-	-	-
2	-	-	-	-	-
4	-	-	-	-	-
6	-	-	-	-	-
8	-	-	-	-	150
10	184	115	-	-	8
12	43	115	50	100	-
14	-	6	50	2	-
16	-	-	-	-	-
18	-	-	-	-	-
20	-	-	-	-	-
22	-	-	-	-	-
24	-	-	-	-	-

Number of animals per haul shown for each of five stations along the fjord ; ring dredge method used .

Garvik is situated at the inner extreme of the fjord .

Text-figure 3.

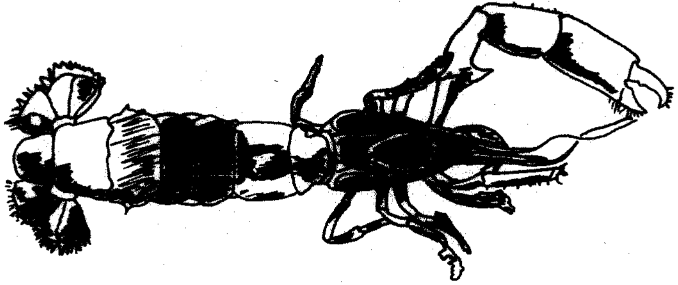
Diagrams of burrowing Crustacea of the family Callianassidae.

1. *Callianassa gigas.*

2. *Upogebia pugettensis.*
    a) Burrow.
    b) Adult male.

1. <u>Callianassa</u> <u>gigas</u> MALE : DORSAL

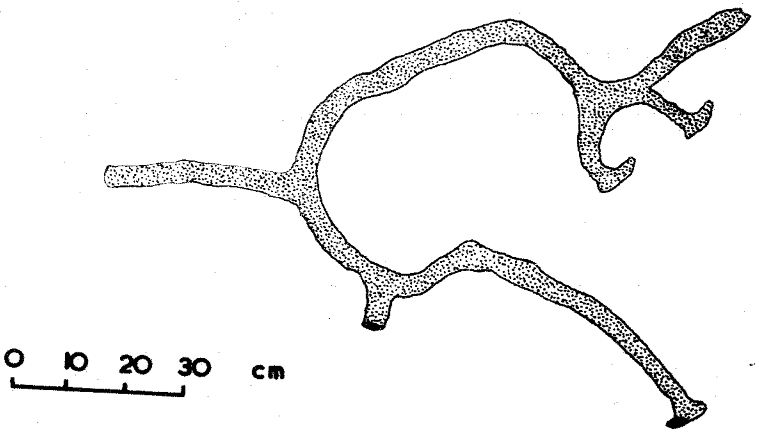
Adult length = 145 mm



Muddy Sand : Restricted distribution

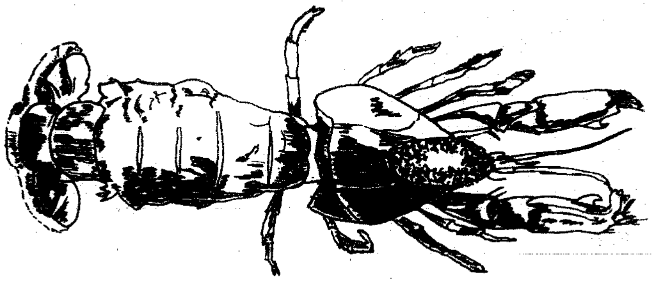
2. <u>Upogebia</u> <u>pugettensis</u> a) BURROW

Plaster Cast



b) MALE : DORSAL

Adult length = 130 mm



Compact gravel , Hard clay :
Widespread distribution

and these are limited to a narrow zone in the rapidly deepening fjords , but are wider amongst the skerries .
Since the distribution of high densities of burrowers is restricted in this way , it is clear that any conclusions about rates of sedimentation in the Swedish fjords based on the degree of "churning" are liable to be in error .

Just how rapidly organisms can completely rework sediment when living under optimum conditions is demonstrated by MACGINITIE (1934) in his study of Callianassa californiensis . This creature , unlike Upogebia, is a deposit feeder , and its burrows therefore ramify to a much greater extent in the quest for food . It is one of the most abundant animals in the muddy sloughs and bays of the west coast of North America , fulfilling a function analogous to that of the earthworm on land . Macginitie calculates that one animal excavates from 20-50cc. of sifted sand in the course of 24hours , and that , on this basis , the population reworks the whole sediment to a depth of 30" in 240days . Certainly , if such a stratum were encountered in the fossil state it would , if interpreted in orthodox fashion , be thought of as marking a prolonged non-sequence or a very slow rate of mud accumulation .

The corollary is probably still more significant . Since this organism , living in its optimum zone , reworks the same sediment every few months , it follows

Text-figure 4.

Diagram of burrow system produced by the Recent crustacean *Callianassa* : plan view of Y-shaped horizontal feeding burrows constructed in littoral mud.

(after Schafer, 1962, fig.186).

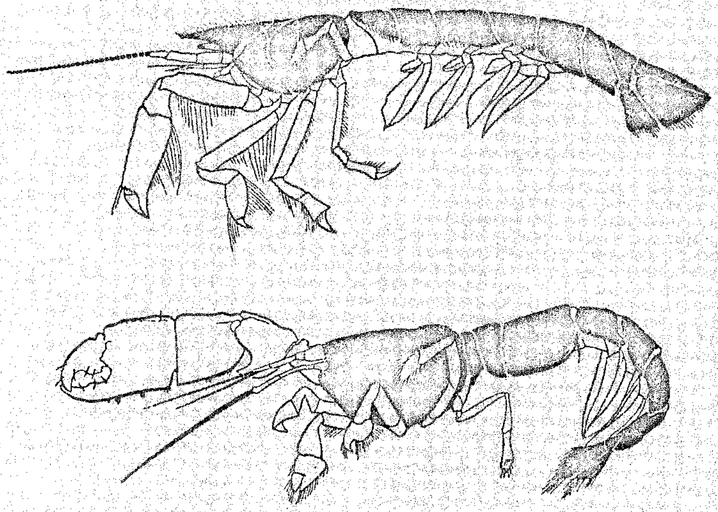


Abb. 185. *Upogebia deltaura* (oben). *Callianassa subterranea.* — Original.

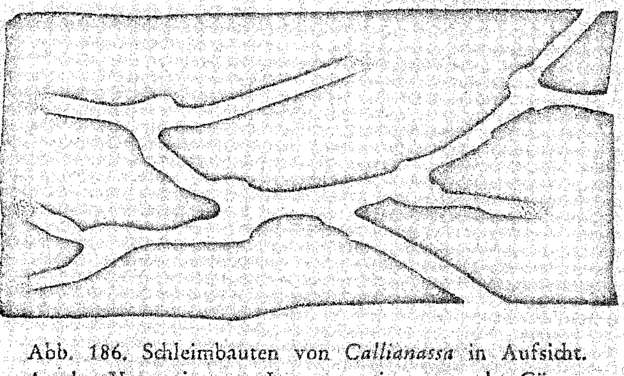


Abb. 186. Schleimbauten von *Callianassa* in Aufsicht. An der Verzweigungen Lumenerweiterungen der Gänge. Original.

that all chance of the preservation of its diagnostic burrow form (Text-fig.4) is lost , with the result that upon fossilization only a confused "bioturbation" effect could be noted .

We therefore have the paradox that due to the vagaries of preservation the characteristic trace of an organism can only be discerned where its activity is less than optimal .

(v) "Fossilization Potential" of nearshore environments

Actualistic studies in Geology in recent years have tended to demonstrate that it is the extraordinary event which is of the greatest significance . Thus a single severe storm accompanying a tidal surge may in one day erode many cubic miles of nearshore sediments which have taken centuries to accumulate . In this way a whole suite of potential trace fossils is lost to the fossil record and may have been so lost in the geological past . Quite clearly , the shallower the water in which a sediment is deposited the more likely is its removal before fossilization . Equally , those burrows constructed nearer to the surface have less chance of being preserved .

A relative scale of "fossilization potential" can be established . Its importance has recently been stressed by GOLDRING (1965) , and REINECK (1960) has estimated that the fossil record of shallow-water sediments represents only 1/10,000 to 1/100,000 of the total time involved . In studying Recent traces , therefore , it is important to consider the likelihood of their preservation .

Consequently a bias is to be expected in the trace-fossil record towards forms originating in a low-energy environment , and the relative abundance of suspected shallow- and deep-water types of trace fossil eventually preserved in the sedimentary record may not reflect in any way the abundance of the populations which formed them .

The degree of protection of a marine sedimentary environment is thus a major factor in determining the preservation of trace fossils . Wave-exposed coasts rarely have shallow burrows preserved , if indeed any are formed initially . Protected estuaries , lagoons and bays stand less chance of having their near-surface features removed by erosion . WEIGELT (1929 , p.24) has shown that conditions are very favourable for the preservation of trace fossils along protected coasts of western Australia , where at Chilli Creek , north of Beagle Bay , the tidal range is 28 feet and the area set free by the ebb is seven miles wide . This coastal strip , enclosed by mangroves , is teeming with millions of burrowing crabs , and Weigelt's observations on the mode of preservation of the burrows are worth quoting :-

" Accomodation to life on land has already made such marked progress that the decapods protect themselves at the start of the flood tide . Ocypode and Mictyris therefore remain in their burrows during the flood tide , the entrances covered and the water-current stopped with sand . The winking crabs are able to close their burrows , like other species , with the big main claw (Text-fig.3) . But the most remarkable behaviour is that of Uca , which closes its burrow during the flood tide with a self-made round lid . This behaviour enables us easily to understand that it is possible , under specific circumstances , for widespread extermination of animals to occur . At the same time their burrows can sometimes be preserved during excessive flooding of the slime and mud area lying behind the lagoons " (translation) .

Such lagoons are often also areas of quite rapid subsidence , as SHEPARD (1953) has demonstrated along the eastern seaboard of America , where silting at the rate of 3 feet / century has been in progress for thousands of years ; so that traces , once formed , are soon covered by sediment .

Regional subsidence is thus an important factor in the preservation of trace fossils . Subsidence is considerable in the vicinity of a prograding delta , and may explain why trace fossils are abundantly preserved in deltaic sediments in the geological record .

(vi) Effect of grain-size on trace-fossil preservation

The detail of preservation of trace fossils often correlates with the particle size of the sediment within which the structure is excavated . Crustacean burrows demonstrate this relationship . A crab , for example , may extend its burrow by scraping material from the walls with its pointed claws , and although the very same process may be used to burrow in muds or in coarse sands , fossil burrows preserved in the latter would never show details of the original scrape-marks which are always preserved in the finer lithologies .

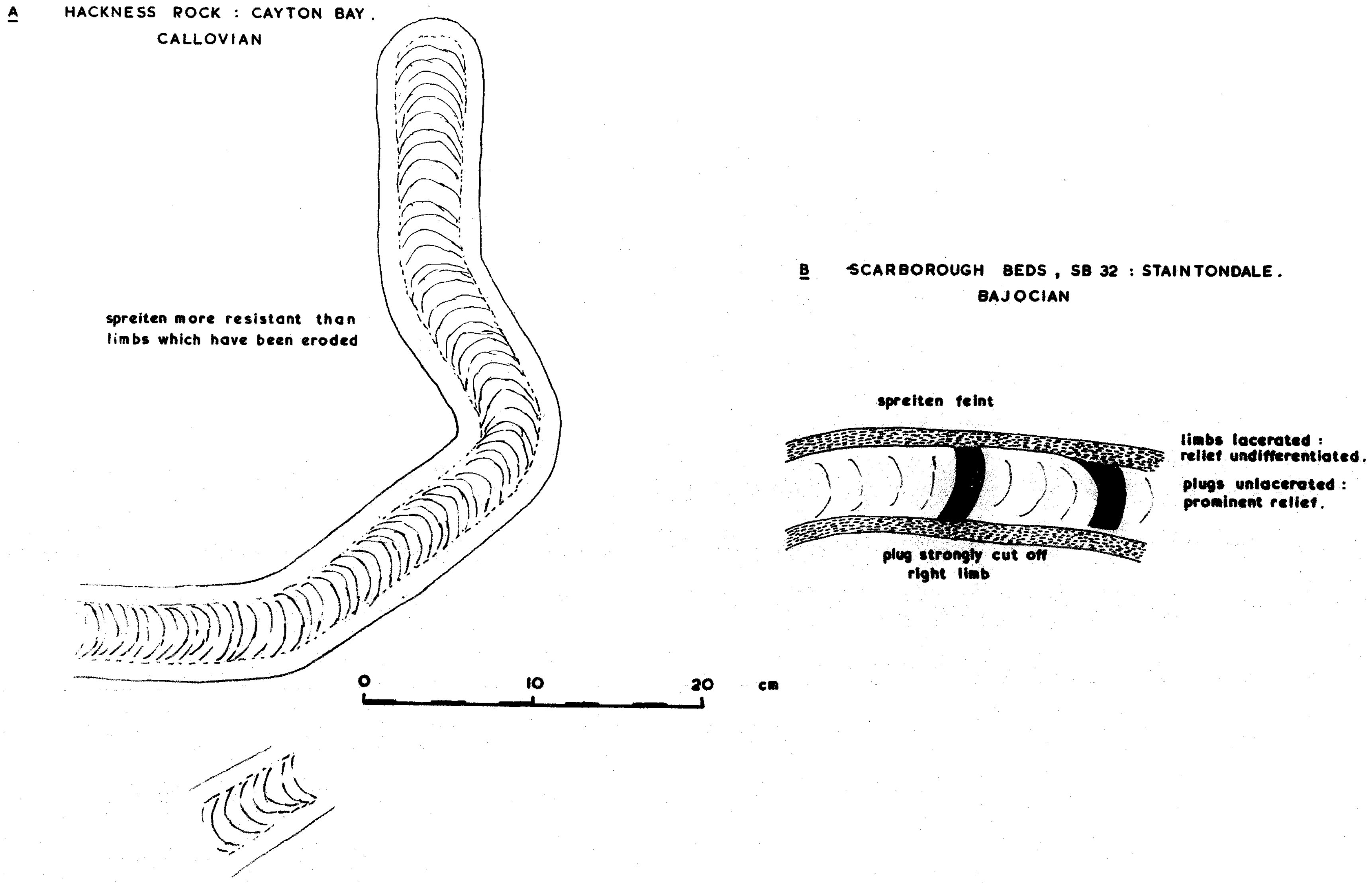
Plate 5 shows specimens of the supposed crustacean burrow Rhizocorallium . In the Middle Lias Ironstone Series of Staithes , Yorkshire , scrape-marks are preserved in great detail (Pl.26~~5A~~) in a chamositic siderite mudstone , and again from the Ellerbeck Bed of Staintondale (Pl. 5) , where they are impressed into kaolinitic silts . The same trace fossil is also illustrated (Text-fig.5) preserved in different lithologies . Within the Scarborough Beds the wall sculpture of Rhizocorallium is discernible in silty limestones , though not **im** calcareous grits . The Callovian example from Cayton Bay shows completely different weathering characteristics in which the burrows are less resistant than the internal spreiten . Comparable lithologies

Text-figure 5.

Diagram illustrating two modes of preservation of the protrusive crustacean feeding burrow *Rhizocorallium commune*.

A. Example from the Hackness Rock (Callovian) of Cayton Bay, Scarborough, with very strongly developed *Spreite* and eroded limbs preserved in ferruginous sandstone.

B. Example from the Scarborough Beds (Bajocian of Staintondale, with feeble *Spreite* and sculptured limbs: preserved in ripple-marked silty limestone (S.D. 32).


A HACKNESS ROCK : CAYTON BAY.
CALLOVIAN
spreiten more resistant than limbs which have been eroded
0
10
20
cm
B SCARBOROUGH BEDS, SB 32 : STAINTONDALE.
BAJOCIAN
spreiten feint
limbs lacerated : relief undifferentiated.
plugs unlacerated : prominent relief.
plug strongly cut off right limb

from the Dorset Corallian present similar Rhizocorallium .

Examples from the Calcareous Grit of Dorset and the Ironstone Series of Yorkshire are two extremes of a continuous series of preservational types . The two end-members are strikingly different in trace-morphology and it is not surprising that they have frequently been treated as separate trace-fossil species , Rh. commune and Rh. jenense . WEIGELT (1929 , p.27) was aware of the danger of this practice of species discrimination on the basis of preservational differences . He observed that examples from marly layers in the Upper Chalk , such as the Koeneni-marl of the Lower Emscherian in Halberstadt , possess an indistinct sculpture comparable with "Moor's lines on a pressed marble cylinder" , whereas occurrences from other Series are often completely devoid of sculpture . As he says :-

> " .... the preservation of such fine digging-traces depends in high degree upon the nature of the surrounding medium " (translation) .

(vii) Thixotropic variation and its influence on preservation

Since Weigelt was able to distinguish Rhizocorallium with various degrees of scraping of the wall preserved in the same lithology , it follows that some other control acts on the type of preservation in addition to the gross grain-size of the sediment . WEIGELT (op.cit.,p.26) considered that specimens with pronounced relief and strongly rounded ribs were impressed in more plastic and less firm materials . Recent experiments show thixotropy to be the cause

The concentration of many burrowing animals in gregarious clusters on intertidal flats results from their burrowing ability being controlled by thixotropy . CHAPMAN (1949) has demonstrated that the lug-worm Arenicola marina is restricted to areas where the substratum retains enough water to keep it soft (Plate 6) . The change in thixotropy across the mudflats is in no way due to any change in grain-size of the sediment , for identical effects are produced by slight changes in the slope of the sediment surface .

This may well be the cause of the random distribution of many vertical burrows in the geological record . HALLAM & SWETT (1966 , p.105) , for example , attribute the absence of trace fossils from certain parts of the Lower Cambrian Pipe Rock , lithologically no different from the rest , to inappropriate thixotropic conditions for burrowing , though admit it could also be a function of preservation .

Thus the ecological limits of many burrowers initially may be controlled by thixotropy , while others formed contemporaneously become obliterated by subsequent flow of the 'gel'-like sediment .

The role of thixotropy cannot be fully appreciated without a consideration of surface-formed trails such as those produced by the gastropod Littorina , and of the various modifications of preservation created by the changing thixotropy of the superficial sediment . RAYMOND (1922) described the trails produced by Littorina ; HANTZSCHEL (1938) presented a more detailed and well illustrated account . The trail is slightly wider than the aperture of the gastropod and is bounded by a pair of lateral ridges between which occur transverse ridges bowed forward in the direction of travel (Plate 7A) . There are many variations from this basic pattern formed on a muddy surface . RAYMOND (op.cit., p.110) mentions that Littorina , when travelling in water , forms lateral ridges which are high and broad , and transverse ridges are absent (c.f. Plate 9C) . The absence of the transverse ridges may also be a function of thixotropy , since occasionally they fail , apparently at random (Plate 7B). Their absence may also be due to more than one animal progressing along the same track , as I have observed on mud-covered rocky foreshores near Whitby , where the main trail becomes markedly overdeepened and the lateral ridges pronounced (Plate 7C) .

Identical phenomena are to be found in trails produced by other creatures . The amphipod Corophium volutator provides a good example (HANTZSCHEL 1939).

The typical trail has a beaded appearance (Plate 8A) , though this is often lost due to subsequent thixotropic flow of the muddy sand (plate 8B) .

Comparable fossil trails are well-developed in the Carboniferous of Northern England . They appear to be absent from the British Jurassic . The form *Eione moniliformis* TATE is very similar in its beaded character to the Recent *Corophium* trail (Plate 9A) when fully preserved , but it is frequently accompanied by a form which is unbeaded and possesses marked lateral ridges . The two forms are seen together at Swath Beck Hush on the Moor House National Nature Reserve (Plate 9B / 9C) in a flaggy fine-grained micaceous sandstone . It is also very noticeable that forms of *Crossopodia* are present here in which the transverse striations generally characteristic of this trace-fossil genus are lacking . This also may be explained by a thixotropy unfavourable to the preservation of fine detail .

These Carboniferous trails show considerable morphological dissimilarity , and their dissociated study would lead to their being placed in different trace-fossil species . Consideration of the range of preservational types exhibited by a single Recent trail clearly demonstrates that thixotropic variation can easily account for widely differing trace morphology . Consequently it is unwise to establish finely-discriminated trace-fossil species , and any diagnosis should be sufficiently broad to cope with such exigences .

(viii) Compaction phenomena

Two types of compaction may occur . The first is syn-depositional , where an originally hollow tunnel collapses behind its producer : this is clearly related to the thixotropy of the surrounding sediment . The second is due to the weight of superincumbent sediment , which may considerably distort the tunnel outline of some trace fossils . SCOTT SIMPSON (1957 , Pl. XXI/1) has illustrated a specimen of Chondrites from the Belemnite Marl of the Dorset Lower Lias , where the initially circular tunnels are now clearly ovoid in cross-section . Commonly this may occur where sediment has passively drifted into a burrow system , and not been actively plugged by the burrowing organism . Where plugging has occurred , however , burrows tend to retain their true cross-sections : in such instances there is often load deformation around the structure . Specimens of Thalassinoides from the Lower Chalk of Hunstanton may even show slickensiding along the burrow walls (A.J.STOYEL , personal communication 1966) .

Compaction distortion effects are thus slight in trace fossils compared with the considerable crushing which may occur with shelly fossils, where tectonic distortion may also cause great difficulty to the taxonomist.

(ix) Trace fossils & Stratinomy

Since many burrows are produced by deposit feeders exploiting the sediment for food it is not surprising that many are related to organic-rich layers. Organic carbon is known to be strongly adsorbed onto clay minerals, so it is to be expected that many trace fossils will be preserved at the interfaces between sandy and clayey sediments. In fact the "sole trail" formed on the lower surface of a greywacke is a very abundant type of trace fossil. Other burrows are constructed in relation to the local ground-water table. In this case also a clay underlying a sand will give rise to "sole trails".

Hence many structures may be related to the lower boundaries of sandstones, rather than the upper, in an alternating sequence of Flysch-like sediments (e.g. SCOTT 1966). It is thus difficult to distinguish sand casts of surface trails which were impressed on clay from internal traces which were produced by activity at an already established sand/clay interface. Seilacher, on the basis of experiments with living animals, has demonstrated that traces formed within sediment ("innenspuren") are <u>more</u>

distinctly preserved. This quality is difficult to assess in the majority of natural cases since it requires something less distinctly preserved for comparison. Thus to use SEILACHER's terminology (1964a), the distinction between a positive exogeneous hypo-relief and a positive endogeneous hypo-relief (Text-fig.6a) is equivocal. Moreover, their separation from epi-reliefs is frequently difficult, especially when the 'way-up' of a specimen may be in doubt.

Regrettably it must be concluded that the theoretically sound stratinomic classification proposed by Seilacher (Table 2) is often difficult to apply in practice when dealing with hypo- and epi-reliefs. Such a scheme does explain the great variation in the type of preservation to be found in any one trace fossil as a result of construction at different levels within the sediment.

WEISS (1940) pointed out this phenomenon in the bilobed gallery Gyrochorte, well known from the German Jurassic and the British Carboniferous (Plate 14). He observed that many of the variations shown on Text-fig,7 were the result of subsequent load compaction of surrounding sediment (e.g. No.9) and that clearly they did not merit the specific identity previously given them; nor did the remaining preservational variants.

The ambiguity associated with hypo- and epi-reliefs reduces the value of the nomenclature proposed

Text-figure 6.

The stratinomic classification of trace fossils (after SEILACHER, 1964, and [illegible], 1965).

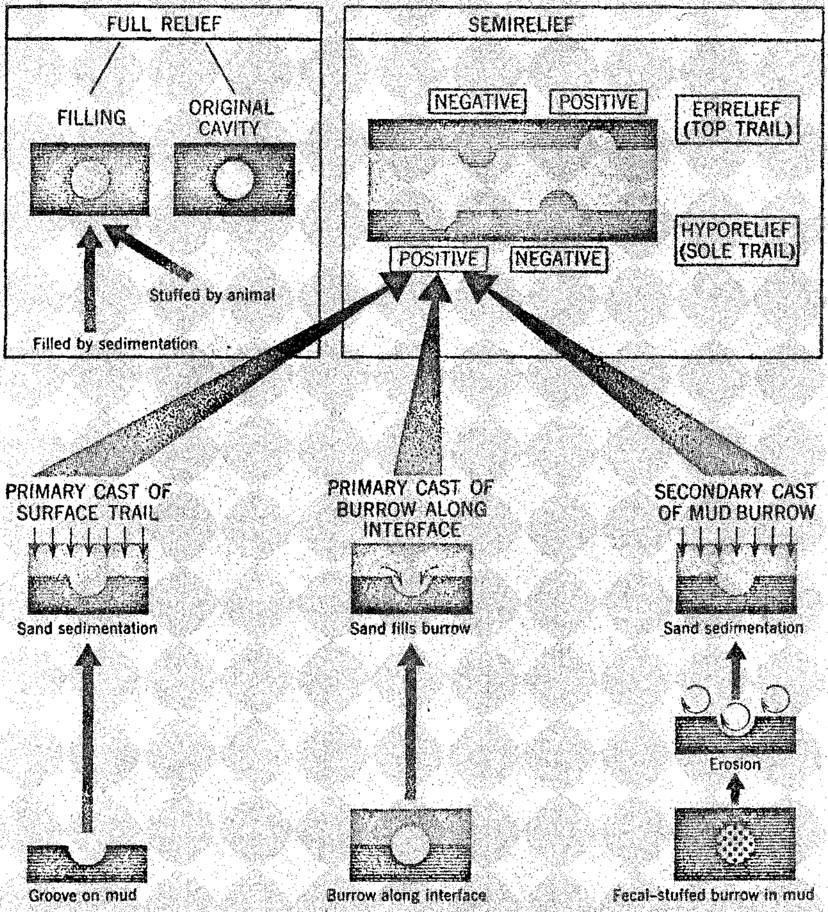


Fig. 1 Preservation of trace fossils. *Since the preparation of this chart a somewhat modified terminology has been suggested to the Committee for the Nomenclature of Sedimentary Structures. This includes the following new terms:* Convex *for positive, and* concave *instead of negative semireliefs.* Exogene *for actual surface trails, versus* endogene *for primary casts of internal origin, and* pseudexogene *for the secondary casts.* *Active fill, if burrow was stuffed by the animal,* passive *fill, if it was filled by sedimentation.*

CHART I

RELATION BETWEEN PRESERVATIONAL PROCESSES AND GENETIC AND DESCRIPTIVE TERMINOLOGY

	Original structure	*Preservational process*[1]	*Genetic term*	*Descriptive terms for fossil*	
				Semireliefs	
				epirelief	*hyporelief*
(*1*)	Surface impression	(*a*) hidden by cover of same sediment †			
		(*b*) covered by different sediment	exogene	concave	convex
(*2*)	Agitation from the surface	top layer protects internal interface impression	endogene	concave	convex
(*3*)	Burrow along sand-mud interface (see also 4)				
	(*a*) open	sand presses into the mud mold	endogene	convex	convex
	(*b*) mud-stuffed	outline against mud disappears	endogene	concave	concave
	(*c*) sand-stuffed	outline against sand disappears	endogene	convex	convex
(*4*)	Burrow within homogeneous sediment				
	(*a*) mud-stuffed burrow in mud	(*a, a*) uncovered by slight erosion; then recast with sand	pseudexogene	—	convex
				Full reliefs	
		(*a, b*) obliterated †			
	(*b*) other stuffed burrows	(*a, c*) preserved and accentuated during diagenesis	active	fill	
	(*c*) open tunnel	(*c, a*) filled by sedimentation	passive		
			weathered	cavity	
		(*c, b*) remaining open	original		
				Biodeformational structures	
			In cross section, any biogenic sedimentary structure may appear this way		

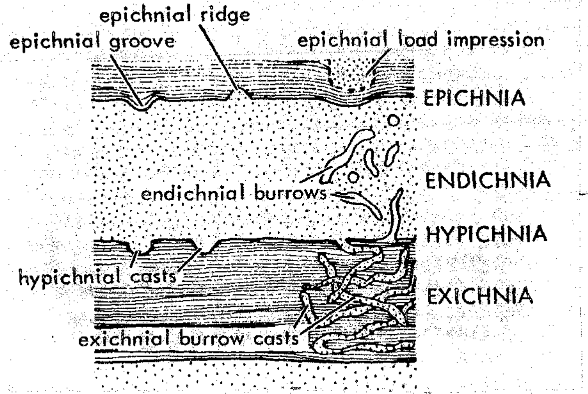
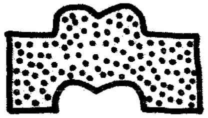
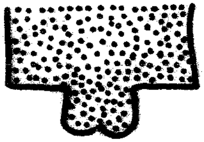


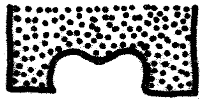
TABLE TWO

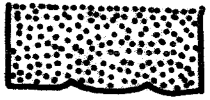
Text-figure 7.

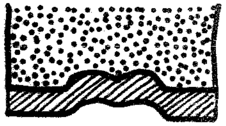
Diagram illustrating the various
modes of preservation of the
trace fossil *Gyrochorte*
(after WEISS, 1940).

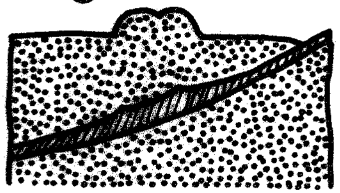
1


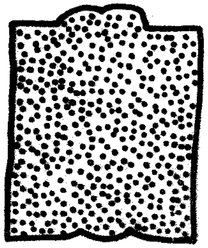
2


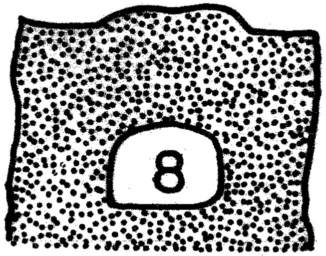
3


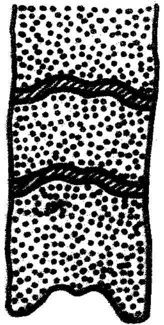
4


5


6


7


8


9


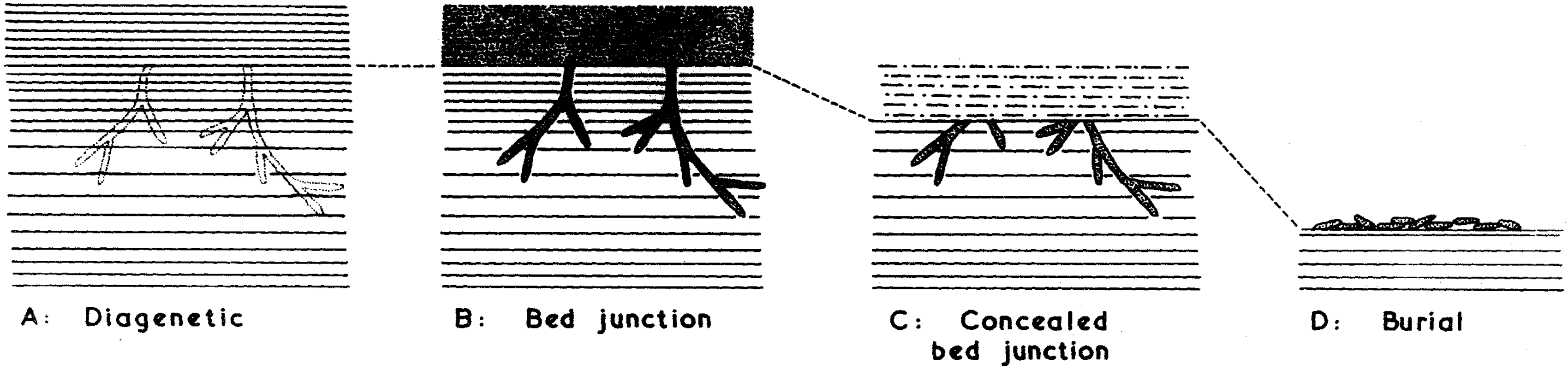
by Seilacher . The slightly simpler classification suggested by MARTINSSON (1965 , pp.202-203) could be used as an alternative (Text-fig.6b) . It serves to describe any trace fossil from a topographic standpoint , and may be used in conjunction with common geological and ethological observations .

Burrows preserved as full reliefs (Text-fig.6a) may offer much interesting , and unequivocal , stratinomic evidence . SCOTT SIMPSON (1957 , pp.479-481) , while making no pretence at an all-embracing classification , has recognised four stratinomic types of preservation in Chondrites . These have subsequently been widely recognised in strata other than the Dinantian and the Lias from which they were initially described . The four types are shown on Text-fig.8 , and each have important sedimentological connotations : they are :-

1) Diagenetic preservation - where there is no change in the type of sediment filling the burrows (Plate 4); generally indicating quiet conditions with lack of penecontemporaneous erosion :
2) Bed-junction preservation - where a change takes place in the type of sediment filling the burrows (Plate 10); sometimes accompanied by slight penecontemporaneous erosion indicated by removal of the proximal shafts :

Text-figure 8.

Diagram illustrating the four different types of preservation occurring in the trace fossil *Chondrites* (redrawn : after SIMPSON, 1957).


A: Diagenetic
B: Bed junction
C: Concealed bed junction
D: Burial

3) Concealed bed-junction - where the sediment filling the burrows is of a type different from that overlying the burrowed stratum; e.g. sand-filled burrows in shale , overlain by siltstone ; indicating considerable local winnowing following a sharp lithological change :

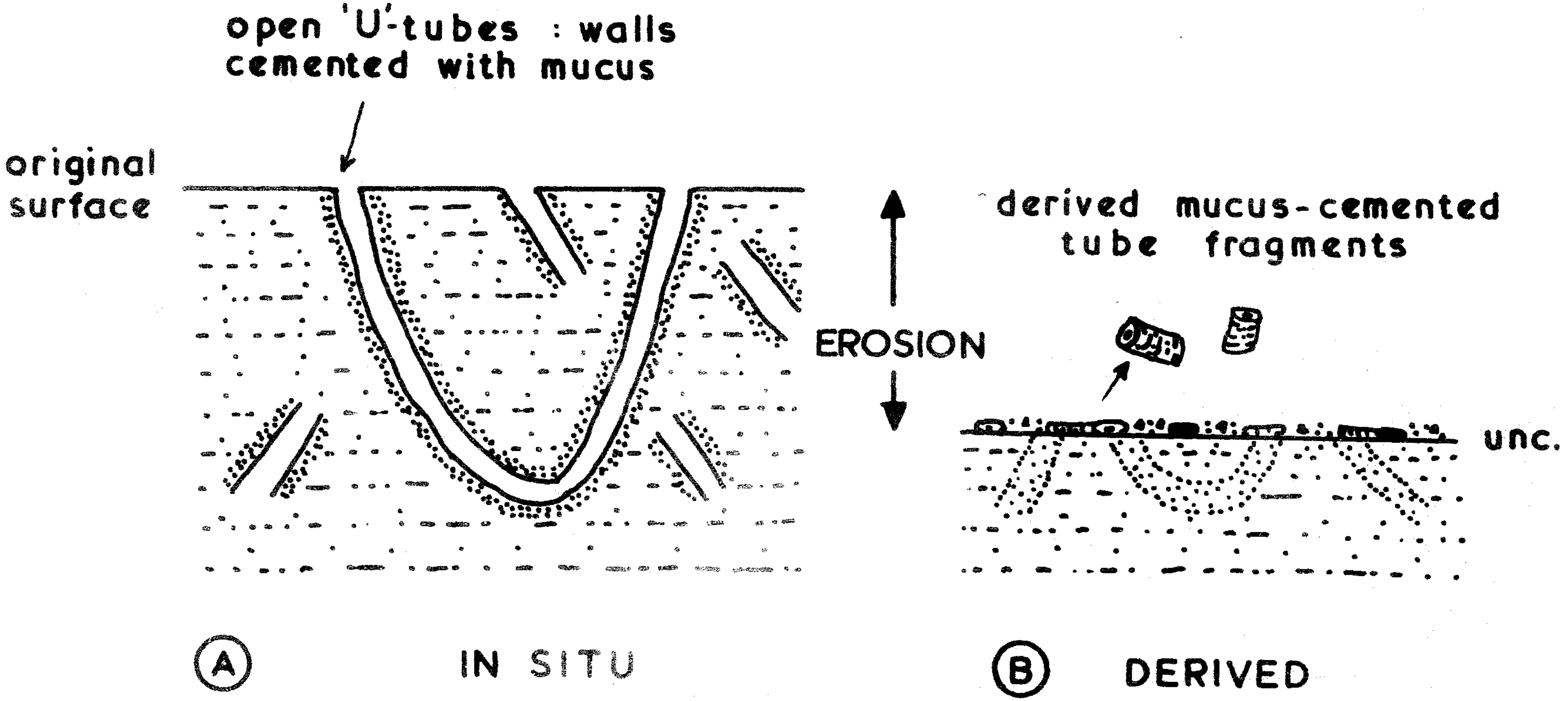
4) Burial preservation - where the sediment surrounding the burrows has been removed to leave a pile of tubes as a minor intraformational conglomerate ; indicating definite erosion and the removal of the surface from which the burrows originated .

Whereas types 1 & 2 represent low energy environments and are common in the Lias and the Carboniferous Limestone of South-West England , types 3 & 4 occur in higher energy environments and are found , for example , in the Upper Emsian Lynton Beds and the Givetian Ilfracombe Beds (GOLDRING 1964 , p.137) where there is a complete absence of near-surface trails . Here burial preservation , unknown in the Lias , is common , and intraformational conglomerates composed of the tubes of Arenicolites curvatus (Text-fig.9) are also found in the neighbouring Baggy Beds .

The presence of derived trace fossils may seem a little alarming , in view of the fact that one of their greatest advantages is generally considered to be their

Text-figure 9.

Diagram illustrating *in situ* and derived preservation of the trace fossil *Arenicolites curvatus* from the Devonian Baggy Beds (after GOLDRING 1964).


open 'U'-tubes : walls cemented with mucus
original surface
EROSION
derived mucus-cemented tube fragments
unc.
Ⓐ IN SITU
Ⓑ DERIVED

truly in situ nature compared with shelly fossils , which are frequently current-sorted and do not represent autochthonous life . However , trace fossils are so completely different in their derived state from their normal mode of occurrence , unlike shelly fossils , that they are easily recognisable .

Moreover , these occasional occurrences of trace fossils preserved by burial preservation reveal the nature of the burrowing process of the organism . The burrow systems must clearly have been strengthened in some way to make them more resistant than the matrix enclosing them . In the examples just mentioned it is logical to assume that the walls of the burrow were lined with mucus during construction . In other burrows , plugging with faecal matter may produce greater resistance to erosion and the structure may be sufficiently cohesive to become incorporated in later conglomerates . Thus HECKER (1965 , p.118 , Pl.XI/3) records abundant derived Rhizoliths in transgressive basal conglomerates from the Palaeogene of the Fergana Bay region of Central Asia . As these are derived steinkerns of the stuffed crustacean burrow *Rhizocorallium* , however , it is possible that collophanous impregnations may have given the structure added rigidity . This secretion is known to be copiously produced by present-day burrowing decapods (WEIMER & HOYT 1964 , p.763) .

CHAPTER FIVE.

CLASSIFICATION AND THE TAXONOMIC PROBLEM.

(1) Classification

It is impossible to classify trace fossils in the same manner as body fossils. This is because many different traces can be produced by the same animal, depending on the type of its activity, and on fortuitous properties of the sediment. Moreover, adaptive modification has led to the production of similar traces in completely unrelated groups of creatures. Thus amphipods, annelids and hemichordates may all produce similar 'U'-shaped burrows. Because of the widespread possibility of homoeomorphy any classification which attempts to arrange trace fossils according to the morphology of their producers is liable to be erroneous.

Classification should ultimately be based on ethological criteria, the morphology of the trace being interpreted as the result of a particular type of behaviour. Many of the earlier attempts at classification (e.g. FUCHS 1895) usefully grouped various morphological types of trace fossil together, such as the 'fucoids', the 'heiroglyphs' and the Spreiten-burrows (which FUCHS termed the "darkest and most enigmatic area in the kingdom of the problematical fossils"), but failed to recognise the ethological significance of each type. Later classifications have been along similar lines, with a number of groups of approximate familial status being created. RICHTER (1927) applied a useful distinction between 'U'-shaped burrows with and without Spreiten (Rhizocorallidae and Arenicolitidae), though some difficulty was experienced when applying this scheme to certain Jurassic burrows from Yorkshire. RICHTER was also one of the first to stress the inadvisability of too narrow a grouping of trace fossils.

Nevertheless, KREJCI-GRAF (1932) presented a very detailed subdivision of trace fossils with isolated examples of each type, but failed in his 'superordinal' units to create a system which in any way improved that of Fuchs nearly forty years earlier. This lengthy classification has found little favour.

A classification is essentially an artifact contrived to aid human thought. According to this definition it should clearly be both useful and usable.

One which not only overcomes the inherent difficulties of a particular group but also takes advantage of any special peculiarities stands the best chance of becoming generally accepted. Such a classification was proposed by SEILACHER (1953a, pp. 432-434) and has not subsequently been improved. It involves five units of approximate ordinal status (Text-fig. 10, TABLE 3):-

TABLE 3

(1) DOMICHNIA - dwelling burrows: constructed vertically: may be simple or 'U'-shaped:

(2) FODINICHNIA - feeding burrows: extensive systems reflecting efficient use of unit *volume* of sediment:

(3) PASCICHNIA - grazing trails: spirals and meanders reflecting intensive use of unit *surface area*:

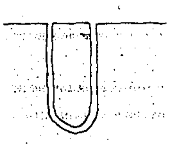
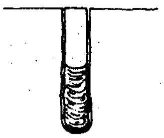
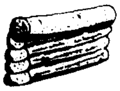
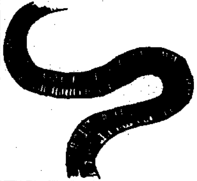
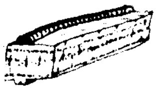
(4) CUBICHNIA - resting trails: outlines corresponding roughly to shape of producer:

(5) REPICHNIA - crawling trails: produced during directed locomotion by vagile benthos.

This classification has several advantages. It collects ecologically similar groups of trace fossils together, so that the group of resting trails (Cubichnia) is as valid for the extinct trilobites as it is for Recent

Text-figure 10.

Diagram showing the distribution of English Jurassic and Carboniferous trace fossils in Seilacher's five-fold ethological classification, with illustrations of comparative examples.

		BAJOCIAN Yorkshire	NAMURIAN Northumberland
DOMICHNIA	Dwelling burrows	*Arenicolites* 	*Diplocraterion* 
FODINICHNIA	Feeding burrows	*Teichichnus* 	*Phycodes* 
PASCICHNIA	Grazing trails	*ABSENT*	*Crossopodia* 
CUBICHNIA	Resting impressions	*VERY RARE*	*VERY RARE*
REPICHNIA	Crawling trails	*Gyrochorte* 	*Gyrochorte* 

arthropods living the same mode of life. Because of this grouping, questions concerning the nature of the trail-producer are of subordinate importance, and Seilacher's classification does justice to, rather than circumnavigates, the peculiar properties of trace fossils. The classification enables any trace fossil, even if it cannot be identified taxonomically, to be placed in a meaningful category. It has also proved to be very useful in distinguishing various ichnofacies, each characterised by a different ecological assemblage of traces and each apparently indicative of a particular major depth zone (SEILACHER 1964b, pp. 307-314).

Occasionally there has been a tendency in the past to read too much into the complicated patterns exhibited by trace fossils, and there have been a few attempts at a 'psycho-physiological' classification (e.g. HUNDT 1932, DESIO 1940) shown in Table 4.

TABLE 4

A) SURFACE TRACES	B) TRACES AT DEPTH
1: thigmotaxes (meanders and free spirals)	1: tubular galleries

2: homostrophies (meanders and obligatory spirals)	2: 'U'-shaped galleries
3: phobotaxes (stelliforms, corymbiforms, pseudocorymbiforms, chondritiforms)	3: 'pocket' galleries
4: straight lines (simple, ramifying)	4: irregular galleries

Apart from the surprise of finding *Chondrites* among the surface traces, there are other more fundamental grounds for not adopting this classification. As LESSERTISSEUR (1955, p. 17) says:-

> "L'incertitude qui règne en bien des cas sur la nature des stimulus mis en jeu, ou l'absence ou la pluralité de ces stimulus permettent de condamner ces classifications, qui font d'ailleurs d'inévitables emprunts aux critères morphologiques".

Furthermore, as SEILACHER (1964b, p. 300) points out, "surface trails and burrows are fundamentally different only to our eyes. For many benthonic animals it makes little difference whether they creep at the surface or along bedding planes inside the sediment, and for the palaeontologist it is often impossible to differentiate these two types of motion". (c.f. p.44).

Clearly then, any classification whose chief distinction is between surface and sub-surface traces (e.g. LESSERTISSEUR 1955, p. 19, tab. 5) will be difficult to apply, and may often create misplaced emphasis. Thus Seilacher's classification remains the most easily applied and the most meaningful.

Recently attempts have been made to rearrange and 'improve' Seilacher's scheme (MÜLLER 1962) by the creation of 'new' superordinal ranks into which Seilacher's original terms, and several additional ones, have to be fitted (Table 5).

TABLE 5

1) CIBICHNIA Muller - eating trails:-
    (i) Fodinichnia Seilacher - extensive tunnel systems;
    (ii) Mordichnia Muller - biting and gnawing trails;
    (iii) Pascichnia Seilacher - grazing trails:
2) MOVICHNIA Muller - moving trails:-
    (i) Repichnia Seilacher - crawling trails;
    (ii) Cursichnia Muller - running trails;

(iii) Natichnia Muller - swimming trails;

(iv) Volichnia Muller - flying trails:

3) QUIETICHNIA Muller - resting trails:-

(i) Cubichnia Seilacher - resting impressions s.s.;

(ii) Domichnia Seilacher - dwelling burrows.

This classification is very sound theoretically, but lacks the brevity and ease of application of Seilacher's simpler scheme: the Volichnia must constitute an exceedingly rare group in Nature. Other terms such as 'Quietichnia' do not improve an already clumsy terminology, and the inclusion in this group of the Domichnia seems a peculiar choice, since vertical 'U'-shaped burrows often show considerable movement in response to penecontemporaneous erosion and sedimentation (e.g. GOLDRING 1964) and are not genetically connected with the Cubichnia.

(ii) Historical basis of the taxonomic problem

There are many anomalies in trace-fossil taxonomy since structures which are now understood to be invertebrate burrows were considered originally to be plant fossils and because the Law of Priority applies, many nomenclatural inconsistencies cannot be avoided. Many genera and species were created on the basis of the shape of the presumed algal "thallus" and according to the angle at which the branches diverged. Much of this division was too narrow. There are thus a great many superfluous names in the literature and these are scattered throughout the world in palaeobotanical, palaeontological, stratigraphical, regional geological and field excursion accounts. This means that the establishing of complete synonymies is a lengthy task and much research is necessary before the creation of new and reliable trace-fossil taxa.

The world-wide distribution and the very long time-range of the majority of trace fossils are very important factors to bear in mind. "New" species founded on isolated, indifferently preserved specimens are particularly suspect, and the warnings of JAMES (1884) went unheeded for many years. In view of the current interest in trace fossils it is as well to repeat them:-

> "When every turn made by a worm or shell, and every print left by the claw of a crustacean is described as a new addition to Science, it is time to call 'halt!' and eliminate some of the old before making any more new species."

(iii) Recent trends in trace-fossil taxonomy

Twenty synonyms of the trace-fossil genus Chondrites are recorded in the Treatise (HANTZSCHEL 1962 W.187) and sixteen for the spreiten burrow Zoophycos (idem, W. 220). These are probably the two worst examples. The problem of generic synonymy has now been alleviated by the publication of the trace-fossil part of the "Fossilium Catalogus" (HANTZSCHEL 1965), though species discrimination still involves extensive consultation of foreign literature.

Many authors therefore prefer not to designate trace-fossil species. SCOTT SIMPSON (1957, p.489) concludes that: "in the present state of our knowledge it is doubtful whether any advantage is obtained by attempting to recognise ichnospecies within Chondrites". VEEVERS (1962) did not attempt to designate species of Rhizocorallium from the Lower Cretaceous of Australia because he was unable to consult the relevant German literature. KSIAZKIEWICZ (1961) published original formal descriptions of three "nova forma", Acanthoraphe, Helicoraphe & Megagrapton, from the Polish Flysh without specific names. This practice may become increasingly popular. Other workers, fully acquainted with the world literature, still prefer not to recognise distinct species of trace fossils.

HANTZSCHEL (1964), in his study of the Upper Campanian trace fossils of Central Westphalia, formally named seven trace-fossil genera, but only differentiated species in one, *Paleodictyon*, and then on the basis of size, a criterion not favoured by other workers.

In view of the widespread morphological variety which may be created by fortuitous properties in the original sediment (*vide* Chapter Four) this "lumping" is sensible. Occasionally, however, it has been taken too far, and attempts have been made to name tracks and trails simply as 'species' of one genus *Ichnium*. In this case the lack of refinement is a drawback to the use of trace fossils as detailed facies indicators.

Provided that "artificial" elements in trace morphology can be satisfactorily eliminated, and that the variant is of sufficiently widespread occurrence to be useful in facies studies, there appears to be scope for establishing trace-fossil species. Within the trace-fossil genus *Rhizocorallium*, for example, the species *Rh. commune* falls into the "artificial" category due to its indistinct wall sculpture being a function of the grain-size of the surrounding sediment (*vide supra*, p.38): *Rh. uliarensis* (FIRTION 1958, p.107) is a valid species, however, since the coiling of the axis of the 'U' distinguishes it from the type species *Rh. jenense*, in whatever lithology it is preserved.

At the present time two opposed concepts of trace-fossil nomenclature exist. The first stems from those authors who decline to name trace fossils formally, not wishing to create a taxonomic system outside ICZN jurisdiction (e.g. RAYNER 1963, p.127). This ideologically justifiable procedure suffers from a considerable practical disadvantage, for experience shows that unnamed forms usually escape notice in later literature.

The second concept is adopted by those authors who recognise that some form of systematic nomenclature is desirable if progress is to be made. In order that any newly created trace-fossil name should be readily distinguishable from a true Linnaean species, it is recommended that the suffix "*-ichnus*" be added. If the name also symbolises some morphological peculiarity of the trace fossil (e.g. *Sagittichnus* SEILACHER), so much the better.

(iv) Taxonomic characters in trace fossils

Just as in body fossils, there is no uniformity of status for any one taxonomic character. The direction of burrowing of certain trace fossils, for example, appears to some workers to be fundamentally important, and to merit generic status. Taking 'U'-shaped spreiten burrows, it seems to me that there is a basic difference between those which are vertical, and generally found in coarse clastic sediments, representing the dwelling burrows (Domichnia) of suspension feeders, and those which are horizontal, and generally found in rocks with considerable admixed clay, representing extensive feeding burrows (Fodinichnia) of deposit feeders. SEILACHER (1953, p.448) evidently did not consider this sufficient justification for retaining the form Diplocraterion TORELL 1870 for vertical spreiten burrows, placing the type species D. parallelum in the earlier trace-fossil genus Rhizocorallium ZENKER 1836. Consequently he refers to the form as Rhizocorallium parallelum (TORELL 1870).

Most subsequent workers (e.g. GOLDRING 1962, p.237) maintain that the distinction between vertical and horizontal spreiten burrows is a fundamental one, and should be recognised at the generic level.

Certainly no one to date appears to have considered the possibility that *Teichichnus rectus* SEILACHER 1955 is simply a vertical form of the horizontal *Zoophycos* MASSALONGO 1855, as seems likely: we may yet see the form treated as "*Zoophycos rectus*" (SEILACHER).

The distinction between vertical and horizontal directions of burrowing has not the same significance in simple structures as in the more complex spreiten burrows. *Planolites montanus* RICHTER 1937 is a simple horizontal sand-filled burrow; *Planolites ophthalmoides* JESSEN 1950 an essentially vertical burrow with an eye-like halo. The much larger burrows of the decapod *Callianassa* are likewise distinguished at specific level according to the dominant direction of burrowing. The type species *Ophiomorpha nodosa* LUNDGREN 1891 has an essentially vertical attitude, whereas *O. borneensis* KEIJ 1965 has a dominantly horizontal orientation.

Size has never been a popular taxonomic character. As already mentioned (p. 62) two species of the honeycomb network *Paleodictyon* are often distinguished on the basis of size, *P. giganteum* PERUZZI and *P. minutum* KINDELAN (SACCO 1939). In the vertical 'U'-shaped burrows, however, no such size distinction is possible since variation is continuous, unlike the discontinuous variation of *Paleodictyon*. WESTERGARD (1931, p.9), in his redescription of the type species of *Diplocraterion*, *D. parallelum* TORELL, stressed the great variation in burrow depth and length of examples from the type horizon at the type locality.

Among the Domichnia it is the nature of the aperture of the burrow which is of greater taxonomic importance than the absolute size, and the character is generally considered to have generic significance. Thus *Diplocraterion* TORELL 1870 is distinguished from the similar *Corophioides* SMITH 1893 by the presence of funnel-shaped apertures: *Monocraterion* TORELL 1870 is similarly distinguished from *Skolithos* HALDEMAN 1840. Since these vertical burrows are usually found in littoral sediments, it follows that their apertures are frequently truncated by erosion, so that the nature of the aperture is not an ideal generic character. Eroded examples of *Monocraterion* are thus indistinguishable from *Skolithos*.

Attempts have been made in the past to differentiate the two on the basis of the degree of crowding of the burrows, though in view of the wide variation in burrow density shown by the type species, S. linearis, this must not be thought of as a diagnostic feature. HALLAM & SWETT (1966, p.102), having stated that "the degree of crowding of a given trace fossil hardly seems a satisfactory character in the diagnosis of that fossil", proceed to point out that in the Lower Cambrian of Durness Skolithos is "frequently but not invariably closely crowded" whereas Monocraterion is "more widely spaced than is usual with Skolithos and never closely crowded". Clearly this character may be useful locally, however undesirable in a diagnosis.

Some palaeontologists have expressed alarm at the considerable stratigraphic range of the majority of trace-fossil taxa, which are known by the same name in the Cambrian as in the Tertiary. Since it is possible that these structures were not produced by the same organism, or even related organisms, it has occasionally been suggested that different names be applied to the same ethological pattern when it occurs in different parts of the geological column (e.g. HOWELL 1957, p.150). There is absolutely no justification for this practice. Trace fossils are virtually useless as zone fossils, and their one supreme advantage, that of facilitating long-range facies comparison, is entirely lost by adopting such a philosophy.

(v) Taxonomic procedure in the description of trace fossils

To describe any trace fossil adequately it is necessary to consider three factors:- the state of preservation, taxonomic and ethological aspects of the specimen. Classifications have been proposed with each of these as the basis. In practice, however, only one can be used and here the classification proposed by SEILACHER (1953, p.432-434) is followed. He recommends the method indicated in Table 6 for describing any given trace fossil: the selected example is the horizontal crustacean burrow Rhizocorallium from the Lower Lias of Helmstedt.

The most satisfactory example of taxonomic method in trace-fossil study is without doubt GOLDRING's (1962) account of the Upper Devonian trace fossils from the Baggy Beds of North Devon. His description of Diplocraterion yoyo (op.cit., pp.235-245) could well be used as a standard for subsequent taxonomic accounts; the detailed steps involved are shown on Table 7. Goldring's method emphasises the considerable value of detailed trace-fossil study in the understanding of sedimentary processes. This method is followed closely in this thesis.

TABLE SIX.

TAXONOMIC PROCEDURE FOR DESCRIBING TRACE FOSSILS
(Model from SEILACHER 1953).

1. ECO-CATEGORY:

'Order': FODINICHNIA

'Family': Rhizocorallidae

2. TAXO-CATEGORY:

Ichnogenus: Rhizocorallium

Ichnospecies: jenense

3. STRATO-CATEGORY:

preservation: hyporelief

position: endogeneous

relief: positive

Based on trace fossil from the Helstedt Lower Lias.

TABLE SEVEN.

TAXONOMIC PROCEDURE FOR DESCRIBING TRACE FOSSILS

(Model from GOLDRING 1962).

1. Seilacherian Ecological type.
2. Genus, Author, Year.
3. Generic Synonymy.
4. Type Species, Author, Year.
5. Generic Diagnosis.
6. Species, Author, Year.
7. Plates and Text-figures.
8. Holotype.
9. Type locality.
10. Introduction.
11. Diagnosis of species, if new.
12. Description:-
    a) general b) aperture and walls c) faecal pellets.
13. Ethological interpretation.
14. Sedimentological interpretation.
15. Comparisons with other figures examples.
16. Occurrence: localities other than type.
17. Geological position and range.

Based on description of *Diplocraterion yoyo*.

CHAPTER SIX.

VERTICAL DWELLING BURROWS.

(Domichnia).

The Domichnia are abundant in the British Jurassic: both simple and U-shaped vertical burrows occur. The latter have been described from the Middle Jurassic of Yorkshire by BATHER (1925) and from the Corallian of Dorset by ARKELL (1939). Occurrences from other horizons such as the Cleveland Middle Lias, Ellerbeck Bed and Millepore Bed have not received adequate study. The simple vertical Domichnia, probably because of their rather nondescript nature, have not been treated adequately in the literature.

In this study the following 'genera' have been identified from the Yorkshire and Dorset Jurassic:- Arenicolites, Diplocraterion, Corophioides, Skolithos and Laevicyclus. Kulindrichnus, believed by HALLAM (1960) to belong to the Domichnia, has not been studied.

Complete synonyms for all 'genera' will be found in HANTZSCHEL (1962).

(i) Vertical U-shaped Burrows

Arenicolitidae RICHTER 1926

Arenicolites SALTER 1857

Type species: *Arenicola Carbonarius* BINNEY 1852, p.192, Pl. 1/1; discussed by RICHTER (1924, p.137).

Generic diagnosis: (HÄNTZSCHEL 1962, p.W183-4).

U-shaped, thick or thin, rounded or compressed burrows without *Spreite*; walls unsculptured, sculptured, or lined; perpendicular to bedding plane.

Arenicolites statheri BATHER 1925

PLATES 12, 13, 14: Text-fig. 11.

1925 *Arenicolites statheri* BATHER, p.198.

Holotype: B.M. A2442, a vertical section.

Paratype: B.M. A2443, a double opening.

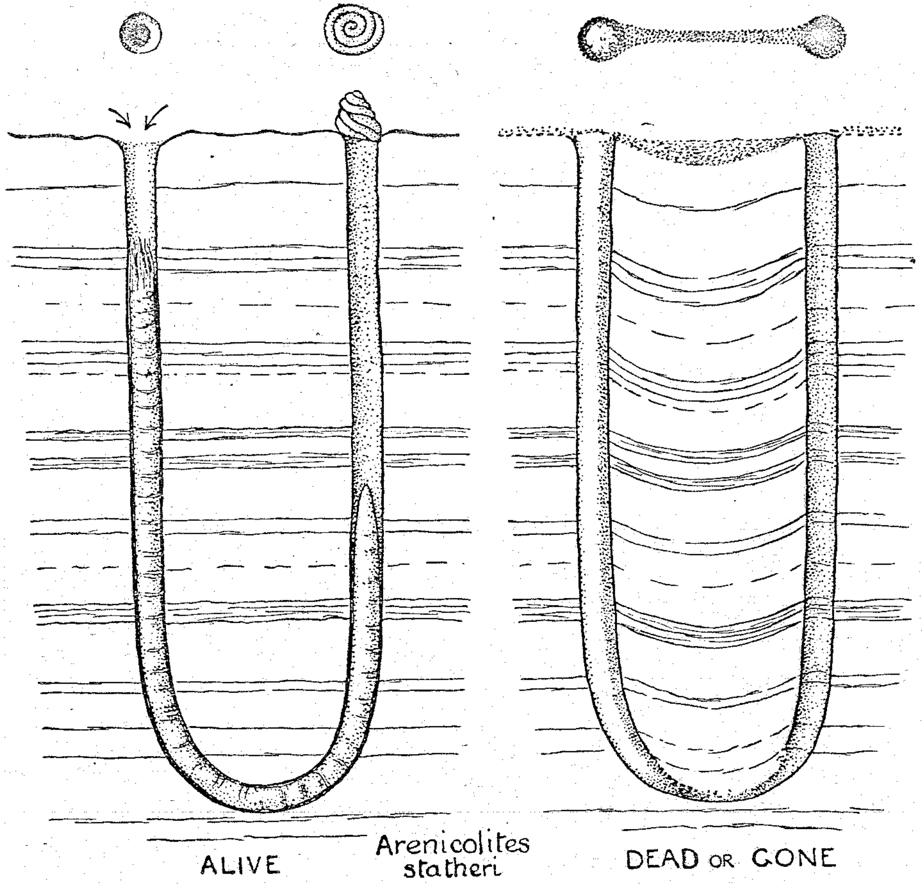
Type locality: southeast of Blea Wyke Point (45/993012).

Discussion.

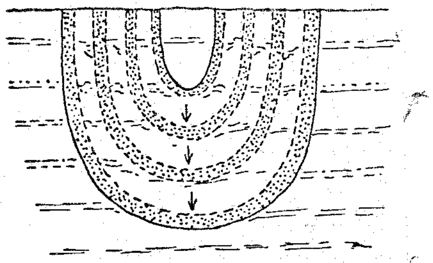
Vertical U-tubes are found *in situ* in the basal sandstone of the Bajocian Scarborough Beds in the cliffs at Ravenscar (45/990010). They are abundant in fallen blocks of this sandstone, especially at the type locality, though they occur at intervals southeastwards along the coast almost as far as Hundale Point (text-fig.40), where they are occasionally accompanied by clearly related *Spreiten* burrows which must be assigned to *Diplocraterion* (Text-fig. 18).

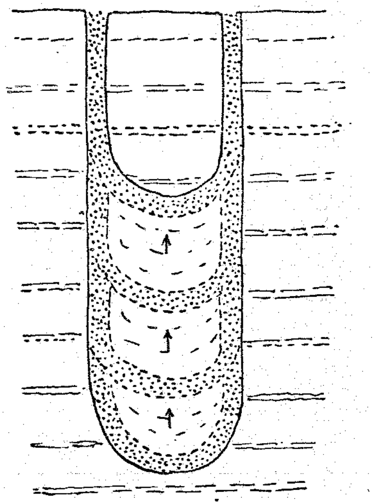
Text-figure 11A.

Diagram of BATHER'S (1925) interpretation of the differences between *Arenicolites*, *Diplocraterion* (=*Arenicoloides*) and *Corophioides*.



Corophioides





Arenicoloides

BATHER (*op. cit.*, p.186) was emphatic that in the true form of *Arenicolites statheri* there were no *Spreite*, but the space was often filled with collapsed laminae (right-hand burrow in Plate 14/A). Since these are continuous with laminae in the surrounding sediment they cannot have resulted from any activity of the burrowing animal. Bather's interpretation of the trace fossil is shown as Text-fig. 11A, which is explained as follows (*loc. cit.* p.187):-

> "So long as the creature lived and filled the bottom of the habitation, it supported the superincumbent sand. But so soon as it died and decayed, or perchance it had migrated or formed another burrow, then the sand between the limbs of the 'U' would gradually sink into the tunnel below and the laminae would sag".

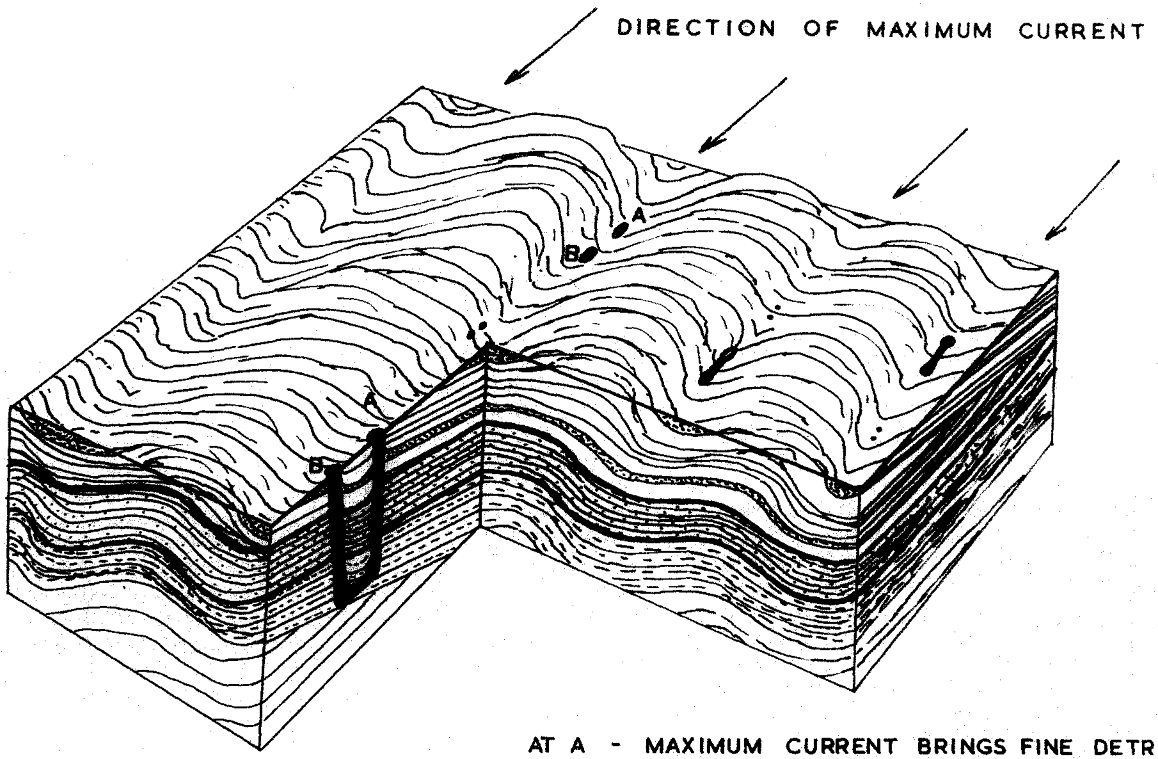
This phenomenon has not been observed in other *Arenicolites* (e.g. the Devonian form *A. curvatus* GOLDRING 1962, p.245), nor has it been found in *Arenicolites* from the Dorset Corallian. Its origin may probably be explained by an unusual thixotropy of the original sand.

Arenicolites statheri occurs in a massive, laminated 4' sandstone (Plate 12: S.B.35 of the writer's notation, Appendix Table IV). It is well-sorted, with the average grain-size 0°1 mm. in diamter, and wholly composed of angular quartz: although the laminae are occasionally marked by carbonaceous blebs the rock is not fissile. The burrows are often preserved as tube-casts in full relief, filled with massive, un-laminated sandstone (middle burrow, rear limb, Plate 14A), though generally only one limb is preserved in this manner, the other limb showing clear evidence of the sedimentary laminae being drawn downwards (middle burrow, fore limb, Plate 14A).

It seems most likely that these represent the plugged tail-shaft and open head-shaft of a burrow formed similarly to that of Arenicola marina (e.g. WELLS 1945, p.170; SCHÄFER 1962, p.341; Text-fig. 12A, B). The base of the 'U' is also occasionally marked by a plugged tube-cast (Plate 13), though there are burrows where there is no evidence for the U-tube having possessed rigidity. It is thus probable that the burrows were lined with mucus, though no intergranular material such as sericite has been found replacing it (c.f. GOLDRING, op. cit., p.254). The tube-casts clearly retain sufficient cohesiveness to withstand incorporation into intraformational conglomerates

Text-figure 11B.

Diagram illustrating the possible functional advantage of alignment of the apertures of *Arenicolites statheri* from S.B. 35 of the Scarborough Beds, Ravenscar.



AT A - MAXIMUM CURRENT BRINGS FINE DETRITUS WHICH REPLENISHES FOOD SUPPLY.

AT B - CURRENT DISINTEGRATES WORM - CASTS PREVENTING BURROW FROM BECOMING CLOGGED WITH EXCREMENT.

<u>Arenicolites</u> & paired <u>Laevicyclus</u> orientated in troughs of "Rib & furrow" Sandstone from S.B. 35: Explanation demonstrating Functional advantage.

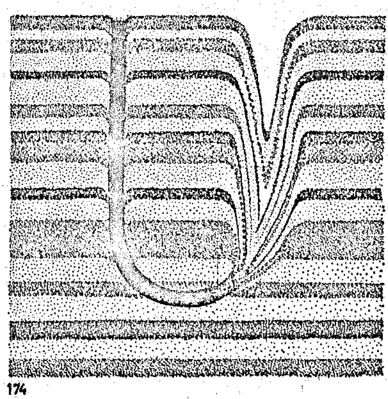
Text-figure 12.

Diagrams of U-shaped burrows formed by the Recent polychaet worm *Arenicola marina* (after Schäfer, 1962).

A. In highly thixotropic sediment : the worm has no feeding tube. (fig.174)

B. In almost nonthixotropic sediment : the worm, of necessity, drives the feeding tube upwards. (fig.175)

C. One closely packed *Arenicola* colony has burrowed to the same level, and by its feeding habits has aggregated coarse particles and built a continuous layer. (fig.269)


174

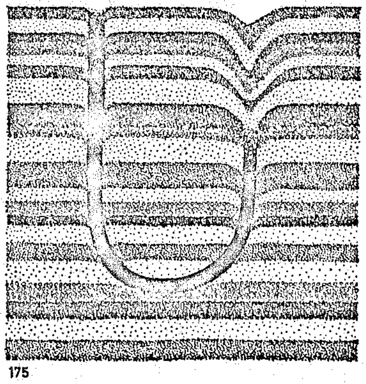

175

Abb. 174. U-Bau von *Arenicola marina* in gut rutschendem Sediment. Der Wurm hat keinen Freßgang (rechts). — Original.

Abb. 175. U-Bau von *Arenicola marina* in wenig nachrutschendem Sediment: Der Wurm muß den Freßgang (rechts) nach oben vortreiben. — Original.

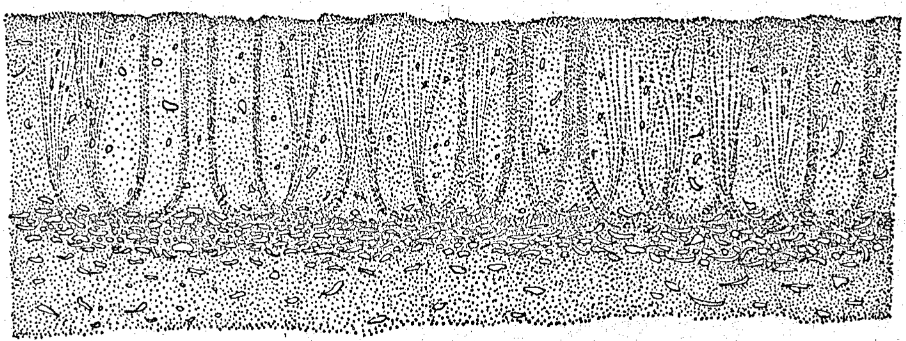


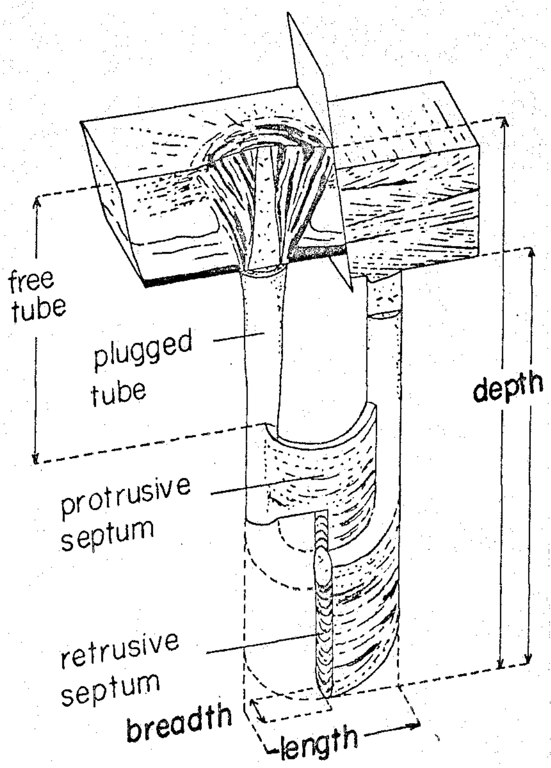
Abb. 269. Am Grund einer dichten *Arenicola*-Siedlung haben sich die in den Freßtrichtern abrutschenden Schille angesammelt und bilden eine kontinuierliche Schicht. Original.

such as those recorded from the Baggy Beds (Text-fig.9) by GOLDRING (op. cit., p.245). Such conglomerates are, however, rare in the Scarborough Beds and no derived Arenicolites statheri are known.

There is no evidence for a funnel-shaped aperture to the burrow: nor for any annulations of the wall. This may be due to the proximal parts in every case having been removed by erosion, but the energy level of the environment suggested by the sedimentology of the surrounding strata does not indicate that this is acceptable. BATHER (1925, p.186) appears to have disregarded the probability of some slight contemporary erosion in occasional instances, for he writes:-

> "Whatever may be the depth to which a tube reached, the upper ~~buds~~ ends are all cut off sharply at the same level - i.e. at what was the sea floor when the tubes were formed".

According to Bather then the tubes must have remained circular in section right to the surface: certainly there are no ringed apertures as are found in Diplocraterion arkelli. The maximum depth attained is 45 cm., the average varying between 20 and 30 cm. (terminology as in Text-fig. 13); the length varies between 4 and 6½ cm. and the tube diameter between



Text-fig. 2. Reconstruction of a partially protrusive, partially retrusive specimen of *Diplocraterion yoyo* sp. nov. One free tube is shown opening to a normal aperture; the other tube is shown as having been plugged before erosion and sedimentation took place.

Text-figure 13.

Diagram showing the terminology used in the description of vertical U-shaped burrows.

Model = Diplocraterion yoyo.

(after GOLDRING 1962).

0.8 and 1 cm. Faecal pellets and castings are unknown (c.f. Diplocraterion arkelli). Arenicolites statheri occurs gregariously. The burrow density is easily measured by the transverse plugged slits (Plate 14B) which are commonly found: it is never very high, the maximum recorded being 30/sq. metre. Generally it is of the order of 10/sq. metre.

Ethological interpretation.

The fact that the burrows occur in an orthoquartzitic sandstone, devoid of admixed clay, suggests that the burrows are the product of a suspension-feeding organism, probably a polychaet worm, rather than a deposit feeder. The absence of faecal pellets strengthens this supposition, since these are copiously produced only by deposit feeders. The worm evidently secreted a mucus lining to the basal part of its 'U'-tube and to the tail-shaft. It was unable to adjust the depth of the base of the 'U', though may have been able to extend the limbs vertically if covered with sediment. All burrows descend to approximately the same depth (c.f. Plate 13) and there are no small burrows. From the inability to adjust the depth of their 'U'-tube bases it is possible that a simultaneous killing of the burrowers took place when appreciable sedimentation overcame the area of colonisation. The polychaetes would thus appear to have been intolerant of frequent severe erosion and heavy sedimentation, unlike *Diplocraterion*, where burrows are usually found at all depths and stages of formation.

The planes of the 'U' in *Arenicolites statheri* are sometimes found to be closely aligned (Plate 14B). Similar alignment, but very much more pronounced, was noted by GOLDRING (*op. cit.*, text-fig. 4, p.246) in *Arenicolites curvatus* from the Devonian. I have noted the same phenomenon in large *Diplocraterion arkelli* (p. 103) from the Dorset Corallian. To my knowledge, no explanation of this feature has yet been published.

If, as has been surmised, the two apertures of these 'U'-shaped burrows were respectively inhalent (head-shaft) and exhalent (tail-shaft), then there would be an obvious benefit to the animal if its castings, when removed by currents, did not pass over the inhalent region. Maximum advantage would be obtained with the plane of the 'U' parallel to the maximum current direction (Text-fig. 11B) and the exhalent opening downstream from the inhalent. This is the orientation commonly observed in the field. If the respective positions of the apertures were reversed the situation would be distinctly disadvantageous to the animal, for faecal matter would tend to drift into the inhalent opening.

Sedimentological interpretation.

Small-scale cross-lamination is the commonest sedimentary structure in the sandstone containing *Arenicolites statheri*. Clay-flake and other intraformational conglomerates are not found, whereas ripple-marks and occasional rain-prints are common (Plate 46). Penecontemporaneous erosion, judging from the sedimentary structures, was slight; especially in comparison with the environment associated with *Arenicolites curvatus* from the Devonian Baggy Beds, where wedges of highly micaceous conglomerate commonly contain derived tube fragments of *Arenicolites* (Text-fig. 9).

The association of *A. statheri* with minor unconformities within the sandstone implies either that the burrows, after construction, were all truncated by erosion to the same level; or that the burrows were initiated from one horizon during a pause in sedimentation. The fact that the burrows extend beneath these minor unconformities (Plate 13) to considerable depths (20-30 cm.) favours the latter hypothesis, though a centimetre-or-so of erosion accompanying the deposition of the capping sandstone may have occurred also.

The fact that trails formed only a short distance beneath the sediment/water interface are found with *A. statheri* suggests that penecontemporaneous erosion was not great. Plate 14B shows the oblique Repichnia *Curvolithus* and the small vertical Domichnia *Laevicyclus* associated with the *Arenicolites*.

J. B. WILSON (1965, p.28) has pointed out that many of the infaunal species in the Solway Firth have only become established in recent years following the attainment of equilibrium conditions within the upper mud-flats. The lack of sufficiently long pauses in the deposition of earlier sediments was considered to be the reason for the absence of any infauna. Thus all burrows could be related to one horizon, the existing surface. Wilson's theory that "many of the apparent complexities in the study of fossil burrows in sections and cores through laminated sediments may be understood if an attempt is made to relate the zones of burrows to prominent bedding planes", is evidently supported by the occurrences of *Arenicolites statheri* from the Scarborough Beds.

Comparisons.

Arenicolites curvatus GOLDRING from the Devonian differs from *A. statheri* in possessing convergent limbs and having an elliptical tube cross-section of smaller diamter than the Yorkshire examples. Both forms extend to the same depth, and both occur in massive sandstones in which other trace fossils are rare. Shallow Repichnia such as *Curvolithus* and simple Domichnia like *Laevicyclus* do not occur with the Baggy form, where all near-surface structures are absent.

Arenicolites graptolithoformis HUNDT (1931, p.184) from the Silurian and *A. sparsus* SALTER (1857, p.203) from the Cambrian are very much smaller forms, the latter having a tube diameter of only 2mm. and a density of over 100 burrows/sq. in. They are associated with ripple-marks, suncracks and rainprints.

Serpula compressa SOWERBY 1839 possesses a strongly tapering tube, a feature not found in other *Arenicolites*. *Arenicolites franconicus* TRUSHEIM from the Muschelkalk shows a distinctly funnel-shaped aperture and is only a quarter the size of the Blea Wyke form. *Arenicolites subcompressus* (EICHWALD 1859) from the Zechstein is nearly twice the size of the Yorkshire Bajocian forms.

A poorly preserved form from the Bencliff Grit of Dorset (Text-fig. 48), described below, has a more quadrate burrow form, rather like the L-shaped galley of *A. marina* described by WELLS (1945, Pl. 1). Compared with this *Arenicolites statheri* more resembles those U-shaped *Arenicola* burrows figured by SCHAFER (1962, p.341, fig.175, p.551, fig.269; Text-fig.12BC).

The form described from the Lower Lias of Somerset and Dorset as *Arenicolites lymensis* by COYSH (1931) is a *Corophioides*, although it was maintained that the internal *Spreite* was produced by sagging of the laminae (*op. cit.*, p.13) as envisaged by BATHER (vide supra). The *Spreite*, however, contains some quantity of material from the overlying stratum, and the individual festoons are discontinuous.

c.f. *Arenicolites* sp.

Poorly preserved J- and U-shaped burrows occur in the unconsolidated yellow sand member of Upper Oxfordian Bencliff Grit on the Dorset coast near Osmington Mills (Text-fig. 48). No definite tube can be observed, for the structure is only rendered apparent by preferential oil staining along the burrow limbs. Individual cross-sets of sand can be followed inside the 'U' and no traces of spreiten are to be seen, so the trace fossil clearly belongs to the Arenicolitidae.

The burrows have a distinctly quadrate outline, but the 'U' is not always complete, so that occasional J-shaped burrows occur. Depth and length are both about 15cm., with the 'tube' diameter about 2cm.

In view of the indifferent preservation and limited number of examples only from one locality, it does not seem justifiable to give the form a specific name.

Arenicolites skeltonensis sp. nov.

Plate 11.1

Holotype. Polished vertical section in the collection of T. CHOWNS, Dept. of Geology, University of Newcastle.

Diagnosis.

Vertical U-tubes without Spreite; vertex of U oriented horizontally. Limbs sub-parallel, slightly flexuous and of variable diameter; annulated. Depth = 100 mm. Length = 28 mm. Limb diameter (average value) = 8 mm.

Description.

Vertical tubes filled with light brown mudstone set in dark brown siderite mudstone occur at the top of the ironstone workings in North Skelton mine, immediately above the sulphur band.

Vertical sections alone are insufficient to fully understand the structure of this trace fossil. Horizontal sections immediately above the Sulphur Band show flattened U-bends connected with the vertical tubes.

When seen in vertical section, the tubes are highly polished on the inside of the walls (Plate 11.1b). In transverse section the polished area is revealed as a dense black film around the circular, light-coloured, tube filling. The annulations of the tube wall occur at precisely the same height in all the burrows on the specimen figured Plate 11.1a. They were clearly not produced by any peristaltic motion of the burrowing organism, therefore, since their origin lies in particularly resistant minute laminae in the siderite mudstone causing periodic constrictions in tube diameter.

One wide tube (on the right-hand side of the holotype specimen, Plate 11.1a) exhibits a funnel-shaped aperture which is itself penetrated by a smaller, more acute, funnel connected to a narrow tube. This narrow tube is filled with transverse laminae which are convex upwards. The convex laminae indicate protrusive activity, probably in response to slight erosion of the proximal part of the shaft (c.f. REINECK 1958, p.11, fig.2c ; GOLDRING 1964, p.138, fig.1c).

ethological interpretation.

The burrows may have been constructed by a marine polychaet resembling Arenicola marina (c.f. Arenicolites statheri). The fine-grained, muddy nature of the substratum agrees with the present-day preference of A. marina (Plate 6) which is known to produce U-tubes without Spreite. RICHTER (1924, p.119) has shown that A. marina is capable of reopening a blocked burrow, but does not produce a Spreite in the process.

The striking change in the orientation of the axis of the 'U' just above the Sulphur Band, which is a pyritous mudstone with megaripples, where the burrows are deflected horizontally, suggests that for some reason the burrowing organism was unable, or unwilling, to burrow into it. If the organism which formed Arenicolites skeltonensis was as tolerant as Arenicola marina it could not be because of abundant hydrogen sulphide in the sulphur band, because A. marina is quite unaffected by it and can even withstand foul water (RICHTER, LOC.CIT.).

It is more likely that diagenesis had proceeded to such an extent that the Sulphur Band was already partially lithified when the burrows were formed, so that the substratum was too solid for further penetration. This is not unlikely in view of the fact that the overlying mudstone possessed many laminae hard enough to cause marked constrictions of the tube.

Moreover, the horizontal portions of the burrows in the region of the vertex are very strongly compacted, as though against a hard foundation.

Sedimentological interpretation.

Arenicolites skeltonensis occurs beneath a disconformity separating the Upper Lias Tenuicostatum Zone from the Middle Lias Apyrenum Subzone, the Hawskerense Subzone being absent (Text-fig.39b). Since the Sulphur Band was already too solid to penetrate when the burrows were formed, it follows that most of the diagenetic alteration of the ironstones must have taken place within the space of one ammonite subzone, probably less.

The upwardly convex laminae within some tubes (Plate 11.1a) imply downward migration of the organism in response to slight erosion. Such erosion would be expected along a line of disconformity.

Comparisons.

No 'species' of Arenicolites has been recorded in the literature with a right-angled deflection of the vertical tube just above the vertex. I have observed tube fragments of an Arenicolites sp. with flexuous limbs and constrictions of the wall from the Lower Lias at Blockley Station quarry in the Cotswolds. These tube fragments possesses longitudinal wrinkles also, and were preserved in calcareous shale. Their cross-section measures about 1cm. This species may well be synonymous with *Arenicolites skeltonensis*.

Arenicolites is recorded by DOUGHTY (1965) from the Tenuicostatum Zone of Lincolnshire, where it is associated with *Teichichnus* and *Chondrites* in the condensed Transition Bed. CHOWNS (1967, personal communication) has also recorded it from the same horizon in Leicestershire. No detailed descriptions of these *Arenicolites* exist.

Occurrence.

Known in Yorkshire only from the base of the Upper Lias at North Skelton mine, where it occurs immediately above the Sulphur Band.

Rhizocorallidae RICHTER 1926

Diplocraterion TORELL 1870

1872 Arthraria BILLINGS, p.467, fig.2

1916 Arenicoloides BLANCKENHORN, p.39

1940 Bifungites DESIO, P.78, pl.8/3

1957 Polyupsilon HOWELL, p.151

Type species. Diplocraterion parallelum TORELL 1870, p.13;
selected by RICHTER (1926, p.213);
discussed by WESTERGÅRD (1931).

Diagnosis (HÄNTZSCHEL 1962, W.192):

U-shaped burrow with Spreite similar to Rhizocorallium, but always built strictly perpendicular to bedding plane; vertex of U-tube built progressively deeper; tubes ending in large funnels, in small, shallow ones or remaining sub-cylindrical to surface.

Emended Diagnosis:

A U-tube, vertical to the bedding, with straight axis, parallel limbs , and , generally , evidence of upward or downward migration". (GOLDRING 1962, p.235).

Diplocraterion arkelli sp. nov.

Plates 15, 16, 17. Text-figs. 14, 15, 16, 17.

Holotype: specimen figured by ARKELL 1939, fig.2. (= Text-fig. 14G).

Type locality: W. of Redcliff Point, Dorset (SY/710817): backshore.

Type horizon: upper gritstone doggers of Bencliff Grit, Upper Jurassic (Oxfordian).

Introduction.

The synonymy and terminology of Diplocraterion have been fully discussed by GOLDRING (1962, pp.235-239) and need not be reviewed here. Within the 'genus', Goldring has distinguished two types: a retrusive form, where the animal moves upwards in response to sedimentation; and a protrusive form, where the animal moves downwards in response to erosion (Text-fig.13). The burrows here assigned to Diplocraterion have been described by ARKELL (1939), who considered them to be the product of marine polychaet worms. They are typically preserved as slits on bedding planes (Plates 15 & 16).

Diagnosis.

A vertical 'U'-shaped burrow with a laminated septum of sandstone, siltstone and faecal pellets: retrusive and protrusive forms sometimes occur in the same burrow: retrusive form dominant. Free tubes generally present; Apertures funnel-shaped, ringed. Plugged tubes 2cm. in diameter. Average length 15cm. (8-21cm.). Width 3-5cm. Depth 18-30cm. Composite burrows formed by rotation about the vertical axis fairly common. Limbs of 'U' generally indistinct. Walls unsculptured. Specimens usually occur in massive calcareous grits in which there is some admixed silt.

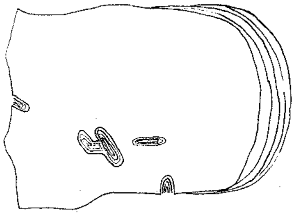
Description.

Protrusive forms. Transverse sections through the septum show a marked dumb-bell shape, with the two circular tubes clearly separated from the septum which is observed as a series of curves parallel to each

Text-figure 14.

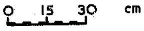
Field sketches of *Diplocraterion arkelli* from the Bencliff Grits of Redcliff Point, Dorset.

A PLAN VIEW OF A 3' LONG DOGGER

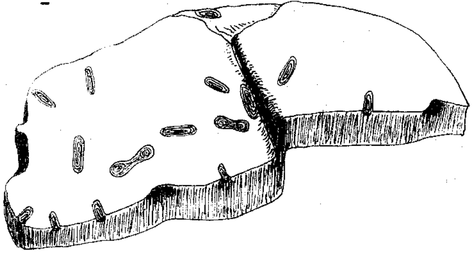


Density: 6/m^2

One composite burrow



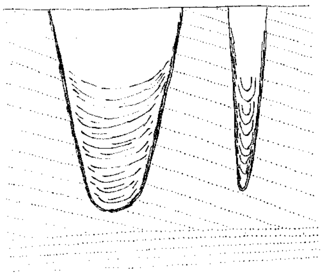
B OBLIQUE VIEW OF A 4'6" LONG DOGGER



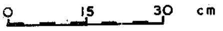
Density: 12 / m^2

Simple burrows, some dumb-bell shaped

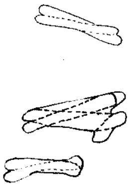
C SIDE VIEW OF A SMALL DOGGER



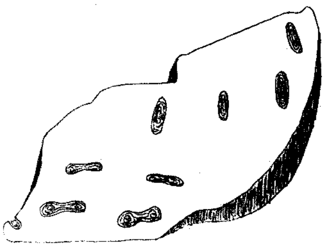
The burrows do not descend perpendicular to the cross-bedded unit

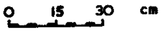


D PLAN VIEW OF COMPOSITE BURROWS IN ROUGH PARALLEL ALIGNMENT

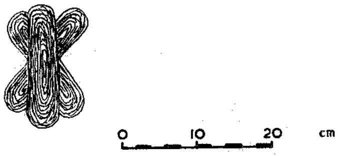


E OBLIQUE VIEW OF BURROWS ALIGNED IN DIFFERENT DIRECTIONS

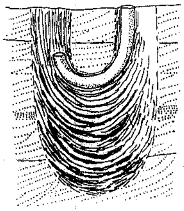




F PLAN VIEW OF COMPOSITE BURROW



G SIDE VIEW OF RETRUSIVE BURROW



The plugged inner tube cast lies above the laminated septum

F & G after Arkell 1939

aperture (Text-fig. 15A).

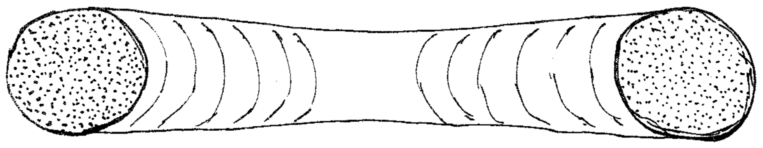
Retrusive forms.

Transverse sections through the septum are generally sausage-shaped; a slight dumb-bell constriction is sometimes seen, but it is not as pronounced as in protrusive forms: (Text-fig. 14A,B,D,E,F). These cross sections are by far the most abundant in all the Jurassic Diplocraterion examined: (Text-figs. 15 & 16; Plate 17). ARKELL (1939, p.456) remarks that the "laminae are all curved upwards also in the direction of the shorter axis (Plate 16B) so that each lamina resembles an inverted mudguard of a bicycle". If this were completely true then all the burrows should be retrusive, but he further remarks (op. cit., p.457) that the "inner U in each burrow....may be anywhere within the laminated area, from top to bottom, and it follows that the movements of the worm that laid down the laminae were not regularly upwards or downwards but fortuitous".

Sections parallel to the length of the burrow generally reveal parallel sides (Text-fig. 14G; Plate 16A), with the laminae between composed of alternating festoons rich in faecal pellets and sand.

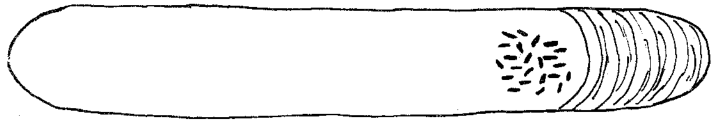
Text-figure 15.

Field sketches of cross-sections of Diplocraterion arkelli from the Scarborough Beds (S.B. 32) beneath Ravenscar



DUMB-BELL-SHAPED <u>Diplocraterion</u> :
ASSOCIATED WITH
<u>Teichichnus</u> only

HEMI-CYLINDRICAL Faecal pellets, ENLARGED



SAUSAGE-SHAPED <u>Diplocraterion</u> PACKED
WITH Faecal pellets : ASSOCIATED WITH
<u>Asterosoma</u>, <u>Daedalus</u>, <u>Teichichnus</u>, <u>Thalassinoides</u>

The laminae are rarely continuous across the septum. Occasionally burrows with sides converging downwards occur (Text-fig. 14C). It is noticeable that they were constructed truly vertically, and not perpendicular to the cross-bedded sediment through which they penetrate. (It is possible that they were constructed perpendicular to a once existing horizontal unit, now eroded).

Free tubes are usually found (Text-fig. 14C, G; Plate 16A), though plugged tube casts are comparatively rare, certainly much rarer than in *Arenicolites statheri*.

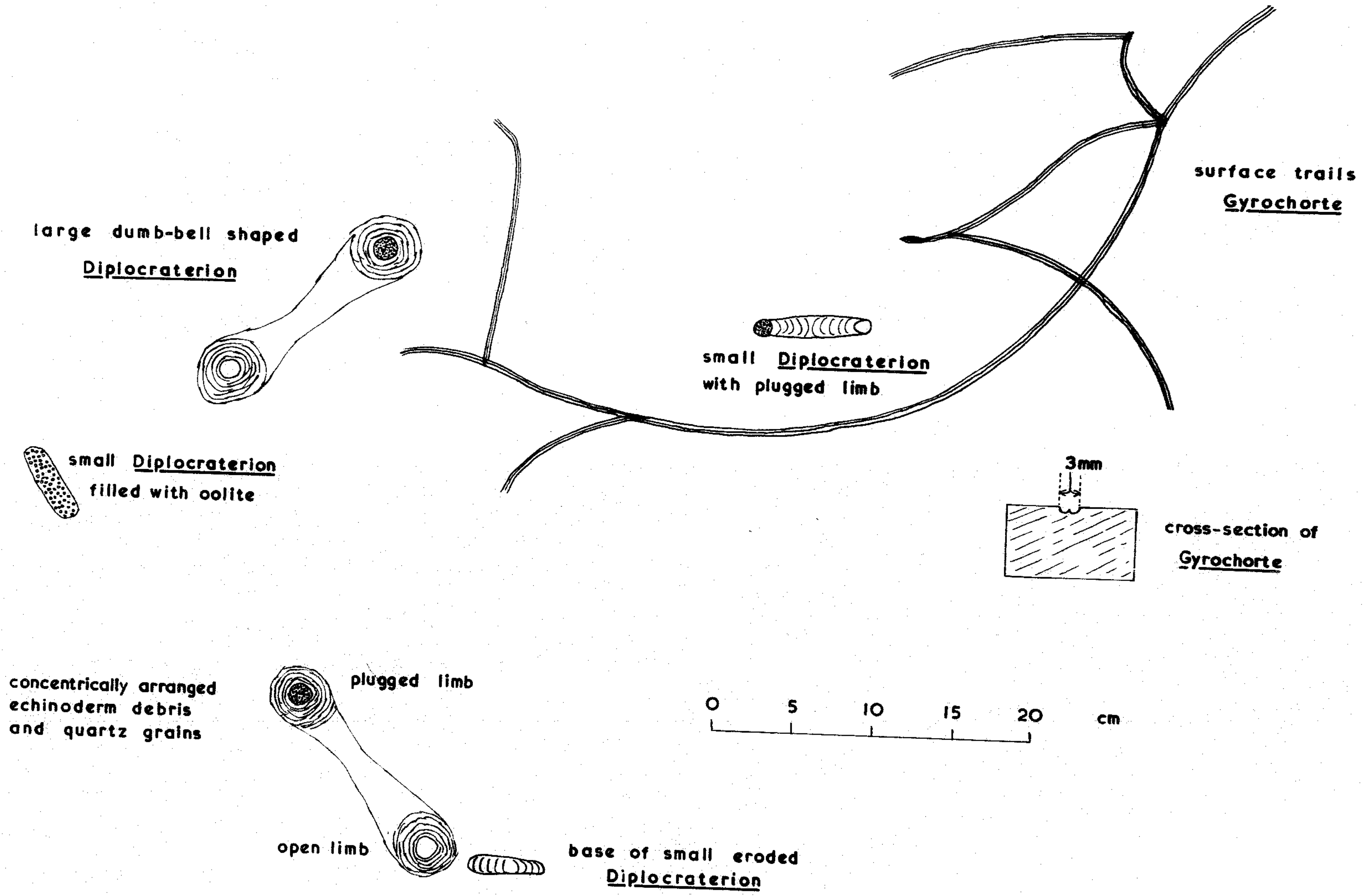
Apertures.

The original apertures have been preserved in several cases: they were observed solely in sections parallel to the bedding. The apertures are seen as a series of concentric rings composed of coarse debris, faecal pellets and sandstone in varying proportions surrounding a central core (Text-figs.14B,E; Plate 16C; Text-fig.16). The central core may be plugged with sandstone, or the central region may be unplugged. In examples from the Millepore Bed of Yorkshire one aperture is commonly plugged and the other open (Text-fig.16: c.f. GOLDRING 1962, Pl.23, fig.8). Both are ringed with comminuted echinoderm debris.

Faecal pellets.

Text-figure 16.

Field sketch of *Diplocraterion arkelli* showing the ringed apertures; from a loose block of Millepore Bed beneath Staintondale ; associated with the near-surface trails *Gyrochorte carbonaria*.



surface trails
Gyrochorte
large dumb-bell shaped
Diplocraterion
small Diplocraterion
with plugged limb
small Diplocraterion
filled with oolite
3mm
cross-section of
Gyrochorte
concentrically arranged
echinoderm debris
and quartz grains
plugged limb
open limb
0
5
10
15
20
cm
base of small eroded
Diplocraterion

Faecal pellets are strikingly associated with almost every specimen. They are apparently most abundant in the septal laminae of retrusive burrows (Plate 16: Text-fig.15B) and may also be observed in the sediment outside the burrow, especially in the vicinity of apertures (Plate 16C). Being very much less resistant to erosion than the sand grains which are the other important septum builders, they weather into small pits or lens-shaped depressions (Plate 16A). Examples from the Scarborough Beds of Yorkshire and the Nothe Grits of Dorset show the best-preserved faecal pellets. They appear to be of flat ended, compressed cylindrical, or hemi-cylindrical shape; dimensions correlating with burrow length. Thus pellets from the Scarborough Beds average 2mm. x ½mm. for a 9cm. long burrow: pellets from the Nothe Grits average 3mm. x ¾mm. for an 11cm. long burrow.

Composite burrows.

Large examples (up to 15cm. long) from the Bencliff Grit at the type locality sometimes show a multiple nature, where the orientation of the vertical plane of the burrow changes (Text-fig. 14D, F). This rotation about the vertical axis commonly results in the two limbs of the burrow being of exaggerated diameter (e.g. the type specimen which is partially composite; Text-fig. 14G) with the plugged tube being much smaller than the limb diameter.

Density.

Density varies quite widely in *Diplocraterion arkelli*. The burrows are gregarious, though not as markedly so as in *Arenicolites statheri*. The large burrows from the type locality commonly attain a density of 35/sq.m. (Plate 15B), though more usually the density ranges between 6 and 12/sq.m. (Text-fig. 14). The highest recorded density of *D. arkelli* is from the Scarborough Beds south of Hundale Point (Text-fig.40) where in S.B.28, an argillaceous, calcareous sandstone of fine grain, the density reaches 50/sq.m.

Ethological interpretation.

The copious production of faecal pellets and the restriction of the burrowing organism to substrates containing appreciable silt and clay suggests that the burrows were constructed by a deposit-feeding organism (cf. *Arenicolites*, p. 81). According to RICHTER (1924, p.119), *Arenicola* itself cannot adjust the base of its 'U', and therefore is not capable of producing the septum found in *Diplocraterion*. *Diplocraterion arkelli* is shorter, wider and thicker than *Arenicolites statheri*, and is very similar in proportions to the burrow of the Recent worm *Echiurus*, figured by HERTWECK & REINECK (1966, Abb.9, p.436) from offshore muds south of Heligoland. *Echiurus* produces a well-developed laminated septum.

The position of the final tube cast, which may be anywhere within the laminated septum, suggests that the spreiten structure was not excavated in search for food, since it is unlikely that the organism would retrace its path. It is more likely that the laminae were produced by the organism slightly adjusting its depth following either a period of minor erosion (in which case the animal migrated downwards to produce a protrusive form) or a phase of sedimentation (in which case the animal migrated upwards to produce a retrusive form).

In the large *D. arkelli* from the type locality at Redcliff Point, occurring in cross-bedded calcareous grits, there is no clear evidence for simultaneous adjustment of depth by a colony of burrows, and the response would appear to have been random. This forced ARKELL (*op*.cit. p.458) to conclude that the adjustments were probably effected rapidly, perhaps with each successive tide. This may well have been the case with the Bencliff Grit examples, though even here the characteristic sausage-shaped slit section tilts the balance in favour of a net retrusive response.

Other *D. arkelli* are less likely to have been formed in an intertidal environment (e.g. Scarborough Beds at Iron Scar, Cloughton, Plate 17). Here the burrows are all retrusive, and are, moreover, associated with the retrusive feeding burrow *Teichichnus*.

At Redcliff Point, where the density of *D. arkelli* is low, parallel orientation of burrows is sometimes observed (Text-figs. 14D,E). A possible explanation for this has been given for *Arenicolites* (*vide supra* p. 82). It may well be that the rotation about the vertical axis which causes the composite burrows (e.g. Text-fig. 14F) is to be explained in terms of the animal changing its orientation in response to a change in the prevalent current direction.

Arenicolites statheri was unable to adjust to the changing sedimentary environment either by rotation or by vertical migration. *Diplocraterion arkelli* was capable of delicate adjustment to environmental change by both rotation and vertical migration.

Sedimentological interpretation.

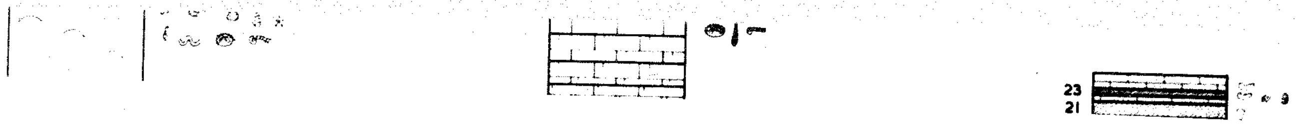
Diplocraterion arkelli from the Dorset Corallian is found in sediments possessing strong deltaic affinities. The largest examples (Pl. 15B: Text-fig. 14G) come from calcareous grits with large scale trough cross-stratification (Plate 15A). Examples from the top of the Bencliff Grit associated with symmetrical linguoid ripples (Pl. 15C) are smaller and clearly retrusive. Protrusive behaviour, common in the cross-bedded unit, is absent.

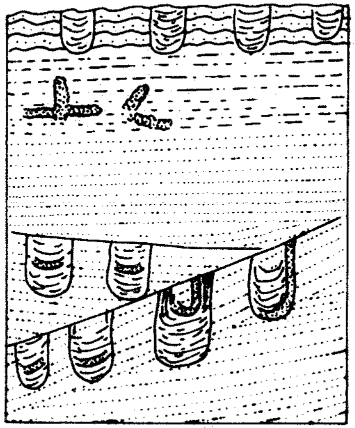
This varying ethology of *D. arkelli* in the different parts of the Bencliff Grit suggests that initially erosion was more important, but later quieter conditions of more uniform deposition prevailed. The response of these vertical burrows therefore suggests an upwards trend of decreasing current velocity, and reinforces the evidence of R.C.L. WILSON (1965, p.58) based on the sedimentology. The two lines of evidence are combined in Text-fig. 17. Although Wilson recognised three cycles of current activity, the *Diplocraterion* contribute substantial evidence only to the last of the cycles.

Trails formed just beneath the sediment/water interface (e.g. *Gyrochorte*) are not found in

Text-figure 17.

Diagram illustrating one cycle of decreasing current activity in the Bencliff Grits of Dorset : evidence from sedimentology and trace-fossil distribution.



ASSOCIATED TRACE FOSSILS	*Diplocraterion arkelli*		LITHOLOGY	SEDIMENTARY STRUCTURES	DEDUCED ENVIRONMENTAL CONDITIONS
Gyrochorte Ophiomorpha	SMALL BURROWS ALL RETRUSIVE		3. CHURNED CLAYS, FINE-GRAINED SANDSTONE AND CALCAREOUS SILTS	Linguoid ripples	LITTLE CURRENT ACTIVITY SLOW DEPOSITION
			2. CARBONACEOUS SANDS	Even lamination	CONTINUOUS UNIFORM DEPOSITION
—	LARGE BURROWS PROTRUSIVE AND RETRUSIVE		1 CALCAREOUS GRITSTONE	Broad trough cross-stratification	STRONG CURRENT ACTIVITY RAPID DEPOSITION WITH INTERMITTENT EROSION

association with the large *Diplocraterion arkelli* from Redcliff Point. If formed, they were eroded together with the proximal parts of the U-tubes. Elsewhere, where there is clear evidence only of retrusive activity, *Gyrochorte* is sometimes observed. As may be expected if the trails were constructed very close to the surface, they accompany *Diplocraterion* showing ringed apertures (Text-fig.16).

Comparisons.

Comparative data for five well-documented 'species' of *Diplocraterion* are presented in Table 8. It can be seen that *D. yoyo* is very similar to the type species *D. parallelum*, but differs in possessing larger funnels, when these are present, and a larger tube diameter. *D. arkelli* is not only much larger, but is relatively longer than other described *Diplocraterion* (D/L = 1.6 compared with 3.0 and 3.1 from Palaeozoic species and 4.7 for *D. statheri*). *D. arkelli* possesses identical faecal pellets to those of *D. yoyo* (c.f. Text-fig.15B and GOLDRING 1962, Pl.28, fig.6); the apertures are also very similar (c.f. Text-fig.16 and *op.cit.* Pl.28, fig.8). *D. statheri*, clearly related to *Arenicolites statheri*, possesses neither faecal pellets nor distinctive apertures; it is a very deep, narrow form.

Occurrence.

TABLE EIGHT. Comparative measurements of five 'species' of *Diplocraterion*.

		Depth av./range	Length av./range	Tube diam.	Aper-ture.	Faecal pellets.	D/L av.
D. parallelum	Cambrian	66(<320)	22(<75)	4	rare small funnels	No.	3.0
D. lyelli		?	(25-9)*	3	large funnels	No.	?
D. yoyo	Devonian	80(10-120)	26(9-55)	6	rare large funnels	Yes.	3.1
D. arkelli	Jurassic	240(180-300)	150(80-210)	20	rare large funnels	Yes.	1.6
D. statheri		350(100-600)	75(70-100)	10	no funnels	No.	4.7

*length variable owing to burrow limbs converging downwards.

Measurements in millimetres.

Type locality as above. Small examples from the Bencliff Grit in Ringstead Bay are less common than the larger examples at Redcliff Point (see Text-fig. 47 for localities). Massive bands from the Nothe Grits in Bowleaze Cove yield abundant examples with a higher density than those from the Bencliff Grit; they are preserved in a fine-grained calcareous sandstone full of ovoid blebs of carbonised plant debris, often one or two centimetres in diameter. A single example was recorded from the Osmington oolite (Bed 7b) at Black Head, ~~Yorkshire~~.

Examples on the Staintondale backshore, north of Hayburn Wyke (Text-fig. 40) coming from the Bajocian Millepore Bed are strikingly similar to the large Redcliff Point examples; they occur in a trough cross-stratified shelly oolite, which contains much comminuted echinoderm debris. Small examples from the Scarborough Beds are found at two horizons (SB.28 & S.B.32). Abundant examples from S.B.28 are found near Iron Scar, south of Hayburn Wyke and occur nearly as far south as Burniston. Rare examples occur in S.B.32, near Ravenscar (995007) and at Hundale Point.

Occurrences from S.B.28 at Cloughton Salt Pans (54/021952) are noteworthy in that Diplocraterion *arkelli* is accompanied by shelly fossils, a unique record. Fairly dense burrows are associated with *Catinula*, *Astarte minima*, *Corbula* and jetified wood debris. Nearby (54/020950) *Diplocraterion arkelli* with a density of 12/sq.m. is associated with traces formed at shallow depth, *Pelecypodichnus* and *Gyrochorte*. South of Scarborough, at Yons Nab (54/085843) silty shales of the Scarborough Beds contain very abundant *Lopha Marshi* accompanied by occasional *Diplocraterion* and very rare *Teichichnus*.

Diplocraterion statheri sp. nov.

Plates 17B, 18. Text-figs. 18, 19, 20.

Holotype: specimen figured as Text-fig. 18.
Type locality: backshore beneath Beast Cliff (54/003995).
Type horizon: uncertain, most probably Ellerbeck Bed.

Introduction.

Further southeast along the strike of the basal sandstone of the Scarborough Beds (S.B.35) 'U'-shaped burrows quite clearly related to the *Arenicolites statheri* occurring to the northwest are found beneath

Rodger Trod, north of Cloughton Wyke (54/020960) and occur sporadically as far as the scar at Hundale Point. They are similar in every respect to the *Arenicolites* except that they show very considerable adjustment of the depth of the base of the 'U' tubes, and must therefore be assigned to *Diplocraterion*.

Diagnosis.

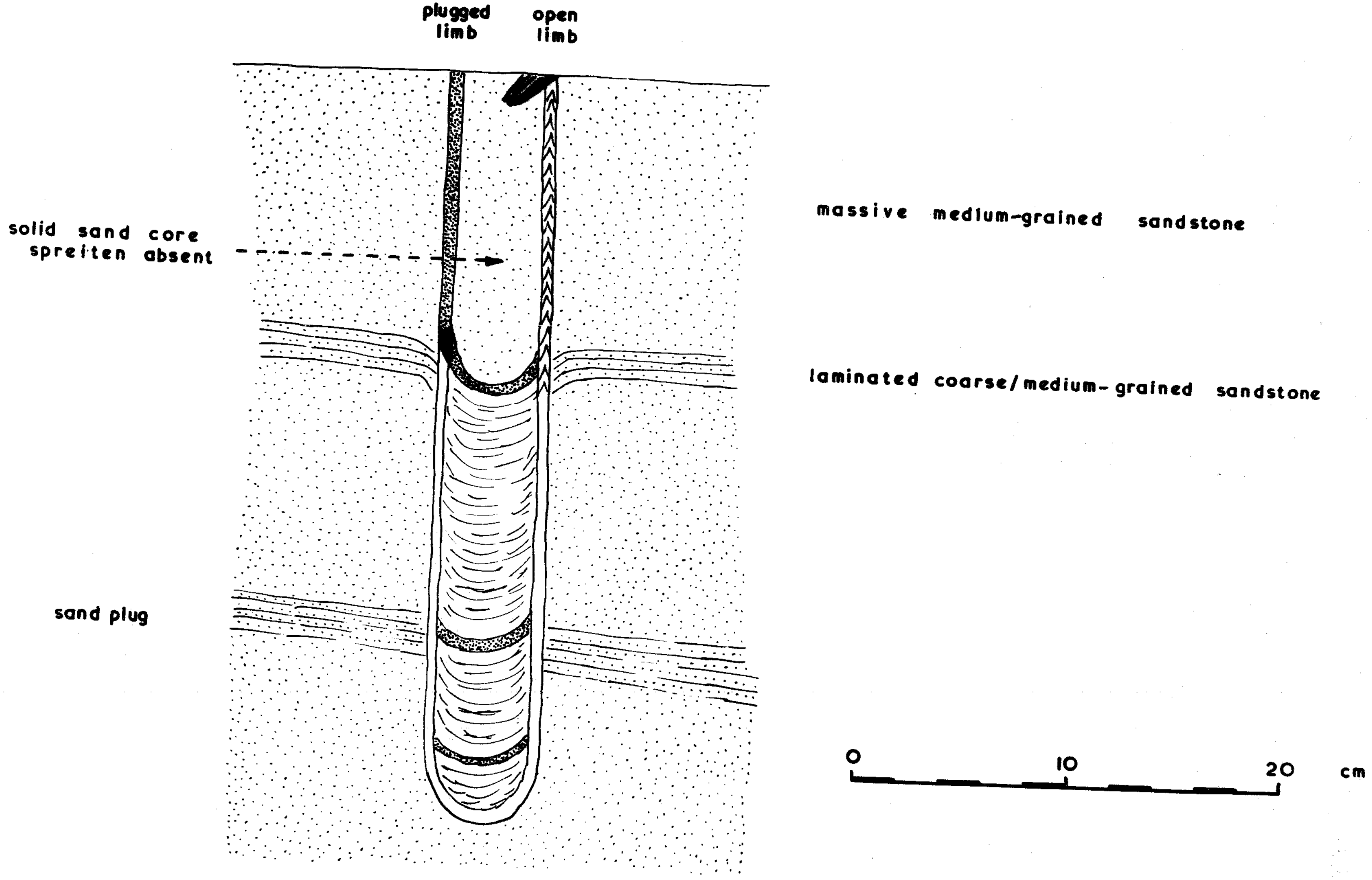
A deep, narrow, vertical 'U'-shaped burrow with an indistinctly laminated septum of sandstone showing evidence of considerable upward migration of the base of the 'U'. Free tubes 15cm. deep; plugged tubes 1cm. in diameter. Limbs cylindrical to surface; no funnels; no faecal pellets. Average length 7.5cm. (7-11cm); average depth 35cm. (max. 60cm.).

Description.

As in *Diplocraterion arkelli* the margins of the burrows are indistinct, due to the retrusive activity of the organism. Within the septum occasional tube-casts occur (Text-fig.18) marking a pause in the upward migration, probably related to a temporary cessation of sedimentation. The burrows are more obviously related to unconformities than are the *Arenicolites*, and their

Text-figure 13.

Field sketch of retrusive *Diplocraterion statheri* from a loose block of Ellerbeck Bed sandstone from the backshore beneath Staintondale.


plugged limb
open limb
solid sand core
spreiten absent
massive medium-grained sandstone
laminated coarse/medium-grained sandstone
sand plug
0
10
20
cm

depth has often been truncated to a much greater extent (Text-fig.19).

The most abundant examples are preserved as deeply eroded slots in loose blocks of Dogger in Saltwick Bay (Plate 18), where the form is very markedly gregarious. Densities here range from a maximum of over 100/sq.m. in the centre of the Bay (45/918107), falling off to 15/sq.m. to the east of Saltwick Nab (45/923106) and rising to over 100/sq.m. again beneath Whitby High Light (45/929102). Some of the Dogger examples possess a distinct dumb-bell shape, and several protrusive burrows may be present. The necessary vertical sections are not available to support this view, since only the basal remnants of the 'U'-tubes are preserved. Although the eroded slots bear comparison with those of D. arkelli from the Dorset coast (Plate 15B) there is no evidence of any composite burrow.

Ethological interpretation

Whereas Arenicolites statheri shows no adjustment of the depth of its U-tube base, Diplocraterion statheri shows evidence of great adjustment. Text-fig.18 demonstrates that the organism migrated upwards for 20cm., with two pauses indicated by plugged tube-casts; Text-fig.19 implies a greater movement, with no intervening pauses. The long burrow has clearly migrated continuously upwards for 50cm.

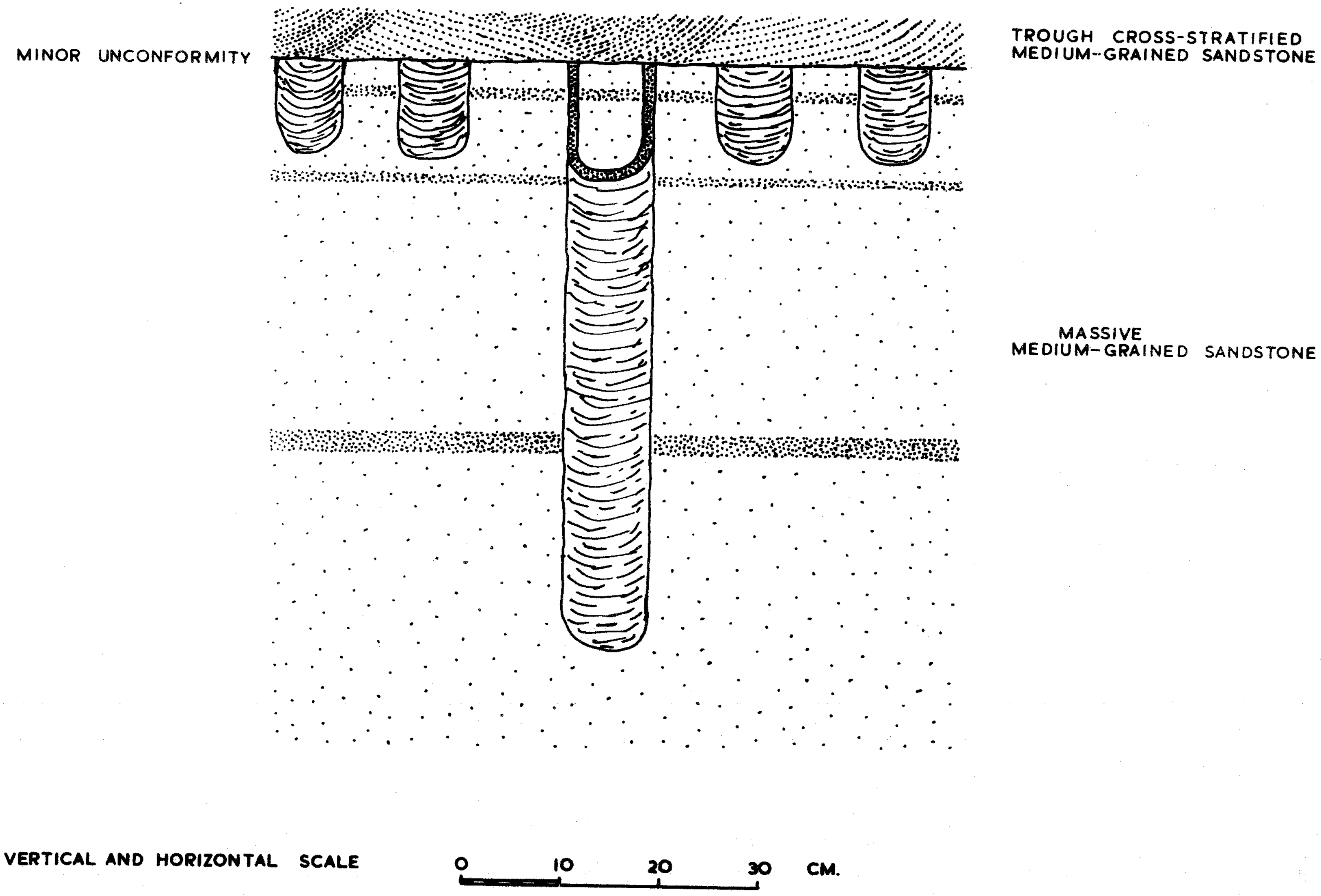
In Text-fig.18 two bands of laminated sandstone occur in the otherwise massive unit. Of these, the upper one has the laminae drawn downwards in the vicinity of the burrow limbs; the lower one is unaffected and the laminae are not depressed. The laminae, on sedimentological grounds, indicate a definite reduction in the rate of sedimentation compared with that for the massive unit. It appears that conditions should have been suitable for the normal feeding pattern of the creature to be resumed, and the plugged tube-cast probably represents the depth reached by the creature while the apertures were situated at the horizon of the upper laminated unit, the depressed laminae being caused by gravitation of sediment towards the openings. If this were the case it gives a direct measure of the true depth of the free tube, viz. 15cm., and indicates that there was probably little erosion of the proximal part of the final stage of the burrow.

Sedimentological interpretation.

For the example just discussed, from the Ellerbeck

Text-figure 19.

Field sketch of Diplocraterion statneri from a loose block of Scarborough Beds sandstone (S.H.35) - showing retrusive burrows truncated by a minor unconformity.


MINOR UNCONFORMITY
TROUGH CROSS-STRATIFIED
MEDIUM-GRAINED SANDSTONE
MASSIVE
MEDIUM-GRAINED SANDSTONE
VERTICAL AND HORIZONTAL SCALE
0
10
20
30
CM.

Bed, the ethology indicates rapid accumulation of 15cm. of massive sandstone followed by a much slower accumulation of 2½cm. of laminated sandstone. The massive bed may have been formed in a single event. For the example illustrated in Text-fig.19 from the Scarborough Beds, the rapidly formed massive unit must originally have been much thicker, and continuous sedimentation punctuated by pauses enabling the establishing of the set of four smaller burrows. Text-fig.20 indicates the simplest possible sequence of events which could have led to the production of the final form shown as Text-fig.19.

Detailed studies of *Diplocraterion* may thus contribute the only evidence for phases of erosion and sedimentation which are unrepresented in the surrounding sediments. Clearly the proportion of the sediment now fossilized is but a small fraction of that originally deposited.

Corophioides SMITH 1893.

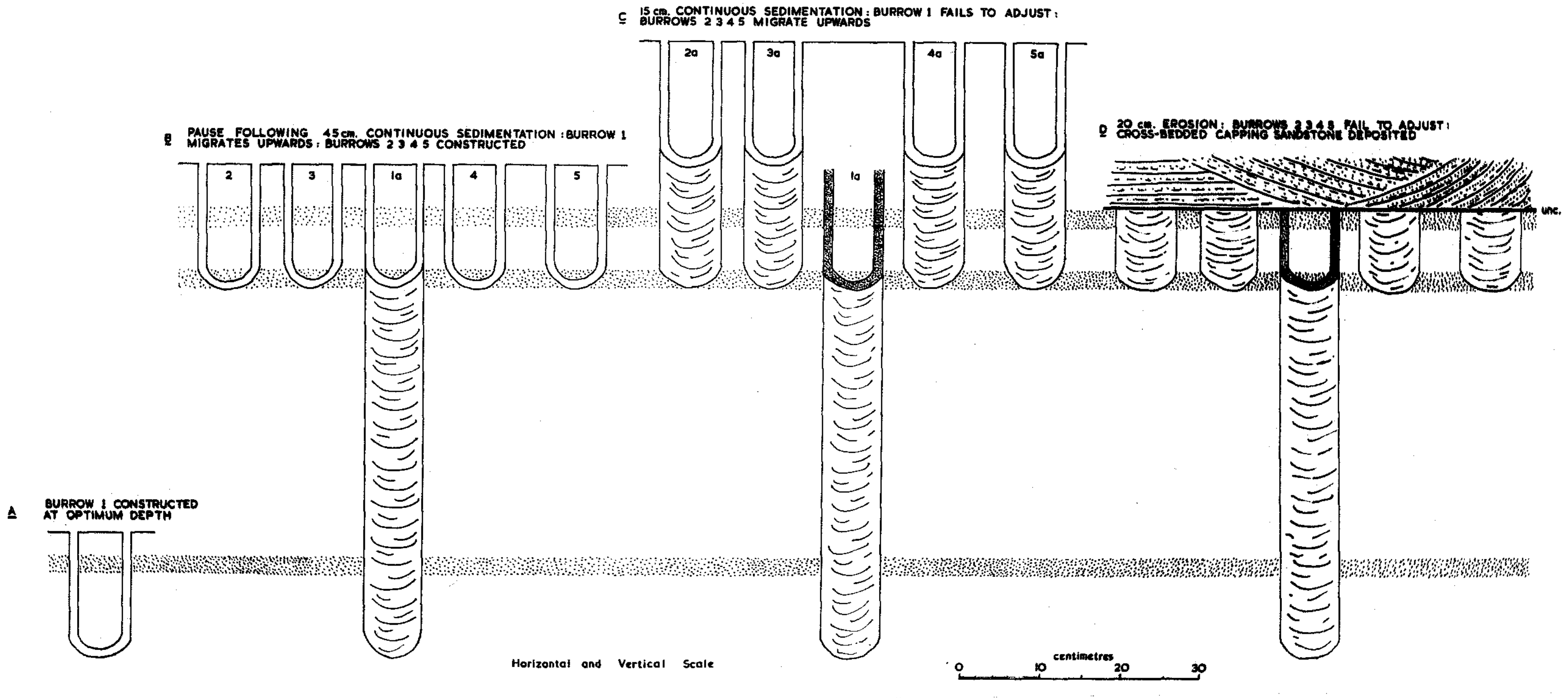
Type species: *Corophioides polyupsilon* SMITH 1893

Generic diagnosis: (HÄNTZSCHEL 1962, W.189).

U-shaped *Spreiten* burrows similar to *Rhizocorallium*

Text-figure 20.

Diagram demonstrating the simplest sequence of events which could have produced the eroded _Diplocraterion statheri_ shown in the previous figure.


A
BURROW 1 CONSTRUCTED AT OPTIMUM DEPTH
B
PAUSE FOLLOWING 45 cm. CONTINUOUS SEDIMENTATION : BURROW 1 MIGRATES UPWARDS : BURROWS 2 3 4 5 CONSTRUCTED
2
3
1a
4
5
C
15 cm. CONTINUOUS SEDIMENTATION : BURROW 1 FAILS TO ADJUST : BURROWS 2 3 4 5 MIGRATE UPWARDS
2a
3a
1a
4a
5a
D
20 cm. EROSION : BURROWS 2 3 4 5 FAIL TO ADJUST : CROSS-BEDDED CAPPING SANDSTONE DEPOSITED
unc.
Horizontal and Vertical Scale
centimetres
0
10
20
30

but shorter and always perpendicular to bedding plane.

Discussion.

This genus has been treated in a rather casual way recently, with some authors merely regarding it as a synonym for *Diplocraterion* (e.g. SCOTT SIMPSON 1957, p.493). WESTERGARD (1931, p.9) distinguished *Corophioides* as a series of tubes not only of different depth but also of different diameter. *Diplocraterion* has U-tubes of equal diameter. GOLDRING (1962, p.236) considers *Corophioides* to be produced by continuous migration from the surface.

A fundamental difference exists therefore between *Corophioides*, with *Spreite* continuous up to the original surface and no free tubes, and *Diplocraterion*, with *Spreite* formed after the production of free tubes. The former shows no response to erosion and sedimentation; the latter always shows upward or downward migration.

To help separate these two trace-fossil genera the following enlarged diagnosis is suggested:-

Revised diagnosis.

Small U-shaped *Spreiten* burrows similar to *Rhizocorallium*, but shorter and always perpendicular to bedding plane. *Spreite* continuous from sediment/water interface, merging into limbs of 'U'; no free tubes. No evidence of vertical migration in response to erosion or sedimentation. Apertures not funnel-shaped. Faecal pellets not found.

Corophioides lymensis (COYSH 1931)

Plate 4, Plate 19.

1931 *Arenicolites lymensis* COYSH, p.13.
Holotype: B.M. A4400.
Type locality: foreshore west of Lyme Regis.

Introduction.

For about a mile southeast of 45/997005 fallen nodules of ironstone speckled with white dickite ooliths, originating from the base of the Ellerbeck Bed, contain at their bases small vertical U-shaped burrows showing very delicate transverse striation. Other larger, oblique, U-shaped burrows have coarser longitudinal striation: these clearly belong to *Rhizocorallium*. The burrows penetrate kaolinitic silts belonging to the Lower Deltaic Series. The detail of preservation is exceptionally good, much better in fact than in the holotype.

Description.

Small, vertical, pocket-like U-tubes with parallel limbs enclosing <u>Spreiten</u> which merge into limbs, giving characteristic key-hole cross-section. Limbs and <u>Spreiten</u> with very fine transverse striations: both filled with identical packing. Average length 18mm. (range 13-22mm): width 5mm (range 4-7mm): depth 36mm. (up to 60mm maximum). Limb diameter (= width) directly correlated with length.

The burrows are normally visible in lateral view, occurring in very high densities. Block E.B.C. contains 20 burrows in 25sq.cm. (a density of 8000/sq. metre). Unlike <u>Diplocraterion</u>, the <u>Spreiten</u> are only visible as superficial ornament; a section parallel to the length would not reveal any lamination. The limbs are not separate entities, and only appear distinct due to their width being greater than that of the septum: any inner margin is lacking. No plugged tubes occur within the 'septal' area, and there is no evidence for any change in the position of the base of the 'U', which is rather more angular than in <u>Diplocraterion</u>.

Small burrows in block E.B.C. with a length of 13mm. possess Chondrites along the margins of both limbs and Spreite (Plate 19). The Chondrites tubes are all of the same diameter (1mm.) and compare remarkably with those along the walls of the Corophioides figured by SCOTT SIMPSON (1957, plate 24, figs. 1 & 2) from the obtusum zone of the Lower Lias at Bishopsworth Bristol, which also came from nodules.

Apertures.

No separate apertures exist.

Faecal pellets.

No faecal pellets have been observed.

Composite burrows.

No composite burrows occur.

Ethological interpretation.

In all cases the burrows appear to have been formed by progressive downward migration within the 'septal' area from the surface to a certain depth. Once at this depth no further migration occurred, the organism dwelling at the periphery of the pocket so formed and there accentuating the width to produce the two apparent limbs. The fact that the width and length of burrows are directly correlated (Table 9) suggests that after ecdysis the organism moved elsewhere and constructed a larger burrow. The very high burrow density may therefore not reflect so high an original abundance of creatures.

Most burrows have closely comparable measurements which agree in detail with those of the holotype and a Corophioides sp. described by SCOTT SIMPSON (1957, p. 493). The salient measurements are compared in Table 9. Only a few reach as much as 3mm. more than the average length. This suggests that in the main the area of colonisation was populated by only one age group. The burrows are very similar in size to those formed by Recent Corophium, known to excavate their burrows by means of gradual downward migration in the 'septal' region (SCHAFER 1962, p.346, fig.179, reproduced as Text-fig. 21). Corophium volutator PALLAS lives at densities even greater than the 8000/sq.metre calculated for Corophioides lymensis, SMIDT (1951) recording densities of up to 24,500/sq.metre. The optimum environment is a grey muddy silt (HART 1930) which never

Text-figure 21.

Diagrams of U-shaped *Spreiten* burrows produced by the Recent amphipod *Corophium volutator* (after SCHÄFER 1962).

A. Burrows constructed exactly perpendicular to the surface of the substratum, however slanting this may be. (fig. 178).

B. Demonstrating the stratification of the *Spreite*, proving its "active" origin (i.e. it is constructed by *Corophium*). (fig. 179).

C. Both limbs of the 'U' have their bends at the same height. This is only possible when the U-burrow was formed before the pocket burrow. (fig. 180).

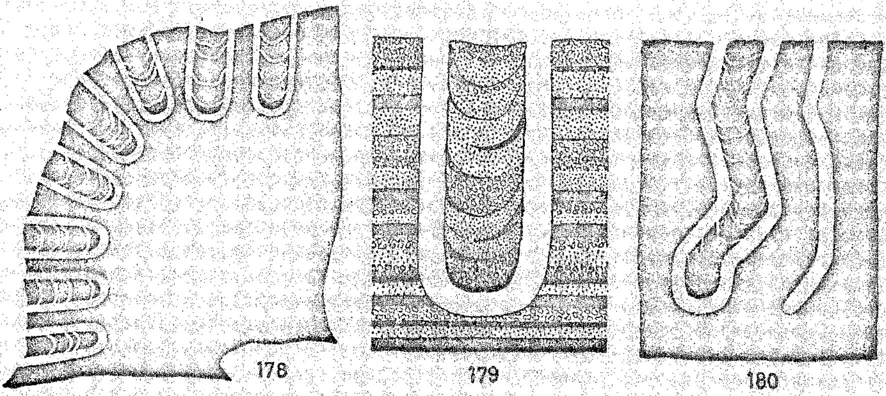


Abb. 178. *Corophium volutator:* Die U-förmigen Spreitenbauten werden ebenso senkrecht in die Tiefe wie schräg und waagerecht in das Substrat eingebaut. — Original.

Abb. 179. Bau von *Corophium volutator:* Die Spreite zeigt an ihrer eigenen Schichtung, daß sie aktiv gemauert wurde. — Original.

Abb. 180. U-Bau von *Corophium volutator:* Die beiden Schenkel des U haben jeweils in gleicher Höhe ihre Abknickungen. Dies ist nur möglich, wenn dem U-Bau ein Taschenbau vorausgeht. — Original.

dries out at low tide; the form being unable to live in putrifying muds with a very high organic content.

TABLE NINE. Data for three blocks of ironstone containing *Corophioides lymensis*.

		Length	limb diam.	Depth	D/L	L/l	
Ellerbeck Bed Yorkshire	E.B. A	18	5	36	2.0	3.6	50% of burrows
		21	7	50	2.4	3.0	largest burrows
	E.B. B	18	5	38	2.1	3.6	70% of burrows
		20	6	45	2.5	3.3	largest burrows
	E.B. C	13	small burrows with *chondrites* along the limb margins				
Lower Lias Dorset	(COYSH)	10-35	4-7	100			
Lower Lias Bristol	(SIMPSON)	30	7-8	100			

Measurements in millimetres.

Sedimentological interpretation.

The very fact that these small vertical burrows are preserved at all suggests that the sedimentary environment was protected from severe erosion. *Corophium* is found today in protected estuaries, and BEANLAND (1940) has related the distribution of the species *C. volutator* to fresh-water stream outlets. SPOONER & MOORE (1940) noted that the species is restricted to sheltered areas where there is little disturbance of the surface sediment.

The stratigraphic occurrence of Corophioides lymensis at the junction between the Lower Deltaic Series and marine Ellerbeck Bed, with the burrows penetrating a typical seat-earth siltstone, suggests that the environment was a very shallow protected embayment on the top of the Jurassic delta. The preservation of the burrows in a pure siderite mudstone further suggests a rather restricted environment. The burrows constitute the first evidence of the slight Ellerbeck transgression, and precede the occurrence of shelly macrofauna (chiefly Nucula, Corbula, Astarte).

Comparisons.

Corophioides luniformis (BLANCKENHORN), from the German Lower Trias apparently shows both protrusive and retrusive behaviour (SEILACHER, 1963, fig.3, p.86) and is difficult to distinguish from Diplocraterion, into which genus it should more properly be placed. Corophioides c.f. rosei DAHMER from the Pakistan Lower Cambrian possesses well defined limbs, and is longer than deep (SEILACHER 1955, p.377). Neither of these forms possesses the characteristic key-hole outline of C. lymensis when seen in cross-section.

Occurrence.

Corophioides lymensis (COYSH) was recorded from many horizons in the Lower Lias by COYSH (1931, p.15), and is widespread in the southwest England province. The type horizon is the Mottled Marl of the Dorset coast (Plate 4). Other horizons include the Planorbis Zone at St. Audries, the Bucklandi Zone at Kilve Pill and Radstock, and the *calcicosta* limestone at Keynsham. The example described by SCOTT SIMPSON (1957, p.493) belongs to *Corophioides lymensis* as here comprehended: it comes from the Obtusum Zone.

The examples from the Ellerbeck Bed of Staintondale constitute the first record of the trace fossil from Yorkshire, and the first record in the Middle Jurassic.

Glossifungites lymensis sp. nov.

Text-fig. 22B

Discussion.

Some authors regard *Glossifungites* LOMNICKI 1886 (p.99) as a synonym of *Rhizocorallium* ZENKER 1836 (e.g. KÄNTZSCHEL 1965, p.38). Both are true rhizocorallids, but the former is characterised by a highly inclined orientation and a flask, or magnet shape (*vide* DOUVILLE 1908, p.366, fig.8; *Taonurus ultimus*; synonym of *Glossifungites saxicava*). In view of its essential differences from the dominantly horizontal *Rhizocorallium s.s.* the genus is retained here, being diagnosed as follows:-

> Vertical or highly oblique *Spreiten* burrows with limbs diverging downwards to give magnet-shaped outline.

Holotype. Specimen in the collection of R.KNOX , Dept. of Geology, University of Newcastle; figured Text-fig.22B.

Type locality. Iron Scar, near Hayburn Wyke, Yorkshire.
Type horizon. Basal ironstone of the Ellerbeck Bed, Bajocian.

Introduction.

About three miles to the southeast of the locality beneath Staintondale and Ravenscar bearing very dense *Corophioides lymensis*, the same horizon at the base of the Ellerbeck Bed has yielded very similar vertical rhizocorallid burrows possessing identical ornamentation of the limbs and *Spreite* but with diverging limbs giving the burrows a constricted flask shape. They must clearly be included in *Glossifungites*.

Diagnosis.

Small, elongate, vertical *Glossifungites*. Limbs parallel proximally, diverging distally producing a shape resembling a long-necked flask or long horseshoe magnet. Limbs and *Spreite* with identical fine transverse striae.

Description.

As in *Corophioides lymensis* there is no distinct separation of limbs and *Spreite*, the two merging to give a vertical pocket burrow. The proximal length of the burrows is identical to that in *C. lymensis* (21 mm.) as is the "limb" diameter (7 mm.). In the bulbous distal region the length increases to 30 mm., though the width of the burrow does not increase.

The burrows are deeper than *C. lymensis* (60 mm. compared with an average of about 45 mm.).

Ethological interpretation.

Glossifungites lymensis appears to represent a burrow produced by an organism which enlarged its burrow as it grew larger. It therefore primarily represents a response to growth and is thus both deeper and longer distally than *Corophioides lymensis* with which it is identical proximally.

The inference is thus that in Corophioides lymensis a series of burrows is produced by one organism as it grows larger, whereas in Glossifungites lymensis the organism remained in one burrow throughout life. The very high density of the burrows of C. lymensis compared with G. lymensis would seem to support such a hypothesis.

Occurrence.

Very much rarer than Corophioides lymensis, of which it is an ethological variant. Known only from the type locality.

Rhizocorallium (Corophioides) jenense ZENKER 1836

Plate 19.1

Discussion.

Rhizocorallium jenense is customarily regarded as being a typical member of the Fodinichnia, and, as the generic diagnosis states, is "horizontal or oblique". However, very highly inclined examples, usually vertical, occur at two horizons in the Yorkshire Jurassic, in both cases descending from marked disconformities.

In the possession of thick, parallel limbs with sculpture identical to that on the *Spreite*, they clearly belong to *Rhizocorallium jenense*. In the vertical attitude of the burrow axis and the reduced length, they clearly belong to *Corophioides*.

In an attempt to portray accurately these two relationships the burrows are described in the Domichnia as *Rhizocorallium* (*Corophioides*) *jenense*.

Description.

Vertical or very highly inclined burrows with deeply scratched limbs and *Spreite* descend from the base of the Dogger pebble bed into the top of the Alum shales at Long Bight, Whitby. The burrows are excavated pockets completely filled with very coarse gritty material identical to that of the overlying Dogger. Differential compaction has caused the Alum Shales to be intensely slickensided along the burrow sides (Plate 19.1B).

The burrows descend up to 45 cm. beneath the disconformity. The limbs are parallel (Plate 19.1A), but the axis is not always strictly vertical, being sometimes 'bent' sharply in the plane of the length. The burrows average 75 mm. in length (=overall gauge of horizontal *Rhizocorallium*) and 19 mm. in 'limb' diameter, which gives a ratio identical to that of *Rhizocorallium jenense* from the Ellerbeck Bed at Ravenscar

(p. 169 ; Plate 25.1). Occasional larger examples are found with a length of 100 mm. and a 'limb' diameter of 26 mm. (Ratio= 3.9; identical to smaller examples). These larger specimens have significantly coarser scratch-markings (Plate 19.1C) and were clearly made by larger organisms.

Vertical examples identical to the average Dogger specimens occur at the base of the Ellerbeck Bed at Iron Scar where they penetrate kaolinitic silts of the Lower Deltaic series. They are associated with Glossifungites lymensis. To the north, beneath Ravenscar, **true** Rhizocorallium jenense (viz. with axis at only 45°) are associated with Corophioides lymensis.

Environmental interpretation.

Highly inclined rhizocorallid burrows often penetrate major unconformities. In Yorkshire, the Dogger Rhizocorallium (Corophioides) jenense occur beneath a disconformity which cuts out the whole of the Yeovilian and several zones of the Aalenian. On the Podolian Plateaux great numbers of Glossifungites saxicava FUCHS descending into the eroded surface of the Upper Senonian are filled with Tertiary sand containing Lithothamnion (FUCHS 1895, p.53). The same form, recorded as Taonurus ultimus SAPORTA by WEIGELT (1929, p.34), descends from the Miocene into the Chalk in Alcoy.

Likewise, specimens of Taonurus saportai DEWALQUE ramify white Chalk but are filled with glauconitic sandstone of the Lower Eocene Landenian.

U-shaped , pocket-like , dwelling burrows scraped out by crustaceans (probably Brachyura, according to WEIGELT 1929) may thus serve to accentuate unconformities by their striking preservation. The fact that the hollows were later filled passively by the overlying sediment drifting into the empty hollows implies that the burrows were probably constructed during the period of non-deposition represented by the unconformity. It also implies that the substratum must have been very solid and unthixotropic, or the burrow sides would have caved in before being filled with sediment. That the substratum was not cemented, in the Dogger examples at least, is shown by the slickensiding along the burrow walls.

Occurrence.

Rhizocorallium (Corophioides) jenense is known from the Dogger and Ellerbeck Bed of the Middle Jurassic of Yorkshire.

SUMMARY : JURASSIC U-SHAPED VERTICAL BURROWS (Domichnia)

Seven 'species' from four 'genera' have been identified and described in detail from the English Jurassic. They may be divided conveniently into two groups:-

Group One : burrows occurring in well-sorted sandstones:-

1. *Arenicolites statheri* BATHER, which is shown to be confined to the Scarborough Beds of Yorkshire;
2. *Diplocraterion statheri* sp. nov., which occurs also in the Dogger and the Ellerbeck Bed;
3. *Diplocraterion arkelli* sp. nov., the most widespread form, invariably associated with faecal pellets.

Group Two : burrows preserved in ironstone, associated with marked disconformities:-

i. *Arenicolites skeltonensis* sp. nov., occurring at the base of the Upper Lias in northeast Yorkshire;

ii. *Rhizocorallium* (*Corophioides*) *jenense* ZENKER, which occurs at the base of the Dogger and the Ellerbeck Bed;

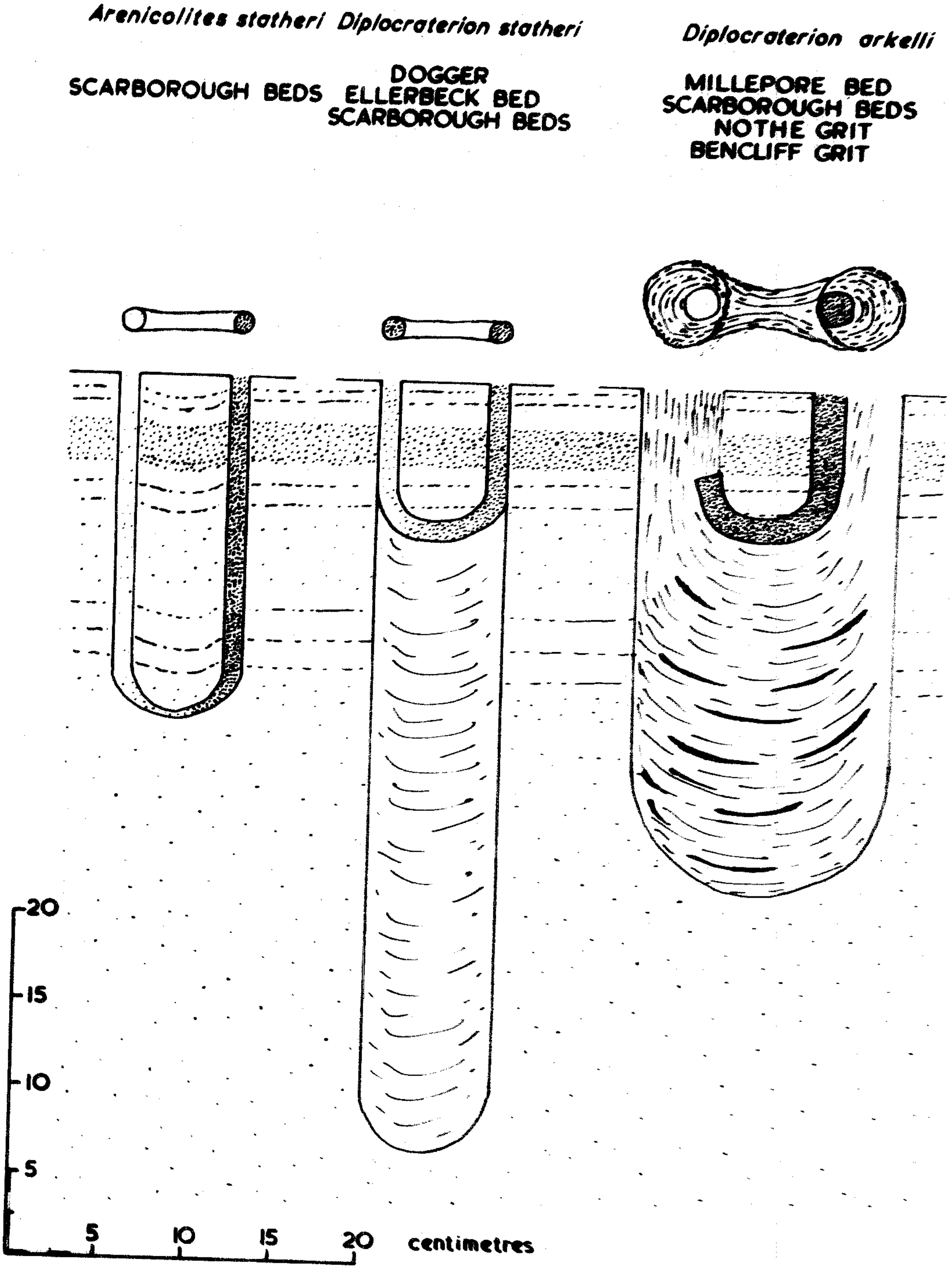
iii. *Corophioides lymensis* (COYSH), occurring in very high densities at the base of the Ellerbeck Bed;

iv. *Glossifungites lymensis* sp. nov., from the base of the Ellerbeck Bed.

The morphological differences between each member of the two groups are shown on Text-fig. 22 A & B.

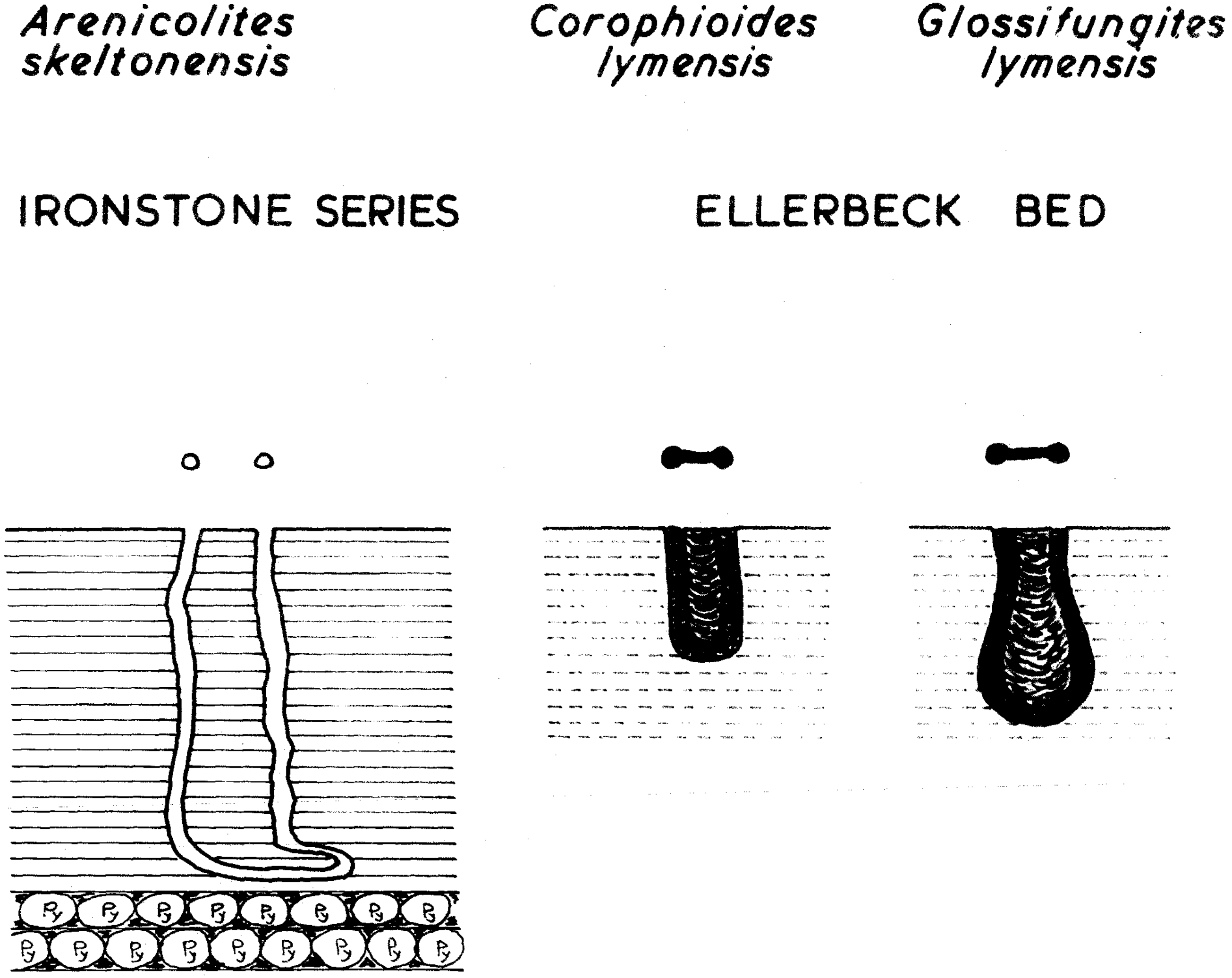
Text-figure 22A.

Summary diagram of Jurassic U-shaped burrows from well-sorted sandstones : x $\frac{1}{4}$.


Arenicolites statheri
Diplocraterion statheri
Diplocraterion arkelli
SCARBOROUGH BEDS
DOGGER
ELLERBECK BED
SCARBOROUGH BEDS
MILLEPORE BED
SCARBOROUGH BEDS
NOTHE GRIT
BENCLIFF GRIT
20
15
10
5
5
10
15
20
centimetres

Text-figure 22B.

Summary diagram of Jurassic U-shaped burrows from ironstone environments: x ½.


Arenicolites skeltonensis
Corophioides lymensis
Glossifungites lymensis
IRONSTONE SERIES
ELLERBECK BED
Py

(ii) Simple vertical burrows.

Skolithos HALDEMAN 1840

1838 *Tubulites* ROGERS (*nom. nud.*)

1847 *Scolithus* HALL (and *auctt*).

1848 *Scolecolithus* ROEMER

1852 *Scolecolithus* GOEPPERT

1857 *Scolites* SALTER

Type species:	*Skolithos linearis* HALDEMAN 1840, pl.1, figs. 1-3.
Diagnosis:	(HÄNTZSCHEL 1962, W.215). Tubes or tube fillings standing vertically in sandstones; diameter 0.2 to 1cm; usually straight, never branched; commonly but not always closely crowded; rarely with fine annulations.

Discussion.

The genus has recently been discussed by HALLAM & SWETT (1966), describing examples from the Pipe Rock of the Scottish Lower Cambrian. A more complete treatment will be found in WESTERGÅRD (1931). The form has been regarded as a set of colonial worm tubes (RICHTER 1920), a phoronid (FENTON & FENTON 1934) or as inorganic, being due to the action of rising air bubbles (HOGBOM 1926). Richter and Westergard (op.cit.) have stated many cogent reasons for regarding it as organic.

Skolithos c.f. linearis HALDEMAN 1840.

Plate 20.

Description.

Straight, cylindrical, unbranched tubes plugged with coarse-grained ooliths set in a matrix of medium-grained laminated oolite, normal to the cross-bedding, which dips at 15°, are found in the Osmington Oolite (Bed 6) at Black Head, Dorset, (Text-fig. 47). They occur beneath bedding planes where an abrupt change in the sediment type occurs (Plate 20A). The tubes are of constant diameter, about 1cm., their depth seldom exceeding 10cm. When seen in cross section the tubes have a truly circular cross section (Place 20C) and a comparatively low density for the genus.

Ethological interpretation.

The tubes occur in well-sorted oolites, devoid of any appreciable clay or silt, and represent the infilled burrows of suspension-feeding organisms, either annelids or phoronids. The top surfaces are conspicuously related to minor non-sequences in the sediment, and the burrows were probably formed during a period of non-deposition, or even slight erosion.

The orientation of the tubes, truly normal to the bedding laminae, which are never depressed near the burrows, is in contrast to that of Diplocraterion arkelli (Text-fig. 14C) where the burrow is truly vertical with respect to gravity.

Sedimentological interpretation.

The tubes are preserved by both bed-junction and concealed bed-junction preservation. Plate 20A shows the former type at the extreme left of the picture, where massive coarse oolite pipes down into grey laminated marly oolite; on the right, immediately above the hammer head, concealed bed-junction preservation is shown, with a massive oolite filling the tubes, which are set in a similar lithology, both being overlain by dark grey marly limestone. Plate 20B also shows concealed bed-junction preservation, with a marked erosion-surface truncating the burrows.

The sedimentary environment appears to have been of high energy, with forset-bedded oolites completely unfossiliferous except for these infilled tubes: on sedimentological grounds alone the region would appear to have been supra-tidal. The comparative rarity of Skolithos from British Jurassic rocks would therefore be explained by the very low fossilization potential of such an environment. The Skolithos zone of SEILACHER (1963, p.85, fig.2) is the most nearshore of his four major bathymetric trace-fossil zones. A supra-tidal, open sea environment is therefore not improbable.

Comparisons.

Except that the Lower Cambrian Skolithos linearis occur in gritty sandstones, they are indistinguishable from the Jurassic examples from the Osmington oolites: the specimen figured by WESTERGARD (1931, Pl.X1/1a,b) is strikingly similar. The density of the Jurassic examples is much less than that in the Pipe Rock example figured by HALLAM & SWETT (1966, Pl.1/1), though this is probably not taxonomically important.

Occurrence.

Skolithos c.f. linearis occurs at Black Head at the base and at the top of bed 6, the Middle White Oolite; at Osmington Mills, the same form occurs at the base of the overlying bed 7, of the Osmington Oolite Series.

Laevicyclus QUENSTEDT 1879.

Text-fig. 23.

Type species: none has been designated.

Diagnosis: (HÄNTZSCHEL 1962, W.201).

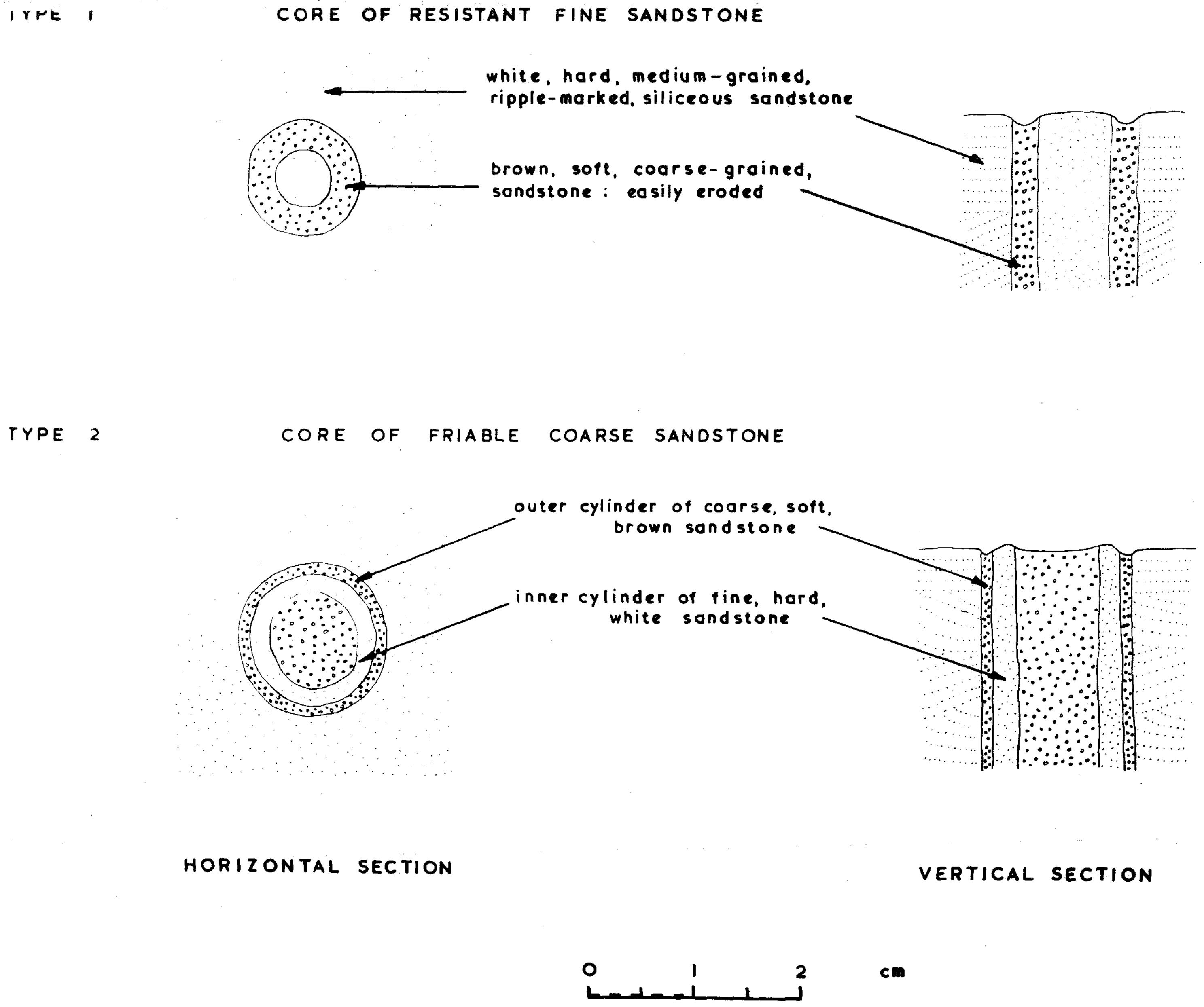
> "Approximately cylindrical bodies standing at right angles to bedding place; diameter variable in same specimen; perforated by central canal; visible on bedding planes as regular concentric circles with diameter of several cm".

Discussion.

The problematical structures were originally interpreted as corals by QUENSTEDT (1879, p.577), and later as inorganic by SCHMIDT (1934, pp.18-27) who considered gas-exhalations and water under pressure within the sediment were responsible. SEILACHER (1953a, p.431, fig.5) has compared *Laevicyclus* with the central dwelling shaft and surrounding scraping circles of the Recent polychaet worm *Scolecolepis squamata*.

Text-figure 25.

Field sketches of two types of
simple vertical burrow (Laevicyclus)
from "non-marine" sandstone blocks
beneath Ravenscar.


TYPE 1
CORE OF RESISTANT FINE SANDSTONE
white, hard, medium-grained, ripple-marked, siliceous sandstone
brown, soft, coarse-grained, sandstone : easily eroded
TYPE 2
CORE OF FRIABLE COARSE SANDSTONE
outer cylinder of coarse, soft, brown sandstone
inner cylinder of fine, hard, white sandstone
HORIZONTAL SECTION
VERTICAL SECTION
0
1
2
cm

Description.

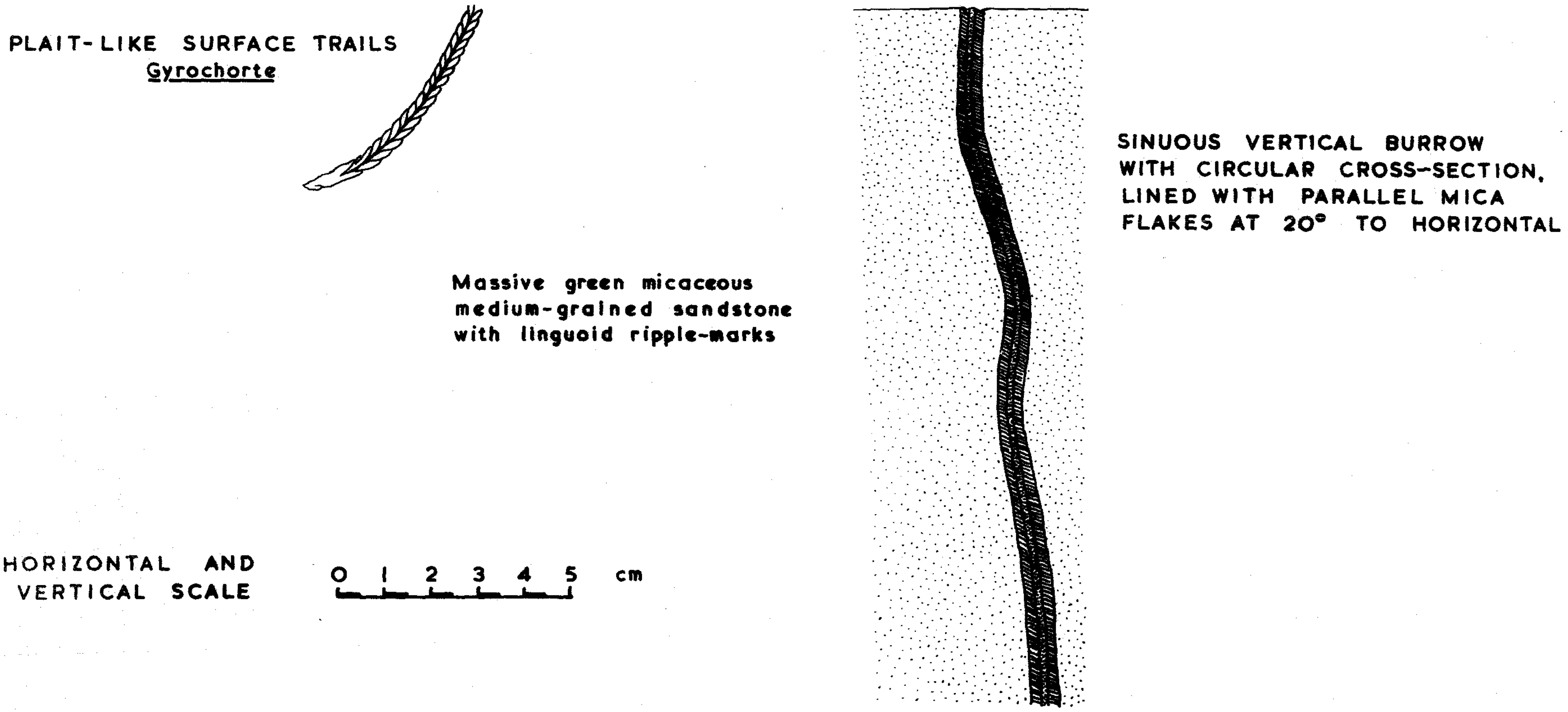
Short vertical tubes (max. depth 8cm.) with a circular cross-section (1-2cm.) and several concentric rings visible on a weathered surface, are common trace fossils in medium-grained sandstones on the backshore beneath Ravenscar. Their horizon can rarely be determined. Occasionally they are found accompanying Arenicolites statheri from S.B.35, but more often they occur with the horizontal bilobed gallery Gyrochorte, probably from horizons in the Middle Deltaic Series.

Two types appear to be common (Text-fig.23). Type 1 consists of a simple shaft, now filled with material identical to that in the surrounding sediment; this shaft is surrounded by coarser, but usually more easily eroded, ferruginous sandstone. This is the predominant type, and the vertical burrows are frequently the starting (or finishing) point for the horizontal Gyrochorte carbonaria trails, whose width matches the internal bore of the tube. The spatial connection is striking, and the connection between vertical burrows and horizontal trails is found also in other morphologically different traces from other lithologies.

Type 2 is rather more complicated, and is rare

Text-figure 24.

Field sketch of two associated trace fossils
from a loose block of Middle Deltaic series
sandstone : A. Gyrochorte comosa - horizontal,
plait-like trail.
B. Vertical burrow lined with
parallel flakes of mica.


PLAIT-LIKE SURFACE TRAILS
Gyrochorte
Massive green micaceous medium-grained sandstone with linguoid ripple-marks
SINUOUS VERTICAL BURROW WITH CIRCULAR CROSS-SECTION, LINED WITH PARALLEL MICA FLAKES AT 20° TO HORIZONTAL
HORIZONTAL AND VERTICAL SCALE
0 1 2 3 4 5 cm

compared with type 1: here the coarser, softer material fills the bore of the tube which is surrounded by two cylinders of sandstone, the coarser occurring outside the finer.

Types 1 and 2 are almost restricted to white, non-micaceous, well-sorted, fine- or medium-grained sandstones. Symmetrical ripples with straight crests are the commonest sedimentary structures, migration of which causes rib-and-furrow structure.

A loose stock of massive green, micaceous, medium-grained sandstone also shows the association between vertical burrows and horizontal trails. Here there is no visible merging of the two, but they are the only two types of trace fossil in the block. The vertical burrows (Text-fig. 24B) are much longer than the orthodox Laevicyclus (15cm.) and a little narrower. The burrows are unique in possessing instead of the coarse ferruginous sandy lining a sheath wholly composed of flakes of mica, each flake parallel to the next, the whole series dipping at about 20° to the horizontal. The associated Gyrochorte comosa (Text-fig. 24A) is a unique specimen also, the obliquely-placed transverse pads being diagnostic of this species. Again the width of the trail, and the bore of the tube are closely comparable.

Interpretation.

The spatial association with trails strongly suspected to be of amphiphod origin suggests that the vertical burrows may also have such an origin. Certainly the Recent amphiphod Corophium volutator is known to produce a simple vertical burrow rather than a 'U' when dwelling in a sandy substratum (SEILACHER 1953a, p.429, fig.4). It is not known whether it lines its burrow, however, either with sand or mica.

It is possible that in Text-fig. 24B, the mica may be secondary, replacing mucus which originally lined the burrow. Sericitic replacement of mucus has been suggested for Monocraterion by GOLDRING (1962, p.235). If the mica is original it is most unusual that the flakes are not oriented parallel to the tube wall, as is generally the case. Alternatively, if it is secondary, the flakes are of a surprisingly large size. If the mica flakes are merely viewed as an alternative selection to sand grains for lining the burrow, the form clearly belongs to type 1.

Type 1 is a simple vertical burrow constructed by one organism using one grade of particle size to line the walls. Type 2 may represent a burrow which was initiated as Type 1, but a later organism re-excavated the central region, the whole of which was later infilled by bed-junction preservation with the coarser sand.

The search for the producer must therefore switch to those creatures known to line their burrows. The worm-like Scleractinian *Cerianthus* lines its burrow with coarse sand-grains (SCHAFER 1956, p.205) but is not as selective as the builder of these *Laevicyclus* appears to have been. Recent polychaetes are more fastidious in their choice, particularly Terebelloids (BATHER 1910, 1911), and these may be considered more likely producers than amphiphods.

Comparisons.

When seen on the surface of a weathered bedding plane the Yorkshire Jurassic *Laevicyclus* are indistinguishable from those figured by HANTZSCHEL (1962, fig.123/3a, W.198) from the Upper Triassic Campiller Beds of Italy. They are superficially similar to the form *Planolites ophthalmoides* JESSEN (illustrated in SEILACHER 1963, fig.1, p.83 and 1964, p.307, fig.6), but this form is surrounded by more resistant eye-like halo caused not by any grain-size differences, but simply by a zone of oxidation around the gallery made visible by subsequent tectonic compression. Moreover, the form is not invariably vertical, but may also be oblique or even horizontal.

Occurrence.

The forms here assigned to Laevicyclus are abundant in fallen blocks of sandstone at intervals along the backshore between Ravenscar and Hayburn Wyke, the horizon from which they originated being impossible to ascertain exactly. Their range does not fall outside the Bajocian however. They may be from either the Lower or (more possibly) the Middle Deltaic Series, and are common in parts of the succession commonly referred to as "non-marine".

SUMMARY: Jurassic simple vertical burrows.

Only two 'species' of simple vertical burrows possess sufficiently diagnostic properties to enable accurate identification. The cylindrical, unlined tube Skolithos has been described from the Osmington oolites of the Dorset coast. The lined, shorter tube Laevicyclus occurs in the 'non-marine' parts of the Middle Jurassic Deltaic Series of Yorkshire.

CHAPTER SEVEN

HORIZONTAL CRUSTACEAN FEEDING BURROWS (Fodinichnia)

I : Y-SHAPED BURROWS (*Ophiomorpha* ; *Thalassinoides*)

The Fodinichnia includes the majority of British Jurassic trace fossils. Generically they constitute the most important group of Seilacher's five categories. Also in terms of burrow densities they are by far the most important group.

Many of the trace-fossil genera within the Jurassic Fodinichnia possess very distinctive geometric shapes and sculpture. Some can be assigned to a crustacean origin with a fair degree of confidence: others are of more doubtful origin. A distinction will therefore be made between these two major categories of feeding burrows.

Feeding Burrows of suspected Crustacean origin.

The following trace-fossil genera fall into this group :-

Ophiomorpha, *Thalassinoides* and *Rhizocorallium*.

Of these, the first is very rare, being known only from the Upper Oxfordian Bencliff Grit and Osmington Oolite of the Dorset coast. The second and third are the two most abundant trace-fossil genera in the British Jurassic, with the possible exception of Chondrites, and must account for well over 50% of the burrows recorded in the present study.

Ophiomorpha LUNDGREN 1891

For complete synonymy, see HANTZSCHEL (1952)

Type species. Ophiomorpha nodosa LUNDGREN 1891, p.114;
Palaeogene, Scania.

Generic diagnosis (HANTZSCHEL 1962, W.205-6):

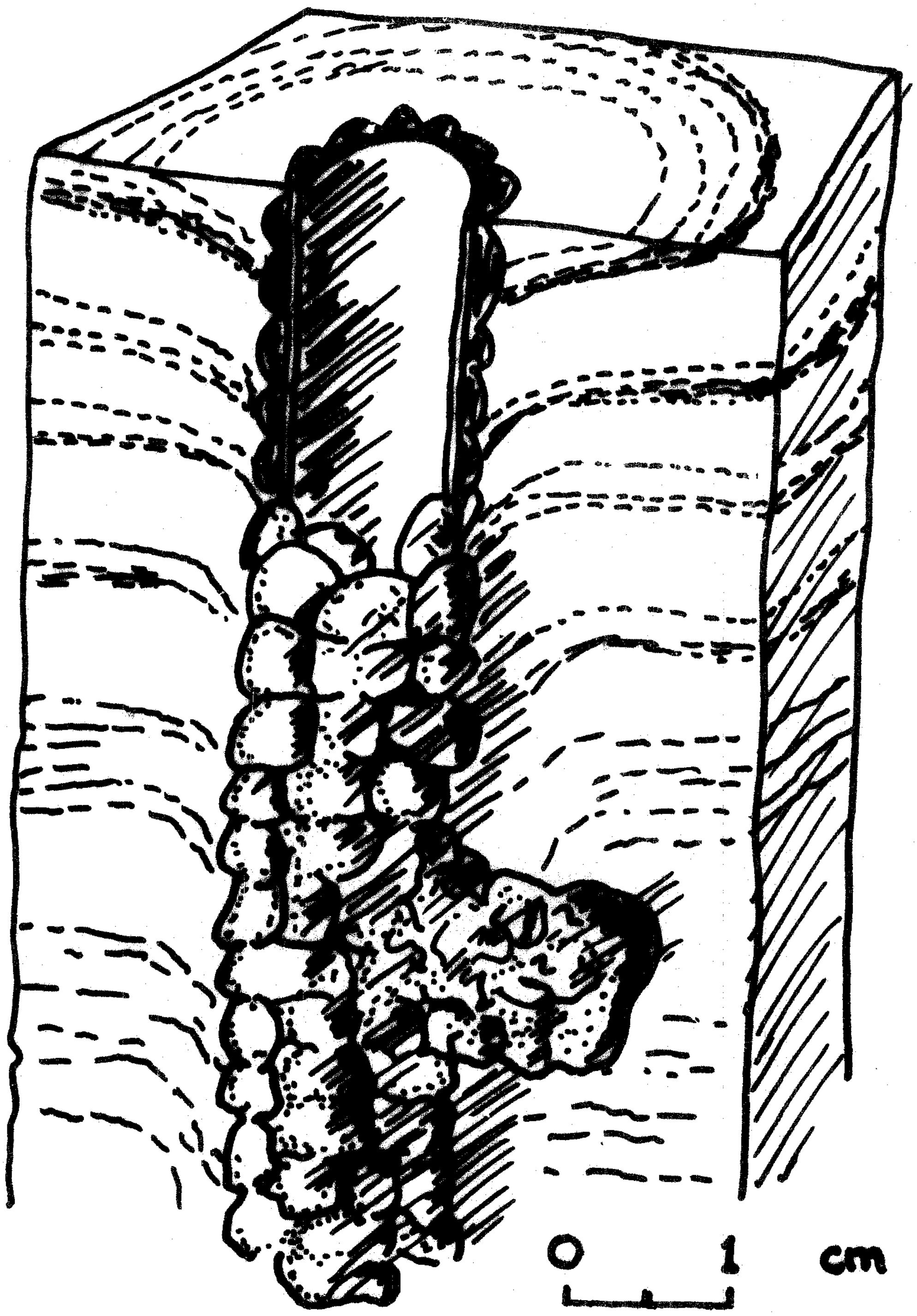
> Tunnel trails with tubercle-like or wart-like ornamentation of outer wall but smooth inside; width 1 to 2 cm.; may be branched, with place of ramification widened in blistered or pear-shaped way.

Ophiomorpha borneensis KEIJ 1965

Plate 21

Text-figure 25.

Diagram of _ophiomorpha nodosa_ LUNDGREN
from the Miocene of Germany
(after HILLMER 1963).


0
1
cm

This species was erected to distinguish forms with a dominantly horizontal orientation (*Ophiomorpha borneensis*) from those where most of the burrows are vertical (*Ophiomorpha nodosa*; Text-fig. 25).

Occasional doggers from the Bencliff Grit at Redcliff Point (Text-fig. 47) show horizontal burrows with a wart-like lining (Plate 21A). The burrows have a circular cross-section varying between 1 and 1½ cm. in diameter, though this increases in the vicinity of burrow branches, which are generally dichotomous. Rare vertical shafts are indicated by the scars of broken tunnels, circular in outline, which are seen as black areas on Plate 21A. No actual vertical trunk has been observed.

Only the dorsal (upper) surface of the burrow-wall could be observed. It is lined with coarse, closely packed, clayey pellets, darker in colour than the surrounding matrix of yellow sandstone, each pellet being separated from the next by deep incisions. KEIJ (1965, p.225) reports that the ventral surface of the burrows is smooth or only sparsely dressed with pellets: this could not be checked in the Dorset material. He also reports (*loc.cit.*) that the pellets on the dorsal surface of the type material are of a conspicuously dark brown colour, possibly caused by collophanite, a substance which is known to be used by *Callianassa major* SAY for strengthening the walls of its burrows (WEIMER & HOYT 1964, p.763).

Within the Osmington Oolite succession at Black Head some small *Thalassinoides*-like trace fossils occur in Beds 6 and 7b (of ARKELL 1949). They branch dichotomously, and consist of a smooth-walled core between 9 and 12 mm. in diameter, filled with coarser ooliths than the matrix, surrounded by a haematite-rich lining about 2½ mm. in thickness (Plate 21B). Within this lining, which is very much less resistant to erosion than the core, a series of regular pits occurs (Plate 21C) at intervals of 2.5 to 3.7 mm., depending on the width of the core.

It seems unlikely that the haematite staining is original, but it may well represent a replacement of some other burrow linign material of the typerrecorded by WEIMER & HOYT, *op.cit.*). The burrows are, like *Ophiomorpha borneensis*, essentially horizontal, but often descend obliquely through the oolite (Plate 21B). Transverse sections in the horizontal plane are more common than in the better preserved examples from the Bencliff Grit.

Ethological interpretation.

The burrows are thought to have been the product of a species of the anomuran genus *Callianassa* (Text-fig. 3) which burrowed horizontally. *Callianassa major* produces vertical structures up to 2 m. long, in all respects identical to the trace fossil *Ophiomorpha nodosa* (Text-fig.25). Other Thalassinidea, including other species of *Callianassa*, are known to produce perfectly smooth walls to their burrows, with no sign of any coarse pellets (Text-fig. 4), but these burrows, assigned to the trace-fossil genus *Thalassinoides*, agree with *Ophiomorpha* in their characteristically dichotomous branches.

Comparisons.

TOOTS (1961) has recorded dominantly horizontal *Ophiomorpha* from the Cretaceous of Wyoming, though in general the trace fossil is more abundant in Tertiary and Quaternary sediments. It has been widely recorded from the Miocene, around Hamburg (HÄNTZSCHEL 1952) and elsewhere in Germany (LUTTIG 1962, p.585), and from Borneo (KEIJ 1965, pp.224-226, pl.29); from the Oligocene (MURAWSKI 1960, p.222) and from the Pleistocene (WEIMER & HOYT 1964).

Occurrences of *Ophiomorpha* in Jurassic rocks are confined to poorly illustrated records from the Upper Jurassic of northern France. BOURSAULT (1889, p.728) described " tubes ou canaux...dont les parois sont criblées de petites cavités hemisphérique de 2 a 3 mm. de profondeur," under the name *Portelia*, which Prof. HANTZSCHEL (1967, personal communication) assures me is pre-occupied by the polychaet *Portelia* de QUATREFAGES.

Environmental interpretation.

The distribution of the trace fossil *Ophiomorpha* is very strongly governed by the nature of the substratum. The Miocene examples from Borneo and Germany previously quoted agree with the Jurassic examples from the Bencliff Grit of Dorset in being preserved in well-sorted, laminated sandstones with abundant coaly matter, often in the form of flakes and pebbles dispersed through the bed, or concentrated into discrete laminae. Association with deltaic sediments is strong, and both the stratigraphic and the sedimentological restriction of *Ophiomorpha* suggest that it may be a useful indicator of proximity to shorelines and may also indicate somewhat brackish conditions.

KEIJ (1965, p.221) notes that the only microfauna commonly associated with *Ophiomorpha* is the *Ammobaculites* association, suggesting a fresh-brackish-water environment of deposition. In Dorset only a few arenaceous groups of Foraminifera are found in very large numbers in the Bencliff Grit. Here also the Ostracoda show an abrupt change in the specimen:species ratio, from 25:1 to 80:1 (WHATLEY 1965, pp.537-8), and the tolerant species are moreover much smaller in size in the Bencliff Grit than elsewhere, and this decrease, like the restriction in the Foraminifera, is probably related to a lowering of salinity (BARKER 1963).

There is thus abundant evidence from localities widely separated in space and time that *Ophiomorpha* was formed in the littoral zone, usually under conditions of reduced salinity. It is typically found in deltaic sandstones, and, in sequences of dominantly freshwater deposits, it may also be used as a sensitive indicator of slight quasi-marine transgressions. Since it occurs unassociated with other fauna it may present the only evidence for such an advance. Thus HILLMER (1963, p.137) points out that beds deposited in a hitherto questionable environment occurring between the Eocene Middle and Upper Coal Groups of Helmstedt could now be definitely stated to be of brackish-marine origin on the basis of the widespread occurrence of *Ophiomorpha*.

Thalassinoides EHRENBERG 1944

1841 *Cylindrites spongioides* GOEPPERT (*nom. nud.*)
1842 *Spongites saxonicus* GEINETZ (*nom. nud.*)
1955 *Vomacispongites* de LAUBENFELS.

Type species. *Thalassinoides callianassae* EHRENBERG 1944, p.358; Miocene, Austria.

Generic diagnosis (HÄNTZSCHEL 1962, W.218):

> Branched burrows and tunnel systems, forkings mostly Y-shaped, without special ornamentation, commonly widened to form pear-shaped cavities.

Thalassinoides saxonicus (*sensu* RIETH 1932)

Plate 22; Text-fig.26C.

1932 *Spongites saxonicus* RIETH, pl.5, figs. a1 and a2.

Hummocky masses of closely-spaced, dichotomously branching burrows with an axial core running through their lower margins occur in the Scarborough Beds south-southeast of Blea Wyke Point on the Yorkshire coast (45/993012). They are confined to one horizon (S.B.28, Appendix IV) and have not been recorded elsewhere in the British Jurassic.

The burrows are wide (about 70 mm. on average), oval in cross-section, and occur in such a high density that they tend mutually to impede one another, so that regularity of dichotomy is not obtained (Plate 22). Similarly, mutual interference appears to be the cause of their irregularly horizontal orientation.

Comparisons.

Thalassinoides saxonicus has been widely reported from the Cretaceous, usually as *Spongites* auctt. RIETH (1932, pl.5) has illustrated two occurrences, both of which are isolated examples, their branching being quite unaffected by interference from adjacent burrows. The nature of the branching seems to be fundamentally different from that in *Thalassinoides suevicus*: it is more angular and less regular (Text-fig.26), varying between 40° and 130°, compared with 100°-140° for the more regular 'species'. In the British Jurassic, *Thalassinoides saxonicus* is much more restricted than the cosmopolitan *T. suevicus*, which lacks the axial core and is more regularly branched.

Interpretation.

In view of the lack of distinctive packing around

Text-figure 26.

Diagrams illustrating various patterns of dichotomous branching in European Mesozoic *Thalassinoides*.

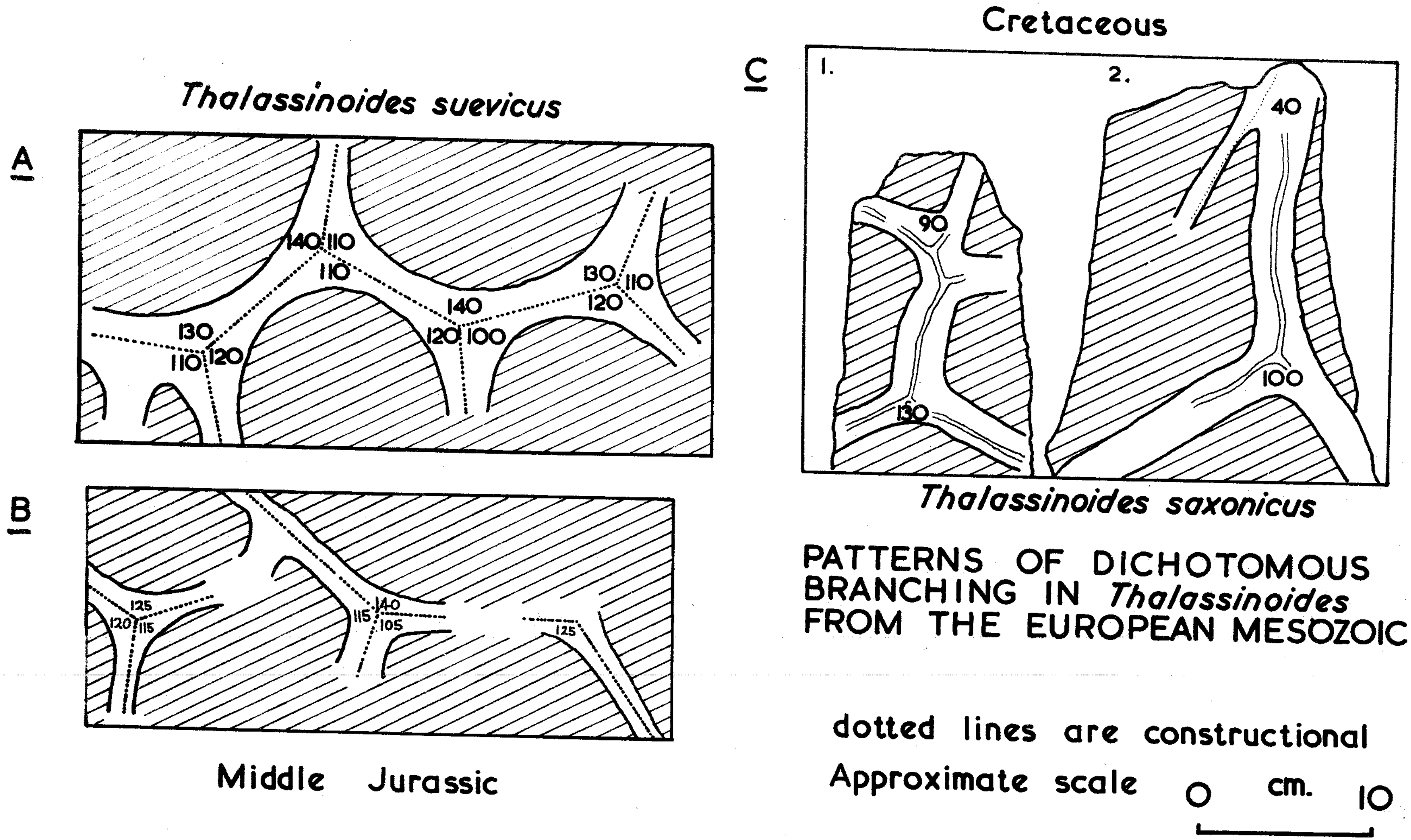
A. T. *suevicus* from the Dogger
of the Swabian Jura.

B. T. *suevicus* from the Scarborough
Beds (S.B.28) of Cloughton Wyke,
Yorkshire (54/020951).

C. T. *saxonicus* :
1. Cenomanian, Bannewitz :
2. Lower Freestone, Welschufa.

A. & C. after RIETH (1932).

B. redrawn from Plate 23B.



PATTERNS OF DICHOTOMOUS BRANCHING IN *Thalassinoides* FROM THE EUROPEAN MESOZOIC

dotted lines are constructional

Approximate scale

the burrow walls (c.f. Ophiomorpha) it is not possible to be very specific about the nature of the trace-fossil producer in this instance. Dichotomously branching cylinders may be formed in a number of different ways (see the discussion of Thalassinoides suevicus, p.). No account exists of a Recent Y-shaped burrow with an axial core analogous to that in Thalassinoides saxonicus, and so the interpretation of this 'species' may conveniently be included with that of the more widespread T. suevicus, for which analogous Recent structures are well documented.

Thalassinoides suevicus (QUENSTEDT 1858)

Plates 23 - 25 ; Text-figs.26A,B, 27.

1858 Spongites suevicus QUENSTEDT

Introduction.

Horizontal Y-shaped cylinders, devoid of axial canal and special ornamentation, are often found in great banks on bedding planes of detrital limestones and are one of the most common of British Jurassic trace fossils. They are also exceedingly abundant in Germany at the same horizons asin Britain.

Description.

The burrows are of ovoid cross-section and vary greatly in width. The smallest only reach 16 mm. (from S.B.32 of the Scarborough Beds, south-southeast of Blea Wyke Point: 45/998003). The largest may attain a width of 100 mm. (in the Osmington Oolite at Black Head, Dorset). The average of 40-50 mm. includes specimens from classic Filey and Dorset localities. The average may be particularly misleading, however, for in one burrow system the width may vary between wide limits in a comparatively short distance.

Frequently the burrows are accentuated by a lining of shell fragments, especially in the coarser, gritty lithologies, and may appear very much coarser than the matrix. This lining may be more easily eroded than the core of the structure, so that a furrow may result on prolonged weathering (Plate 23A).

Laceration of the burrow wall has been observed in a system of burrows from S.B.32 of the Scarborough Beds beneath Staintondale (Text-fig. 27). The burrows are here preserved in a fine-grained sandy limestone. In the majority of cases, where the burrows are preserved in much coarser lithologies it is doubtful whether any laceration of the wall would be preserved.

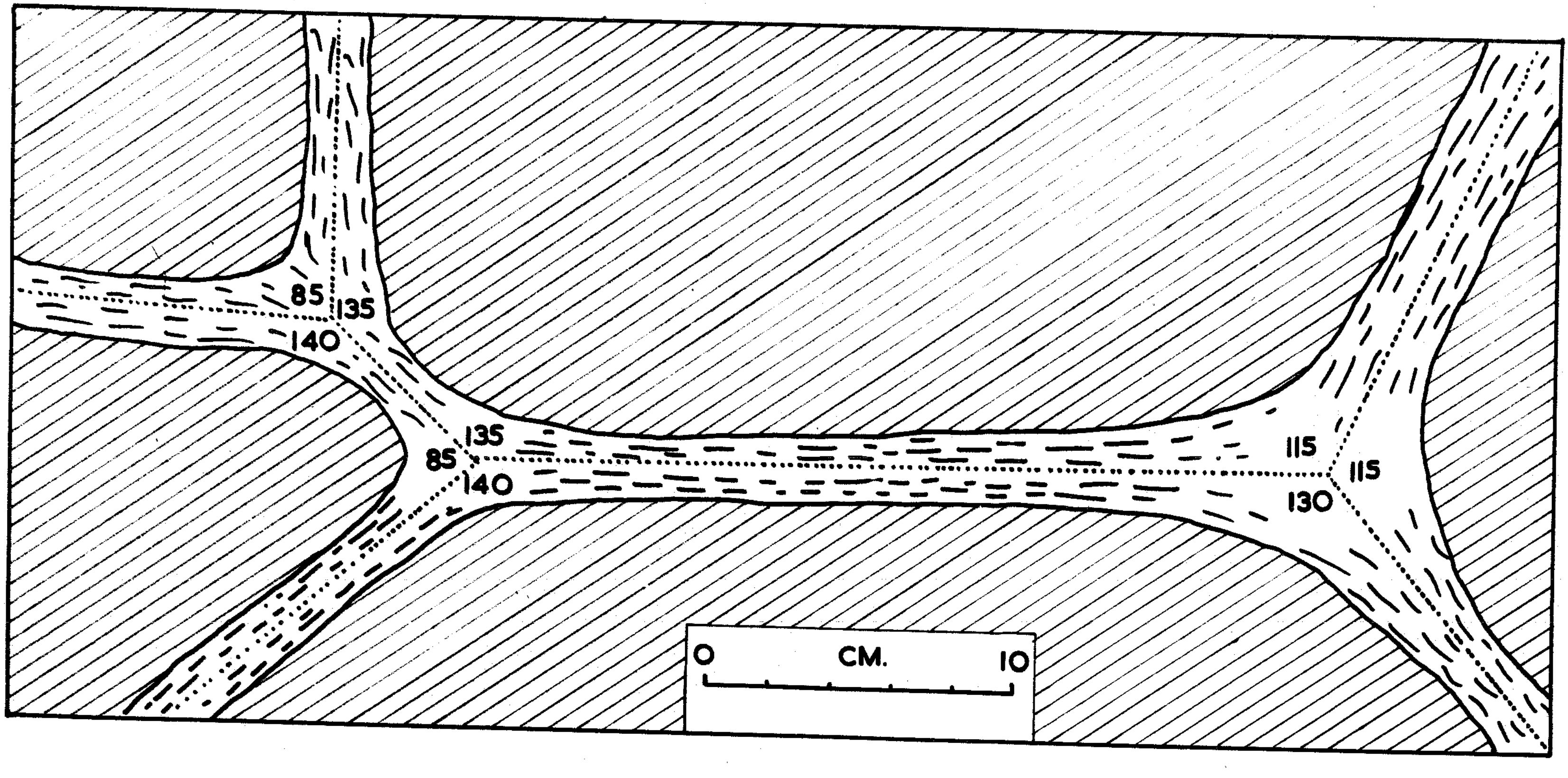
Where the burrows of *Thalassinoides suevicus* do not occur in very high densities, and thus interfere with each other's development, remarkably constant values for the dichotomy of the branches are obtained (e.g. in the Filey Brigg Hambleton Oolites; Table 10).

TABLE TEN. DICHOTOMOUS BRANCHING IN *Thalassinoides*.

Horizon	Locality	Source	Number of angles measured	Average variation from 120°
Thalassinoides suevicus				
Dogger β	S.Germany	Fig.26	12	10°
S.B.32	Staintondale	Fig.27	9	18°
S.B.28	Cloughton	Fig.26	7	8°
Hambleton Oolite	Filey	Pl. 24	33	12°
		Pl. 25	16	20°
Thalassinoides saxonicus				
Cretaceous	S.Germany	Fig.26	4	35°

Text-figure 27.

Field sketch of lacerated Thalassinoides suevicus from loose block of Scarborough Beds (S.B.32) beneath Staintondale, showing the dichotomous branching.


85
135
140
135
85
140
115
115
130
0
CM.
10

Interpretation.

The characteristic mode of preservation of *Thalassinoides suevicus* is as semi-reliefs projecting from the lower surface of coarse clastic sediments. This fact has played a significant part in the evolution of ideas on the origin of these structures.

The classical view, that they represent the casts of ancient sea-weeds, originated in the early days of palaeontology (GOEPPERT 1842), and led to the general "sack" term 'Fucoid' becoming established for these, and most other problematical fossils.

Later they were compared with horny sponges by many authors (e.g. RIETH 1932), although this view had been challenged by REIS (1910) who demonstrated that they were definitely burrows. The sponge origin is still held by de LAUBENFELS (1955).

V.WILSON (1949, p.262) suggested that they represent the weathered-out remnants of infilled suncracks. There are several objections to this inorganic hypothesis:-

a) Suncracks do not develop in coarse detrital limestones;
b) When developed, suncracks are sharply polygonal;
c) The structures are of sub-circular cross-section;
d) They are peripherally rimmed with detrital debris;
e) Isolated examples occur in neritic sediments.

Recently the trace fossil *Thalassinoides* has been compared with the Y-shaped burrows produced by anomuran crustaceans of the family Callianassidae, species of which also produce the burrows *Ophiomorpha* to which reference has previously been made (p. 149)

STEVENS (1929) states that the burrows of *Callianassa* and *Upogebia* (Text-fig. 3) are cylindrical, with a diameter of 1 to 1½ inches, and are vertical. The junctions of the Y-shaped burrows are of enlarged diameter due to the animal's activity, which involves a somersault in order to reverse its position after digging and transport excavated material to the surface. This turning accounts for the cylindrical form of the burrow. As a reslut of the pressure of the animal's body in many trips back and forth, the walls are smooth, as if plastered.

STEVENS further notes that whereas *Upogebia pugettensis* achieves a wide distribution, being found in coarse compact material, *Callianassa californiensis* is more restricted, and most common in ground which is more sandy than muddy.

MACGINITIE (1934) has considerably added to our knowledge of the ecology of *Callianassa*. He has stressed the importance of thixotropy in determining the distribution pattern,; it is not found either in very loose sand or in very soft mud, in neither of which lithologies can permanent burrows satisfactorily be constructed.

MACGINITIE (*op.cit.*) observes that *Callianassa* is wholly occupied in extending or adding new tunnels to its burrows, which often connect with those of other individuals. This latter point has important bearing on the origin of fossil *Thalassinoides*, for these burrows are invariably interconnected (Plate 24).

Since *Callianassa* is a deposit feeder (c.f. *Upogebia*) it follows that its burrows are likely to exploit any horizon especially rich in organic matter, which would account for fossil *Thalassinoides* being preserved as "sole-trails" at an interface between two lithologies. SCHÄFER (1962, p.353, fig.186; reproduced as Text-fig. 4) illustrates a plan view of a horizontal system of Y-shaped dichotomously branching Recent burrows produced by the feeding activity of *Callianassa*.

Such extensively developed dichotomous branching is not known to be produced by any burrowing creatures other than Decapoda. Moreover, the mass appearance of great densities of these fossil structures is in complete harmony with the present-day occurrence of burrowing decapods, which are distributed over wide areas as the dominant benthos.

Comparisons.

Among the first to draw attention to the similarities between fossil 'Fucoids' and 'Concretions' and the burrows produced by Decapoda were NOMURA & HATAI (1936), who compared some " forked branch-like concretions of Y-shape " from the Japanese Upper Miocene / Lower Pliocene Suenomatuyama Group with Recent *Ocypoda* burrows described from Formosa by TAKAHASHI (1935). These "concretions" were 22 - 30 mm. in diameter, and oriented horizontally (unlike *Ocypoda* burrows), being situated just above a major unconformity. Like the Jurassic *Thalassinoides* illustrated on Plate 23 the Japanese Tertiary structures are rimmed peripherally with clastic matter, in the latter case believed to be Foraminifera.

The Corallian 'Fucoids' of Filey Brigg (Plates 24 & 25) agree with the Tertiary examples from the Suenomatuyama Group in their dichotomy, though the latter do not exhibit the anastomosis shown by the Filey trace fossils. Both Y-shaped sets of burrows are preserved in coarse detrital limestones with pectinids as common faunal associates.

RIETH (1932) has recorded four horizons from the German Jurassic which possess *Thalassinoides suevicus* almost identical to the English examples (Text-fig. 26).

Thalassinoides suevicus is the most abundant trace fossil occurring in nearshore deposits. Its abundance is very much reduced in Jurassic neritic sediments, where Chondrites is the dominant trace fossil, though it has been widely recorded from the Chalk, especially from the hardgrounds (BROMLEY 1967). This distribution pattern at first appears anomalous. Why should Thalassinoides, after being of minor importance in Jurassic neritic sediments, assume dominance in the Chalk, presumably a neritic deposit ?

The answer is probably to be found in the phenomenon of 'submergence' which is exhibited by the majority of marine animals at the present day. Thus creatures which are in high latitudes inhabitants of the intertidal zone occur at great depths in the tropics, where the temperature of the water is identical. Small-scale examples of this principle have been demonstrated by HOLME (1961) among Bivalvia in the English Channel.

Thus either a variation in latitude or an alteration of oceanic temperature can cause the 'submergence' of whole animal communities. It is not too much to expect an overall change in oceanic temperature from the Jurassic to the Cretaceous, and with it a change in the bathymetric faunal zonation.

CHAPTER EIGHT

HORIZONTAL CRUSTACEAN FEEDING BURROWS (Fodinichnia)

II : U-SHAPED BURROWS (*Rhizocorallium*)

Rhizocorallium ZENKER 1836

1846 *Spongia rhizocorallium* GEINITZ

1876 *Chorcophyllites* TATE, R. & BLAKE

1908 *Lissonites* DOUVILLE (*nom. nud.*)

1929 *Cavernaecola* BENTZ

1941 *Upsiloides* BYRNE & BRANSON

1951 *Rhizocorallum* SULLIVAN & ÖPIK (obj.)

Type species. *Rhizocorallium jenense* ZENKER 1836, p.219, Muschelkalk, Thuringia.

Generic diagnosis (HÄNTZSCHEL 1962, w. 210):

> U-shaped tubes with *Spreite* and nearly parallel legs which are distinctly set off from the vertex arch; tubes relatively thick; mostly oblique or parallel to bedding; preponderantly feeding burrows; prolongation of dwelling tube by removal and redeposition of sediment in vertex; may show lateral flaps and at outer side of tube scratch

markings (indicative of crustaceans); ellipsoidal excrement pills may be incorporated.

Discussion.

MAYER (1952, p.111) has remarked that Rhizocorallium is very often mentioned in stratigraphic studies without due effort being made to designate 'species'. This unwillingness is perhaps justifiable, for the degree of perfection of preservation is of major importance in the taxonomy of the Rhizocorallidae.
Thus Rhizocorallium jenense differs from R. commune in having more marked sculpture. It is generally found penetrating fine-grained lithologies which would be expected to retain fine structural detail.

However, there are other differences. R. jenense possesses a diagonally-reticulate sculpture both on the limbs and internal Spreite. R. commune has a longitudinally striated sculpture, confined to the limbs; the Spreite, formed of bow-shaped arches, is devoid of sculpture. MAYER (loc.cit.) considers this a sufficient difference for specific discrimination, though SCHMIDT (1936, p.20) and WEIGELT (1929, p.27) consider that R. jenense and R. commune are merely different states of preservation of the burrows of one creature.

Other 'species' of *Rhizocorallium* are not based primarily on sculptural details; e.g. *R. hohendahli* (HOSIUS 1893) from marine bands in the Wealden of Westphalia has a tripod form; *R. uliarensis* (FIRTION 1958) has a spirally coiled axis.
These 'species' are not open to question, as is *R. commune*.

Rhizocorallium jenense ZENKER 1836

Plates 5, 19 & 25.1

Oblique examples descending at angles of 45°- 60° with an overall gauge of 42 mm. and a limb diameter of 11 mm. occur in the basal ironstone of the 'marine' Ellerbeck Bed beneath Ravenscar and Staintondale (Text-fig. 40). They are associated with great numbers of *Corophioides lymensis* (Plate 25.1). Both walls and *Spreite* are sculptured, the former with deep, long scratches sub-parallel to the long axis of the burrow (Plate 5). The *Spreite* is about 7 mm. in thickness, its base being at the same level as the base of the limbs.

Other examples have an overall gauge of 60 mm. and a limb diameter of 16 mm. In both cases the ratio of gauge:limb diameter is reasonably constant (3.9 and 3.75).

In neither set do the burrows descend to any great depth, 90 mm. being the maximum observed. The lithology is a fine-grained kaolinitic silt, the kaolin immediately calling to mind the great tripod banks of *Rhizocorallium hohendahli* in the German Wealden, where the environment was very similar to that of the Yorkshire Middle Jurassic.

Examples of *Rhizocorallium jenense* from the Lower Lettenkohle of Enzberg (MAYER 1952, pl.VI/2) compare very closely with the Ellerbeck Bed examples.

Rhizocorallium jenense is customarily regarded as belonging to the Fodinichnia (SEILACHER 1953, p.440), and accordingly is described at this point in the thesis. However, in the Ellerbeck examples described there are indications that they belong more fittingly in the Domichnia. First, the burrows are highly oblique, and of no great length (Maximum depth= 10 cm.). Second, a few miles to the southeast on the same horizon at Iron Scar, related rhizocorallid burrows are large, and truly vertical, but possess identical sculpture to the Ravenscar burrows: these were described under the Domichnia as *Rhizocorallium (Corophioides) jenense*.

In contrast to these short, essentially vertical structures, true rhizocorallid feeding burrows are often over 100 cm. long and essentially horizontal. However, it is unlikely that a sharp division exists in Nature between the two categories, and the *Rhizocorallium jenense* from Ravenscar, with their 45° orientation, constitute an intermediate assemblage which could be placed satisfactorily in either the Domichnia or the Fodinichnia.

Rhizocorallium *cicatricosus* (TATE & BLAKE 1876)

Plates 26, 27, 28A,C, 29.

1876 *Chordophyllites* *cicatricosus* TATE & BLAKE, p.474, pl.14/9

Introduction.

This form was considered by TATE & BLAKE (*loc.cit.*) to represent a fucoid, and they drew attention to its resemblance to the "strands of the common tangle". Such an origin for these structures is unlikely since the tubes, which are packed with faecal pellets, exhibit phobotaxis. The trace fossil was sufficiently well illustrated for the specific name to stand, though it is now necessary to place it in Zenker's 'genus' *Rhizocorallium*.

Undoubtedly, *R.* *cicatricosus* would be placed in synonymy with the type species *R.* *jenense* were it not for the lack of the necessary *Spreite* possessing sculpture identical to that along the outer margin of the limbs.

Diagnosis (prepared):

A 'species' of *Rhizocorallium* closely allied to

R. *jenense* but lacking a sculptured *Spreite*. Limbs circular in cross-section with coarse diagonally-reticulate scratches intersecting at very low angles; plugged, containing ellipsoidal faecal pellets. Overall; range 50 - 60 mm., limb diameter 15 - 18 mm. (Ratio = 3.3). Axis tortuous but limbs parallel; often of great length (up to 300 cm.), terminating in simple U-turns.

General morphology and Occurrence.

In the Cleveland Ironstone Series of the Middle Lias *Rhizocorallium* attains the status of an horizon indicator, for it is only found with the above dimensions and characteristics at one level within the Main Seam. It is recognisable over many tens of square miles, and always occurs at precisely the same horizon.

At the type locality of Old Nab, southeast of Staithes (45/794187; Text-fig. 38) a great bank of *Rhizocorallium* extends along the length of the outcrop of the lower half of the Main Seam for several hundred yards. Most of the burrows are very long (Plate 27C) and have tortuous axes. Occasionally the axis is smoothly curved to the right (looking towards the vertex), a characteristic also noted in *Rhizocorallium* from the Lower Cretaceous of Australia.

VEEVERS (1962, p.13) observed that all but two of the sixteen trails examined by him showed this phenomenon. However, these Australian trails occur at a lower density than that found in the Middle Lias at Staithes, where proximity to other burrows causes many irregularities in ethological pattern. The examples figured on Plates 27A and 29C have been formed without interference from neighbouring burrowers, with the exception of the 'kink' in the specimen shown at the top of the photograph, which is a commonly observed feature in Rhizocorallium commune from other horizons (Text-figs. 29, 31, 33).

Plate 28 shows one of these 'kinks' in detail. It can clearly be observed that one limb is bent in such a way as to avoid a vertical obstruction which was lying directly in its path. Similar 'kinking' occurs more frequently with R. commune, often taking place at the vertex, where it cannot be established that the organism was attempting to avoid an obstacle (Plate 32). In this instance it seems possible that such an ethological modification was adopted to ensure a better coverage of sediment while feeding.

Although the density of burrows is often high, it is exceptional for branched burrows to occur (Plate 29A), and intersections of unrelated burrows are unknown. Oblique burrows are numerous where the density is high

(Plate 29B), a phenomenon also observed with Rhizocorallium commune from the basal Osmington Oolites at Bran Point. They never descend at angles greater than 20° (c.f. R. jenense from the Ellerbeck Bed, p. 169) unlike the Rhizocorallium illustrated by VEEVERS (1962, p.18, pl.1/5).

Faecal pellets.

Sections cut at right angles to the axis of the limbs reveal circular areas about 2 mm. in diameter which are distinctly greyer in colour than the rusty siderite-rich limbs (Plate 30A). Some of these are very long for faecal pellets when seen in longitudinal section, often 2 or 3 cm. in length (Plate 30B). It seems likely that these are not faecal pellets at all, but sections of Chondrites probing along the limbs subsequent to the vacation of the burrow by the original occupant.

Chondrites is known to probe down the limbs of vertical burrows (KREJCI-GRAF 1938; SCOTT SIMPSON 1957, pl.24). Other darker areas are irregularly drawn-out ellipsoids less than ½ cm. in length. These are more likely to be true faecal pellets.

Walls.

There is no evidence that the burrows were actively lined in the same way as Ophiomorpha. Occasionally, ooliths of chamosite are to be found packed around the periphery, but the fact that the deep lacerations on the burrow sides are consistently preserved in great detail (Plate 26) tends to suggest that this packing of chamosite ooliths along the burrow wall was not a common feature.

Ethological interpretation.

The great horizontal extent of the burrows of *Rhizocorallium cicatricosus*, their occurrence in a fine-grained muddy lithology, and the presence of numerous faecal pellets, all indicate that the burrows are the product of a deposit-feeding organism. The deep lacerations on the burrow margins could only have been the work of crustaceans, for the appendages of other creatures, even sabellid annelids or spionids are most unlikely to produce such deep indentations.

WEIGELT (1929), in the most useful discussion on the origin of *Rhizocorallium* which has yet appeared, has stated that species of the stomatopod *Squilla* (Plate 33) which burrow in muddy substrata produce *Rhizocorallium*-like structures (*op. cit.*, p.13). Later in the work WEIGELT attributes rhizoliths in the Pomeranian drift to: "the digging passages of cray-fish" (*op. cit.*, p.29).

It is remarkable that the gauge of *Rhizocorallium cicatricosus* is so constant. This is more easily understood in *Rhizocorallium commune*, where the *Spreite* obviously constitute a control, but there is no such connection in *R. cicatricosus*. A satisfactory explanation can only be found in the highly developed powers of chemotaxis which Brachyura and other Crustacea are known to exhibit.

LUTHER (1930) showed, in the laboratory, that *Carzinus maenas* will remain in contact with a cylinder containing organic-rich sediment by rheotaxis (where the antennae are used) and by chemotaxis (where the maxillipeds are used). Stomatopods have extraordinarily developed maxillipeds.

Since it is obviously unsatisfactory to re-ingest sediment which has already passed through the stomach, and since this sediment is readily perceptible by chemotaxis, it follows that some critical distance must exist, inside which the organism finds conditions unsavoury for feeding. The organism therefore remains just beyond the limit of tolerance of its own faecal matter (determined by chemotaxis), the course of its return path being guided precisely by the existing plugged tube of the initial burrow.

This limit of tolerance should remain reasonably constant for any one species of burrowing crustacean, and this is compatible with the evidence of a strict relationship between tube diameter and overall gauge.

The phenomenon of chemotaxis explains why burrows of *Rhizocorallium cicatricosus* are never seen to penetrate one another, and are often seen avoiding sediment which has been burrowed by other creatures.

Variations in ethology which may be related to chemotaxis are discussed further in the interpretation of *Rhizocorallium commune*.

Comparisons.

The most closely comparable trace fossil with *Rhizocorallium cicatricosus* is the type species, *R. jenense*, from which it differs in possessing a very poorly developed, unsculptured *Spreite*, and having coarser wall scratch markings (c.f. WEIGELT 1929, pl.2/4,5).

Horizontal U-shaped burrows with finely lacerated limbs and no *Spreite* have been recorded from the Upper Jurassic of Pomerania (*loc.cit.*, fig.1) ; they were attributed to *Callianassa*. Here the overall gauge is 70 mm. and the limb diameter 21 mm., giving a ratio of 3.3, which is identical to that in the Middle Lias examples from Staithes.

Rhizocorallium commune SCHMIDT 1876

Plates 27B, 29C, 31, 32; Text-figs.28-34.

Description.

True *Rhizocorallium*, with well-developed *Spreite*, occur at many horizons in the English Jurassic. Compared with *R. jenense* they have narrower limbs and unsculptured, simple, crescentic *Spreite*.

Dimensions vary from a minimum of 48 mm. overall gauge and 9 mm. limb diameter (from the Yorkshire Yeovilian and Bajocian) to 77 mm. overall gauge and 14 mm. limb diameter (from the Corallian of Dorset). Table Eleven, overleaf, gives comparative data for occurrences from six horizons.

The average gauge : limb ratio of 5.6 is significantly different from the 3.3 for *R. cicatricosus*, and this, together with other features, merits specific discrimination.

A great deal of variation is exhibited in the development of *Spreite* in *Rhizocorallium commune*. To a certain extent there is a correlation between increasing grain-size and increasing prominence of the crescents of the *Spreite*. *R. commune* from calcareous grits (S.B.28) of the Scarborough Beds at Ravenscar possesses strong *Spreite* (Text-figs. 30 & 31), as also do examples from

TABLE ELEVEN. DATA FOR GAUGE AND LIMBS OF *Rhizocorallium commune* FROM SELECTED JURASSIC HORIZONS.

Locality	Stage	Horizon	Illustration	Gauge mm.	Limb mm.	Ratio
Peak	Yeovilian	Grey Beds	Pl.27B	48	9	5.3
Blea Wyke	Aalenian	Dogger *	Pl.29C	25	5	5.0
Ravenscar	Bajocian	S.B.32	Pl.31	54	9	6.0
			Pl.34	57	10	5.7
Staintondale			Fig.32	48	8	6.0
			Fig.33	60	12	5.0
Ravenscar		S.B.28	Fig.31	60	10	6.0
Cayton Bay	Callovian	Hackness Rock	Fig.5A	65	13	5.0
Redcliff Pt.	Oxfordian	*Hudlestoni* Bed	Fig.28	77	14	5.5
				58	10	5.8
Average	(of nine samples)			59	10½	5.6

* = small example, poorly preserved, apparently lacking *Spreite*; doubtfully placed in *R. commune*; not in average.

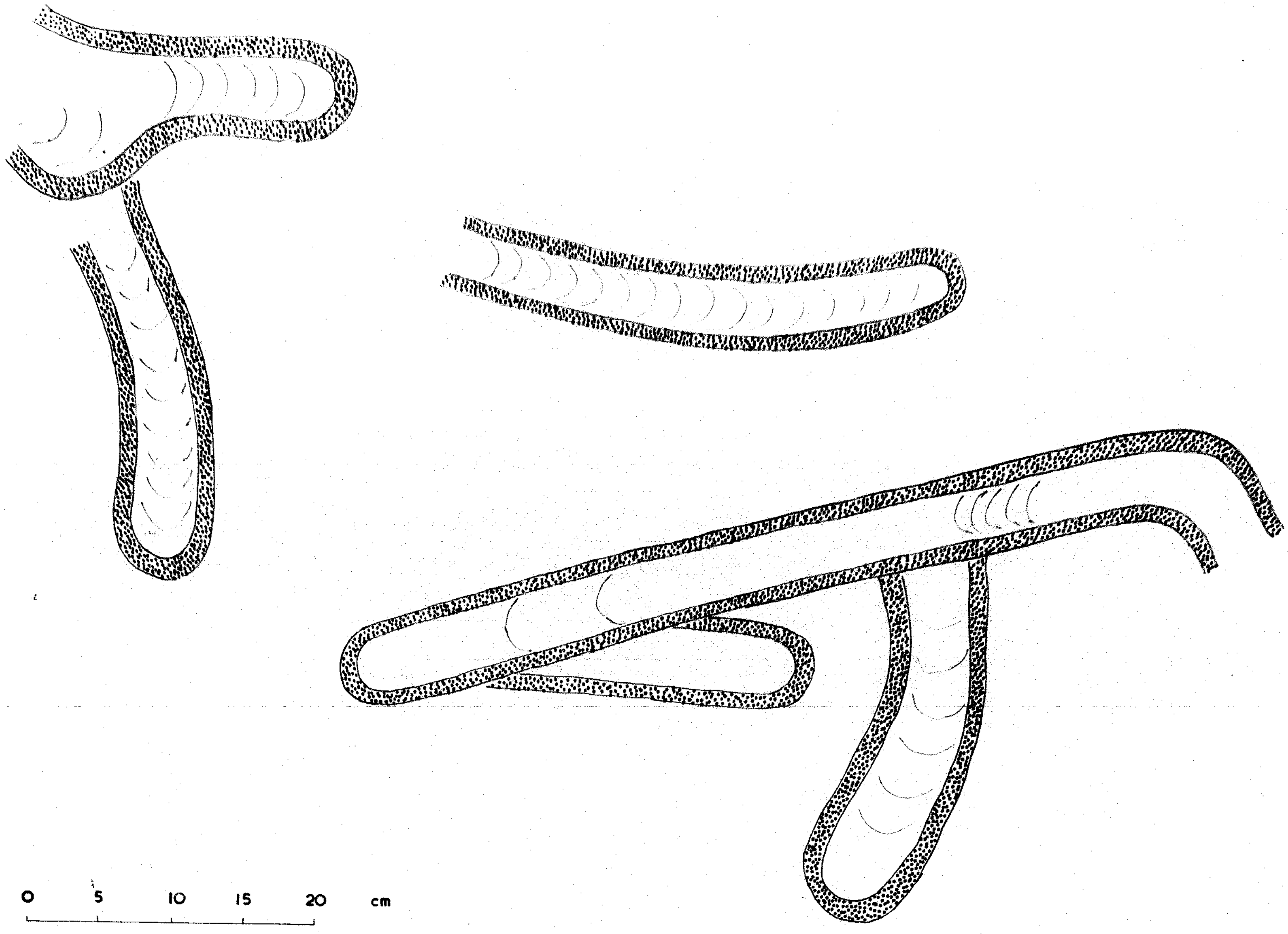
---

the Hackness Rock of Cayton Bay (Text-fig.5A), where the *Spreite* are more resistant than the limbs. In finer-grained lithologies the *Spreite* tend to be feebly developed (e.g. S.B.32, Plates 31 & 34, Text-fig.29).

Text-fig. 28 illustrates the typical appearance of

Text-figure 28.

Field sketch of *Rhizocorallium commune* from the *Trigonia hudlestoni* Bed of Redcliff Point, Dorset.


0
5
10
15
20
cm

Rhizocorallium commune in the *Trigonia hudlestoni* Bed at Redcliff Point. The burrows are fairly dense, straight or slightly curved to right or left, and the *spreite* are strong. The limbs do not show any sculpture, probably as a result of the coarse grain of the gritty limestone, but are lined with comminuted shell fragments. Other examples from this horizon have limbs lined with well-rounded quartz grains, all of identical size.

That the development of strong *spreite* is not solely related to increasing grain-size of the sediment is suggested by the presence of a very long *Rhizocorallium* (over 100 cm.), 75 mm. in overall gauge and 9 mm. in limb diameter lacking *Spreite*, in the same stratum as examples with very strong *spreite*. There are also many examples of *R. commune* in the very coarse calcareous Nothe Grits at Nothe where *Spreite* are not developed. Here the tubes are rimmed with haematite (c.f. *Ophiomorpha borneensis*, p. 161), the margins also being lined with *Chlamys* debris.

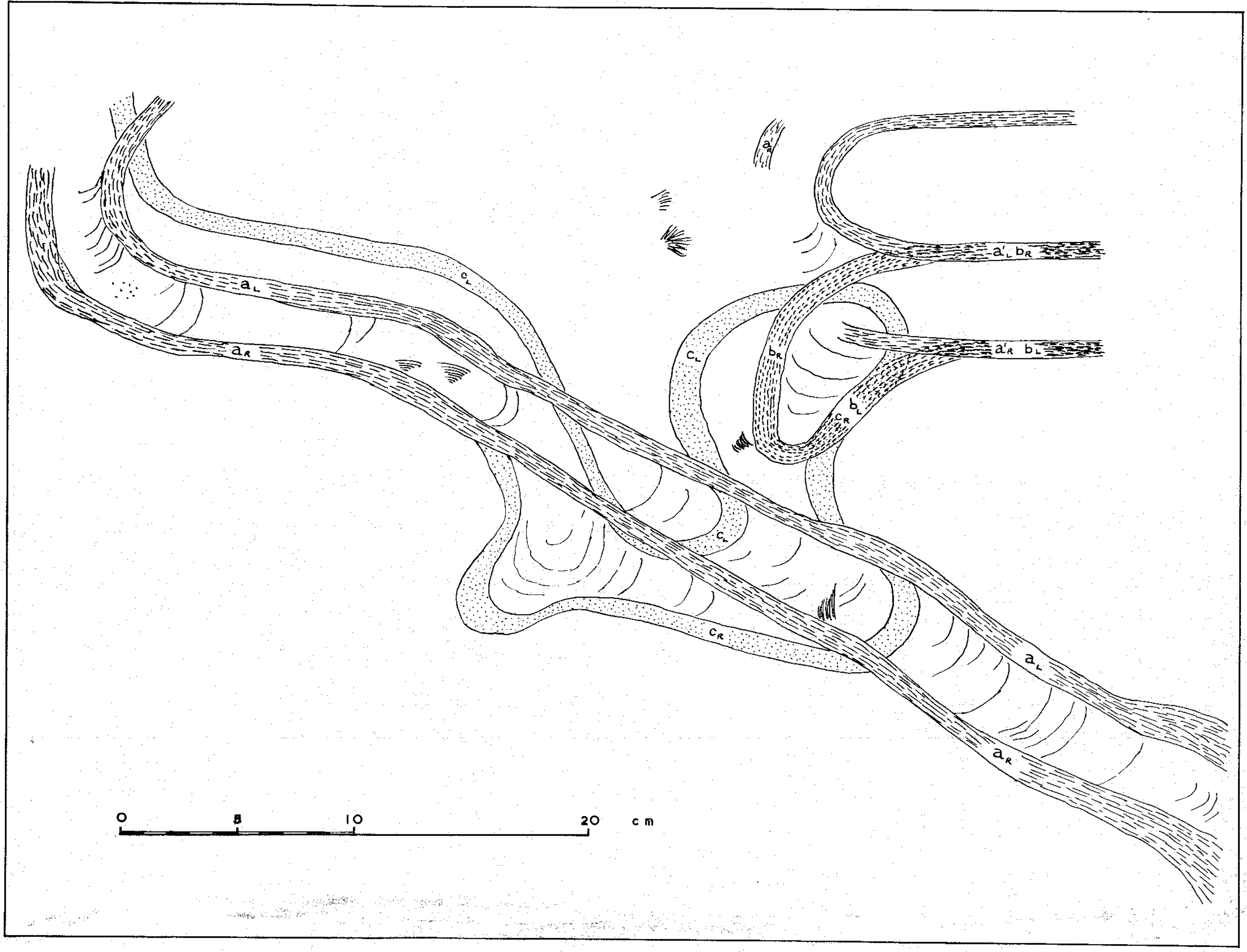
In the finer-grained lithologies such as the silty, ripple-marked limestone from the Scarborough Beds (S.B.32), the limbs show distinct scratch markings (Plate 34A). No faecal pellets have been observed within the limbs of *Rhizocorallium commune*. This is probably because of the generally coarse nature of the preservation of the limbs, which makes the observation of detail difficult.

Text-figure 29.

Diagram illustrating the different ethological patterns of successive burrows of Rhizocorallium commune in ripple-marked argillaceous limestone (S.B.32) from the Bajocian Scarborough Beds 2000 m. south-southeast of the Blea Wyke Point.
Note the great length and straightness of the first-formed burrow 'a'.

N.B. This block has been overturned.

Diagram drawn from Plate 21.



a'R
a'L bR
a'R bL
bR
bL
cR
cL
cL
aL
aR
cL
cR
aL
aR
0
5
10
20
cm

The highest burrow density achieved by *Rhizocorallium commune* occurs at the base of the Osmington Oolite Series at Bran Point, where in Bed 1 (of ARKELL 1949) examples with very resistant *spreite* and eroded limbs occur, often obliquely, up to 20° from the horizontal. Most of the burrows are very markedly curved, unlike examples at lower densities from the *Hudlestoni* Bed, and elsewhere, which are straight or only slightly curved (Text-fig.28).

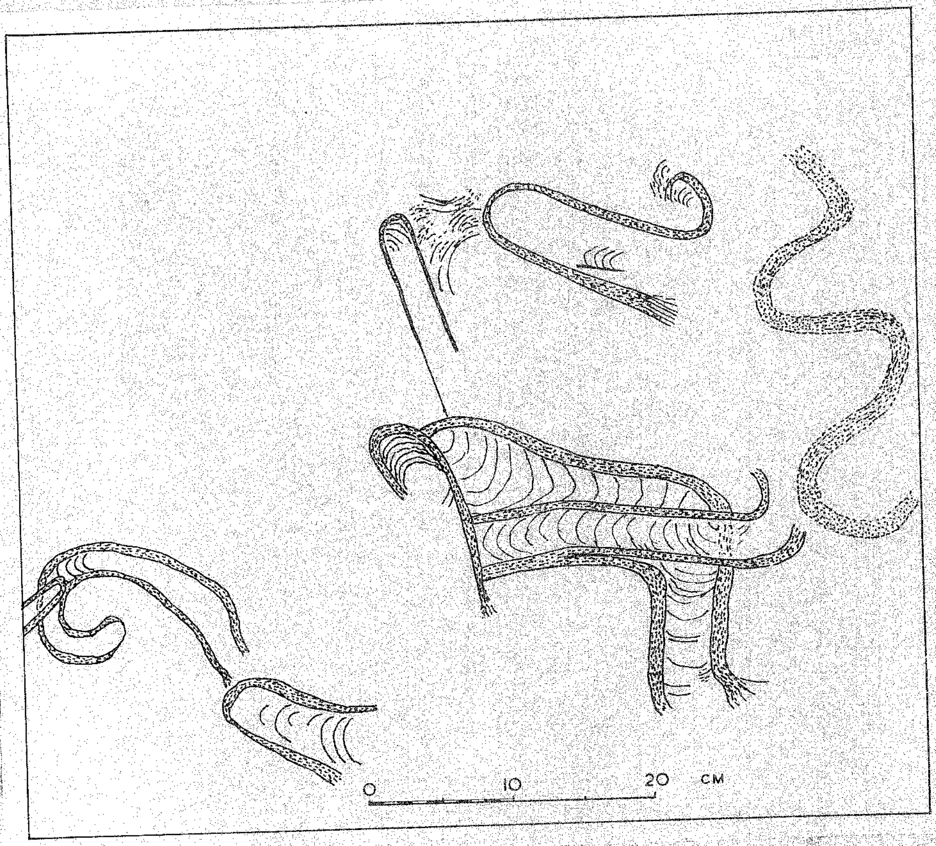
The occurrences bear comparison in obliquity and curvature of the axis with the Middle Lias examples of *Rhizocorallium cicatricosus*. There is abundant evidence that the ethological pattern is noticeably affected when the burrows occur at sufficiently high densities to cause mutual interference.

Variations in ethological pattern.

The orthodox, simple, U-turn typical of the majority of *Rhizocorallium* is present in most *R. commune* (e.g. Text-figs.5A & 28; Plates 27B & 34). Occasionally, though, modifications in terminal ethology are found. Plate 32 illustrates how the vertex is sometimes modified from a 'U' into a 'T'. In Text-fig. 31 the development of a large T-shaped vertex is associated with retrusive activity. The final position of the plugged tube lies

Text-figure 34.

Field sketch of *Rhizocorallium commune* from calcareous grit (S.B.28) of the Bajocian Scarborough Beds; backshore south-southeast by 1200 m. of Blea Wyke Point; showing the marked parallelism of many of the burrows.



within earlier positions of the 'U', which was more extended. One other burrow nearby also shows evidence of retrusive activity in the form of a plugged section of tube within the main elongated 'U'.

These appear to be rare instances of a reversal of the normal protrusive activity. In the latter a simple long U-tube is produced : if internal plugged tubes occur, they are sharply truncated at the sides by the two main limbs (Text-fig.5B). Text-fig. 33 shows both retrusive and protrusive burrows occurring together on the same bedding plane. Both are oriented in the same direction and both must have been constructed at approximately the same time, so that it appears unlikely that any one environmental factor can be the cause of the ethological change (c.f. *Diplocraterion*, Ch. 6).

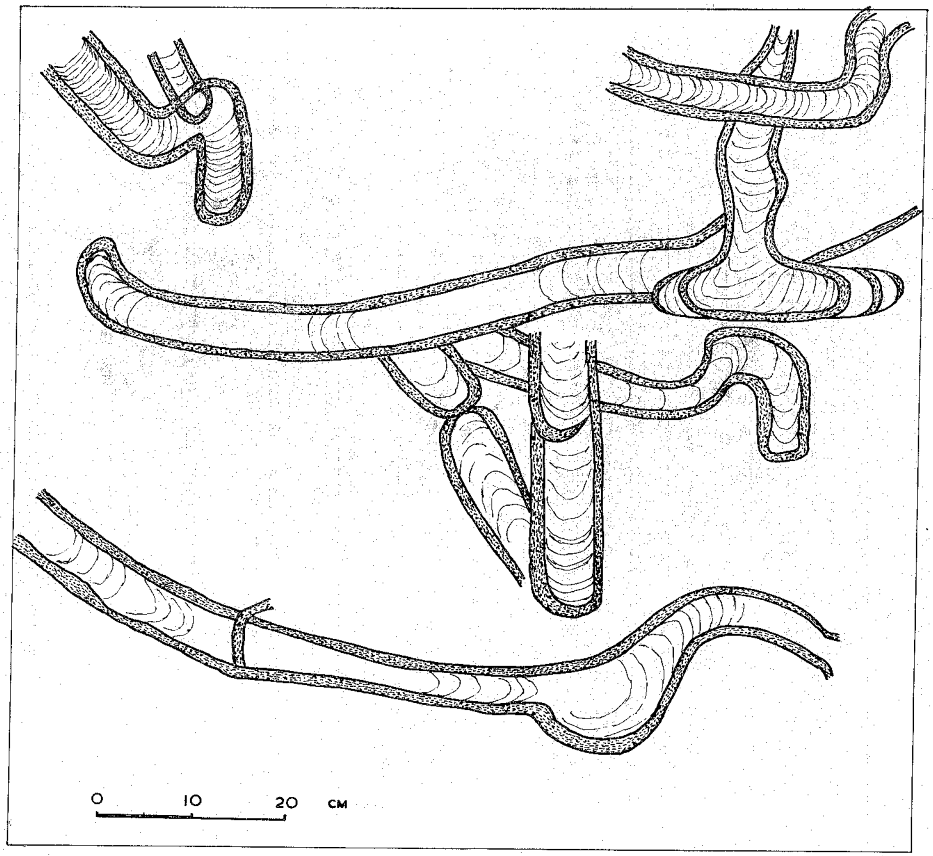
The possibility that chemotaxis had played some part in the development of ethological patterns in *Rhizocorallium* has been discussed already with reference to *R. cicatricosus* (p. 176). This possibility can now be examined for *R. commune* using a greater number of specimens from different horizons.

Evidence of phobotaxis is commonly observed at some localities (e.g. Staintondale; Text-fig.33) but not at others (e.g. Ravenscar; Text-fig.29) at precisely the same stratigraphic horizon. In the former case it would appear

Text-figure 31.

Field sketch of very long Rhizocorallium commune from coarse calcareous grit (S.B.28) of Bajocian Scarborough Beds; backshore 1500 m. south-southeast of Blea Wyke point.

Note retrusive activity associated with T-shaped vertex of burrow at the top right of the sketch, and the strong Spreite.



that the burrows shown top left in the diagram were being constructed simultaneously. The limbs stuffed with faecal matter would be identified by chemotaxis, and avoided.

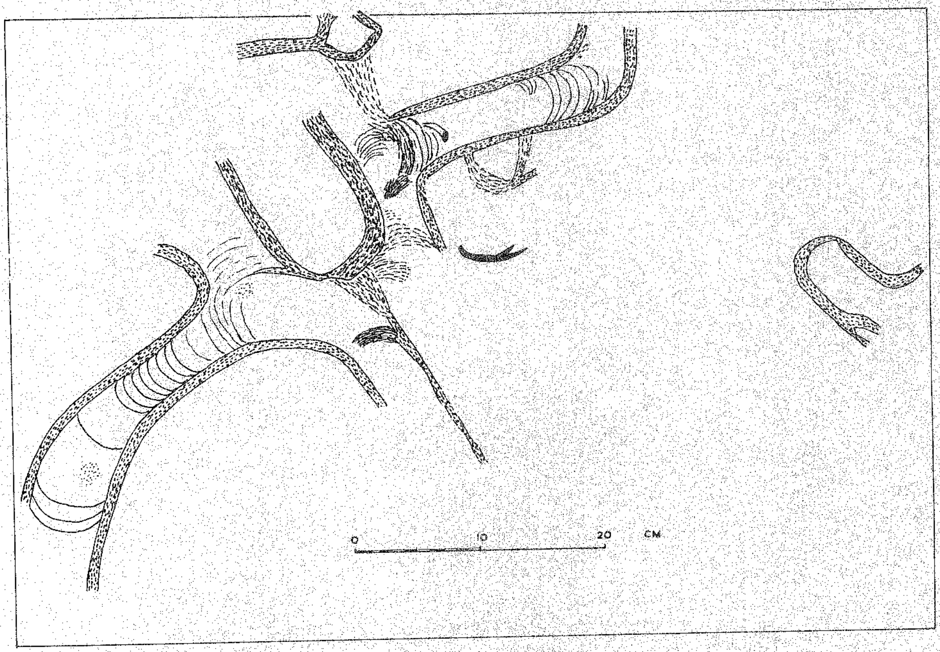
Interpretation is more complex in the system of burrows illustrated on Text-fig. 29. Burrow 'a' was constructed initially, and agrees with most Rhizocorallium formed without interference from adjacent burrows in being straight (c.f. Text-fig. 28). Burrow 'b' was constructed next; it has a trend nearly perpendicular to burrow 'a' but stops short of it, with the formation of a simple U-shaped vertex. It is reasonable to infer that the organism constructing burrow 'b' detected the tubes of 'a' chemotactically.

Text-fig. 32 shows one of the more peculiar ethological patterns developed by Rhizocorallium commune. The burrows all appear to converge on one point. Close examination reveals that only one burrow is a complete U-tube, the limbs of the remainder having been deflected when nearing the nodal point so that they trend parallel to other limbs not of their own construction.
Such a relationship is explained if all the trails were constructed at about the same time, so that the deflections are again the result of the chemotactical perception of kindred burrows in the direct path of the trail producer. In this instance the limb of one burrowing organism runs

Text-figure 32.

Field sketch of eccentric *Rhizocorallium commune* from ripple-marked argillaceous limestone (S.B.32) of the Bajocian Scarborough Beds; backshore 1900 m. south-southeast of Blea Wyke Point.
Note the nodal pattern of the burrows, the scratch markings, and the rarity of orthodox U-shaped vertices.

No other trace fossils are associated with these burrows on this bedding plane.



for some length parallel to the limb of another, an apparent case of mistaken chemical identity ; but these exceptions strengthen the view advanced previously for *Rhizocorallium cicatricosus* (p. 176) that the orientation of the 'return' limbs is governed by a chemotactical response.

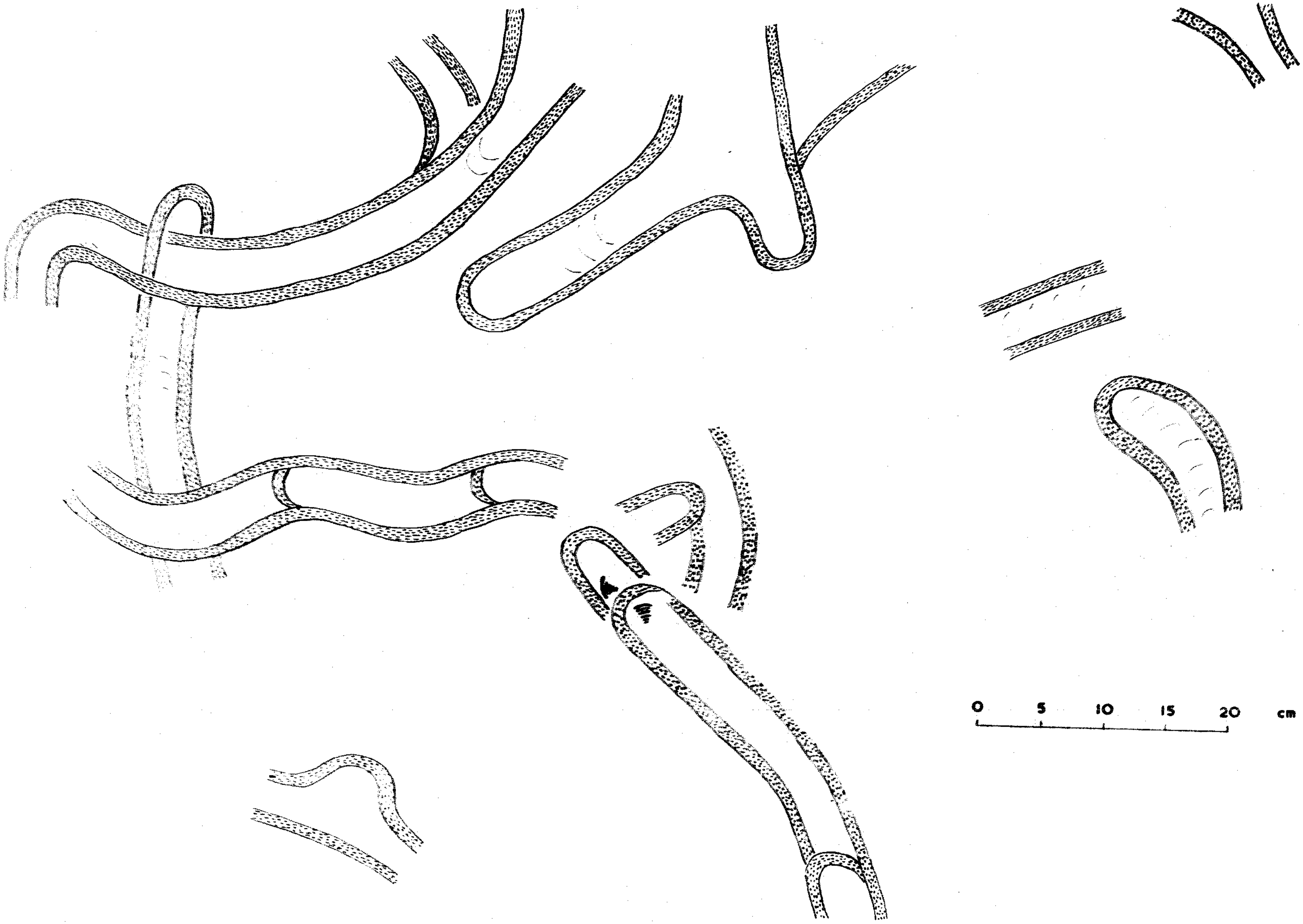
A common morphological feature associated with many of the U-turns, especially when in the vicinity of other burrows, is a set of scatch-markings within the *Spreiten* area (Text-figs. 29, 32 & 33). They generally have a fan-like disposition, usually at variance with the bow-shaped arches of the *Spreite*. Plate 32 shows an exceedingly well preserved set of scratches accompanying a T-shaped vertex. They are particularly marked immediately forward of the conspicuous vertical obstruction, which is a *Pelecypodichnus*.

The mode of construction of *Rhizocorallium commune* and the nature of the producer.

It is possible to argue almost indefinitely about how the burrows were formed. Most of the arguments refer to the internal *Spreite*. VEEVERS (1962, pp.10-13) has presented three possible interpretations, each of which, as he explains, is unsatisfactory on some grounds.

Text-figure 93.

Field sketch of *Rhizocorallium commune* from a loose block of ripple-marked argillaceous limestone (S.B.32) from the Scarborough Beds : beneath Staintondale.


0
5
10
15
20
cm

The basic premise is that the burrow is formed by an animal making a succession of U-shaped horizontal tubes which overlap to form a compound U-in-U structure. The trace is thus essentially protrusive in character.

RICHTER (1927) considered that all pocket-like constructions with U-shaped outline and internal Spreite originated from worms. Diplocraterion, Corophioides and Rhizocorallium were all thought to represent one uniform group. However, it is unsatisfactory to group together burrows with Spreite composed of material of a different kind from the matrix (viz. the faecal-rich Spreite in Diplocraterion) and those where the Spreite are merely impressions made in sediment. As WEIGELT (1929, p.29) suggests: " ...we are here concerned with the traces of cray-fish and the scratches of their claw ends."
He was merely reverting to the view expressed many years earlier by FUCHS (1895) that Rhizocorallium, in this instance from the Chalk, was formed by "scrapings and scratchings" and not constructed of sand grains and faecal pellets.

Scratch markings do not a priori indicate a crustacean origin for Rhizocorallium, for as DOUVILLE (1908, p.361) points out, the spionid worm Polydora possesses hooks on the segments which are specially adapted for scraping. But there are several objections to a spionid origin.

First, Polydora bores only into hard substrata like limestones and oyster shells. Thus DOUVILLÉ (op.cit., fig.1) illustrates Polydora borings penetrating the Miocene / Jurassic unconformity at Arrabida in Portugal, which was almost certainly cemented at the time of construction.

Second, the structures are oriented perpendicular to the surface of the substance being penetrated : Rhizocorallium is horizontal.

Third , the structures are several orders of magnitude too small. The overall gauge of the Arrabida borings is only 2.5 mm. compared with 60.0 mm. for Rhizocorallium.

Fourth, the Spreite in Polydora is very weak and incoherent due to the difference in hardness between the solid rock and the scraped particles : in Rhizocorallium the Spreite is as resistant as, or sometimes more resistant than, the limbs.

Fifth, Polydora, being a suspension feeder, does not produce the pellet-packed limbs characteristic of many Rhizocorallium.

On several counts therefore, a spionid origin cannot be entertained, and the very great horizontal extent of the burrows, together with the morphological features outlined, suggest that a deposit-feeding crustacean is a more likely originator. WEIGELT (1929, p.30) arrived at the conclusion that Rhizocorallium from Finkenwald are mesh-like passage s of crustaceans which had developed through the digging out of the Spreite into pocket-like galleries in which the crabs probably carried out ecdysis. It would be gratifying if there were on record carapaces within the Spreiten area. WEIGELT (op.cit.pp.36-7) has recorded the occurrence of numerous Callianassa in strata surrounding Spreite-less Rhizocorallium from the lowest horizon of the Middle Kimeridgian of Zarnglaff (WEIGELT op.cit.pp36-7). The same organism is thought to be responsible for Rhizocorallium in the Upper Chalk of Kieslingswald (FINCKH in WEIGELT, loc.cit.)

It is possible on the evidence of the English Jurassic material examined in the present study to add to the already numerous ideas on the origin of Rhizocorallium. VEEVERS (1962,p.17, fig.8) illustrated a Lower Cretaceous example where the first-formed portion of the burrow possessed an undisturbed plug of sediment separating the limbs before the Spreite commenced. Here the limbs are of equal length on either side of the plug. The distance along each of the free tubes plus the distance around the first curve of the Spreite should give the length of the animal responsible for constructing the burrow. In the figured specimen, with overall gauge 52 mm. and limb diameter 13 mm. (Ratio 4.0), an animal about 11 cm. in length appears to have been involved.

A specimen from the (Upper Lias) Grey Beds (Plate 27B) shows a small Rhizocorallium at an even earlier stage of development than Veevers' example. The Spreite merely consists of three arches. Here the 'U' is unequally developed on either side of a very short undisturbed plug of sediment. The right-hand limb is shorter than the left: the former ending in a blunt symmetrical curve, the latter in a sharp point produced by the intersection of the straight inner boundary and the gently convex outer boundary. An animal only 4 cm. long appears to have produced this Rhizocorallium, with a gauge of 36 mm. and a limb diameter of 9 mm.

The differing termination of right and left limbs was not observable in Veevers' specimens. The evidence of the Upper Lias specimen shows that the head of the burrower was always on the right and the tail on the left side of the burrow. From the greater length of free tube on the 'tail' side it may be concluded that the burrow originated as a series of thrusts forward from the left tube and curved to the right, the animal retracting after each thrust and advancing further forward. This forward thrust directed to the right may well explain why many of the unimpeded burrows possess a marked axial curvature in that direction; (Plate 27A) the force being chiefly unilateral.

Concerning the producer of Rhizocorallium commune, there is one specimen (Plate 32) from the Scarborough Beds which shows sets of diamond-shaped claw impressions - lying immediately inside the tube. This striking piece of trace morphology may indicate the nature of the burrowing organism. There are six to each set, and they occur in such a fashion that it appears that all six were made by one appendage. It is unlikely, if not impossible for six separate appendages to produce such a regular set of equidistant similar impressions.

Examination of the appendages of the various orders of recent crustacea reveals that only the genus Squilla of the Stomatopoda possesses, on the second maxilliped, a sub-chela which has six equidistant spines.

A stomatopod origin is compatible with other known facts about Rhizocorallium. A non-decapod origin is suggested by the fossil record, since the Decapoda are not recorded from the Palaeozoic whereas Rhizocorallium has been reported from the Lower Cambrian SEILACHER 1955 (pp. 377-8) and every other Palaeozoic system. The Stomatopoda have a very poor fossil record, but Squillites is known from the Carboniferous of Montana WOODS 1961 (p.405). Second, the Stomatopods are very well equipped functionally for extensive burrowing and detritus feeding.

The five anterior pairs of thoracic appendages have no exopodites and are directed forwards as maxillipeds, while the six sharp points of the sub-chelae are excellent adaptations for scraping sediment from the burrow walls.

Third, the long, dorso-ventrally flattened shape of Squilla fits the trace morphology of Rhizocorallium much better than does a crab with its short abdomen and greater lateral extent.

Fourth, the stomatopods are among the few Recent creatures which are known to produce Rhizocorallium-like structures WEIGELT, 1929, (p.13). Many of the other known producers cannot be considered, chiefly on grounds of magnitude. These include insect larvae and the spionid Polydora. There thus remains Corophium, which generally produces vertical structures, and Squilla as possible producers. Of these the former is rather small and lacks the functional adaptations of the **stomatopod**, but both are elongate, and both are deposit feeders, with similar modes of life. Other elongate crustacea like Callianassa may also produce these structures, but they have not yet been identified in Recent biota.

It is perhaps wise, in view of the 600 m.y. range of Rhizocorallium, to conclude that the producer was merely an elongate, deposit-feeding crustacean. Only in very isolated cases do outstanding features of trace morphology make it possible, or desirable, to be more specific.

Comparisons.

R. commune differs from R. jenense and R. cicatricosus in possessing limbs with more subdued scratch-marks and Spreite consisting of simple crescents. The former occurs in coarse clastic lithologies, the latter in finer-grained muds and ironstones. The former has a gauge : limb ratio of 5.6, the latter of 3.3. R. commune may exhibit peculiar ethological patterns, particularly at the vertex, which do not occur in R. jenense.

SEILACHER 1955 (pl.24, fig.3) has figured as R. jenense an example of R. commune from the Neobolus Beds of Pakistan which possesses strongly raised crescent-like Spreite. VEEVERS (1962) described Rhizocorallium from the Lower Cretaceous rocks of Australia without specific identification. All his examples, preserved in sandstone, possess simple Spreite which are often strongly developed. The gauge : limb ratio is about 5.0, with limbs 9-11 mm. in diameter. In the presence of oblique burrows up to 20° from the horizontal and coarse Spreite the occurrence bears strongest comparison with the Osmington Oolite R. commune on Ringstead Ledge.

The *Spreite* in the Australian examples from Godfrey Tank (*op. cit.* pl.1 fig.4) are much more strongly developed than any English *Rhizocorallium commune*.

Occurrence.

Rhizocorallium commune is one of the most widespread Jurassic trace fossils. The horizons from which it has been recorded will be found on Text-figs. 37 & 46, and in the stratigraphical part of the text.

Rhizocorallium aff. *uliarensis* FIRTION 1958 Text-fig. 34A. One burrow, 62 mm. in overall gauge, and with a spiral axis, clearly related to *R. commune*, occurs in the Oxfordian *Hudlestoni* Bed at Redcliff Point, associated with *Thalassinoides suevicus* and vertical *Pleuromya uniformis*. The only known spiral *Rhizocorallium* is *R. uliarensis* from the French Portlandian, from which this differs in its more open coiling, so that the burrow crosses itself almost at right angles (Text-fig. 34A). In *R. uliarensis* the spirals increase in diameter downwards without crossing earlier portions of the burrow.

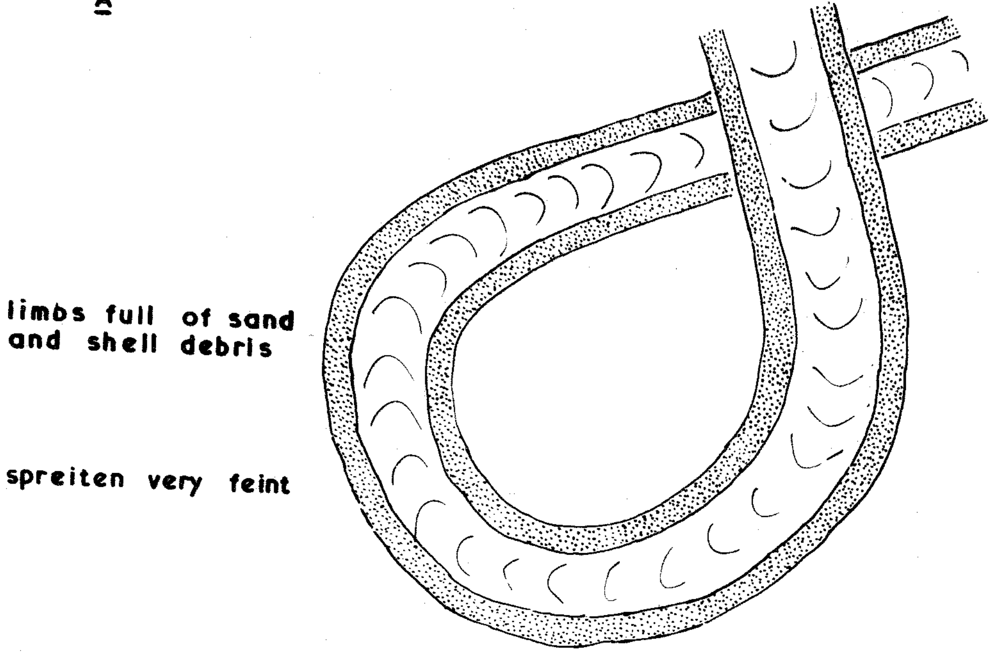
R. uliarensis appears more closely related to *R. jenense*, since faecal pellets and *Chondrites* are figured in association with the limbs. FIRTION 1958 (pl.2 figs. 1 & 4). *R. uliarensis* measures 57 mm. in gauge and has a gauge : limb ratio of 3.8 (c.f. 3.8 for *R. jenense*

Text-figure 34.

A. *Rhizocorallium* aff. *uliarensis* from the *Trigonia hudlestoni* Bed of Bowleaze Cove, Dorset.

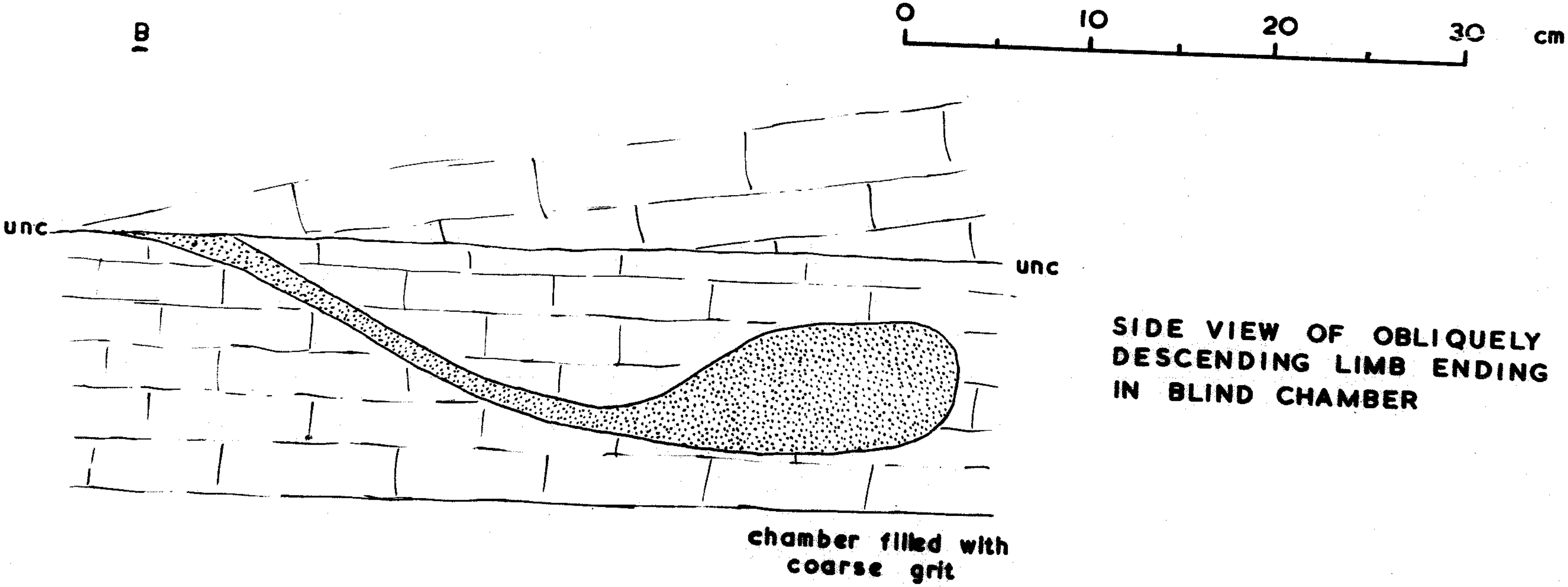
B. obliquely descending *Rhizocorallium commune* limb, ending blindly in a large chamber.

A



PLAN VIEW OF UNUSUAL
SPIRAL PATTERN

B



SIDE VIEW OF OBLIQUELY
DESCENDING LIMB ENDING
IN BLIND CHAMBER

5.6 for R. commune)

The Dorset example is associated with an obliquely descending Rhizocorallium commune which ends in a large blind chamber (Text-fig. 34B)

Summary.

The English occurrences of Rhizocorallium from Jurassic strata are summarised in the following table (Table 12), which shows the essential morphological criteria used for 'specific' discrimination.

TABLE TWELVE. THE ENGLISH JURASSIC 'SPECIES'

'Species'	Gauge : Limb Ratio.	Spreite.	Axial Trace.
GROUP ONE			
R. *jenense*	3.8	Sculptured.	Straight.
R. *cicatricosus*	3.3	Absent.	Tortuous.
GROUP TWO			
R. *commune*	5.6	Simple bows.	Curved: may be T-shaped at vertex.
R. aff *uliarensis*	5.6	Simple bows.	Spiral.

OF *Rhizocorallium*.

Orientation.	Limb Sculpture.	Lithology.	Typical horizon.
45° - 70°	long, coarse striae	Siderite.	Ellerbeck Bed.
0 - 15°	long, coarse striae	Siderite.	Ironstone Series.
0 - 20°	short, subdued striae or lined with shell fragments.	Calcareous grit.	Nothe Grits.
10°	lined with shell fragments.	Calcareous grit.	*Hudlestoni* Bed.

CHAPTER NINE

OTHER FEEDING BURROWS & FAECAL PELLETS

Fodinichnia

As has been mentioned (p. 147), a useful distinction may be made between burrows of suspected crustacean origin and those of more doubtful origin. This chapter deals with burrows of the second group.

Feeding burrows of non-crustacean origin

It would be foolhardy to state categorically that a certain burrow was definitely not formed by a specific group of creatures, but there is a residuum when all burrows firmly attributed to the Crustacea on the basis of particularly outstanding features of trace morphology have been described. The trace fossils in this residual group are of five kinds :-

III: Star-shaped burrows (Asterosoma)
IV : Spiral burrows (c.f. Daedalus)
V : Simple, retrusive burrows (Teichichnus)
VI: Multi-branched tunnel systems (Chondrites)
VII: Irregular, sand-filled burrows (Planolites).

No uniformity in designating 'species' is possible in this group. Three 'species' of *Asterosoma*, two of them new, are described from the Yorkshire Middle Jurassic. The trace fossil *Chondrites* is not so amenable to the designation of trace-fossil species, since it does not show the morphological variety of *Asterosoma*, except in the wide range of tube size, which is not a satisfactory taxonomic criterion.

Thus no 'species' have been recognised within *Chondrites* (c.f. SCOTT SIMPSON 1957) or *Teichichnus*.

III : STAR-SHAPED BURROWS

Stelloglyphidae VIALOV 1964

Asterosoma VON OTTO 1854

Type species: *A. radiciforme* VON OTTO 1854. Turonian

Generic diagnosis (HÄNTZSCHEL 1962, W. 184):

> Big stars (diameter about 20cm.) with elevated centre : rays bulbous, tapering towards ends, longitudinally wrinkled.

Asterosoma fosteri sp. nov.

Plate 35

Holotype. D.LW 2.

Type locality. Loop Wyke, backshore; northwest of
Whitby (45/848148).

Origin of name. After the discoverer of the trace
fossil, Mr. R. Foster, of Imperial College.

Diagnosis:

Stellate mounds with five or six radiating lobes. Lobes often curved; bulbous, widest distally, narrowing to centre which is strongly raised. Average diameter of complete structure = 9cm. Average height = 3.5cm.; maximum distal lobe width = 3cm.

Description.

Asterosoma fosteri is preserved as positive endogeneous hyporeliefs in a medium to coarse-grained sideritic sandstone. Individual lobes have a well-marked internal concentric structure with central passively-filled core. At the type locality the stars occur at a low density of 1 or 2 /sq. m.; they are radially complete.

Further to the southeast, just north of Maw Wyke Hole, Hawsker Bottoms, the density is much higher, though the specimens have been planed down by erosion, so that the lobes are only seen in section.

The lobes are filled with siderite mudstone concentrically arranged with elongate phosphatic particles. The lobes are thus much richer in siderite than the matrix (c.f. Rhizocorallium cicatricosus; Plate 34B) which is more sandy and also contains clay flakes and a little chamosite.

The lobes do not converge on one single central point (Plate 35A), but stop short, so that each lobe is in fact a separate entity. The height of the lobes becomes greater with each successive lobe when followed round in an anti-clockwise direction, so that the locus of the highest point of each lobe is a spiral.

Ethological interpretation.

Each lobe represents the accumulation of concentric layers of faecal matter, which become more and more compacted around the margins with each successive fill, until a hollow the exact width of the animal responsible remains to be filled later with matrix. The next lobe is formed in the same way, but is initiated above, and to one side of the previous lobe, so that eventually, with the lobes widening appreciably towards their distal ends, the maximum amount of faecal matter is dispersed with a minimum risk of contamination, especially about the central region.

After five or six lobes have been completed in successive anticlockwise positions, the circle is complete, but, as a result of the gradual stepping up in height of each lobe, the animal may continue to form faecal lobes in similar fashion since these would be placed higher than those formed earlier. This appears to be the case in the specimen figured on Plate 35B.

The burrow is thus interpreted in its final form as representing a series of faecal lobes distributed around a central vertical axis: (there is, however, no hint of a vertical burrow preserved in the central position). Originally, though, there must have existed an empty lobe into which the faecal matter could periodically be discharged. This implies that the lobe must first have been excavated before being filled, and therefore that the lobes were probably originally formed by a deposit-feeding organism systematically working through the sediment on all sides of a central vertical burrow. The faecal matter produced while grazing in the first lobe would have to have been discharged at the surface, but thereafter the faecal matter resulting from the grazing of the next lobe could be plugged into the previous lobe.

Therefore the final ethological interpretation should be that the geometric form of *Asterosoma fosteri* is primarily a reflection of an efficient method of feeding on the maximum amount of sediment while remaining in one position. The fact that the lobes are not simply filled with matrix but concentrically plugged means that the cavities produced by feeding were secondarily used for the purpose of disposing of faecal matter with minimum risk of contaminating ungrazed sediment nearby.

Stellate grazing patterns forming on the surface of the sediment are well-known at the present day. They may be produced by many different creatures :- *Corophium volutator* (SEILACHER 1953, p.429, fig. 4) and *Scopimera inflata* (McCULLOCH & McNEILL, 1923; PANZER 1935) among the Crustacea ; *Scrobicularia plana* (SCHAFER 1962, p.305, fig.157; reproduced on text-fig.35) and *Macoma balthica* among the Bivalvia.
In each of these cases the principle is the same: efficient sediment-feeding while remaining in one central vertical

Text-figure 35.

Diagram of the stellate feeding trail of the Recent bivalve _Scrobicularia plana_ (after SCHÄFER 1962, fig. 157) formed on an intertidal mud surface.

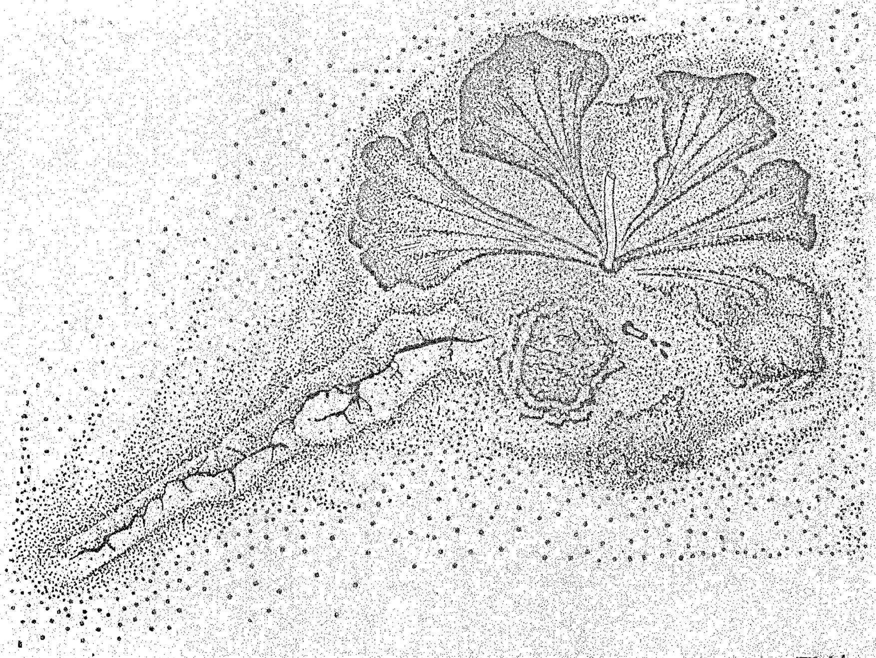


Abb. 157. Oberflächen-Weidespur von *Scrobicularia plana.* Zur sternförmigen Weidespur führt eine Sackungsbahn, erzeugt durch die in der Tiefe herangewanderte Muschel. Original.

burrow. The bivalves feed by way of their extensile siphons, one of which is long and sucks the sediment from the surface, forming the radiating lobes (Text-fig.35), while the other shorter siphon discharges faecal matter at the surface. The shell of the bivalve is thus actually stationary: it is the siphons which move.

It is not known whether such stellate patterns are developed beneath the sediment surface at the present time. Technical difficulties are such that it would be a considerable sampling problem to obtain an actualistic *Asterosoma*. However there is no reason why the same feeding principle should not be adopted within the sediment. As SEILACHER (1964, p.300) says:-

> "Surface tracks and burrows are fundamentally different only to our eyes. For many benthonic creatures it makes little difference whether they creep at the surface or along bedding planes inside the sediment".

So far as *Asterosoma fosteri* is concerned the only modification of the *Scrobicularia* principle required is that the faecal matter should be emplaced within a previously excavated lobe rather than emitted at the surface. There are several reasons why the faecal matter should not be discharged at the surface. First, unless discharged siphonally , it would bring the organism to the surface and attract predators. Second, unless the burrow was formed intertidally , faecal matter around the burrow would not be dispersed effectively. On these two counts it may thus be advantageous to dispose of faecal matter within voids already created in the sediment.

Sedimentological interpretation

Since the radiating lobes of Asterosoma fosteri are constructed in succession, it follows that the degree of completeness of the radial pattern gives an indication of the energy level of the environment, unless the life-span of the organism occupies less time than that required the completion of one circumference. In the absence of strong scour and periodically high sediment accumulation, the organism has time to develop the radial patterm completely. More unstable conditions would result either in the erosion of the whole structure or in the burrow being abandoned and another constructed with reference to a new, higher, sediment/water interface. In the latter case a few, radially incomplete lobes only would be found.

Thus radial symmetry implies environmental stability: unilateral asymmetry, instability. The fewer the number of lobes, the greater the instability. All the specimens of *Asterosoma fosteri* which I have examined are radially complete. The implication is therefore that environmental conditions were stable at the time the burrows were constructed. Certainly the Dogger is of remarkably constant thickness over a wide area around Whitby (RASTALL & HEMINGWAY 1940, p.194), and channelling and cross-bedding features are absent.

Comparisons.

Asterosoma fosteri differs from the type species *A. radiciforme* (figured by HÄNTZSCHEL 1962, fig.111/2) in possessing smooth, wide lobes devoid of longitudinal wrinkles, which expand rather than taper distally: it is also only half the size, but has a more elevated centre. It differs from *A.* c.f. *radiciforme* (Plate 36A) which may be asymmetrical. *A. multilobatum* (Plate 36C) has twenty much stouter lobes in higher relief.

The spiral locus of the lobe summits suggests that *Asterosoma fosteri* may be related to *Gyrophyllites* GLOCKER 1841, which although only one fifth as wide, consists of a vertical shaft from which "rosettes" of short, simple tunnels radiate at levels "as in a mine" (HANTZSCHEL 1962, p.260). Little vertical development was visible in the specimens of *Asterosoma fosteri*, so it is not possible to say whether it possesses the conical shape which typifies *Gyrophyllites*. The two trace-fossil genera may best be distinguished on the basis of their lobes, which are bulbous in the former and flattened, with *Spreiten* sculpture, in the latter.

Occurrence.

Type locality as above. Also common in the Dogger at Maw Wyke Hole, Hawsker Bottoms. In the Dogger at Loop Wyke it is associated with *Chondrites*; at Hawsker Bottoms with c.f. *Daedalus*.

Geological Range.

Asterosoma fosteri is known only from the Dogger of Yorkshire. Other 'species' of *Asterosoma* are known from the Scarborough Beds and the Corallian rocks of Dorset, where a specimen has been reported from the Bencliff Grit (TALBOT 1966, personal communication). Outside England it is known from the Upper Cretaceous of Germany, and the Lower Palaeozoic of Oslo (SEILACHER & MEISCHNER 1964).

Asterosoma c.f. *radiciforme* VON OTTO 1854

Plate 36A,B.

Description.

Specimens agreeing with the type species in all respects except for size and radial completeness occur on the backshore south-southeast of Blea Wyke Point among loose material fallen from S.B.32 of the Bajocian Scarborough Beds (45/997006). Stellate mounds with, in complete specimens, about twelve narrow, longitudinally wrinkled lobes occur as positive endogeneous hyporeliefs on the surface of bedding planes of argillaceous limestone. Occasionally the lobes appear to bifurcate (Plate 36A,B).

In the Ravenscar area, to the northwest, radially incomplete specimens occur (Plate 36A). Cross sections of lobes present a spiral rather than a concentric arrangement of sediment. To the southeast, rare complete specimens can be found (Plate 36B), but they are noticeably ovoid in plan, not circular. Their longer diameter is about 12cm., their shorter about 8cm. The average radial length for incomplete specimens is 4.5cm. Like *Asterosoma fosteri* at Loop Wyke they occur at low densities, never more than 3 / sq. m.

Ethological interpretation.

Owing to imperfect preservation it is difficult to ascertain whether the wrinkles on the Scarborough Bed specimens are scratch-marks. They bear a superficial resemblance to the markings sometimes found on the walls of *Rhizocorallium commune*, but the lobes of the type species figured by HÄNTZSCHEL (1962, fig.111/2) have very long, sinuous markings unlike those in *Rhizocorallium*. It is thus not established that the ornamentation is due to scratching by crustaceans. The markings could as easily have been produced by a contracting siphon or proboscis during the process of feeding.

Sedimentological interpretation.

The radially incomplete pattern of the majority of *Asterosoma* c.f. *radiciforme* probably implies rather unstable bottom conditions, causing frequent vacation of the burrows before the whole structure could be completed. Accordingly, a lateral passage from incomplete to complete structures along the same horizon may be used as an indication of proximity to shoreline, for, in the general case, instability of the bottom increases towards shallow water and decreases towards deeper water as wave-base is approached.

Comparisons.

The form is very similar to the type species, but possesses more lobes when complete, though it is generally only unilaterally developed. SEILACHER & MEISCHNER (1964, p.619, fig.4) have illustrated an *Asterosoma* resembling *A. radiciforme* but possessing only two lobes: the lobes, like those in the Jurassic examples from Yorkshire appear to bifurcate.

Geological Range.

Asterosoma c.f. *radiciforme* is confined to S.B.32 of the Bajocian Scarborough Beds in Yorkshire, though comparable examples occur in the Lower Silurian of the Osle region.

Asterosoma multilobatum sp. nov.

Plate 36C

Holotype. Specimen figured on Plate 36C.

Type locality. Cloughton Wyke, northwest of Scarborough; backshore (54/020951).

Diagnosis.

Strongly-raised stellate mounds with up to 20 short, stubby lobes which become very bulbous at their distal ends. Lobes unwrinkled, smooth. Rarely incomplete radially.

Description.

The diameter of Asterosoma multilobatum varies from 7 - 10 cm. The form may occur at densities up to 8 / sq. m. It is preserved in very strong relief as positive endogeneous hyporeliefs. The lobes vary greatly in size and inclination: some are inclined at almost 70° to the horizontal, possessing a flat longitudinal profile (Plate 36C). The lobes do not unite centrally but stop short at a flat platform which may be erosional.
The specimens are preserved as argillaceous mounds in a sandy, argillaceous limestone.

Comparisons.

Asterosoma multilobatum compares most closely with A. fosteri: both have similar lobe structure and occur in a similar grade of sediment.

Asterosoma multilobatum, however, has four times as many lobes, which are shorter and more bulbous. It may be distinguished from *A. fosteri* and *A.* c.f. *radiciforme* most easily by the exceptionally strong relief and the high inclination of the lobes. No form of *Asterosoma* comparable with *A. multilobatum* appears to exist outside S.B.28 of the Scarborough Beds, and even at this horizon it is only found around Cloughton Wyke.

SUMMARY.

Three 'species' of the stellate trace fossil *Asterosoma* VON OTTO have been described from the Middle Jurassic of Yorkshire. Table 13 summarises the morphological criteria distinguishing them, and the horizons at which they occur.

TABLE THIRTEEN. *Asterosoma* FROM THE YORKSHIRE JURASSIC

'Species'	No. of lobes	ornamentation	shape	radial symmetry	lithology	horizon
fosteri	5-6	smooth	bulbous	complete	Fe-Sst	Dogger
cf. *radiciforme*	12	wrinkles	narrow	onesided	Slt-Lst	S.B.32
multilobatum	20	smooth	v.bulbous	complete	Sdy-Lst	S.B.28

IV : SPIRAL-SHAPED BURROWS

Daedalus ROUAULT 1850

Type species. *Vexillum desglandi* ROUAULT 1850 p.734
Ordovician, Brittany.

Generic diagnosis (HÄNTZSCHEL 1962, W.191):

> *Spreiten* structures, J-shaped at beginning, later spirally twisted; *Spreiten* surface may cut through itself, as in *Dictyodora*.

c.f. *Daedalus desglandi* (ROUAULT 1850)

Text-fig. 36

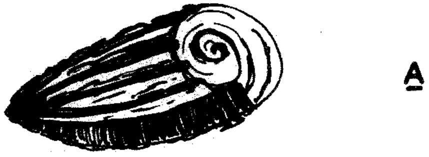
Description.

At two horizons in the Yorkshire Middle Jurassic there occur burrows with a "swiss-roll" cross-section. Rare examples with the axis oblique to the bedding occur in S.B.32 of the Scarborough Beds, associated with *Asterosoma* c.f. *radiciforme* at Ravenscar (45/997006). The burrows have their blunt apices directed downwards and their upward termination in a flat transverse section at about 140° to the axis of the burrow (Text-fig. 36A). This inclination varies with the degree of obliquity of

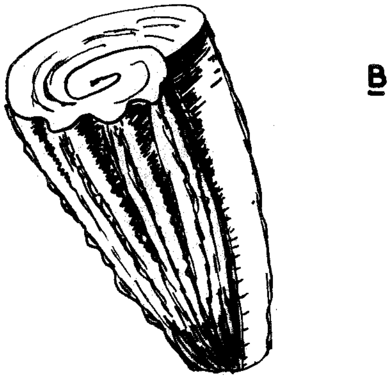
Text-figure 36.

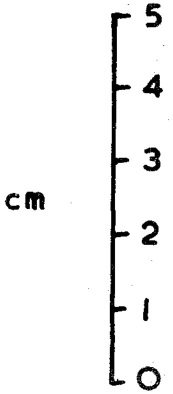
Field sketches of c.f. *Daedalus desglandi*
from the Yorkshire Middle Jurassic.

TWO OBLIQUE EXAMPLES FROM S.B. 32
SHOWING THE 'Swiss-Roll' CROSS SECTION
AND THE WRINKLED LONGITUDINAL RIDGES



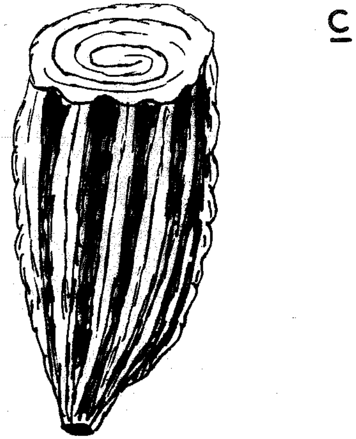
Rare examples : generally oblique





VERTICAL EXAMPLE FROM THE DOGGER

Abundant examples, with high density :
mostly vertical.



the burrows, so that in a vertical example it is exactly perpendicular (Text-fig. 36B,C). These oblique examples from the Scarborough Beds are very rare and occur at densities of about 1 / sq.m.

In loose blocks of Dogger at Maw wyke Hole, Hawsker Bottoms, there occur abundant examples which are nearly all vertical (Text-fig. 36C). Here the density may reach 50 / sq. m., and here also they are associated with Asterosoma, in this case A. fosteri.

Both in vertical and oblique examples the depth is about 50mm. and the diameter between 15 and 25mm. Both Dogger and Scarborough Bed examples show a coarse longitudinal wrinkling.

Interpretation.

The constant association of c.f. Daedalus desglandi and Asterosoma suggests that both may be the product of the same organism. In cross section an Asterosoma lobe, with its concentrically arranged material, strongly resembles this trace fossil. Occasional specimens of A. c.f. radiciforme have even been recorded with spiral rather than concentric lobe structure. Moreover, the longitudinal wrinkling of the A. c.f. radiciforme lobes, though less strong than that in c.f. Daedalus desglandi, is of the same style.

It appears probable, therefore, that these trace fossils are ethological variants of the more usual stellate pattern of *Asterosoma*.

KREJCI-GRAF (1935 p.25, fig.5) has illustrated short vertical burrows with a spiral internal arrangement of the sediment, forming at the present day around Hong Kong. They are caused by crabs seeking temporary refuge in the sediment by means of a rapid spiralling burrowing action. If c.f. *Daedalus desglandi* had a similar origin, then the structures should be placed in the Cubichnia or Domichnia. *Spreiten*-structures, however, are generally regarded as belonging to the Fodinichnia.

Comparisons.

The Yorkshire Middle Jurassic examples agree with the type species in possessing the "swiss-roll" transverse section, the coarse longitudinal wrinkling, and in their orientation with respect to the bedding. However, the J-shaped commencement of the structure (illustrated by HÄNTZSCHEL 1962, fig.120/1b) was not found. The type specimen is twice the size of the average Yorkshire specimen.

Geological Range.

Daedalus is known from the Ordovician and Silurian of Europe and North America, and the Jurassic of Yorkshire.

V : MULTI-BRANCHED TUNNEL SYSTEMS

Chondrites STERNBERG 1833

1876 *Nulliporites furcillatus* TATE & BLAKE

For full synonymy, see HÄNTZSCHEL (1962, W.187)

Type species. *Chondrites targionii* STERNBERG 1833, p.25

(= FUCOIDES informally)

Generic diagnosis (HÄNTZSCHEL *loc.cit.*):

> Very plantlike, regularly ramifying tunnel structures which neither cross each other nor anastomose; should be interpreted as dwelling burrows or feeding burrows; width of tunnels remaining equal within a system, otherwise varying from large (e.g. *Buthotrephis*) to small (e.g. *Chondrites*); very common trace fossil, usually named "fucoid"; some with transversely built in ellipsoidal excrement pills; surface pattern commonly very regular, effected by phobotaxis.

Discussion.

SCOTT SIMPSON (1957) has presented a full account of

Chondrites. He concludes that the burrows are produced by the systematic grazing of sediment from a fixed point on the surface, probably by a sipunculoid worm. The account is full and well illustrated, so that all that remains to be mentioned here are the horizons from which Chondrites has been recorded in Yorkshire (these supplement Scott Simpson's localities), the associated trace fossils; and any features of trace morphology which add to Scott Simpson's original interpretation.

Plate 37 illustrates the orthodox variety of Chondrites, which is abundant on the surface of the upper block of the Main Seam at Old Nab, near Staithes (45/794187). The tube diameter is 1.5-2.0mm. Comparable examples occur in the Sandy Series north of Skinningrove, in the Cementstone nodules of the Upper Lias at Whitby and in the Grey Beds at Blea Wyke. An example from the Ironstone Series at Hawsker Bottoms (Plate 38) shows two of the characteristics noted by Scott Simpson as peculiar to Chondrites. First, there are two sizes of tube, 2.0 and 0.5mm. in diameter, both forming separate tunnel systems. Second, the constriction at the point of branching is very noticeable in the larger system of tunnels.

One striking feature of the field occurrence of

Chondrites at this level in the Middle Lias is the association with the horizontal trace fossil Curvolithus (='Cylindrites' autt.). This was noted by Scott Simpson, but the two burrows were not seen to be directly connected. However, a specimen from the Middle Lias of Chideock in Dorset, kindly brought to my attention by Dr. G. Larwood, shows indubitably that Chondrites may originate from Curvolithus (Plate 39A). The occurrence at this particular locality is further noteworthy from the sedimentological viewpoint, for Chondrites is preserved by bed-junction sedimentation in a coarse, almost conglomeratic sandstone containing Chlamys: the tubes are filled with finer, calcareous sandstone.

In the Middle Jurassic of Yorkshire Chondrites has been recorded from the top of the Dogger at Blea Wyke; from the basal ironstone of the Ellerbeck Bed at Staintondale; and from the Scarborough Beds at White Nab. In the second example Chondrites occurs as 1mm. tubes penetrating the walls and Spreite of Corophioides lymensis (c.f. KREJCI-GRAF 1938, p.464): Plate 19. In the last example, two tube sizes are again found.

The most significant discovery of Chondrites in Yorkshire is undoubtedly the occurrence of borings, preserved in siderite mudstone, in the shell of a now-decalcified bivalve, which, from the branching characteristics, must be included in Chondrites (Plate 39B). It immediately raises the question of the nature of the substratum penetrated by Chondrites at other horizons in the Jurassic and elsewhere. Were these in the nature of "hardgrounds" (sensu VOIGT, 1959) ? There is often evidence that Chondrites occurs in condensed sequences, and it is particularly abundant in carbonate nodules, both sideritic and calcareous, but the question cannot be answered without renewed study of the horizons concerned. It may be that the Chondrites organism was merely very versatile, and could as easily burrow into soft substrata as bore into hard shells.

If many of the horizons bearing Chondrites were shown to be "hardgrounds" then it would remove a serious objection which has been levelled against Scott Simpson's ethological reconstruction. This involves the emplacement of sediment within long tunnels which may be horizontal and over a hundred times longer than broad. Although the tunnels may have been lined with mucus it is hard to appreciate how they became so completely filled with sediment without any trace of collapse. FERGUSON (1965) has attempted to overcome this difficulty by supposing that the vacuum caused on retraction of the proboscis was the force drawing sediment into the tunnels. Nevertheless, if the sediment did not possess very high rigidity the walls would still cave in. If the substratum were already partially cemented by early diagenesis into an embryonic "hardground", then collapse of the tube walls would be most unlikely to occur.

SUMMARY : Additions to, and modifications of, Scott Simpson's ethological interpretation of Chondrites based on newly described material from the Yorkshire Jurassic.

1. The occurrence of branching tunnel systems of Chondrites diverging from horizontal burrows of Curvolithus indicates that not all Chondrites originated from a fixed point on the sediment surface as a system of radiating burrows: some originated from within the sediment.

This in no way detracts from Scott Simpson's suggestion of a sipunculoid origin, for Sipunculus nudus is known to construct extensive horizontal burrows (SCHAFER 1962, p.311, fig.160).

2. The Chondrites organism was capable of boring into solid calcareous substrata: this is proved by its occurrence in a bivalve shell. It could also therefore have bored into calcareous "hardgrounds". The absence of any indications of mechanical boring action may imply that burrowing and boring were acid-assisted.

VI : SIMPLE RETRUSIVE Spreiten BURROWS

Teichichnus SEILACHER 1955

Plate 40 & 41

Type species. Teichichnus rectus SEILACHER 1955, p.378, plate 25, fig.1 ; Lower Cambrian, Pakistan.

Generic diagnosis (HÄNTZSCHEL 1962, W.218):

> Spreiten-Bauten formed by vertical (mostly upward) displacement of horizontal burrows; somewhat flexuous; rarely branched; feeding burrows.

Description.

Teichichnus is a common Jurassic trace fossil both in Yorkshire and Dorset. In Yorkshire it occurs abundantly in the Blea Wyke Series and the Scarborough Beds: in the Dorset Corallian, in the Nothe Grits of Bowleaze Cove and the Little-more Clay facies of the Osmington Oolite.

The burrows vary in width from 3-7mm. and exhibit varying degrees of retrusive activity. No protrusive Teichichnus have been recorded. The degree of upward displacement exhibited by the burrows varies considerably. The maximum appears to occur in S.B.32 of the Scarborough Beds at Ravenscar (45/999002). Here there is also some horizontal displacement of the burrows. Plate 40A shows a specimen with 4cm. of vertical displacement accompanied by a slightly greater horizontal translation: Plate 40B, 2cm. upward migration with little horizontal translation.

In all specimens examined there was no trace of branching, though occasional apparent T-junctions occur (Plate 40D). These are neither straightforward branches nor simple intersections, for it is noticeable that the spreite of the later burrow truncate those of the earlier burrow, but only on one side of the latter; they do not completely cut through the earlier burrow.

The axis of the burrows is seldom straight; it is generally curved smoothly in one direction, and may sometimes be associated with a general spiral disturbance of the surrounding sediment (Plate 41A). The axis is usually almost horizontal, though inclined examples, dipping at nearly 20° occur in S.B.32 (Plate 41B) where they are accompanied by truly horizontal Gyrochorte c.f. comosa.

One of the most distinctive features of well preserved examples of Teichichnus from the Scarborough Beds is that each spreital lamella is composed of two very thin adjacent lamellae (c.f. Plate 40A & 41A).

These lamellae are always more resistant to erosion than the matrix, but do not differ from it petrographically. It is rare for any of the Yorkshire Teichichnus to be followed horizontally for more than 10cm.

Ethological interpretation.

Plate 40C illustrates the trace formed by the lateral and upward migration of several dwelling tubes of the Recent annelid worm Nereis (SCHÄFER 1962, p.407, fig.214). It compares very closely with the Scarborough Bed Teichichnus, particularly the specimen shown in Plate 40A. The dual lamellae are rendered more resistant by the compression caused by the annelid's migration. In fact, the Recent Nereis trace was observed by washing away the surrounding, less compacted mud.
Since no other organism at the present time is known to produce Teichichnus structures other than Nereis, it is reasonable to assume that this polychaet was the producer.

An important point of contrast with other Fodinichnia which have been considered (e.g. Asterosoma and Chondrites) is that the organism was not feeding on the sediment, it was merely travelling through it. This is shown by the petrographic identity of the sediment inside and outside the trace fossil. The mode of life of Nereis diversicolor is entirely compatable with this evidence, for it is a voracious predator (MACGINITIE & MACGINITIE 1949, p.207). Nevertheless, even predators benefit by a systematic coverage of the sediment, so Teichichnus definitely belongs in the Fodinichnia.

Sedimentological interpretation.

The occurrence of Teichichnus is very strongly dependent upon lithology (Appendix II). It occurs only in fine-grained, muddy sandstones and siltstones. It often forms 90% or more of the ichnofauna, and is often accompanied by retrusive Diplocraterion arkelli (e.g. in the Nothe Grits of Bowleaze Cove).

This suggests that the retrusive ethology of Teichichnus may be a direct response to gradual sedimentation rather than a systematic feeding pattern. It is more commonly associated with Thalassinoides suevicus and Chondrites than with Rhizocorallium commune.

Comparisons.

The Jurassic examples of Teichichnus bear closest comparison with the type species, Teichichnus rectus, from the Lower Cambrian Neobolus Beds of the Salt Range Pakistan (SEILACHER 1955, p.378). The burrows are slightly wider in T. rectus, but exhibit the horizontal translation found in the Scarborough Bed examples. DOUGHTY (1965, p.147) has recorded Teichichnus from the basal Upper Lias Transition Bed of Lincolnshire in densities far greater than are normally attained in Scarborough Bed examples. The average width of 13mm. for the Lincolnshire examples is slightly in excess of the 8mm. for the Yorkshire examples. He records that branching is occasionally seen.

A feature not observed in Yorkshire specimens is parallelism of adjacent Teichichnus. This evidently occurs in Lincolnshire, where sets of burrows run parallel for a length of almost 30cm.

SEILACHER (1957, pp.203-4, plate 23/1) was apparently the first to compare Teichichnus with the burrows of Nereis diversicolor.

Occurrence.

Widespread in fine clastic sediments throughout the Jurassic and other Systems. For detailed horizons and localities refer to the stratigraphic section.

Geological range.

Teichichnus occurs in strata from the Lower Cambrian to the Recent. It is particularly abundant in the Mesozoic Era.

VII : IRREGULAR SAND-FILLED BURROWS

Planolites NICHOLSON 1873

Type species. *Planolites vulgaris* NICHOLSON & ETHERIDGE
1875, p.139. Lower Silurian of Ontario.

Generic diagnosis (HÄNTZSCHEL 1962, W.210):

> Fillings of burrows, about 1cm. wide, penetrating sediment in irregular course and direction; sand and silt of filling brought in by animals (presumably worms) after passing alimentary canal.

Planolites c.f. *montanus* RICHTER 1937

Structures complying with the generic diagnosis, and strongly resembling the burrows figured by SEILACHER (1963, p.83, fig.1) as *Planolites montanus* occur in fallen blocks of sandstone at intervals on the backshore between Blea Wyke Point and Ravenscar. The structures consist of a plexus of smooth-walled tubes about 1cm. in diameter running sub-parallel to, but penetrating the bedding planes. They are enriched in iron and devoid of which is abundant in the matrix.

The burrows rarely branch.

RICHTER (1937) originally described *Planolites montanus* from "non-marine" sandstones in Coal Measure cyclothems. The Jurassic sandstones containing *P.* c.f. *montanus* are devoid of diagnostically marine fossils, and are lithologically similar to many Lower Deltaic sandstones, but until their horizon can be firmly established, it can only tentatively be suggested that the Yorkshire Middle Jurassic *P.* c.f. *montanus* occurs in a similar environment to that of the Ruhr Coal Measures. Sound sedimentological grounds exist for such a comparison.

Planolites ophthalmoides JESSEN 1949

Plate 42

Description.

Burrows with the characteristic eye-like halo around a central core occur in loose blocks of grey, micaceous, fine-grained sandstone with rib-and-furrow structure beneath Beast Cliff, Ravenscar. The horizon of the fallen material cannot be established for certain, but it does not fall within any of the recognised "marine" bands.

The burrows are chiefly vertical or highly inclined with a diameter of 5-10mm. They are accompanied by occasional sub-horizontal burrows where the halo is clearly more resistant to erosion than the core: (this is not invariably the case with vertical examples). Occasionally burrows appear to be paired, but this may be fortuitous.

Interpretation.

The halo has been interpreted as either an oxidation or a cementation zone around a gallery made visible by tectonic compression (SEILACHER 1964, p.306). While this interpretation may hold for the Westphalian examples from the Ruhr and Pennsylvania, it is not applicable in the Yorkshire Middle Jurassic where tectonism is negligible. Diagenesis alone must be sufficient.

It is difficult to place Planolites ophthalmoides in Seilacher's classification. Were it not for the sub-horizontal examples, the form could well be placed in the Domichnia. However the genus Planolites is customarily regarded as belonging to the Fodinichnia, since most 'species' are clearly feeding burrows: P. ophthalmoides is unique among them in having a dominantly erect attitude.

Comparisons.

The trace fossils figured on the left of Plate 42 are identical with P. ophthalmoides figured from paralic deposits of the Ruhr Basin (SEILACHER 1964, p.307, fig.6). There it occurs at the boundary between shales containing non-marine bivalves and shales with Lingula.

Planolites ophthalmoides JESSEN is very similar to Laevicyclus QUENSTEDT. It is difficult to distinguish the two forms except on the basis of their size, sedimentological associations and orientation, not all satisfactory criteria. However, Laevicyclus never shows the occasional sub-horizontal tunnels which always accompany the vertical examples of Planolites ophthalmoides. The material surrounding the core supplies the best means of distinguishing the two. In Laevicyclus there is a difference in grain-size: in P. ophthalmoides there is no difference. If these differences are held to be trivial, then Planolites ophthalmoides JESSEN 1949 is synonymous with LAEVICYCLUS Quenstedt 1879 (erected without type species).

P. ophthalmoides differs from P. montanus RICHTER in being dominantly erect, possessing a halo (even when sub-horizontal) and in having a circular cross-section. P. montanus is irregularly horizontal, lacks a halo, and has an ovoid cross-section.

Occurrence.

Planolites ophthalmoides occurs in the Middle Jurassic of Yorkshire, and the Upper Carboniferous of Europe and North America; all areas of "non-marine" sedimentation.

Faecal Pellets

Faecal pellets are often strikingly associated with particular burrows (e.g. Diplocraterion arkelli, Plate 16, Text-fig. 15; and Rhizocorallium cicatricosus, Plate 30). In these instances it is pointless giving the faecal pellets separate names, though this was at one time advocated, RICHTER & RICHTER (1939, p.163) proposing the name Coprulus as a subsidiary 'mechanical-ecological' term for excrement in the form of isolated, loose pills. If used at all, it is only informal.

A more complicated terminology for the description of faecal pellets has been adopted by PAREJAS (1948), who described three 'new' species of Coprolithus (op.cit., p.512), all believed to be crustacean faecal pellets, from the Upper Jurassic of Switzerland and Turkey. Subsequently HÄNTZSCHEL (1965, p.25) has pointed out that one of the 'new' species C. saleviensis was originally "organism β" JOUKOWSKY & FAVRE (1913, p.315). Meanwhile it became independently described by two further authors. The taxonomy of trace fossils is confused enough, without such additional problems of synonymy.

Faecal pellets, not visibly connected with any identifiable trace fossil, have only been recorded from a single loose block of finely laminated sandstone on the backshore at Peak (Plate 43A). It is probably from the Lower Deltaic Series. The pellets are circular or ellipsoidal capsules of bonded fine-grained sand, about 5mm. in diameter. Although isolated pellets are dispersed across the whole bedding plane, several centres are visible, around which faecal pellets are densely packed (Plate 43B). Exposure was not sufficient to reveal any vertical burrow at the centre of the accumulations which may have housed the producer of the pellets. Plate 43B also shows the impressions of very many smaller pellets which have been removed by erosion: they are about $\frac{1}{3}$ to $\frac{1}{4}$ the size of the larger ones.

The fossil pellets compare in detail with the Recent pellets of many crabs living in the littoral zone. KREJCI-GRAF (1935, p.24, fig.4; Plate 44, reproduced) has illustrated two sizes of pellet from laminated sands around Hong Kong. The larger pellets have a diameter of 5mm., and are very noticeably concentrated into discrete areas.

CHAPTER TEN

MEANDERING GRAZING TRAILS

Pascichnia

This major group of trace fossils appears to be completely absent from the Jurassic rocks of England (Text-fig.10).

The absence of the Pascichnia is, in itself, a very useful environmental indicator, as SEILACHER (1959, 1964) has shown, for the group is exceptionally rare in the majority of shallow-water sediments, though abundant in deep-water sediments of the Flysch type showing evidence of 'turbidite' sedimentation.

Not all shallow-water sediments, however, are devoid of Pascichnia, for the group is extremely abundant in cyclothemic Carboniferous rocks of Europe and America, where several 'genera' are known, of which the best-known is probably Crossopodia (Plate 45). Alongside Crossopodia there exist in the Carboniferous other Pascichnia which occur also in the Jurassic, though not in Britain. These include Helminthopsis and Phycosiphon.

The Pascichnia form only one part of the trace-fossil assemblage in the Carboniferous cyclothems. Repichnia such as Gyrochorte carbonaria (Plate 47) indicate a nearshore, probably intertidal habitat for the trace-fossil producing benthos. This view is strengthened by the stratigraphic position of the burrows.
There is thus an apparent anomaly in the Carboniferous, with supposedly diagnostic deep-water trace fossils occurring in littoral, laminated siltstones. The "cock's tail" Zoophycos also appears to occur in shallower water in the Carboniferous than elsewhere.

The anomalous nature of the Namurian trace-fossil fauna of Northumberland may be seen on Text-fig. 54, where it is compared with the Jurassic assemblage, and also with the Flysch. Clearly, the problem merits further study.

CHAPTER ELEVEN

RESTING IMPRESSIONS

Cubichnia

This major division of trace fossils is very rare in the British Jurassic (Text-fig.10), especially when compared with its abundance in the German Jurassic, where <u>Asteriacites</u> SCHLOTHEIM 1820 is very common (e.g. HANTZSCHEL 1962, fig.130/4). It is the more surprising when the widespread "Starfish Beds" are remembered, especially those of the Middle Lias of Dorset and Yorkshire, where resting trails of <u>Ophioderma</u>, for example, may have been expected.

<u>Pelecypodichnus</u> SEILACHER 1953a

Plates 32 & 45

The only resting trace to be found in the present study was <u>Pelecypodichnus</u>. A small loose block of sandstone from the backshore at Ravenscar (45/997006) shows seven pod-like impressions tapering to sharp and obtuse points at each end (Plate 45): it originates from either the Lower or Middle Deltaic Series.

It is interesting to note that the freshwater mussel

Unio kendalli has been found in lithologically identical Deltaic sandstones. However the two do not occur together.

Similar pod-like structures, though standing vertically in silty limestone, are found in the Bajocian Scarborough Beds (S.B.32) at the same locality. One example has been found penetrating the Spreite of Rhizocorallium commune (Plate 32).

Pelecypodichnus is thus recorded from both 'marine' and, tentatively, 'non-marine' horizons in the Middle Jurassic of Yorkshire. SEILACHER (1953a, p.105, pl.10/1 & 12) described the type species from the Keuper, only questionably, and the Dogger β of Wurttemberg. There it is often found with Asteriacites.

CHAPTER TWELVE

CRAWLING TRAILS

(Repichnia)

Gyrochorte HEER 1865

1879 *Gyrochorda* SCHIMPER , p.51

Type species: *Gyrochorte comosa* HEER 1865 , p.142; plate 9, fig. 12 (lect. HÄNTZSCHEL 1962, W.196) Middle Jurassic ; Switzerland.

Diagnosis: (HÄNTZSCHEL, *loc. cit.*) :

Zopf-traces of German literature, *i.e.*, ridges on bedding-planes with biserially arranged, obliquely placed transverse pads, both series separated by a median furrow.

Gyrochorte comosa HEER 1865 p.142

Text-fig. 24A ; Plate 41B

A single loose block of green micaceous sandstone with linguoid ripple-marks, probably fallen from the Middle Deltaic Series at Ravenscar (45/997006) contains several trails identical to those figured by HÄNTZSCHEL (1962, fig. 122/1). They are plait-like trails 5mm. in width with a central axis bordered by alternating oblique pads (Text-fig. 24A).

Small examples, about 2 or 3mm. in width, are sometimes found in the Scarborough Beds (S.B.32) at Ravenscar accompanying Teichichnus (Plate 41B). Here the pads are sub-circular rather spindle-shaped. This form strongly resembles Neonereites biserialis (SEILACHER 1960, p.47). However I am informed (SEILACHER 1966, personal communication) that the resemblance is illusory.

ABEL (1935, p.275) records plait-like trails from the Lias and Middle Jurassic of Germany. A specimen from the α Lias of Hüttlingen (Württemberg) strongly resembles the Yorkshire Gyrochorte comosa, and is attributed by ABEL (op. cit., p.276; fig.248) to the amphipod Corophium. Further similar examples occur in the Upper Toarcian at Baxilliers, southwest Belfort (p.277; fig.251) and are accompanied there by Gyrochorte carbonaria, a form lacking the transverse pads.

Gyrochorte carbonaria SCHLEICHER 1954

Plates 45-48

Description.

Long horizontal bilobed galleries lacking the transverse pads of Gyrochorte comosa HEER are very common trace fossils in the British Jurassic. The galleries vary in width from 2mm. (from the Forest Marble of the Fleet, Dorset) to 6mm. (from the Ellerbeck Bed of Goathland, Yorkshire). The greatest variation shown is in ethological pattern.

The galleries are generally of great length, often several decimetres, and they often cross one another (Plate 45). At some horizons they are randomly disposed (e.g. the Scarborough Beds, ripple-marked sandstone with Catinula casts; Plate 46). At others, like the ripple-marked sandstone of the Ellerbeck Bed at Water Ark, Goathland, Gyrochorte carbonaria shows parallel orientation with respect to the crests of ripples (Plate 47A). From the same locality , several galleries on one block of sandstone describe broad U-turns (Plate 48), with the limbs of the 'U' again sub-parallel to the trend of the ripple crests.

Comparisons.

Gyrochorte carbonaria from the Namurian of Haltwhistle Burn, Northumberland (Text-fig. 2) shows a more pronounced parallelism than occurs at any British Jurassic horizon. A similar strong orientation occurs at several horizons in the German Jurassic (e.g. WEISS 1940, pl.12/1,2). ABEL (1935, p.276, fig.249) has illustrated a very straight example from the Brown Jura of Wasseralfingen (Wurttemberg). The Carboniferous examples are preserved in a purple, laminated siltstone with very strong parting lineation (Plate 47B). In nearly every case the trails are orientated perpendicular to the lineation (Plate 47B,C,D). U-turns, similar in style to those of the Ellerbeck Bed, but with a sharper turning circle, are common. Plate 47C shows U-turns developing in adjacent burrows: Plate 47D shows a very regular example.

Gyrochorte carbonaria from the Ruhr Coal Measures occurs in association with non-marine bivalves and ostracodes (JESSEN & KREMP 1954, p.284). Elsewhere, however, it occurs in fully marine environments, dominantly in the Cruziana Facies of SEILACHER (1964, p.309), though it has been recorded from the Eocene Flysch of Austria. The trace fossil cannot therefore be regarded as diagnostic of any particular environment, though it may locally prove useful in a stratigraphic sense for subdividing paralic cyclothems (SEILACHER 1963, fig.1).

Ethological interpretation.

The trace fossil Gyrochorte has been interpreted as the trail of a polychaet annelid by WEISS (1940) and SEILACHER (1955, fig. 2), but is generally regarded as the product of amphipod crustaceans (e.g. HANCOCK 1858, ABEL 1935, pp.275-279). In both interpretations the structure is thought to have originated just beneath the sediment surface, though WEISS (1940, p.335, fig.2; text-fig. 7) has demonstrated that the structure is transmitted to adjacent bedding laminae. This suggests that the trace was formed by the pushing apart of the laminae, and not by the organism's feeding on the sediment; which definitely places Gyrochorte in the Repichnia.

Orientation in Gyrochorte carbonaria : cause and environmental significance.

There are two main features of the trace morphology of G. carbonaria which require explanation: both are ethological. The first is the widespread occurrence of parallelism of adjacent galleries. The second is the frequent presence of U-shaped tunnels.

NEWELL (1958a, p.231) has said of Recent Littorina littorea trails from Whitstable:-

> "...the very fact that all tracks pursue a fairly straight course for some considerable distance is in itself suggestive of orientated responses".

Since the terrain on which the trails were constructed was flat and featureless NEWELL (1958b, p.241) suggested that light was the operative factor. This he proved convincingly in a series of experiments which showed that winkles orientate by means of "light-compass reaction" (sensu FRAENKEL & GUNN 1940).

It was found that 95% of the trails of Littorina consisted of an outward and a homeward limb, so that trails preserved completely, formed in bright sunlight, were U-shaped. NEWELL (1958b, p.252) showed experimentally that Littorina is initially photopositive, but after five minutes (during which time the average winkle travels 14cm.) the response becomes photonegative. This response enables animals which are mainly sedentary to maintain their ecological station on shore but also undertake grazing excursions. NEWELL (op. cit., p.264) concludes that:

> " winkles ... are, perhaps, representative of the vast majority of shore animals, although this is not to say that the environmental clues selected, and the reactions to them, are identical in all instances ".

Essentially U-shaped traces are known to be produced by other Mollusca. BRAFIELD & NEWELL (1961, p.84, fig.2) have illustrated the same phenomenon in Macoma balthica from Whitstable and Cleethorpes. It also occurs in Cardium edule, where 13 out of 14 trails examined were

U-shaped. They stress, however, that the majority appears straight because the outward limb tended to be formed under water and was obliterated.

The orientation of amphipods with respect to their position on the shore has been studied by PAPI & PARDI (1953) and PARDI & PAPI (1953). They have shown that Talitrus saltator orientates by means of a light-compass reaction, moving up and down the beach at right angles to the shore, no matter what time of day, and so returning to the zone of moist sand whence they originated.

The examples of the amphipod trace fossil Gyrochorte carbonaria from the Ellerbeck Bed (Plate 47A, 48) have a trend dominantly parallel to the ripple crests: examples from the Namurian (Plate 47B,C,D) invariably at right-angles to the parting lineation. Both these directions are normal to the current direction of the water which deposited the sediment, and if this current were of tidal origin, as seems likely from the sedimentology, it would indicate movement parallel to the shoreline (assuming the simplest case), not at right angles to it (c.f. PAPI & PARDI 1953). This, however, cannot be proved. What remains strikingly certain is the constancy of the orientation with respect to sedimentary structures produced by current action, which suggests a response acting on a population as a whole, not on isolated individuals within a population (c.f. SCHWARZ 1932).

From the regularity of the sedimentary laminae in the Namurian siltstones it is clear that the terrain must have been flat, and that light could have been a significant factor (NEWELL 1958b, p.241). The fact that U-turns are here very common (Plate 47C,D) lends further support to the notion that the producer of Gyrochorte was living in an environment in which phototropism played an important part.
The only environment in which such responses are exhibited by benthonic organisms is in the intertidal zone, for under water, particularly turbid water such as is found in estuaries, illumination is drastically reduced, for example at Whitstable, by 95% in a 6" depth of water (NEWELL 1958b, p.254).

Thus the evidence of the ethological pattern of Gyrochorte carbonaria reinforces the sedimentological evidence in suggesting an intertidal origin for the sandstone at the base of the Ellerbeck Bed, and the Namurian siltstones of Haltwhistle Burn. At the majority of other horizons, such as the Scarborough Beds, the ethological patterns are random, and there is no evidence in the trace morphology for an intertidal environment of deposition.

Summary.

Parallel orientation and U-turns are characteristic ethological patterns of Gyrochorte carbonaria SCHLEICHER, both in English Jurassic and Upper Carboniferous deltaic sediments. By analogy with Recent traces of amphipods and other benthonic creatures, such patterns can only be satisfactorily explained by phototaxis.
Phototaxis cannot take place in submarine environments.
Where widespread parallelism and abundant U-turns are present, an intertidal environment is indicated.
Sedimentological evidence supports such a conclusion.

PART THREE:

STRATIGRAPHIC DISTRIBUTION
AND PALAEOECOLOGY

CHAPTER THIRTEEN.

THE SEQUENCE OF TRACE FOSSILS IN THE YORKSHIRE JURASSIC

Introduction.

For much of Jurassic time the Yorkshire Basin was completely separate, both faunally and lithologically from basins to the southwest. The changes take place in the region of the Market Weighton "axis" - a region of relative uplift: it is to the subsiding sedimentary basin on the northern side of this axis that this paper is confined.

The well-exposed cliffs of the northeast coast have long attracted the attention of British geologists, many of whose classic works form the starting point for all research into the area; such are the works of TATE and BLAKE (1876) and FOX-STRANGWAYS (1892). Sadly, after the heyday of the late nineteenth century, the pace of research slackened, not to regain impetus until the 1930's, with the works of BLACK (1929, 1934) on the drifted plant beds and washouts of the Deltaic horizons, and SMITHSON (1942) and RASTALL and HEMINGWAY (1940-1949) on the sedimentary petrology, particularly of the heavy minerals and the Dogger (Middle Jurassic).

In the ensuing years comparatively little was published until quite recently, with the notable exception of papers by WILSON (1949) on the Corallian Limestones, and HEMINGWAY (1951), DEAN (1954) and HOWARTH (1955) on the Liassic. Very recently the pace of research has again stepped up, with the works of BATE (1959, 1964, 1965) on the Middle Jurassic ostracodes, HOWARTH (1962) on the Upper Liassic, MUIR (1964) and HARRIS (1961, 1964) on the palaeobotany of the Deltaic Series. There has however been a sad neglect of the sedimentological and molluscan aspects of the Middle Jurassic, where much remains to be done.

Cycles of Bioturbation.

The Jurassic Succession of the Yorkshire Basin is summarised in Fig. 37, which shows the levels at which sediment is extensively burrowed by annelids and crustaceans. It is evident that the occurrences follow a cyclic pattern.

In the Lower Jurassic it is of the following form:

(1) Cephalopod shale.

(3) Chamositic ironstone with essentially concordant crustacean burrows.

(4) Massive sandstone with essentially discordant annelid burrows.

(3) Ripple-marked, fine-grained sandstone.

(2) Sparsely fossiliferous laminated micaceous siltstone.

(1) Cephalopod shale.

The complete cycle is exhibited by both the Lower-Middle Liassic and Upper Lias-Dogger sequence, where each unit can be matched. The Blea Wyke Series is the analogue of the Middle Lias Sandy Series, both being particularly replete with Chondrites (Plates 11, 27B), while the Middle Liassic Ironstone Series are repeated by the Dogger - both with essential chamosite and siderite as rock-forming minerals, and both containing Rhizocorallium (Plate 28).

HEMINGWAY (1951) has compared these Liassic cycles with the successively shallower sediments now forming in the Black Sea. He points out that every member of the sequence possesses its analogue in the Black Sea with the exception of the ironstones, which mark, sedimentologically, a complete reversal of the trend towards increasing oxygenation. This seems to point to some restriction in the environment of deposition such as would result in the formation of partially enclosed bays or lagoons. These must have remained at near normal salinities, for the Middle Liassic Ironstones contain a very prolific stenohaline fauna including *Pleuroceras* spp., while the Dogger of the Blea Wyke area, though not containing ammonites, is full of "*Terebratula trilineata* auctt." and *Trigonia costata* PARKINSON. Above the shell bank composed of these remains, however, is a band dominated by *Nerinea cingenda* PHILLIPS, a high-spired gastropod typical of many European Mesozoic deposits of lagoonal character (D. V. Ager, personal communication, 1965). Today, high-spired gastropods seem especially adapted for life in anoxygenic environments (YONGE, 1946), and their abundance towards the top of the Dogger, above which occurs *Thalassinoides* seems to support the contentions of petrographers that these chamositic and sideritic ironstones were laid down under reducing conditions. Significantly, burrowing decapods (responsible for forming *Thalassinoides*) are most abundant at the present day in the upper part of the intertidal zone of bays estuaries and lagoons along the Pacific coast of America (RICKETTS and CALVIN, 1962, pp.256-269).

A considerable change takes place in the nature of cyclic sedimentation above the Dogger, where, after a period of relative stability during which a thick pile of deltaic sediments were accumulated at or around sea-level, the cycles are mostly of the typical Jurassic form (ARKELL, 1933, pp.54-55):

(a) Cephalopod clay.
(c) Oolitic limestone (with crustacean burrows)
(b) Massive calcareous sandstone (with annelid burrows).
(a) Cephalopod clay.

These Middle and Upper Jurassic cycles are not so thick as those of the Lower (see Fig. 37), averaging 280ft., compared with 420ft. or more, and differ essentially in their culmination, where the highly oxygenated oolites show no signs of the restricted environment typical of the ironstones lower in the succession, frequently achieving a well-developed reef association (WILSON, 1949).

There are four cycles in the Middle and Upper Jurassic, of which the first is very protracted, being represented by a thin, lagoonal incursion into the deltaic area - the Ellerbeck Bed, which contains Corophioides, vertical burrows, in ironstone nodules from below Beast Cliff.

Late in Bajocian times the deltaic area was inundated by the sea which deposited the Scarborough Beds, forming the next cycle, beginning with a massive sandstone full of the 'U'-shaped lug-worm burrow *Arenicolites statheri*, while later limestones contain an outstanding variety of trace fossils, including, near Blea Wyke, *Rhizocorallium* and *Thalassinoides*.

The succeeding cycle has unit (a) represented by the condensed Upper Cornbrash Limestone with *Macrocephalites macrocephalus*, while the overlying Kellaways Rock is very poorly fossiliferous, except for some obscure vertical burrows. Above is the Hackness Rock, a coarse calcareous sand full of *Gryphaea bilobata* and many *Rhizocorallium* and *Thalassinoides* (Fig. 5A).

The last cycle is best developed, with the Oxford Clay containing many cephalopods being overlain by a thick development of the Lower Calcareous Grit of the Corallian Series containing annelid burrows, with the Hambleton Oolites above full of *Thalassinoides* on Filey Carr Naze (WILSON, 1949, Plate X, figured as "fucoids", though described in the text as infilled suncracks, pp.262-263).

In view of the distinct differences between the sedimentology of the two series of cycles it seems unlikely that a common origin is feasible. HALLAM (1963) has suggested major eustatic control for some of the important Jurassic transgressions, which would account for the first two cycles (in the Liassic). The second group seem to require a more local mechanism since they are neither so completely developed nor so extensive laterally; local isostatic readjustments influencing only the Yorkshire Basin of deposition provide a possible origin for these minor cycles.

CHAPTER FOURTEEN

YORKSHIRE LIASSIC AND DOGGER TRACE FOSSILS

(i) Lower Lias.

Compared with other basins of deposition, the trace fossils in the Lower Lias of Yorkshire are noticeably rare. The odd flask-shaped trace fossil *Kulindrichnus langi* (HALLAM 1960), abundant in Dorset, Glamorgan and Lincolnshire, is not common in Yorkshire. It occurs in Lower Sinemurian limestones at Redcar.

One occurrence worthy of note is the record of *Rhizocorallium* c.f. *cicatricosus* beneath the Rocket Post southwest of Ness Ruck, Robin Hood's Bay (45/957058) in the *Jamesoni* Beds.

The rarity of Lower Liassic trace fossils in Yorkshire contrasts sharply with other areas of deposition, particularly Dorset and Glamorgan (SCOTT SIMPSON 1957, HALLAM 1960a), and the Hebridean area (HALLAM 1966) where *Thalassinoides*, *Rhizocorallium*, *Diplocraterion* and *Chondrites* are frequently found.

The difference between Yorkshire and other areas in Lower Lias times is probably a reflection of original differences in sedimentary regime and depth of deposition.

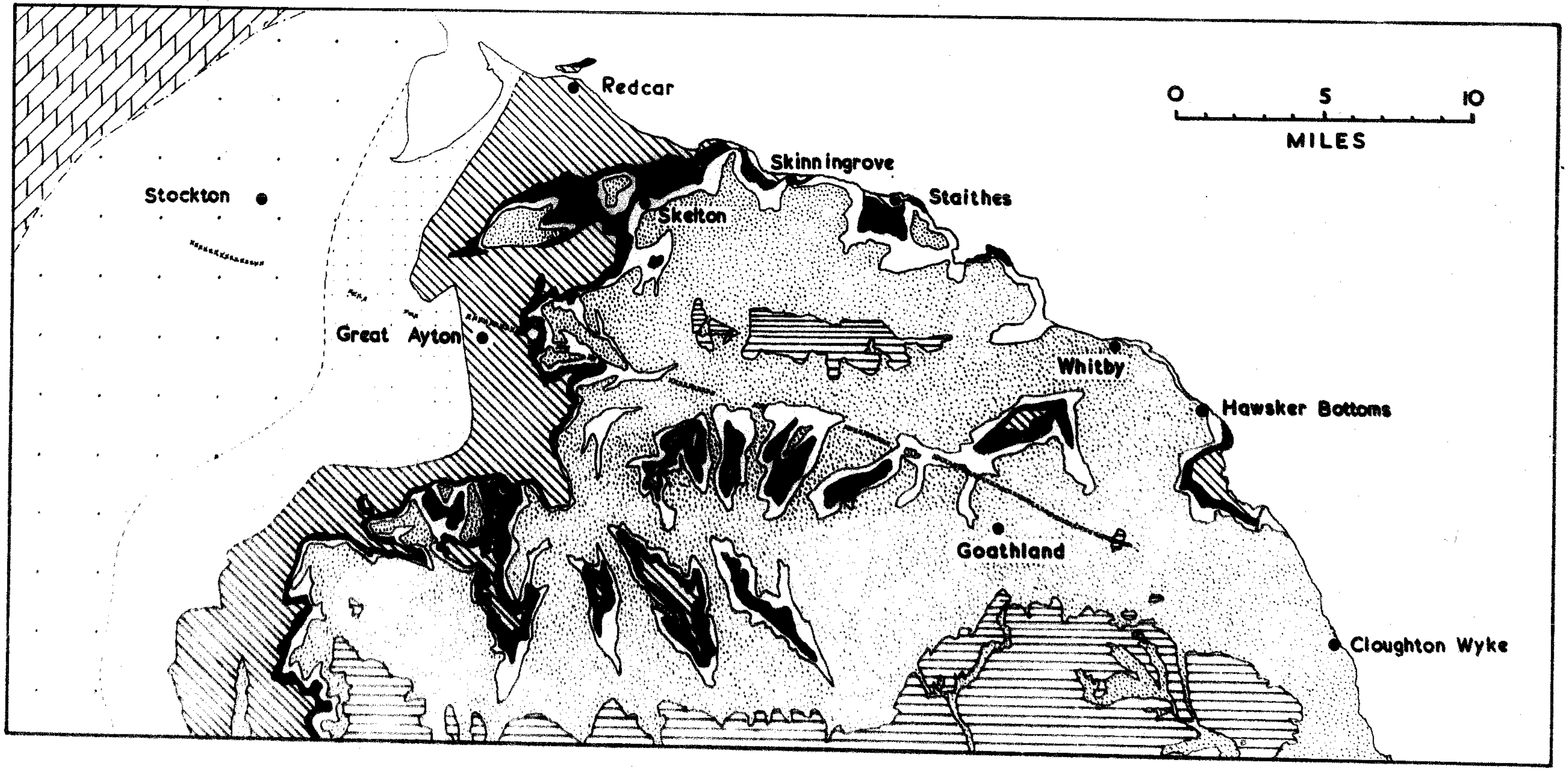
Dorset, Glamorgan and the Hebrides have notably more in-shore Lower Liassic sediments than Yorkshire, where coarse clastic material is unknown, and limestones are rarer than elsewhere. It is not wise, therefore, to use the evidence of the striking difference in trace fossil assemblage between Lincolnshire and Yorkshire as a point in favour of a faunistic barrier in the Market Weighton area, since the differences may be explained in terms of differing depths of deposition, with the shallower, trace fossil-bearing strata unexposed in Yorkshire at the present time.

(ii) Middle Lias : Sandy Series.

The Sandy Series of Yorkshire has not been the subject of a detailed sedimentological study of the type carried out on the neighbouring Lower Lias and Ironstone Series. However, an excellent stratigraphic account exists of the whole of the Middle Lias (HOWARTH 1955) on which such a study could be based. The associated non-cephalopod molluscan fauna has not receievd attention for ninety years (TATE & BLAKE 1876) and would benefit especially from a systematic study of the Bivalvia, through which worthwhile palaeoecological studies could be carried out, as the fauna is prolific, varied and well-exposed.

Text-figure 38.

Map showing the distribution of outcrop of the Jurassic rocks in north-east Yorkshire, including the major trace-fossil localities.


Redcar
Stockton
Skinningrove
Staithes
Skelton
Great Ayton
Whitby
Hawsker Bottoms
Goathland
Cloughton Wyke
0
5
10
MILES

PERMIAN

▨ Magnesian Limestone

TRIASSIC

░ Rhaetic and Keuper Marl

□ Keuper and Bunter Sandstone

JURASSIC

▤ Upper

░ Middle

Lower
- □ Upper Lias
- ■ Middle Lias
- ▧ Lower Lias

TERTIARY

-·-·- Faults

xxxxxx Cleveland Dyke

The trace fossils are comparatively uniform throughout the outcrop, Chondrites being dominant. Some of the best localities for Chondrites and Curvolithus are along the coast northwest of Skinningrove (45/702213) (Text-fig. 38) where well-sorted, fine-grained calcareous sandstones contain isolated Chondrites with a very regular pinnate outline, preserved by concealed bed-junction preservation. Nearby, silty sandstones contain more abundant Chondrites preserved by the usual bed-junction sedimentation (Plate 10A).

Inland, at Cliff Rigg Quarry (45/575116) near Great Ayton (Text-fig. 38) the Cleveland Dyke has baked the Sandy Series, resulting in the striking preservation of bleached Curvolithus and Chondrites in a green, laminated, fine-grained sandstone also containing Entolium (Plate 10B).

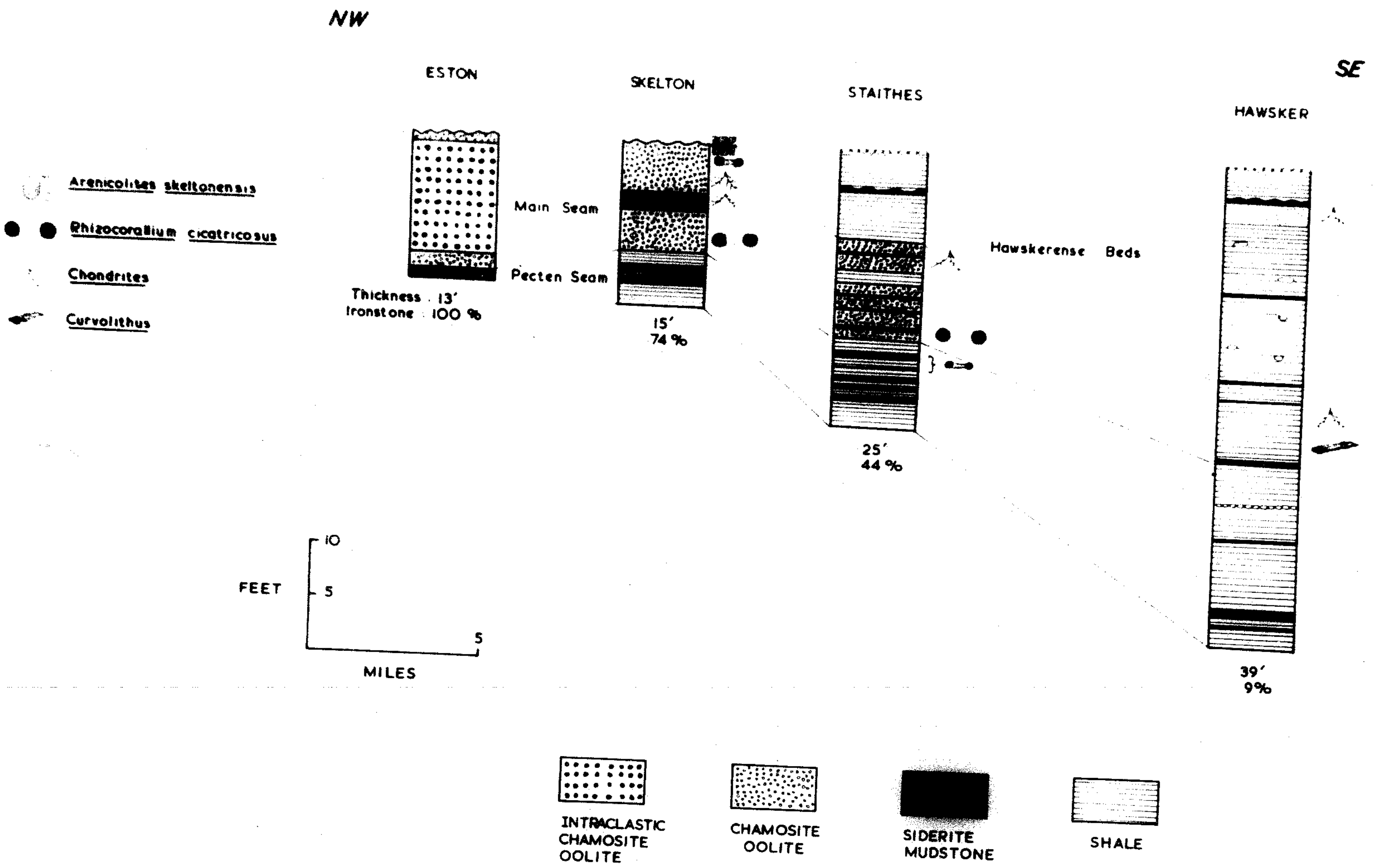
(iii) Middle Lias : Ironstone Series

The Cleveland Ironstone Series presents a most interesting example of the economic use of trace fossils, as horizon indicators in a complex sequence of chamositic and sideritic ironstones. There are four seams in Cleveland, recognisable over the whole of the iron-mining area (approximately 14 x 6 miles ; Text-fig. 38). Three are defined palaeontologically; they are as follows:-

Text-figure 39A.

Diagram illustrating the lateral variation in sedimentary and trace-fossil facies of the Middle Liassic *Spinatum* Zone of north-east Yorkshire.

The percentage of ironstone relative to shale in each of four successions is shown. Compiled from CHOWNS (1966), HOWARTH (1955) and field observations by the author.


NW
SE
ESTON
SKELTON
STAITHES
HAWSKER
Arenicolites skeltonensis
Rhizocorallium cicatricosus
Chondrites
Curvolithus
Main Seam
Pecten Seam
Hawskerense Beds
Thickness 13'
Ironstone 100 %
15'
74 %
25'
44 %
39'
9%
FEET
10
5
5
MILES
INTRACLASTIC CHAMOSITE OOLITE
CHAMOSITE OOLITE
SIDERITE MUDSTONE
SHALE

4. Main Seam

3. Pecten Seam, with Pseudopecten aequivalvis

2. Two-foot Seam

1. Avicula Seam, with Palaeoxytoma cygnipes.

It may be seen that only two are defined in terms of shelly fossils. The highest seam , the Main, is defined by the trace fossil Rhizocorallium, otherwise known to the ironstone miners as 'dog cocks' (CHOWNS 1967, personal communication). Within the Main Seam, which is the thickest of all, various blocks are typified by various sizes of 'dog cock', and these traces enable a subdivision to be undertaken.

At North Skelton Mine (45/675183: the last to close, in 1964) the Main Seam is ten feet thick and divided into three parts (Text-fig. 39a), identified by the miners as follows :-

c. Top Block ; small 'dog cocks'

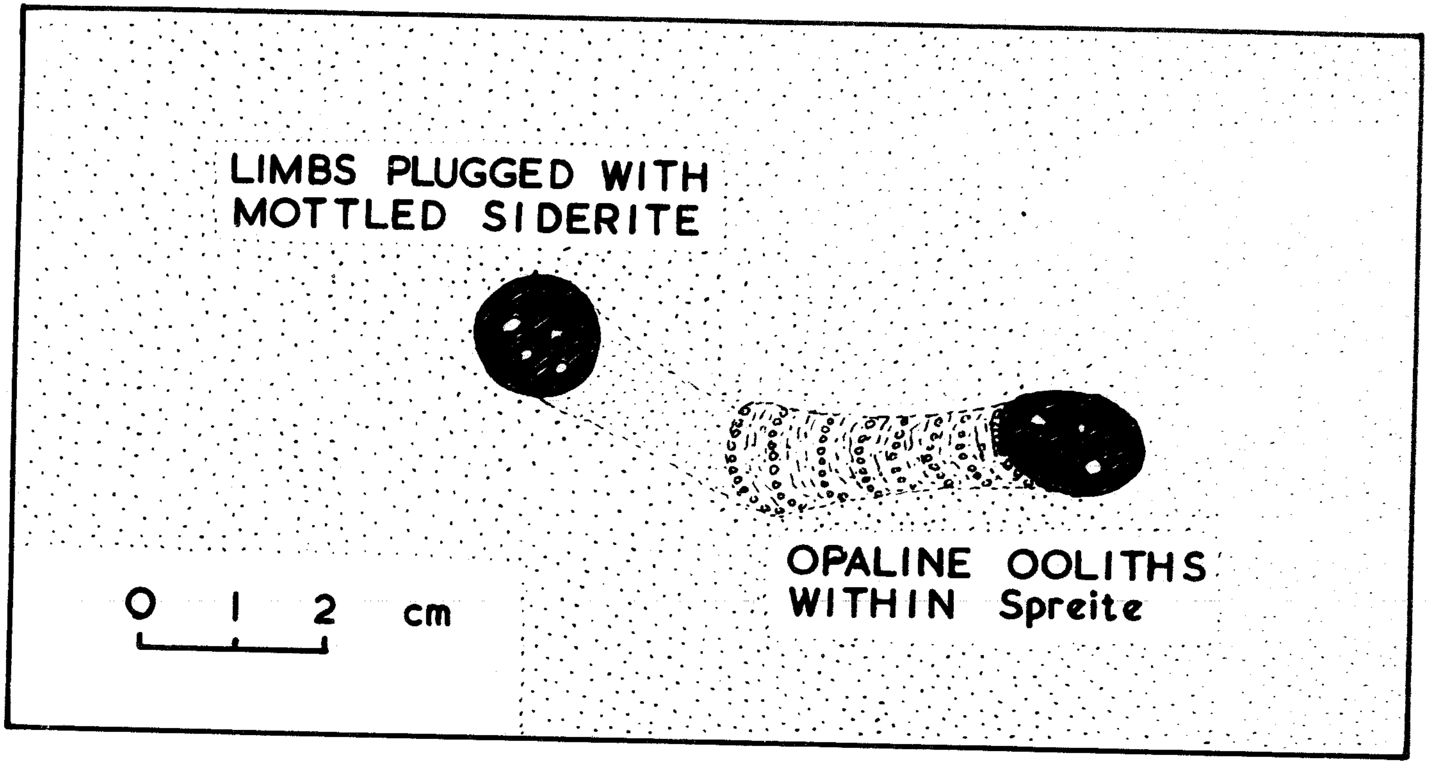
b. Middle Band ; 'dog cocks' rare

a. Bottom Block ; large 'dog cocks' in Black Hard at base.

The small 'dog cocks' from the Top Block generally show Spreite, often composed of chamosite ooliths in marked contrast to the siderite-filled limbs (Plate 34B), though it is apparently lacking in some, while others have the Spreite filled with siderite. The average dimensions of these small 'dog cocks' are 28mm. overall gauge and 7mm.

Text-figure 39B.

Sketch of an oblique section through the *Spreite* of a *Rhizocorallium* from North Skelton ironstone mine : Middle Band of Main Seam. Drawn from a polished vertical block of ironstone in the collection of T. Chowns, University of Newcastle. Note the *Spreite* divided into two parts : on the left typically indistinct : on the right packed with concentric opaline oolites marking the outward migration of the right-hand limb.


LIMBS PLUGGED WITH
MOTTLED SIDERITE
OPALINE OOLITHS
WITHIN Spreite
0 1 2 cm

limb diameter (Ratio = 4.0). The traces can only be examined in vertical section, so they must be placed in Rhizocorallium sensu lato. It was not possible to determine the nature of the surface of the Spreite.

In the Middle Band rare larger examples of Rhizocorallium accompany the typical smaller 'dog cocks' of the Top Block. One oblique section through a pair of limbs showed opaline ooliths packed concentrically about one limb only, within the area of the Spreite (Text-fig. 39b), suggesting that this limb had gradually migrated 43mm. away from its original position only 26mm. from the other limb. The fact that the migratory limb appears elliptical in section, though the second limb is circular, implies that the two limbs were not parallel.

Throughout the Main Seam the burrows of Chondrites are particularly noticeable in the siderite mudstone where they are preserved by a combination of bed-junction and diagenetic processes. They are especially evident in the upper half of the Seam.

In the higher part of the Bottom Block there are no 'dog cocks'. Here Dentalium is common, and this scaphopod may be responsible for the obscure oblique burrowing which occurs at this horizon.

It is in the Black Hard (8' 4" to 10' 0") that the large 'dog cocks' abound. Although seen only in vertical section they agree in size and density with *Rhizocorallium cicatricosus* from Old Nab, Staithes, and occur at precisely the same horizon. Many of the Skelton examples are seen to possess a *Spreite* composed of fine chamosite mudstone or fine opaline ooliths. This apparently contradicts the statement made earlier that *R. cicatricosus* from Staithes possesses no *Spreite*. However, this failure to recognise a *Spreite* may have been due to inadequate vertical sections through the burrows, for even in polished vertical blocks containing the Skelton 'dog cocks' the *Spreite* are only discerned with difficulty.

Lateral variation in the trace fossils of the Main Seam.

Text-fig. 39a illustrates the changes which take place in the sedimentology and the trace fossil assemblage of the Main Seam when traced from northwest to southeast. Following the work of HOWARTH (1955) the stratigraphic detail is very precise, and the correlations shown are not open to doubt.

Evidence for a shoreline to the northwest is substantial (CHOWNS 1966). The various ironstone seams by their lateral facies changes portray increasing depth of deposition when traced southeastwards. The sequence of off-shore, or off-shoal environments, with their associated trace fossils, is as follows:-

1. Intraclastic chamosite oolite, devoid of burrows;
2. Chamosite oolite, with *Rhizocorallium* ;
3. Siderite mudstone, with *Chondrites* ;
4. Shale with siderite concretions, with *Chondrites*.

It is evident that the distribution of the trace fossils is related to the depth of sediment deposition, but only because the sediments themselves change facies rapidly. Thus any bathymetric zonation of the trace fossils essentially parallels changes in the lithology of the substratum, which in the first approximation decreases in grain-size with increasing distance from shore. It is therefore a secondary zonation, being primarily dependent on the sedimentary facies.

This is scarcely surprising, however, for the nature of the substratum is the strongest ecological factor affecting the distribution of most infaunal creatures at the present day.

Nevertheless, study of the Middle Liassic trace fossils of Yorkshire presents evidence for very shallow, probably littoral conditions during the *Hawskerense* sub-zone in the northwestern part of the ironstone field. Text-fig. 39a demonstrates the gradual thinning of the *Hawskerense* Beds towards the northwest, from 18' at Hawsker Bottoms to 9' at Staithes, until they are absent at Skelton, where a disconformity cuts out the whole of this sub-zone. At Skelton the disconformity is penetrated by the vertical U-shaped burrows of Arenicolites skeltonensis. In the absence of such characteristically littoral trace fossils it would not be possible to fully appreciate the significance of this non-sequence. The fact that nowhere to the southeast do such U-shaped burrows occur further strengthens the view that the chamosite oolites were produced in very shallow water.

(iv) Upper Lias.

Most of the Yorkshire Whitbian shales are strikingly devoid of organically disturbed sedimentary laminae, especially the Jet Rock Series. This absence has frequently led to the inference that the bottom conditions were probably anoxygenic.

In the Alum Shales beneath East Cliff, Whitby (45/904115) occasional horizontal, pyritised, twig-like burrows occur. These are quite unlike any other Jurassic burrows discovered in the present study, and most closely compare with Acanthoraphe KSIAZKIEWICZ (1961), described as one of three nova forma without specific names from the Polish Flysch. Chondrites occurs in cementstone nodules from the very top of the Whitbian at Long Bight.

Bioturbation is very extensive in the Yeovilian Blea

Wyke Series. The Grey Beds at Peak and Blea Wyke are completely "churned" by Chondrites, Taenidium and Teichichnus. Occasional specimens of Rhizocorallium commune, all very short (Plate 27B), and Thalassinoides suevicus sometimes accompany these traces.

The commonest macrofaunal associates are circular colonies of Serpula, up to a foot in diameter, accompanied by Pinna and Lingula beani, of which the former, often 8" long, occurs in its original vertical position, while the latter is distributed parallel to the bedding, clearly not in life position.

Elsewhere in Yorkshire the Yeovilian strata are absent, except in some inland dales such as Rosedale, where these beds fill shallow pre-Dogger tectonic depressions of Caledonoid trend (RASTALL & HEMINGWAY 1949). Here the bioturbation of the Yellow Sandstone is so characteristic as to merit the designation "worm-chewed" by the authors. These fine-grained sandstones bear very close comparison with those of the Middle Lias Sandy Series, which are also extremely "chewed" by Chondrites (e.g. at Cliff Rigg, Great Ayton).

These sandstones are good examples of the 'Tunnel Sandstone' of SCOTT SIMPSON (1957).

(v) The Dogger

The detailed sedimentological investigations of RASTALL & HEMINGWAY (1940) gave rise to a precise picture of the palaeogeography of northeast Yorkshire during the period of accumulation of the Dogger (probably *Murchisonae* times).

To the northwest of the Peak Fault a marked disconformity separates the Alum Shales and the Dogger. The occurrence of remanie Yeovilian ammonites (particularly grammoceratids) in the basal pebble-bed of the Dogger at Sawdon's Road, Hawsker Bottoms and Long Bight, Whitby is proof that the Yeovilian strata were originally present, but subsequently removed before the deposition of the Dogger.

In Long Bight, Whitby large vertical U-shaped pocket burrows descend from the base of the phosphatic pebble-bed into the Alum Shales. The burrows are completely filled with gritty Dogger material, and on the sides the Alum Shales are intensely slickensided as a result of differential compaction. The burrows are deeply scratched both along the limbs and across the area of the *spreite*: they belong to *Rhizocorallium*

(*Corophioides*) *jenense* (Plate 19.1).

RASTALL & HEMINGWAY's palaeogeographic reconstructions enable the following facies of the Dogger in the coastal region to be identified (Text-fig. 39c):-

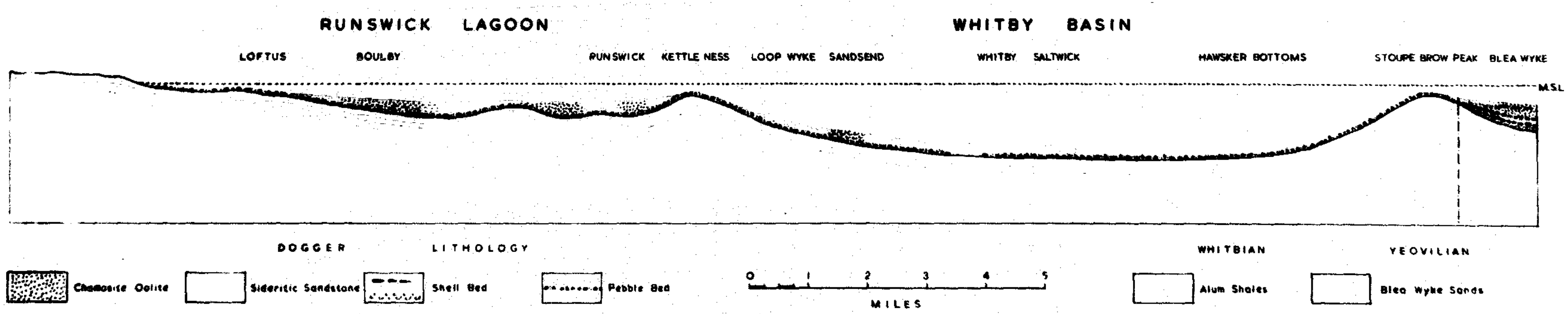
1. Shoreline facies - basal phosphatic pebble-bed;
2. Runswick Lagoon facies - chamosite oolites;
3. Whitby Basin facies - sideritic sandstones.

The Long Bight vertical crustacean burrows are the only recorded trace fossils from the shoreline facies. No trace fossils are known from the Runswick Lagoon facies, but immediately on the seaward side of the Kettleness Ridge (Text-fig. 39c), at Loop Wyke, *Asterosoma fosteri* (Plate 35) occurs with *Chondrites* in the sideritic sandstone of the Whitby Basin facies. The same trace fossil occurs on the other side of the Basin at Maw Wyke Hole, Hawsker Bottoms, where it is more densely crowded and accompanied by dense c.f. *Daedalus desglandi* (Text-fig. 36). Near Whitby, in Jump Down Bight, occasional small, horizontal, poorly preserved *Rhizocorallium* sp. occur in the sideritic sandstone (Plate 29C).

In the centre of the Basin, around Saltwick Bay, *Diplocraterion statheri* (Plate 18) occurs in widely varying densities for about a mile to the southeast past Black Nab, often reaching over 100 / sq. m.

Text-Figure 39C.

Diagram illustrating the Palaeogeography
of the coastal region of north-east Yorkshire
during the period of formation of the Dogger,
also showing the sedimentary facies and
important trace-fossil localities.
(after RASTALL & HEMINGWAY, 1940).


RUNSWICK LAGOON
WHITBY BASIN
LOFTUS
BOULBY
RUNSWICK
KETTLE NESS
LOOP WYKE
SANDSEND
WHITBY
SALTWICK
HAWSKER BOTTOMS
STOUPE BROW PEAK
BLEA WYKE
M.S.L.
DOGGER
LITHOLOGY
Chamosite Oolite
Sideritic Sandstone
Shell Bed
Pebble Bed
0
1
2
3
4
5
MILES
WHITBIAN
YEOVILIAN
Alum Shales
Blea Wyke Sands

Throughout the whole of the Dogger outcrop along the North Sea coast the thickness remains remarkably constant until, southeast of the Peak Fault, it thickens very rapidly (Text-fig. 39c), as do many Jurassic formations. Here it contains both Thalassinoides and Chondrites at the top of the Dogger.

It seems unlikely that a considerable bathymetric gradient existed across the Whitby Basin. Both the uniformly coarse lithology of the Dogger (which is an angular gritstone at Saltwick Alum Works, almost along the axis of the Basin) and the trace-fossil assemblage (with U-shaped burrows in the axial region) indicate very shallow conditions.
Such conditions are also implicit in the stratigraphic position of the Dogger, before the deposittion of which there was a prolonged planation of the whole of north-east Yorkshire.

CHAPTER FIFTEEN

TRACE FOSSILS FROM THE ELLERBECK BED, MILLEPORE BED AND DELTAIC SERIES, YORKSHIRE.

(i) Ellerbeck Bed.

The Ellerbeck Bed of Yorkshire is a marine band separating the Lower and Middle Deltaic Series. It is more persistent laterally than the Millepore Bed which overlies it, and was originally used as the boundary between the Lower and Middle Estuarine Series (FOX-STRANGWAYS 1892). The terminology adopted here is that suggested by HEMINGWAY (1949).

Over much of northeast Yorkshire the Ellerbeck Bed may be divided into a basal ironstone overlain by fairly thick, medium-grained sandstones. The sedimentology is at present the study of R. KNOX (University of Newcastle), so more detailed information on lateral variation at this horizon should shortly become available.

Two distinctive suites of trace fossils occur: an ironstone and a sandstone assemblage. The former has so far been identified only in the coastal region from the north end of Beast Cliff, Ravenscar to Iron Scar, south of Hayburn Wyke: the latter has also been identified from inland exposures.

The Ellerbeck ironstone trace-fossil assemblage comprises the following forms :-
Corophioides lymensis, Glossifungites lymensis, Rhizocorallium jenense and Chondrites.
All the burrows are strikingly preserved as ironstone fillings in white kaolinitic silts of the Lower Deltaic Series. In the north high densities of Corophioides lymensis occur (several hundred burrows per square metre). Some of the burrows are penetrated by Chondrites (Plate 19), visible along the burrow walls, though this trace fossil is otherwise not noticeable. Oblique Rhizocorallium jenense descending at angles of 45° - 70° accompany the vertical Corophioides lymensis (Plate 5): they are variable in gauge, between 42 and 60 mm., and limb diameter, 11 to 16 mm.

To the southeast, in Hayburn Wyke itself (54/011972), nodules fallen from the base of the Ellerbeck Bed apparently contain only Chondrites, though a little further southeast at Iron Scar (54/ 017964) where the Ellerbeck Bed descends into the sea and is finally lost, Glossifungites lymensis appears. This is a small U-shaped, pocket-like burrow identical in ornament to Corophioides lymensis but flask-shaped and slightly deeper (Text-fig.22). The form is also accompanied by *Rhizocorallium (Corophioides) jenense*, here highly oblique and occasionally vertical (c.f. its occurrence in the Dogger, p. 275): it is larger than in the north, with a gauge of 76 mm. and a limb diameter of 18 mm. The gauge : limb ratio , however, remains constant (between 3.75 and 4.0).

The Ellerbeck sandstone trace-fossil assemblage comprises the following forms:-
Diplocraterion statheri, *Gyrochorte carbonaria*.
The former has been observed on the backshore and undercliff below Ravenscar and Staintondale (Text-fig.15) where *Gyrochorte carbonaria* is also found. Inland, at the type section near Water Ark, Goathland, *Gyrochorte carbonaria* occurs in the massive ripple-marked sandstone at the top of the bed. Here parallelism and U-turns are common ethological patterns (Plate 47A, 48): their significance has been discussed previously (p. 252).

(ii) Millepore Bed

Loose blocks on the backshore below Staintondale (54/000000) have yielded large *Diplocraterion arkelli*, and *Gyrochorte carbonaria*. The former show good ringed apertures (Text-fig. 16) with concentric echinoderm debris packed around them. The latter, unlike the Ellerbeck Bed examples of *Gyrochorte*, lack any specific orientation.

Nearly three miles to the southeast, where the Millepore Bed crosses the foreshore 300 yards north of Cloughton Wyke (54/022955) there are no trace fossils.

In contrast to the Ellerbeck Bed the Millepore Bed exhibits marked lateral variation. At Cloughton Wyke it is half as thick as at Yons Nab, Scarborough (54/084844), less oolitic and more ferruginous (HEMINGWAY et.al. 1963, p.18). The thickness gradually diminishes northwestwards, and the horizon cannot be identified north of the Peak Fault. This has been understood to indicate a shoreline in a northerly direction (BATE 1959). The trace fossils *Diplocraterion arkelli* and *Gyrochorte carbonaria* therefore occur within two miles of the inferred position of the shoreline. Five miles to the southeast their place is taken by abundant bivalves, particularly *Lima duplicata* and *Pholadomya seamanni*. Fourteen miles to the southeast the fauna is dominated by the polyzoan *Haploecia straminea* and echinoderms.

At all localities the Millepore Bed is noticeably cross-bedded, and it seems unlikely that there was any great bathymetric gradient from northwest to southeast, such as is thought to have existed later in the Bajocian.

(iii) Lower and Middle Deltaic Series.

The trace fossils stated to occur from one or both of these horizons were selected by a process of elimination. The designation of their horizons must thus be regarded as tentative.

It was found from field experience that a detailed knowledge of the in situ cliff stratigraphy of the "marine" horizons enabled an accurate assessment of the stratigraphic position of much fallen material to be made. There nevertheless remain many blocks whose horizons are not accurately known. Trace fossils from these blocks comprise :-

Planolites ophthalmoides (Plate 42), Planolites montanus, Gyrochorte carbonaria (Plate 45), Gyrochorte comosa (Text-fig. 24), Pelecypodichnus (Plate 45), Laevicyclus (Text-fig. 23), and faecal pellets (Plate 43).

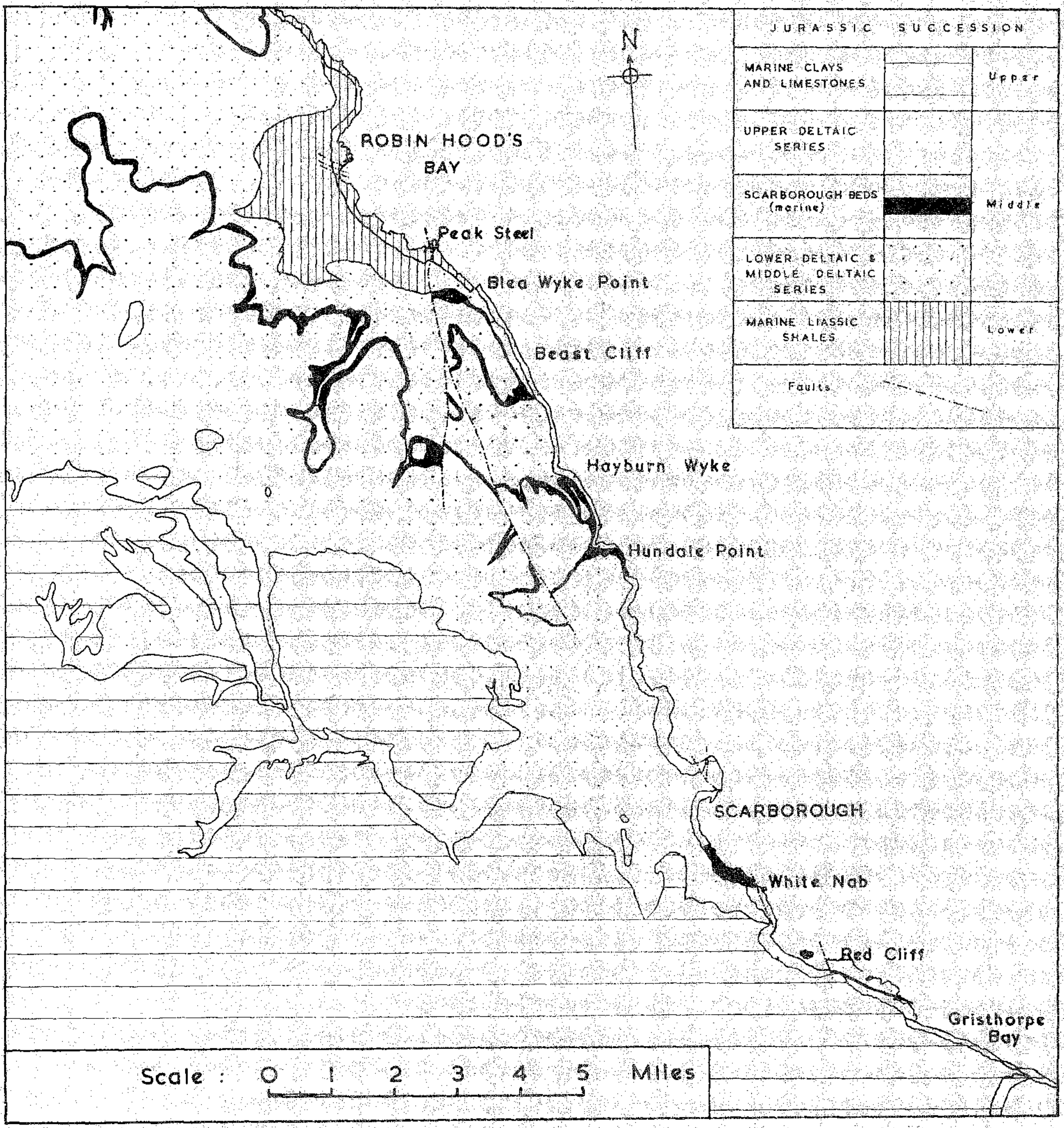
It may be significant that the first three trace fossils in this list occur in "non-marine" sandstones from the Upper Carboniferous (JESSEN & KREMP 1954, SEILACHER 1963).

CHAPTER SIXTEEN.

THE STRATIGRAPHY AND PALAEOECOLOGY OF THE SCARBOROUGH BEDS OF NORTH EAST YORKSHIRE.

Text-figure 40.

Location map showing the distribution of outcrop of the Scarborough Beds along the Yorkshire coast.



Introduction.

A consideration of the detailed stratigraphy of the Scarborough Beds between Robin Hood's Bay and Scarborough provides clear evidence confirming a bathymetric zonation of the major trace fossil genera. Here trace fossils are very abundant and the bed-by-bed stratal sequence can be traced for over 5 miles in the lofty cliffs beneath which, on the backshore, the traces are beautifully preserved.

The distribution of outcrop of the Scarborough Beds is shown on Fig.40, while the lateral variations of individual strata from Blea Wyke south-eastwards are shown in Fig.41. The area under consideration forms a small part of the outcrop of the Scarborough Beds; to the northwest of the area the facies becomes a very coarse grit full of crinoid ossicles; limestone is important to the east and south around Scarborough which accounts for the original name of the series.

Sedimentary and faunal succession near Blea Wyke

The detailed bed-by-bed sequence of the Scarborough Beds was worked out at the north end of Beast Cliff (54/993006), where exposure is most complete at the present time. The succession measured by the survey (FOX-STRANGWAYS, 1892, p.233) lies further to the north (54/987014) and is poorly exposed today. The stratal numbers used in the text are as shown in Fig. 41, while the major marker beds may be seen in Plates 49, 60, 50. For complete stratigraphic details refer to Appendix IV.

The two successions are closely comparable and divide readily into four basic units (Table 14). They begin and end with flaggy sandstones containing abundant casts of Pleuromya, Catinula and the pteriid Meleagrinella lycetti - the most characteristic mollusc of the whole series. Bioturbation is common in S.B. 35, though rare in S.B.36, where small-scale foreset bedding (Plate 50) probably represents a fossil beach strand, accounting for its rapid diminution in thickness southeastwards, forming an environment of low fossilization potential (sensu GOLDRING, 1965, p.863).

Arenicolites statheri (Plates 12-14) is very common at this horizon, which is frequently ripple-marked. The ripples are a common variety with flattened crests, idential to the type illustrated by MCKEE (1957, p.1737, fig.E) from the recent tidal flats of Cholla Bay, Mexico: the parallel ripples are formed by the incoming tide, the crests being flattened by the ebbing tide; their wavelength is generally 17.5cm. Lamination, too, is common (Plate 14A); massive clean, medium-grained sand alternating with thin bands of fine sand, the dual lamination being several millimetres, or rarely centimetres in thickness. OTVOS (1965) has described very similar lamination, of tidal origin, from the beaches of Long Island Sound. Some thin, coarse layers of clean sand probably represent the level, about 30cm below the original sedimentary surface, at which the lugworms thrust aside sand grains too large to be ingested (cf. WELLS, 1963, p.80, fig.1; VAN STRAATEN, 1952, 1956; SCHAFER, 1962, p.551, fig.269; Text-fig. 12C).

TABLE 14. The major subdivisions of the Scarborough Beds (Bajocian) in the Blea Wyke area, Yorkshire.

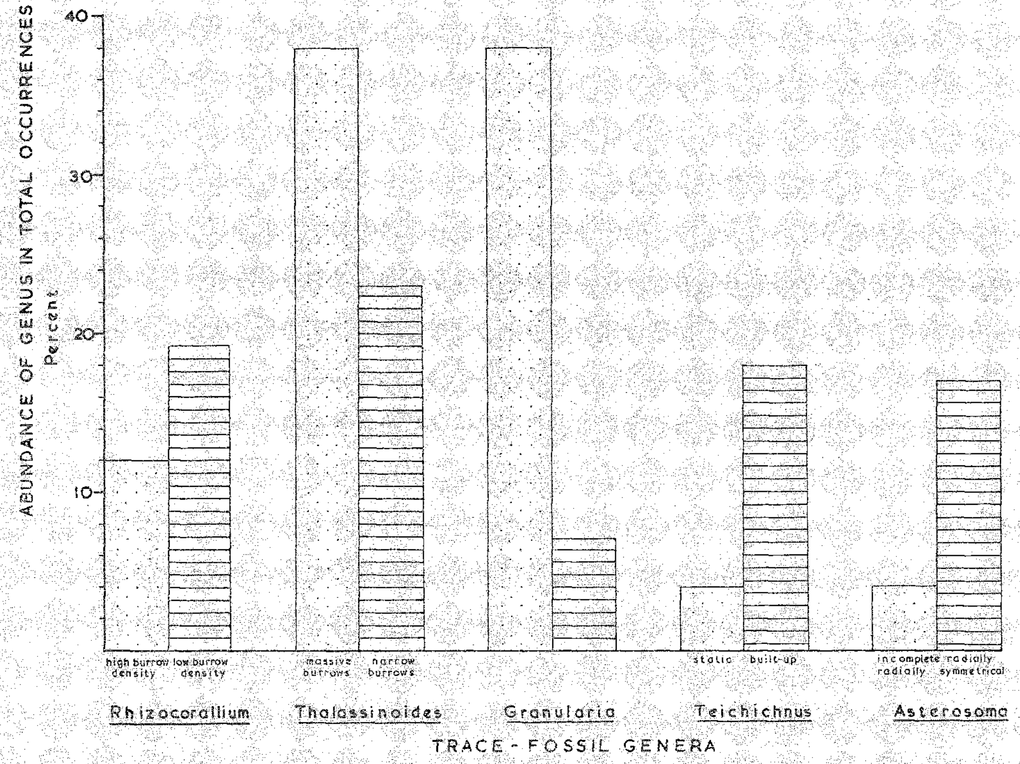
Bed	Lithology	Thickness	
		North End Beast Cliff	Blea Wyke
S.B. a-e, 1-26	Flaggy sandstones with <u>Pleuromya</u> casts	13.ft.8ins.	15ft.
S.B. 27	Silty shales with much shelly debris	51ft.	55ft.
S.B. 28-34	Impure limestones, shales and calcareous sandstones	18ft.	19ft.
S.B. 35,36	Flaggy sandstones with <u>Pleuromya</u> casts	10ft. 4ins.	15ft.

The lug-worm burrows are distinctly gregarious and often aligned parallel. This is particularly well seen where erosion has produced a horizontal section showing the bases of the "U"-tubes: the density can then also be worked out using a simple quadrat. The burrows, originally described by BATHER (1925) from Blea Wyke, are densest in the northwest, where they are associated with *Laevicyclus*, and reach 28/m^2 (Plate 14B). This is very much less than the density achieved by *Arenicola marina* at the present day under optimum conditions. However, the sediment grade of S.B. 35 is relatively high and conditions would not have been optimal, since highest density is reached today in mudy sand which is moisture-retentive at low tide (WELLS, 1945, 1963, p.79). There are nevertheless other species of *Arenicola*, e.g. *A. claperedii*, which habitually lives in sand bars with a similar lithology to S.B. 35, (MACGINITIE & MACGINITIE, 1949, p.205). The density is less towards the southeast, where *Diplocraterion statheri* supercedes *Arenicola* (Figs. 19 & 20) and eventually S.B. 35 pinches out altogether before Hundale Point is reached (Fig. 41).

In the second major group (Table 14), with dominantly limy beds, S.B. 33 contains an abundance of the first of the important bysally-attached pernid

Text-figure 42. Comparison of the trace fossils from different limestones of the Scarborough Beds near Blea Wyke. Histogram shows the relative abundance of the major trace-fossil genera from S.B.28 and S.B.32.

N.B. *Granularia* = *Thalassinoides* with coarse shelly lining to burrows, seldom dichotomously branched.



DATA

S.B.28		GENUS	S.B.32	
		Rhizocorallium		
3	12%	dense	0	-
0	-	sparce	8	19%
		Thalassinoides		
10	38%	massive	0	-
0	-	narrow	10	23%
10	38%	Granularia	3	7%
		Teichichnus		
0	-	built-up	8	18%
1	4%	static	0	-
		Asterosoma		
1	4%	incomplete	0	-
0	-	symmetrical	7	17%
1	4%	Other traces	7	17%
26		TOTAL OCCURRENCES	43	
⁙			▤	

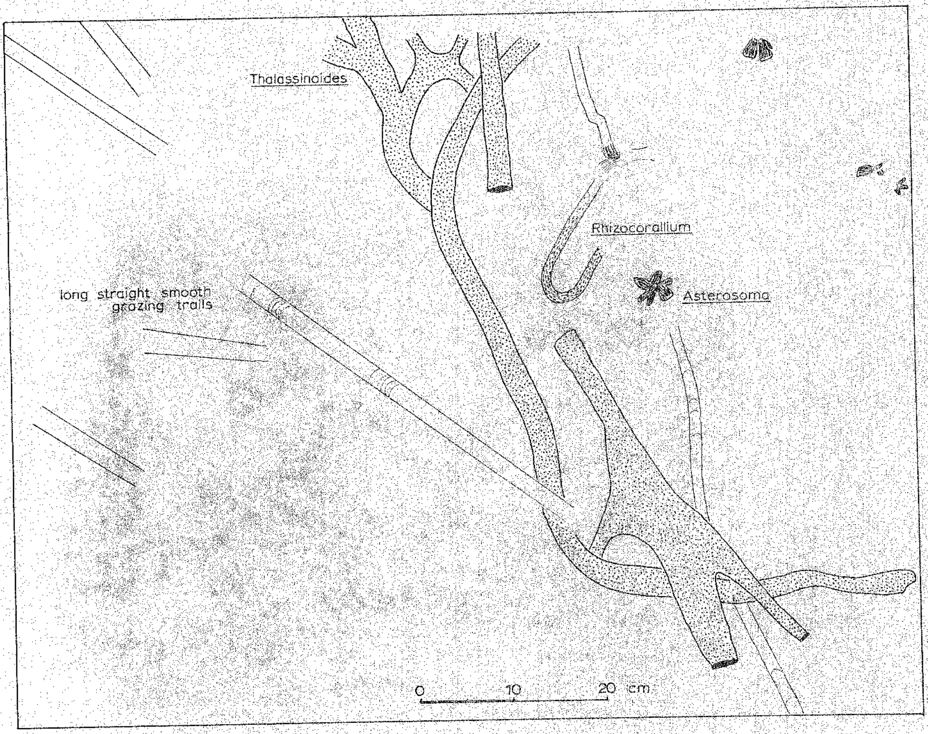
bi-valves, *Gervillella scarburgensis*, a form which is characteristic of the majority of the limestones, with the exception of those which are extensively burrowed, as S.B. 32, where molluscan remains, other than the finest shell detritus, are absent.

It is S.B. 32, a massive argillaceous limestone covered with stalactite, which contains the majority of the trace fossils (Fig. 42). The degree of sediment reworking is almost 100%, burrowing activities having completely destroyed any original lamination (Plate 3) with the result that a freshly-fractured hand specimen appears homogeneous (cf., MOORE and SCRUTON, 1957, p.2743). S.B. 32 shows two facies; a more sandy facies in the northwest around Blea Wyke with a distinctive suite of ichnogenera dominated by *Thalassinoides*, c.f. *suevicus* and long, straight, smooth grazing trails, tending to parallel alignment (Fig. 43) and a finer-grained facies to the southeast with fewer *Thalassinoides*, and *Rhizocorallium commune* (Plates 31, 32, 34), *Asterosoma* (Plate 36A, B) and *Teichichnus* (Plates 40, 41) assuming dominance, with no distinct parallelism of the traces.

The overlying limestone S.B. 31 is a nodular

Text-figure 43.

Field sketch showing the trace-fossil assemblage on a loose block of S.S.32 (littoral facies); backshore 900 m. south-southeast of Blea Wyke.



bioclastic limestone with pernids again the commonest faunal element, *Isognomon isognomonoides* and *Pteroperna plana* being most abundant. The succeeding unit contains a similar limestone, S.B. 30f, the surface of which is plastered with randomly oriented *Gervillella* and *Isognomon*. These two forms are sufficiently abundant in this 5-inch band to form majore rock-building constituents. Although quite thin, the band is persistent laterally, being typified by gregarious clusters of *Gervillella*, whose mode of occurrence is strongly suggestive of modern *Mytilus* mussel banks. S.B. 30f. is sandwiched between two shale bands containing highly fragmentary *Gervillella* material.

The purplish weathering os S.B. 29, a ferruginous limestone, serves to distinguish fallen blocks from this horizon. Less argillaceous than S.B. 32, it contains much chemically precipitated carbonate, in strong contrast to the bioclastic limestones S.B. 31 and S.B. 30f. The fauna suggests slightly deeper water than earlier, with *Entolium corneolum* and belemnites being common. *Isognomon*, *Pteroperna* and other thick-shelled Mollusca are absent.

An abrupt shallowing preceded the deposition of S. B. 28, which is a massive calcareous grit devoid of

TABLE EIGHTEEN

FAUNAL SUCCESSION IN BASAL 15 FT. OF S.B. 27

Depth (ft.)	*Faunas*
15	Fragment of fish fin: *Tancredia planata*
14½	Highly fossiliferous: *Quenstedtia bathonica, Anisocardia loweana, Pterocardia subminuta*
14	Sparcely fossiliferous, *Isocyprina dolabra*
13¾	Bituminous shales with many small fossils: *Astarte minima,* small *Meleagrinella lycetti*
13½	Very fine slightly bituminous shale: *Pterocardia subminuta Cucullaea cancellata*
13	Light grey shale *Meleagrinalla lycetti, Astarte minima*
12½	*Pholadomya ovalis* in life position: *Sphaeriola oolithica*
12	Small *Platymya scarburgensis: Meleagrinella lycetti*
11¾	Soft crumbly shale with crinoid debris and belemnites
11½	Oyster bank: *Lopha marshii, Isognomon isognomonoides, Serpula intestinalis, Eopecten tegulata*
11	Shell bank composed of *Pteroperna plana*
10½	Shelly shale with large *Meleagrinella lycetti; Pinna beani, Lima schimperi*
10	Ferruginous shelly nodules, *Modiolus leckenbyi:* ammonite camera (? derived)
9½	Comminuted shell limestone composed of *Pterocardia* and *Tancredia: Meleagrinella lycetti* occurs
9¼	Calcareous concretions with *Cylindrobullina gigantea: Camptonectes rigidus* with epifaunal *Serpula plicatilis*
9	Ferruginous shale, very fossiliferous: *Gervillella scarburgensis, Cucullaea, Modiolus leckenbyi*
8¾	Highly fossiliferous, *Entolium* very common: *Arcomya tumida* and *Meleagrinella* occur
8½	Calcareous shale: *Gervillella, Pteroperna, Isognomon, Oxytoma inequivalve, Pterocardia*
8	Calcareous shale: *Trigonia signata, Entolium, Pholadomya seamanni*
7½	Hard blocky shale, very fossiliferous: *Gervillella, Entolium, Modiolus, Cucullaea*
7	Silty shale with *Catinula* and *Liostrea:* some l-inch *Pentacrinites* stems
6	Grey shale, very fossiliferous: *Meleagrinella* very common: *Tancredia* occurs: *Platymya* in life position
4	Speckled calcareous band, hard, unfossiliferous
3	Grey shale, sparcely fossiliferous, occasional vertical *Pinna: Meleagrinella*
2	Fine shaly ironstone: common *Meleagrinella,* some *Entolium*
1	Coarse sandy ironstone, sparcely fossiliferous, occasional *Meleagrinella*

shelly remains but containing dense, large, parallel crustacean burrows, both Thalassinoides saxoniars (nearer Blea Wyke) and Rhizocorallium commune (Plate 22, figs. 30, 31). It weathers into large sphaeroids, whose interstices are full of impure stalactite, (Plate 49), and is the most distinctive bed in the succession.

Owing to poor exposure of the large shale unit S.B. 27, it was necessary to trench the cliff in order to establish the nature of the fauna: this was only possible for the basal fifteen feet, where the succession of shallow-water faunas is summarised in Table 15.

The flaggy sandstones at the top of the succession, S.B. a-e, 1-26, forming the last of the four major units, are similar to S.B. 35, 36. They differ principally in fauna rather than lithology, lacking Arenicolites and Laevicyclus - being much less bioturbated, and containing the casts of Astarte minima, Pleuromya, Chlamys, Meleagrinella and Catinula - a more diverse fauna than that of S.B. 36, occurring as shell banks above local erosion planes within the low-angle cross-bedding.

Correlation with cliff sections to the southeast.

Two points immediately emerge from a consideration of Fig. 41: (1) a wholesale stratal thinning from 104ft. at Blea Wyke to 7ft. at Gristhorpe Bay, with the wedging out of all the coarse clastic horizons; (2) a marked faunal change from the dominance of bysally-attached pernids, plicate oysters and an abundance of trace fossils in the north, to the appearance of large ammonites (Teloceras blagdeni) in siderite nodules from black shales in the south. This suggests an appreciable bathymetric gradient, with the Blea Wyke area lying very close to shore and the Gristhorpe area offshore, out of reach of the effects of tractive currents, where uniform suspensions (sensu PASSEGA, 1964, p.830) are responsible for sediment deposition.

The flaggy sandstones at the base and top of the successions at Beast Cliff and Blea Wyke are the least persistent of all the horizons, fading out before Hundale Point (Plate 51), a distance of less than four miles. In that they contain lenticular shell banks, dense lug-worm burrows and such sedimentary features as parallel, flat-crested ripples and frequent lamination they strongly indicate intertidal sands, a supposition which is supported by their stratigraphic position.

S.B. 36/35 immediately succeed Middle Deltaic delta-top silts with plant remains; S.B. a-e immediately precede very coarse distributary channel sands of the Upper Deltaic Series (the Moor Grit).

The overlying limestones are more persistent: in particular S.B. 32 grades laterally from a sandy limestone with *Thalassinoides* at Blea Wyke (Fig. 43) through an argillaceous, symmetrically-rippled limestone with *Rhizocorallium*, often showing odd ethological patterns (Figs. 29, 32, 33) to a non-rippled limestone with *Asterosoma* and *Teichichnus* (Plate 36A, Plate 40, 41) beneath Beast Cliff. Around Iron Scar the dominance of *Teichichnus* is supplanted by an isolated occurrence of dense *Rhizocorallium commune* (54/018964), which grades 300yds. further south into aa mixed *Rhizocorallium* and *Thalassinoides* association (Plate 52). S.B. 32 eventually reaches Hundale Point as a pure non-detrital limestone with *Gervillella*. These changes suggest a shore-line in a direction west of north.

Considerable lateral variation follows in succeeding horizons until the level of S.B. 28, which is more persistent. This bed thins very gradually from a maximum of 5ft. at Blea Wyke, where it is the coarsest member of the Scarborough Beds. It contains exceptionally dense burrows of a large distinctive variety of *Thalassinoides*, *I. saxonicus*, in most of which there is an annelid-like core (Plate 22). Beneath Beast Cliff, S.B. 28 is 4ft. thick and contains aligned *Rhizocorallium* (Figs. 30, 31), achieving a greater density than in S.B. 32. ¼ mile north of Petard Point the whole of S.B. 28 consists of *Teichichnus* and "*Cylindrites*", though just north of the point it is full of shelly debris and *Serpula* balls (54/004991). At the foot of Rodger Trod (54/020980) *Diplocraterion arkelli* appears in large numbers associated with *Teichichnus* (Plate 17A). A little further south very large specimens of *Camptonectes* occur (54/021958). At Hundale Point it is reduced to 3ft. 6ins. with abundant *Teichichnus*, and *Asterosoma multilobatum* (Plate 36C) in a sandy limestone - the "fucoid sandstone" of early survey officers (e.g. FOX-STRANGWAYS 1892, p.232). *Teichichnus* may form up to 90% of the burrows, and is often accompanied by the more orthodox form of *Thalassinoides*, *I. suevicus* (Plate 23B) and *Diplocraterion arkelli*: *Rhizocorallium* is very rare. At White Nab (Fig. 41) S.B. 28 is probably represented by part of the thick pure limestone, though correlation is less certain here because of exposure failure in the intervening six miles from Hundale Point.

It is impossible to subdivide accurately the thick shale member S.B. 27 at Blea Wyke as exposure is poor. Such digging as was possible revelaed that the silty shales were calcareous in the lower part and possessed sideritized shelly nodules in the upper part. In the lower half there is a southeastward increase in calcium carbonate at the expense of silt, until at White Nab the horizon is represented *in toto* by a pure calcilutite.

The overlying sandy limestone at White Nab is something of an enigma, since it cannot be correlated either to the north or the south. It probably represents either sediment derived from another source, or the localized reworking of an earlier sandy deposit such as S.B. 28 or S.B. 30.

Fundamentally then, the series consists of relatively inshore sediments showing an appreciable lateral change which is most easily interpreted as the result of a considerable original bathymetric gradient. It is in this broad environmental light that the variations, not only in relative abundance of trace fossil genera but also in their ethology, must be viewed.

Palaeobathymetry: Variation in trace fossils

The trace fossils from S.B. 32 and S.B. 28 commonly comprise four genera: *Thalassinoides*, *Rhizocorallium*, *Teichichnus* and *Asterosoma*, of which the first two are considered to be of crustacean origin, the next of annelid origin, and the last may be either crustacean or annelid. In different limestones, and at different points along the outcrop of the same limestone, the relative proportions of the various genera, their size and their behavioural patterns vary: these are summarised in Fig. 44.

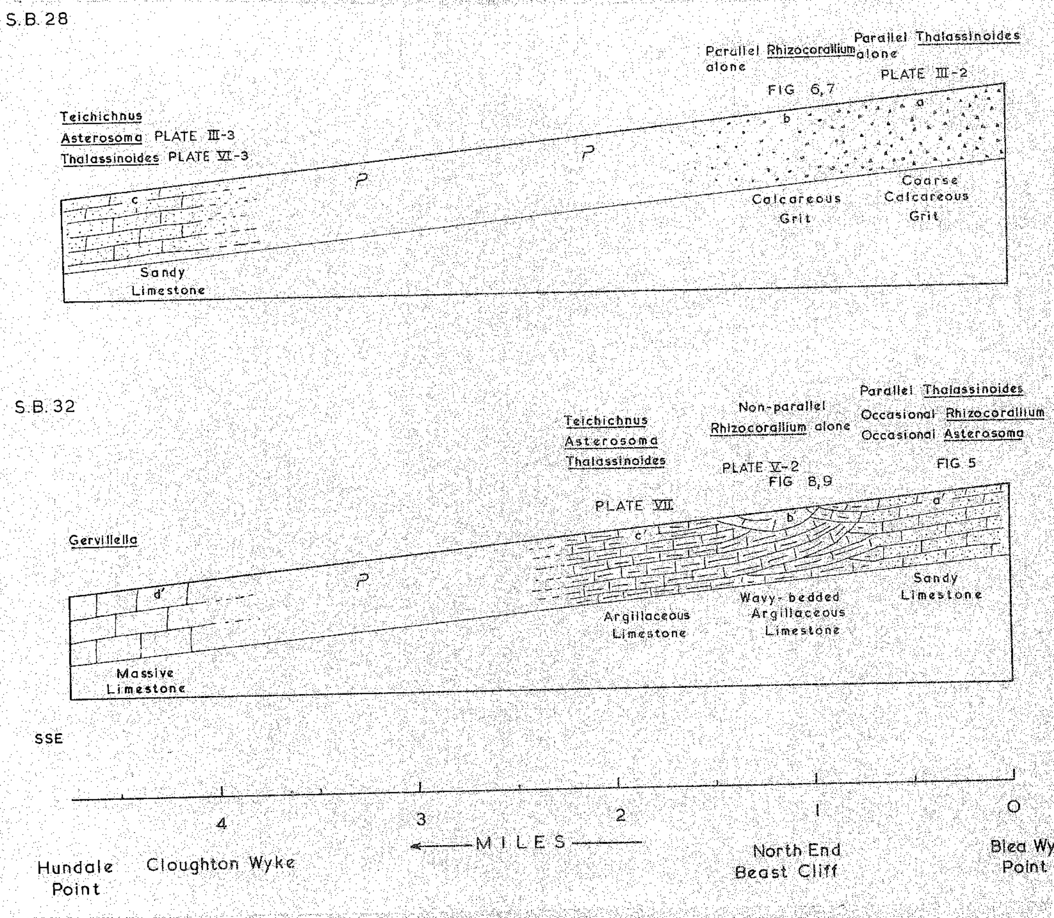
An analysis of these variations is presented below, and provides a detailed picture of the life zonation within the Bajocian sea floor in this part of Yorkshire - a pattern formed dominantly by creatures either with non-preservable exoskeletons (like the chitin of crustaceans) or entirely soft-bodied. Thus an ecological picture emerges which would be difficult to achieve were it to be solely based on epifaunal mollusca, notoriously rare from bioturbated horizons.

Relationship between bathymetry and ethology

The tendency for many of the more inshore traces to be aligned parallel is one which requires explanation. Since this orientation is most marked in burrows

Text-figure 44.

Lateral variation in lithology and trace fossils of S.B.28 and S.B.32 from Blea Wyke to Hundale Pt. (Horizontal scale accurate; vertical scale diagrammat



generally recognised to be crustacean origin (WEIGELT, 1929; ABEL, 1935; HANTZSCHEL, 1962) it is on the Crustacea that attention is now focussed.

Tertiary and Recent decapod crustacea **which** construct burrows resembling Thalassinoides are commonest in the zone a few metres above mean tide level (RICKETTS and CALVIN, 1962, pp.256-259; HECKER, 1965, p.33; WEIMER and HOYT, 1964). Physiological studies of present day Decapoda show them to be highly developed for oriented locomotion, possessing special cells in the region of the dactylopodite-propodite joints promoting synchronous activity (WIERSMA, 1959). This movement sense has been discerned in all groups of the Reptantia, and is possibly found in other Arthropoda.

To produce oriented movement in a group of burrows there must therefore exist some external force acting on different creatures which stimulates a similar reaction in each of them: this force at the present day is that of tidal flux. As an example of the effect which a rising tide may have on the behaviour of a burrowing decapod, it is instructive to note the sensitivity of the fiddler crab, Uca crenulata, which inhabits the highest zone of the high-tide region in Pacific bays and lagoons (RICKETTS and CALVIN, 1962, pp. 256-259) and builds oblique burrows up to 3ft. in length. Between tides the burrow is open, but at the approach of high-water the crab plugs up the burrow entrance. It must therefore sense the advancing water, but as it inhabits the burrow perpetually sight cannot be the effective stimulus. Changes in the local ground-water circulation affecting the walls of the burrow seem to provide the necessary stimulus, especially as _Uca_ is a deep burrower.

Emerita analoga, the mole crab, is also provided with a sense of orientation not dependent upon sight: this appears to be a function of slop (RICKETTS and CALVIN, p.191), so that during low-tide there is a tendency to move further offshore.

An annual migration is also to be found in most crustacean groups, either by the construction of a deeper burrow or by movement into deeper water away from the vicissitudes of intertidal life in winter months. Tides, however, provide a more regular mechanism inducing parallel orientation, and it seems that the movement is to be explained in terms of the search for food.

In the ability to return along a path exactly parallel to that of the exploratory trail, Rhizocorallium possesses the very marked advantage of returning inately to its original position on the shore, thus maintaining its station. This enables it to make very long journeys (e.g. Plate 27C) without losing its optimum ecological zone.

It would seem, therefore, that aligned behaviour in burrowing Decapoda cannot easily be explained without invoking tidal action as a modus operandi. It is in consequence reasonable to infer that where the Jurassic burrows are strongly aligned, the rocks in which they occur were deposited intertidally, (c.f. Gyrochorte carbonaria, Ch. 12), or at least within the sphere of influence of tidal flux. Correspondingly, where the ethological pattern of the same genera is random it is probable that the enclosing sediments lay in deeper water below the level of the lowest tides, though still within wave base, since they frequently show symmetrical, oscillation ripples.

Littoral and sublittoral ichnofacies

A statistical treatment of the trace fossils from S.B. 32 and S.B. 28 found on the backshore south-south-east of Blea Wyke Point (Fig. 42) demonstrates the essential differences between a calcareous grit (littoral) and an argillaceous limestone (sublittoral, nearshore) facies.

Table 16 summarises the distinguishing features of the two environments.

The most obvious difference is the density of Thalassinoides and the restricted number of genera, in the littoral zone compared with the more varied assemblage of the sublittoral zone. In the latter, occasional Cubichnia (Pelecypodichnus) and Fodinichnia (Chondrites) accompany some much shallower Repichnia (Gyrochorte; Plate 41B) which formed just beneath the sediment-water interface (SEILACHER, 1955, fig. 2). Teichichnus with as much as 5cm. vertical development is common in this zone (Plate 40A; fig.44). The absence of these genera from the intertidal zone may be attributed to the high energy level of that habitat.

Fig. 45 shows the suggested bathymetric zonation of the infauna, compiled from data in Table 16, fig. 44 and from the text.

TABLE 16. Differences between littoral and sub-littoral trace-fossil assemblages in limestones from the Bajocian Scarborough Beds near Blea Wyke, Yorkshire.

	Littoral (e.g. S.B. 28).	Sub-littoral (e.g. S.B. 32).
Dominant ichnogenera	*Thalassinoides*	No clear dominance
Rhizocorallium	High burrow density Parallel orientation	Low burrow density Randon orientation
Thalassinoides	Exceptionally dense *T. saxonicus*	Low density *T. suevicus*
Teichichnus	Very rare	Very abundant, often <90%; deeper than *Rhizocorallium*.
	Never vertically developed.	Great vertical development, often 5cm.
Asterosoma	Rare	Abundant; deeper than *Rhizocorallium*
	One-sided	Radially symmetrical
Diplocraterion arkelli	Absent	Often abundant, associated with *Teichichnus*.
Chondrites	Absent	Occasionally found
Near-surface trails	Rarely preserved	*Gyrochorte* sometimes found with *Teichichnus*
Resting traces	Absent	*Pelecypodichnus* rare
c.f. *Daedalus*	Absent	Occasionally found
Taxonomic composition	Restricted number of genera	Greater generic diversity

Stratigraphic implications

Palaeoecological and sedimentological data suggest that in Late Bajocian times, during the deposition of the Scarborough Beds, the intertidal zone was situated in the region of Blea Wyke with deeper water to the southeast. There were occasional northward transgressions, but for much of the time the position of the shore lay very close to the line of the Peak Fault (Figs. 40, 45). The much greater thickness of predominantly littoral and shallow sublittoral sediments on the downthrow side of the fault, and their thinness both on the upthrow side and away to the southeast, where deeper water existed, implies a degree of subsidence of the same order as the thickness of the succession immediately southeast of the fault.

Such subsidence is known to occur at the present day in enclosed bays and lagoons on the eastern seaboard of America (SHEPARD, 1953), where silting at the rate of three feet per century appears to have been in operation for thousands of years without appreciable change in water depth, so that thick sequences of wholly lagoonal sediment result.

This provides strong evidence for penecontemporaneous movement along the Peak fault, which at this stage clearly seems to have acted as a hinge, with progressive downwarping on the southeastern limb. Significantly, an horizon 20ft. below the base of the Scarborough Beds shows considerable evidence for contemporaneous slumping (HEMINGWAY et al., 1963, p.12). It outcrops above Blea Wyke, a few hundred metres on the downthrow side of the fault.

CHAPTER SEVENTEEN

TRACE FOSSILS FROM THE CORALLIAN ROCKS OF DORSET

Introduction.

In order that the conclusions concerning the facies distribution of Yorkshire Jurassic trace fossils could be tested, it was decided to investigate a different basin of deposition and a different series of strata. The Corallian of Dorset was chosen because, in its well-exposed coastal sections and well-documented stratigraphy, it provided 'experimental' conditions analogous to those in Yorkshire.

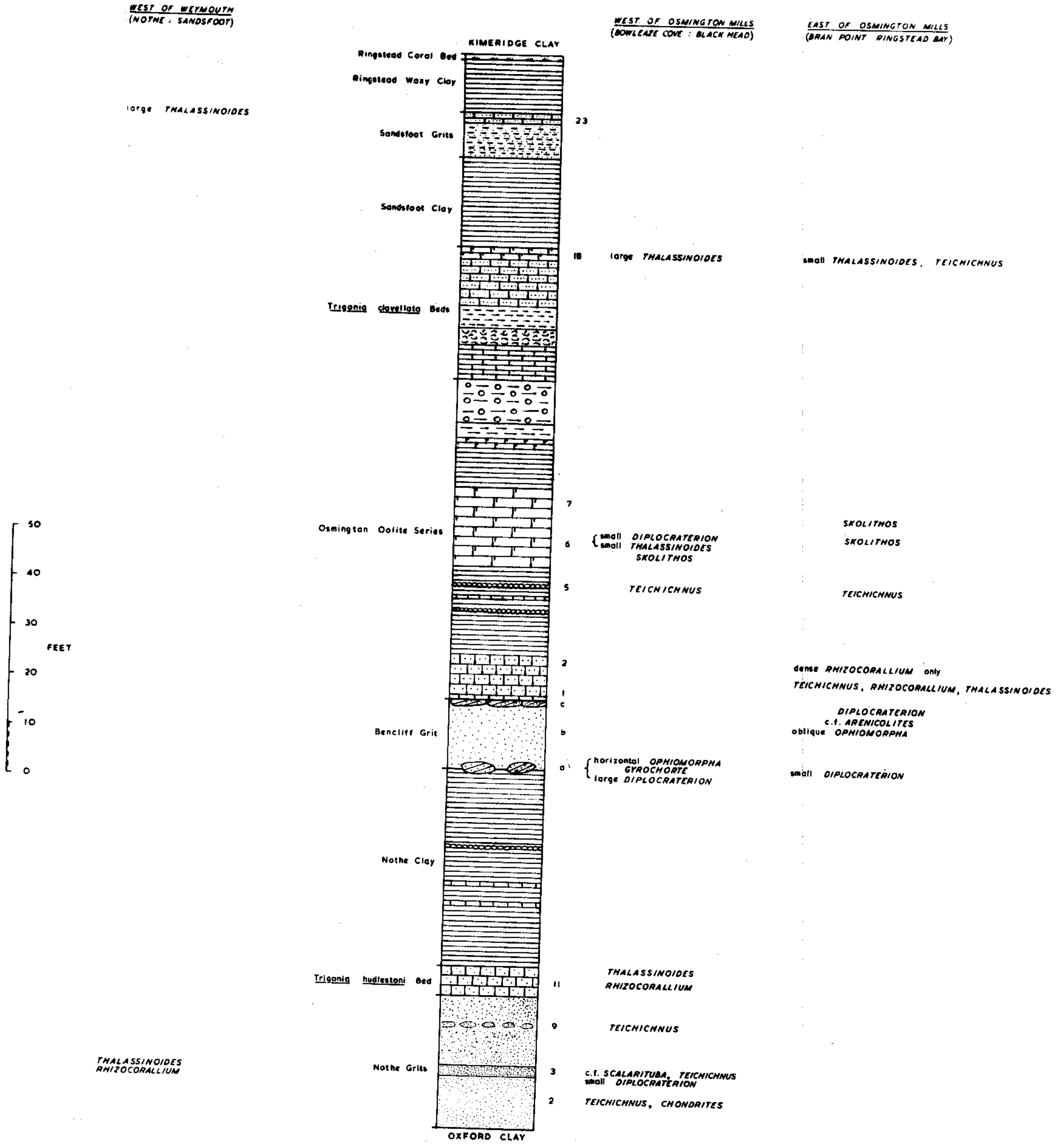
The field procedure adopted was identical to that followed in Yorkshire. The bed numbers in Text-fig. 46 are those of ARKELL (1947). Characteristic horizons have been labelled: most of them date from BLAKE & HUDLESTON (1877).

The following trace-fossil genera have been identified from the Dorset Corallian :- *Thalassinoides*, *Rhizocorallium*, *Diplocraterion*, *Arenicolites*, *Gyrochorte*, *Teichichnus* and *Chondrites*, all of which occur in the Bajocian Scarborough Beds of Yorkshire; and

Text-figure 46.

Diagram showing the stratigraphic distribution of identifiable trace fossils in the complete Corallian succession of the Dorset coast. Bed numbers from ARKELL (1947).

Note: the "pitted *Thalassinoides*" recorded from the Osmington Oolites are described in the text as *Ophiomorpha borneensis*.


WEST OF WEYMOUTH
(NOTHE : SANDSFOOT)
WEST OF OSMINGTON MILLS
(BOWLEAZE COVE : BLACK HEAD)
EAST OF OSMINGTON MILLS
(BRAN POINT RINGSTEAD BAY)
KIMERIDGE CLAY
Ringstead Coral Bed
Ringstead Waxy Clay
large THALASSINOIDES
Sandsfoot Grits
23
Sandsfoot Clay
18
large THALASSINOIDES
small THALASSINOIDES, TEICHICHNUS
Trigonia clavellata Beds
7
Osmington Oolite Series
6
small DIPLOCRATERION
small THALASSINOIDES
SKOLITHOS
SKOLITHOS
SKOLITHOS
5
TEICHICHNUS
TEICHICHNUS
2
dense RHIZOCORALLIUM only
1
TEICHICHNUS, RHIZOCORALLIUM, THALASSINOIDES
c
DIPLOCRATERION
c.f. ARENICOLITES
Bencliff Grit
b
oblique OPHIOMORPHA
a
horizontal OPHIOMORPHA
GYROCHORTE
large DIPLOCRATERION
small DIPLOCRATERION
50
40
30
FEET
20
10
0
Nothe Clay
Trigonia hudlestoni Bed
11
THALASSINOIDES
RHIZOCORALLIUM
9
TEICHICHNUS
THALASSINOIDES
RHIZOCORALLIUM
Nothe Grits
3
c.f. SCALARITUBA, TEICHICHNUS
small DIPLOCRATERION
2
TEICHICHNUS, CHONDRITES
OXFORD CLAY

Skolithos, c.f. *Scalarituba* and *Ophiomorpha*, which do not occur in the Scarborough Beds.

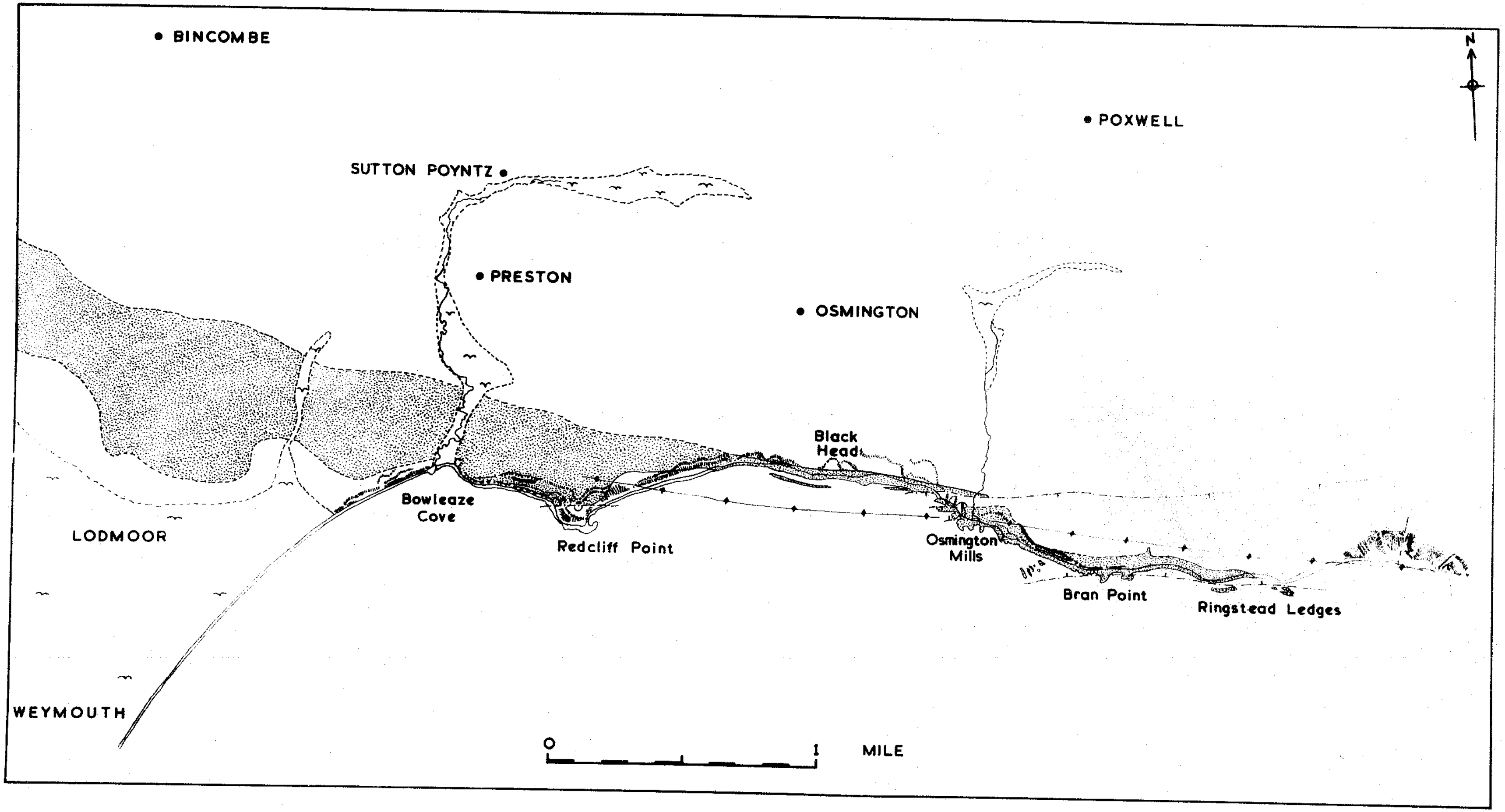
The horizons from which the various trace fossils have been recorded are shown on Text-fig. 46. They include localities both on the northern and southern limbs of the Weymouth Anticline (HOUSE 1961).

The preponderance of *Thalassinoides* and *Rhizocorallium commune* in rocks very similar lithologically to the calcareous grits in the Scarborough Beds (S.B.28) is most striking (c.f. Plates 49 & 53A). Moreover, the high percentage of *Teichichnus* in the finer-grained Nothe Grits and Littlemore Clay merits comparison with deeper-water facies of S.B.32, where *Teichichnus* forms 90% of the recognisable trace-fossil assemblage.

With a view to examining in detail a series of sediments rather different from the non-oolitic, impure limestones of the Scarborough Beds of Yorkshire, it was decided to examine in detail the Osmington Oolite series of the Dorset coast. Two easily studied sections just over a mile apart enable the lateral persistence of individual horizons to be investigated, though not over distances comparable with those in the Yorkshire Middle Lias and Bajocian.

Text-figure 47.

Map showing the major sampling localities in the Corallian rocks to the east of Weymouth from which trace fossils have been described.


N
BINCOMBE
POXWELL
SUTTON POYNTZ
PRESTON
OSMINGTON
Black Head
Osmington Mills
Bran Point
Ringstead Ledges
LODMOOR
Bowleaze Cove
Redcliff Point
WEYMOUTH
0
1
MILE

Nothe Grits.

The Corallian sequence begins with the highly bioturbated Nothe Grits which succeed the Oxford Clay conformably. They represent the Dorset equivalent of the Lower Calcareous Grit of Yorkshire. Although the development at the type area can no longer be seen *in situ*, many fallen blocks remain beneath the Nothe fortifications. These are full of very dense *Rhizocorallium commune* and *Thalassinoides* which occur mutually exclusively, as in the nearshore facies of S.B.28. It may also be noted here that dense *Thalassinoides* occur at the same horizon over much of Yorkshire, especially around Sutton Bank in the Hambleton Hills. On the northern limb of the Weymouth Anticline the Nothe Grits are well-exposed in the cliffs and on the backshore in Bowleaze Cove (Text-fig. 47). Here a more varied suite of trace fossils occurs, with *Teichichnus* ranging through most of the Grits, accompanied by *Chondrites*: in the middle (Bed 3) c.f. *Scalarituba* and *Diplocraterion arkelli* (Plate 16) occur.

There is thus a notable difference between the trace fossils of the two areas, with the Bowleaze Cove region bearing comparison with the slightly deeper water facies of S.B. 28 & 32 , even to the extent of *Teichichnus* forming 90% of the identifiable trace-fossil assemblage. The evidence of the trace fossils therefore indicates a westerly shoreline, with the sea deepening to the east around Redcliff Point.

Trigonia hudlestoni Bed.

Fallen blocks from this horizon have only been identified with certainty from Redcliff Point, where their in situ characteristics are remarkably similar to those of S.B. 28, both horizons producing great, rounded, rectangular blocks as a result of sphaeroidal weathering. Furthermore, the trace fossils of the two horizons are identical, with dense Thalassinoides and Rhizocorallium commune, again occurring mutually exclusively; (Plate 23A; Text-fig.28).
From this horizon a unique specimen of Rhizocorallium aff. uliarensis has been recorded; (Text-fig.34).

The abrupt change in the trace-fossil assembalge from the preceding Nothe Grits implies a marked shallowing, and the sudden appearance of a prolific molluscan fauna in this thin gritty limestone suggests that this horizon may be condensed. Elsewhere, dense Thalassinoides and Rhizocorallium commune occur in otherwise unfossiliferous strata (e.g. S.B. 28 of Yorkshire).

Nothe Clay.

The absence from Text-fig. 46 of any recognisable trace-fossil genera in the Nothe Clay is explainable on two counts. First, the absence of good sections of unslipped clay : second, the difficulty of generic identification in the absence of good planar surfaces.

The apparent absence of trace fossils from this horizon may therefore have little environmental significance.

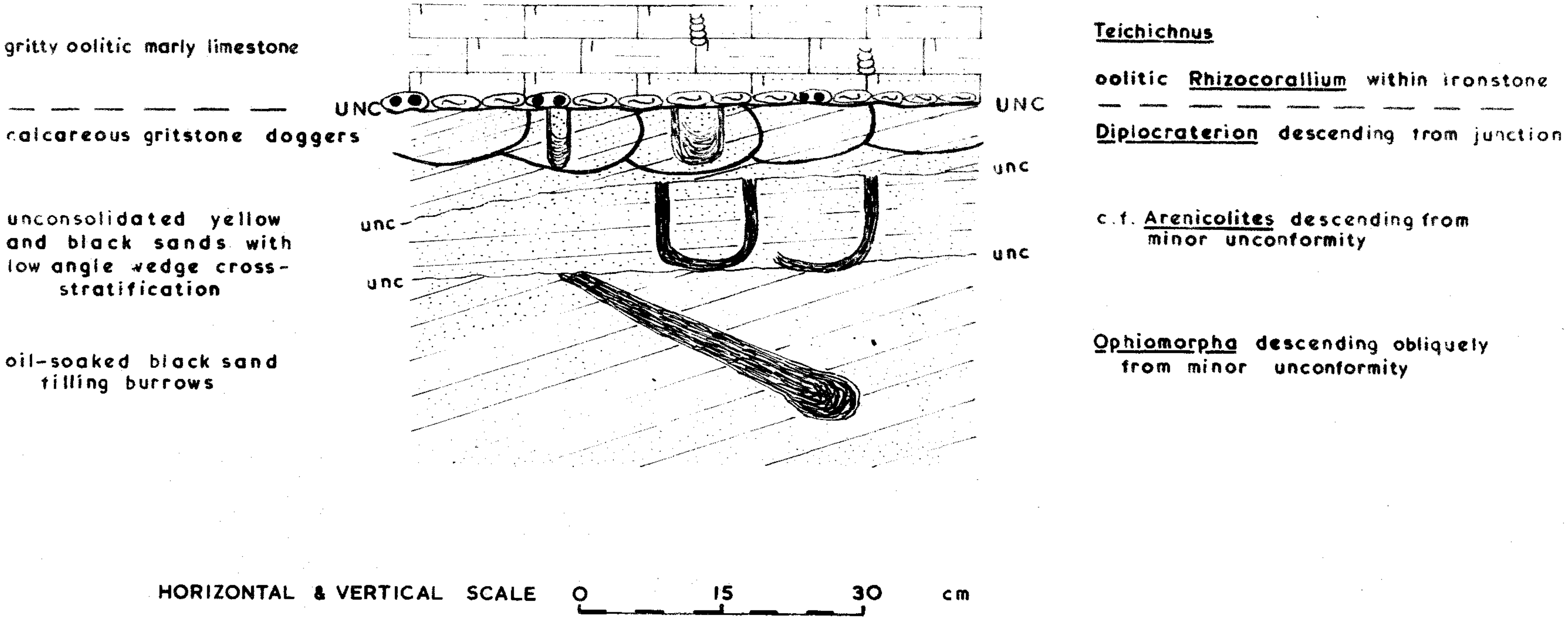
Bencliff Grits.

The huge gritstone doggers from the base of the Bencliff Grits (Plate 15A) contain well-preserved trace fossils both at Redcliff, where they are abundant though not _in situ_, and east of Osmington Mills, where they may be conveniently examined _in situ_ but are less abundant.

Below Redcliff Point large _Diplocraterion arkelli_ are very common (ARKELL 1939). Their characteristic appearance is as deep slots, either with a 'sausage'- or 'dumbbell'-shaped cross-section, on the upper surface of doggers (Plate 15B, Text-fig.14). Occasional horizontal _Gyrochorte carbonaria_ occur in doggers not

Text-figure 48.

Field sketch showing the concentration of burrows associated with the Osmington Oolite/ Bencliff Grit unconformity to the east of the waterfall at Osmington Mills.


gritty oolitic marly limestone
calcareous gritstone doggers
unconsolidated yellow and black sands with low angle wedge cross-stratification
oil-soaked black sand filling burrows
UNC
UNC
unc
unc
unc
unc
Teichichnus
oolitic Rhizocorallium within ironstone
Diplocraterion descending from junction
c.f. Arenicolites descending from minor unconformity
Ophiomorpha descending obliquely from minor unconformity
HORIZONTAL & VERTICAL SCALE
0
15
30
cm

showing cross-bedding (Plate 45), though they are absent from Osmington Mills. Likewise, rare horizontal *Ophiomorpha borneensis* (Plate 21A) occurring at Redcliff are not found east of Osmington.

On the low cliff between Osmington Mills and the waterfall (Text-fig. 47) the huge doggers of bed 'a' may be examined *in situ*. One dogger shows a peculiar early diagenetic 'slump' which has fractured the cross-bedding, apparently near the side of a distributary channel (Plate 15A). Other doggers show *Diplocraterion arkelli* slots, though these are smaller and less dense than those at Redcliff Point, and are accompanied by symmetrical ripples (Plate 15C).

In the oil-soaked unconsolidated sand member (bed 'b') burrows are imperfectly preserved, though preferential oil seepage along vertical burrows such as c.f. *Arenicolites* serves to delineate their vague outlines (Text-fig. 48).

Osmington Oolite Series.

The basal member of the Osmington Oolites at Bran Point contains a prolific suite of burrows, beginning with a few horizontal *Rhizocorallium commune*, preserved as oolitic casts in a nodular ironstone immediately above the unconformity with the Bencliff Grit. These are followed by *Teichichnus*, then by an horizon containing *Rhizocorallium* and rare *Ophiomorpha*. On the surface of Bed 1 very dense *Rhizocorallium commune* are found to the exclusion of all other traces. The *Spreite* are very pronounced, and more resistant to erosion than the limbs (c.f. Text-fig. 5A). Many burrows are somewhat oblique to the bedding, but not at more than about 20° (c.f. VEEVERS 1962, pl.1/5).

The great concentration of burrows above and below the unconformity (Text-fig. 48) points to a reduced rate of sedimentation: the truncated *Diplocraterion* and c.f. *Arenicolites* to frequent intra-stratal erosion. It is most likely that the Osmington region remained fairly close to shore for a prolonged period at this time.

This is also suggested by further horizons, the shell-banks represented by the *Qualicosta* Bed and the condensed Pisolite, which at Black Head is full of rolled phosphatic nodules.

Whether subsidence followed or merely quieter conditions of sedimentation, only *Teichichnus* is found in the succeeding Littlemore Clay facies, and there it is only recognisable in the cementstone nodule bands.

Conditions were reasonably uniform between Black Head and Ringstead, for at both localities the thickness of the Littlemore Clay is identical (Text-fig. 49). There is, however, a slight increase in calcareous content at Black Head, where cementstones and marly limestones are common.

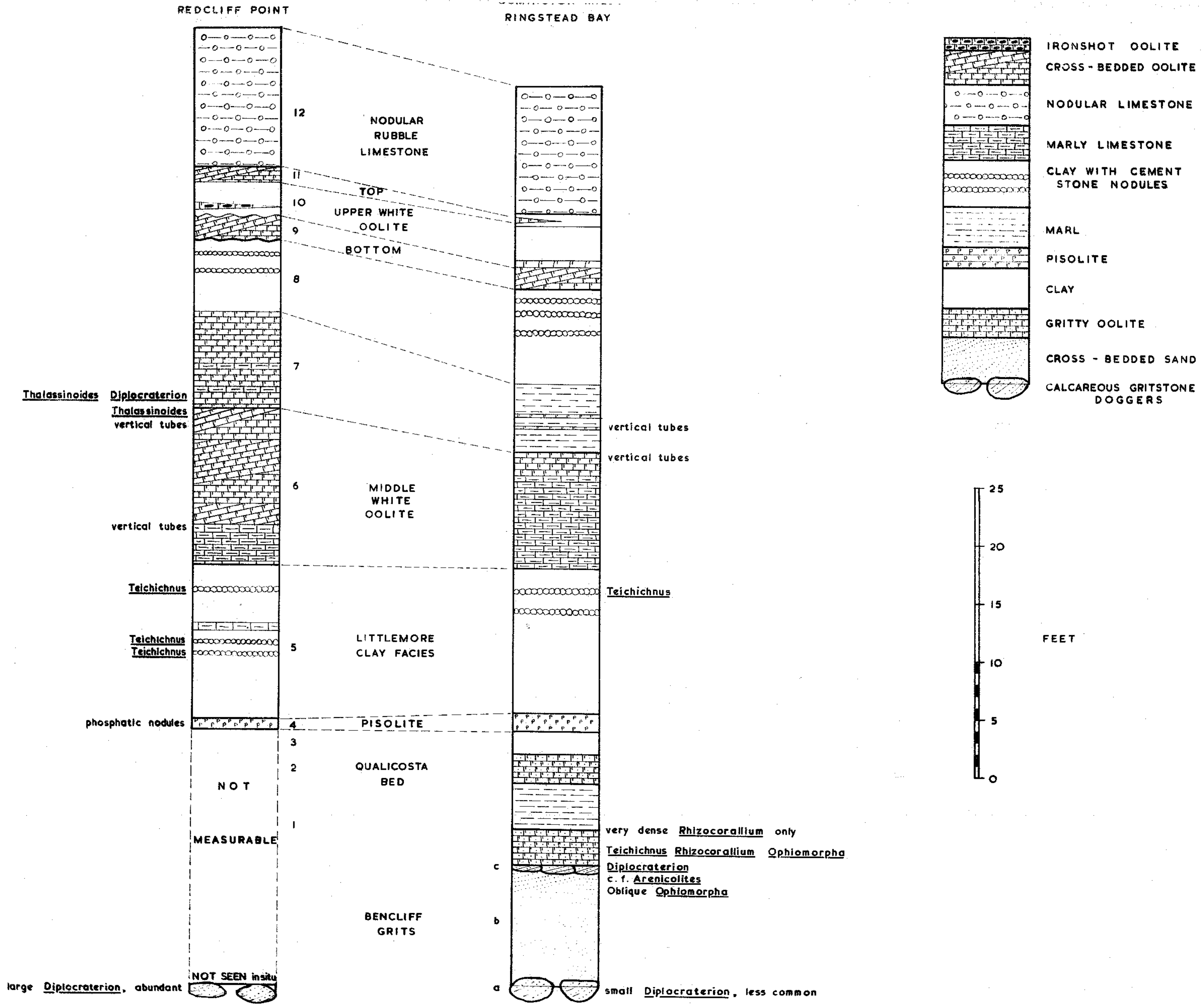
Compared with the stable Littlemore Clay facies, the overlying Middle White Oolites exhibit extreme facies variation within the short distance from Black Head to Bran Point (Text-fig. 47). Most noticeable, especially when considered with Bed 7, is the dominance of oolitic limestone, often cross-bedded, in the west compared with the marls and marly limestones of the east.

At Black Head *Skolithos* occurs as oolitic tubes at the base of the massive 10' cross-bedded oolite penetrating the underlying interdigitated marly limestone and oolite. Both horizons are markedly cross-bedded, and the *Skolithos* descend perpendicular to the cross-bedded units; they are not strictly vertical (Plate 20A).

The solid Middle White Oolite has large-scale foreset bedding on such a scale as to be reminiscent of the massive channel sandstones in the Lower Deltaic Series of Yorkshire. No trace fossils occur in this unit. Presumably the sea bottom was far too unstable to permit the establishment of benthonic life. Comminuted shell debris, clay-galls, micromorphic

Text-figure 49.

Diagram illustrating lateral variation in limestone sedimentology and trace-fossil assemblages of the Osmington Oolites between Black Head and Bran Point.


REDCLIFF POINT
RINGSTEAD BAY
12
NODULAR RUBBLE LIMESTONE
11
TOP
10
UPPER WHITE OOLITE
9
BOTTOM
8
7
Thalassinoides Diplocraterion
Thalassinoides
vertical tubes
6
MIDDLE WHITE OOLITE
vertical tubes
Teichichnus
5
LITTLEMORE CLAY FACIES
Teichichnus
Teichichnus
phosphatic nodules
4
PISOLITE
3
2
QUALICOSTA BED
1
NOT MEASURABLE
BENCLIFF GRITS
NOT SEEN insitu
large Diplocraterion, abundant
vertical tubes
vertical tubes
Teichichnus
very dense Rhizocorallium only
Teichichnus Rhizocorallium Ophiomorpha
Diplocraterion
c. f. Arenicolites
Oblique Ophiomorpha
c
b
a
small Diplocraterion, less common
IRONSHOT OOLITE
CROSS-BEDDED OOLITE
NODULAR LIMESTONE
MARLY LIMESTONE
CLAY WITH CEMENT STONE NODULES
MARL
PISOLITE
CLAY
GRITTY OOLITE
CROSS-BEDDED SAND
CALCAREOUS GRITSTONE DOGGERS
25
20
15
10
5
0
FEET

surf-sorted gastropods and marl lenses are all common along planes of erosion within the cross-bedding, pointing to a probable supra-tidal environment for Skolithos.

The top 3" of the Middle White Oolite stands in marked contrast to the rest, for it has been highly "churned" by burrowers, particularly Ophiomorpha borneensis (Plate 21B) whose tubes are filled with coarse ooliths and lined with haematite: the walls are regularly pitted in a highly distinctive fashion.

Bed 6 at Bran Point is dominated by marly limestone, oolites only being developed for 2' at the top of the bed, though here it is full of Skolithos. Ophiomorpha is not found.

The overlying Bed 7 shows a similar eastward diminution in total oolite, with concomitant marl increase. At Black Head seven oolitic limestone 'tiers' are separated by thin marl partings (Appendix V). At Bran Point only two 'tiers' are recognisable within a reduced thickness of marl. Sharp boundaries between 'tiers' are rare owing to the severe "churning" which has taken place.

Compared with the massive oolites of Bed 6, the seven 'tiers' of Black Head lack clay-galls, seldom have visible cross-bedding, do not contain shells, even comminuted, and

are highly bioturbated. There is abundant evidence of repeated inter-stratal erosion, in spite of apparently non-erosive boundaries, for many examples of Diplocraterion from the first 'tier' have been reduced nearly to their basal ends. It is merely that ensuing thorough "churning" has obliterated a once erosive boundary (Plate 53B).
The second 'tier' has a phosphatic nodule bed at the base.
The third 'tier' is the most coarsely oolitic of all, and is also the most highly bioturbated, with Skolithos.
The coincidence of Skolithos and the coarser oolites is again noticeable, as in Bed 6. The same horizon at Bran Point is also oolitic, and bears Skolithos.
The fifth 'tier' is most striking. At the top occurs a band, 2 or 3" thick, of marcasite nodules varying in size from 2 to 20 mm. The nodules have very sharp boundaries with the oolite, and there is no evidence of gradual replacement of oolitic or faecal matter.

Clavellata Beds.

Apart from a few isolated Skolithos and Thalassinoides from Bed 9, recognisable trace fossils have not been recorded from the remainder of the Osmington Oolites, and dense identifiable burrows do not occur again until Bed 18, at the top of the Trigonia clavellata Beds.

at Black Head, in a sparsely oolitic, grey and red mottled limestone, occur dense large *Thalassinoides* within which coarse shelly debris, abundant in the matrix, is absent. Occasionally it is found packed along the burrow walls when not eroded because of its low cohesivity. The same horizon at Bran Point is represented by an identical rock type, slightly less thick and containing perisphinctid ammonites identical to those at Black Head (ARKELL 1949, pp.46, 49) as the sole molluscan fauna. The trace fossils are markedly different, with *Thalassinoides* subordinate to *Teichichnus*. This again suggests a shoreline in the west, with sea-depth increasing eastwards.

Sandsfoot Grits.

The final 'fucoid' development in the Dorset Corallian occurs within the Sandsfoot Grits, where trace fossils are abundant both on the southern limb in the vicinity of the type area, and on the northern limb in Ringstead Bay. Around Sandsfoot Castle large *Thalassinoides suevicus* abound in a haematite-rich sandy limestone. They were originally noticed by BLAKE & HUDLESTON (1877, p.271) who commented thus on their preservation:-

> "...the strange interlacing fucoid or sponge-growths... weathering out in a purplish tint on a greenish ground, give a very curious aspect to the surface."

Their ideas on the origin of the structures are of interest since they reflect the orthodox contemporary view, yet to be challenged by NATHORST (1881). They continue (*loc.cit.*):-

> " What we see here, indeed, is not drifted material brought from a distance to be deposited along with its organic remains, but the actual spot on which colonies of fucoids and sponges luxuriated, and on which they left their remains, their most constant Molluscan companion being the great *Lima pectiniformis*."

SUMMARY: Direction of shorelines in the Corallian identified by lateral variation in the trace fossils.

Within short distances the gross lithology of many of the Corallian horizons changes only slightly, and diminution in grain-size of detrital constituents is not an easily applied criterion for determining the probable source direction. However, appreciable changes in the assemblage of trace fossils occur, and these may be used to indicate relative bathymetry. Thus the trace fossils in the Nothe Grits, Bencliff Grits and Sandsfoot Grits all indicate a shoreline in the west with slightly deeper water to the east of region. *Skolithos* in the Osmington Oolite Series is an indicator of supra-tidal environments.

CHAPTER EIGHTEEN.

THE PALAEOECOLOGICAL SETTING OF THE HAMBLETON OOLITE *Thalassinoides* OF FILEY BRIGG, YORKSHIRE.

The Lower Corallian rocks of northeast Yorkshire supply clear proof of the hypothesis, erected on the basis of studies of lateral variation in the Bajocian Scarborough Beds, that horizons bearing burrows of *Thalassinoides* in high densities occupy a zone very close to ancient shorelines.

In the Scarborough Beds it was possible to trace several assemblages of trace fossils laterally through calcareous grits to silty limestones (Text-figs. 44 & 45). In the Lower Corallian Hambleton Oolites (Costicardia and Cordatum Zones) calcareous grits pass into oolitic limestones, and only the *Thalassinoides* facies, devoid of other trace fossils, occurs.
Thus the bathymetric gradient cannot be established using lateral variation of trace-fossil taxa and their ethological modifications. Recourse must be made to stratigraphical and palaeoecological evidence, evidence which nevertheless clearly demonstrates the restriction of dense *Thalassinoides* to the most nearshore detrital limestone facies.

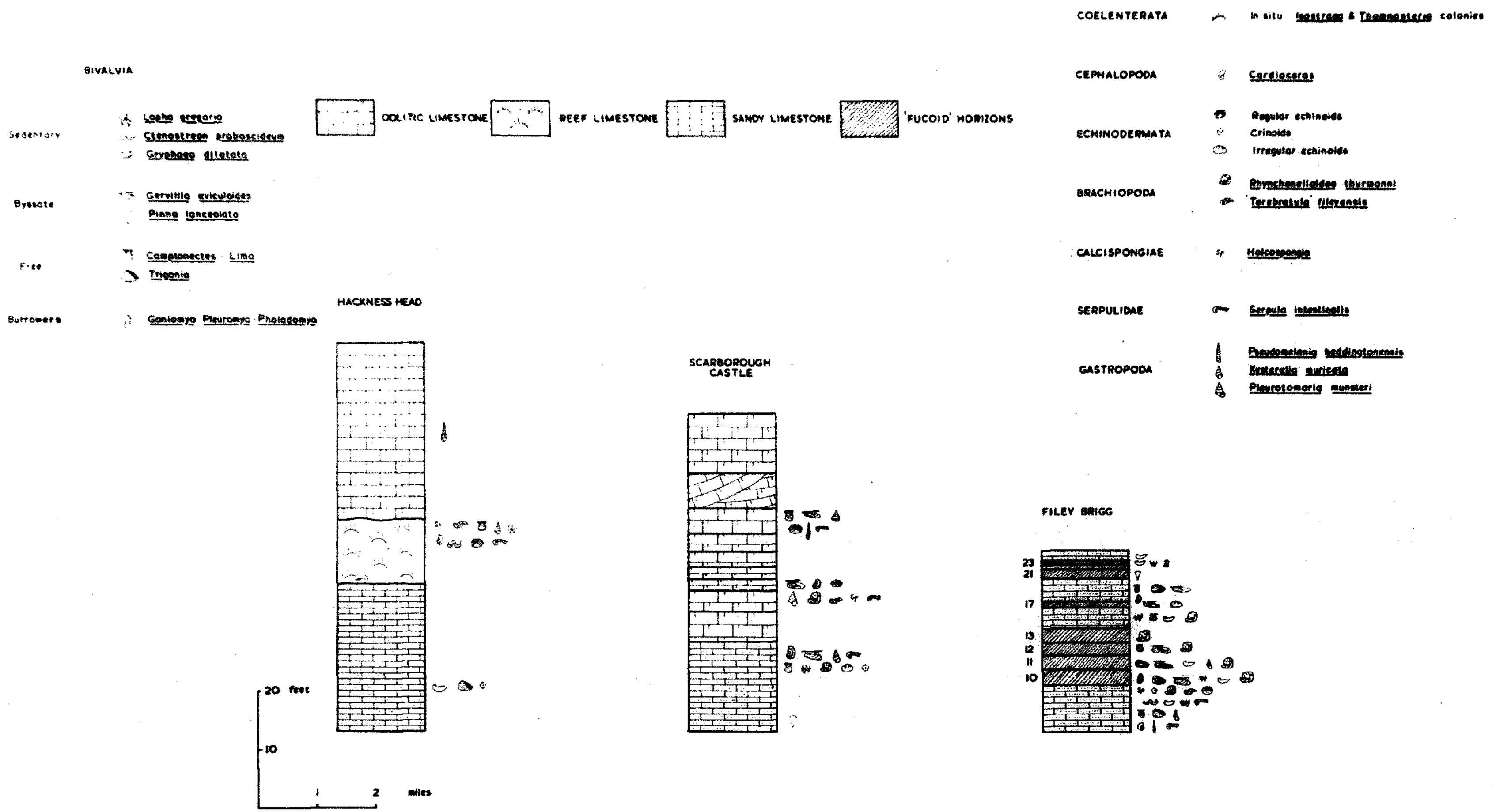
Through the meticulous bed-by-bed studies of SMITH (1829) and V.WILSON (1949) the stratigraphy of the Lower Corallian rocks in this part of Yorkshire is accurately documented.
When traced from west to east across northeast Yorkshire the whole Corallian sequence becomes attenuated. The Hambleton Oolites illustrate this easterly attenuation very well, being oolitic throughout their main outcrop in the Tabular Hills, but passing laterally into condensed sandy limestones and calcareous grits in the coastal region between Scarborough and Filey (Text-fig.50). Thus at Hackness Head the Hambleton Oolites total 66', of which the upper 30' comprise the typical oolites found throughout the main outcrop, while on the north side of Scarborough Castle, six miles to the east of Hackness, they total 54', with 26' of impure oolite. On Filey Brigg the succession is devoid of oolitic limestone, being wholly represented by indurated calcareous grits and sandy limestones, in the upper part of which occur seven beds with the horizontal Y-shaped burrows of Thalassinoides suevicus.

The dominant faunal assemblage at each horizon in the three successions has been shown diagrammatically on Text-fig. 50. It is readily apparent that the lower

Text-figure 59.

Diagram showing the stratigraphic equivalents of the Corallian Hambleton Oolite Series in the region around Scarborough, and the occurrence of Thalassinoides in highly condensed "fucoid" beds at Filey.

(drawn from data in V. WILSON, 1949).


BIVALVIA
Sedentary
Lopha gregaria
Ctenostreon proboscideum
Gryphaea dilatata
Byssate
Gervillia aviculoides
Pinna lanceolata
Free
Camptonectes · Lima
Trigonia
Burrowers
Goniomya Pleuromya Pholadomya
OOLITIC LIMESTONE
REEF LIMESTONE
SANDY LIMESTONE
'FUCOID' HORIZONS
COELENTERATA
in situ Isastraea & Thamnasteria colonies
CEPHALOPODA
Cardioceras
ECHINODERMATA
Regular echinoids
Crinoids
Irregular echinoids
BRACHIOPODA
Rhynchonelloidea thurmanni
'Terebratula' fileyensis
CALCISPONGIAE
Sp
Holcospongia
SERPULIDAE
Serpula intestinalis
GASTROPODA
Pseudomelania heddingtonensis
Littorina muricata
Pleurotomaria munsteri
HACKNESS HEAD
SCARBOROUGH CASTLE
FILEY BRIGG
23
21
17
13
12
11
10
20 feet
10
1
2
miles
Sp
w

part of the Scarborough succession is faunally very similar to the Filey sequence, except that the very common *Thalassinoides* of Filey Brigg do not occur at Scarborough. A very detailed study of the relative abundance of the various macrofaunal elements at the two localities would be necessary to discern any significant palaeoecological difference if the true nature of the *Thalassinoides* burrows were not appreciated.

A much greater palaeoecological difference exists between the Scarborough and Hackness successions, with the development at Hackness of a unique Coral/Sponge Reef at the boundary between the sandy limestones, here notably less fossiliferous than at Scarborough or Filey, and the oolitic limestones, thicker, purer and less fossiliferous than at Scarborough.

In order to investigate major lateral variation of the shelly fauna it is first necessary to eliminate the many forms which occur throughout the sandy limestones at the base of the Hambleton Oolites. These include a host of typical fossils:-

Exogyra nana, *Chlamys fibrosa*, *Gervillia aviculoides*, *Gryphaea dilatata*, *Lopha gregaria*, *Rhynchonelloidea thurmanni*, *'Terebratula' fileyensis* and the ubiquitous *Serpula* spp.

Of the remainder, the siliceous sponge *Rhaxella perforata* and the bivalve *Ctenostreon proboscideum* are more common at Filey, while gastropods, the byssate bivalves *Oxytoma* and *Meleagrinella*, and echinoderms are more common at Scarborough.

Other more subtle palaeoecological differences would undoubtedly present themselves upon further study, and an analysis of variation in the morphology of the widespread *Exogyra* would probably reveal many of the adaptive modifications noted by JOURDY (1924).

The Coral/Sponge Reef of the Hackness district is the lateral equivalent of the 'fucoid'-rich Filey sequence and the gritty oolites of Scarborough. The Reef fauna is unique in Britain in that calcareous sponges are the dominant element, unlike the later Upper Corallian Reefs where calcareous sponges do not occur. V.WILSON (1949, p.239) notes that this is also the earliest horizon from which a small molluscan community confined to the Reef habitat occurs: it comprises *Lima zonata*, *Lithophaga inclusa*, *Chlamys nattheimensis*, *Lopha gregaria* and *Xysterella muricata*. These forms together with very abundant terebratulids constitute the Reef dwellers, a fauna remarkable for the paucity of species compared with other Corallian Reefs.

The easterly attenuation of the Hambleton Oolites indicates a shoreline in that direction. Likewise, the changing sedimentology of the limestones, for SVERDRUP et.al.(1942, pp.997-1004) have observed that there is a tendency for calcium carbonate to increase in sediments away from coastlines. Thus on this basis the Oolites of Hackness, with their high calcium carbonate content, would be deposited offshore, while onshore, sandy limestones and calcareous grits would be deposited around Scarborough and Filey. As the grain-size of the detrital quartz increases southeastwards from Scarborough to Filey, the zone nearest shore was probably situated in the region of the Brigg. Thalassinoides only occurs in this zone.

Since a greater environmental difference existed between localities from west to east (viz. Hackness to Scarborough) than from northwest to southeast (viz. Scarborough to Filey) it follows that the coastline in Hambleton Oolite times must have been situated in what is now the North Sea, to the east.

CHAPTER NINETEEN.

TRACE-FOSSIL FACIES IN THE ENGLISH JURASSIC.

The British Jurassic rocks present a multiplicity of shallow-water sediments. Since the distribution of trace fossils is very strongly affected by the nature of the contemporary substratum it follows that a useful distinction may be made initially between the sediments of the major sedimentary "regimes" and their trace-fossil assemblages. They are :-

(i) Impure calcareous clastic "regime" :
(ii) Ironstone "regime" :
(iii)Well-sorted sandstone and oolite "regime" .

Each of these major "regimes" of sedimentation possesses a characteristic assemblage of trace fossils. Some trace-fossil 'genera' may be common to two or more divisions, but they are generally represented by different 'species'.

(i) Trace-fossil facies in the impure calcareous clastic "regime" of sedimentation.

Text-fig. 51 illustrates the complete set of trace-fossil facies belonging to this "regime". The diagram is based on detailed field observations of the Yorkshire Scarborough Beds and the Corallian limestones of Yorkshire and Dorset.

In order of decreasing grain-size of detrital constituents, and therefore as a general indication of increasing depth of water, the facies are as follows:-

A) *Thalassinoides* facies - dense, large, Y-shaped, horizontal burrows preserved in coarse, indurated calcareous grits;

B) *Rhizocorallium commune* facies - dense, horizontal, U-shaped burrows preserved in calcareous grits: may be aligned;

C) *Teichichnus* facies - vertically built-up horizontal burrows up to 90% preserved in sandy and silty limestones: *Asterosoma*, *Diplocraterion* and *Thalassinoides* may form up to 10% : occasional *Rhizocorallium commune*;

D) *Chondrites* facies - multi-branched tunnels predominate in siltstones and calcareous shales: accompanied by *Curvolithus*: occasional *Teichichnus*, *Diplocraterion*, *Thalassinoides*, *Rhizocorallium commune* & *Corophioides*;

Facies A) and B) are monotypic, *Thalassinoides* and *Rhizocorallium commune* being respectively the only trace fossils present. Facies C) and D) possess a varied suite of trace fossils and are demonstrably gradational : they are defined in terms of two dominant 'end-members'.

The restricted number of trace fossils occurring in high densities in the more inshore facies is in keeping with the present-day high specimen:species ratio of the littoral fauna.

The absence of any traces clearly formed at a shallow depth beneath the sediment/water interface suggests an exposed, high-energy, environment.

(ii) Trace-fossil facies in the ironstone "regime"

Text-figure 52 illustrates the complete set of trace-fossil facies belonging to this "regime". The diagram is based essentially on detailed observations on the Yorkshire Middle Liassic Ironstone Series, with additions from the Dogger and Ellerbeck Bed. The following facies may be recognised, in order of increasing distance from shore :-

A) _Corophioides_ facies - vertical U-shaped burrows, comprising either _Arenicolites skeltonensis_ or _Corophioides lymensis_ & _Rhizocorallium (Corophioides) jenense_; penetrating various lithologies beneath marked disconformities.

B) Glossifungites facies - flask-shaped vertical burrows; penetrating deltaic siltstones beneath minor disconformity.

C) Rhizocorallium cicatricosus facies - very long, horizontal U-shaped burrows; ramifying condensed sideritic chamosite oolites.

D) Chondrites facies - multi-branched tunnels; penetrating siderite mudstone and shale.

The occurrence of the trace fossils in facies A) and B) beneath disconformities, and in facies C) in condensed deposits, stresses the inshore nature of these three facies.

The fact that the small vertical pocket burrows of Corophioides lymensis are preserved at all suggests that the environment was protected in the inshore regions.

(iii) Trace-fossil facies in the well-sorted sandstone and oolitic limestone "regime".

Text-fig. 53 illustrates the complete set of trace-fossil facies found in this "regime". It has been compiled from observations on the Corallian rocks of Dorset and the Scarborough Beds of Yorkshire. The following facies may be recognised :-

A) Skolithos facies - simple, vertical tubes; penetrating coarse, cross-bedded oolitic limestone :

B) Arenicolites facies - vertical U-shaped burrows with no evidence of migration; horizontal, tuberculate burrows of Ophiomorpha borneensis may occur instead; preserved in trough cross-bedded sandstones and oolites :

C) Diplocraterion facies - vertical, migratory, U-shaped burrows; divided into two sub-facies:-

  a) protrusive and retrusive burrows; preserved in foreset-bedded sandstones;

  b) retrusive burrows; preserved in laminated sandstone; often accompanied by Gyrochorte carbonaria.

These three facies possess notably inshore characteristics. With the exception of facies C)b) there are no traces formed at shallow depth beneath the sediment/water interface. The sedimentology of the enclosing rocks indicates a highly mobile substratum.

In all probability no significant bathymetric variation exists between facies B) and C) : certainly the difference is negligible when compared with "regimes" (i) & (ii).

Of all the facies, those in group (iii) indicate the greatest degree of environmental exposure.

CHAPTER TWENTY.

A COMPARISON OF ENGLISH JURASSIC TRACE FOSSILS WITH THOSE OF OTHER GEOLOGICAL SYSTEMS, AND THEIR BATHYMETRIC SIGNIFICANCE.

One of the greatest advantages which the study of trace fossils can contribute to the science of Geology is the facility for detailed facies comparison.

The shelly fossils of two Systems widely separated in time may be so completely unrelated that facies comparisons based on the macrofauna are very difficult. The basic types of trace fossil, however, have altered little in the course of Phanerozoic time, many forms such as Chondrites, Teichichnus and Rhizocorallium being as common in the Lower Palaeozoic as in the Tertiary.

The restriction of certain trace fossils to particular "regimes" of sedimentation enables four major trace-fossil facies to be identified throughout the Phanerozoic (SEILACHER 1964).
If trace fossils are allocated to their correct ecological category (SEILACHER 1953), this four-fold

grouping provides a meaningful picture of environmental differences which are chiefly related to the contemporary sea depth.

The characteristics of the four universal trace-fossil facies are shown on Table 17.

TABLE SEVENTEEN. DIAGNOSTIC FEATURES OF THE FOUR MAJOR UNIVERSAL TRACE-FOSSIL FACIES.

Facies	Typical traces	Water agitation	Bathymetric zone	Dominant ecological category	Associated sedimentary structures
Skolithos Facies	simple vertical burrows	surf-zone	supra-littoral	DOMICHNIA	Cross-beddin
Cruziana Facies	long horizontal burrows	rough-water zone	littoral sub-littoral	FODINICHNIA	Symmetrical ripplemarks
Zoophycos Facies	*Spreiten* burrows	still-water zone	neritic	FODINICHNIA	Massive
Nereites Facies	meandering grazing trails	turbidity currents	bathyal	PASCICHNIA	Graded bedding

---

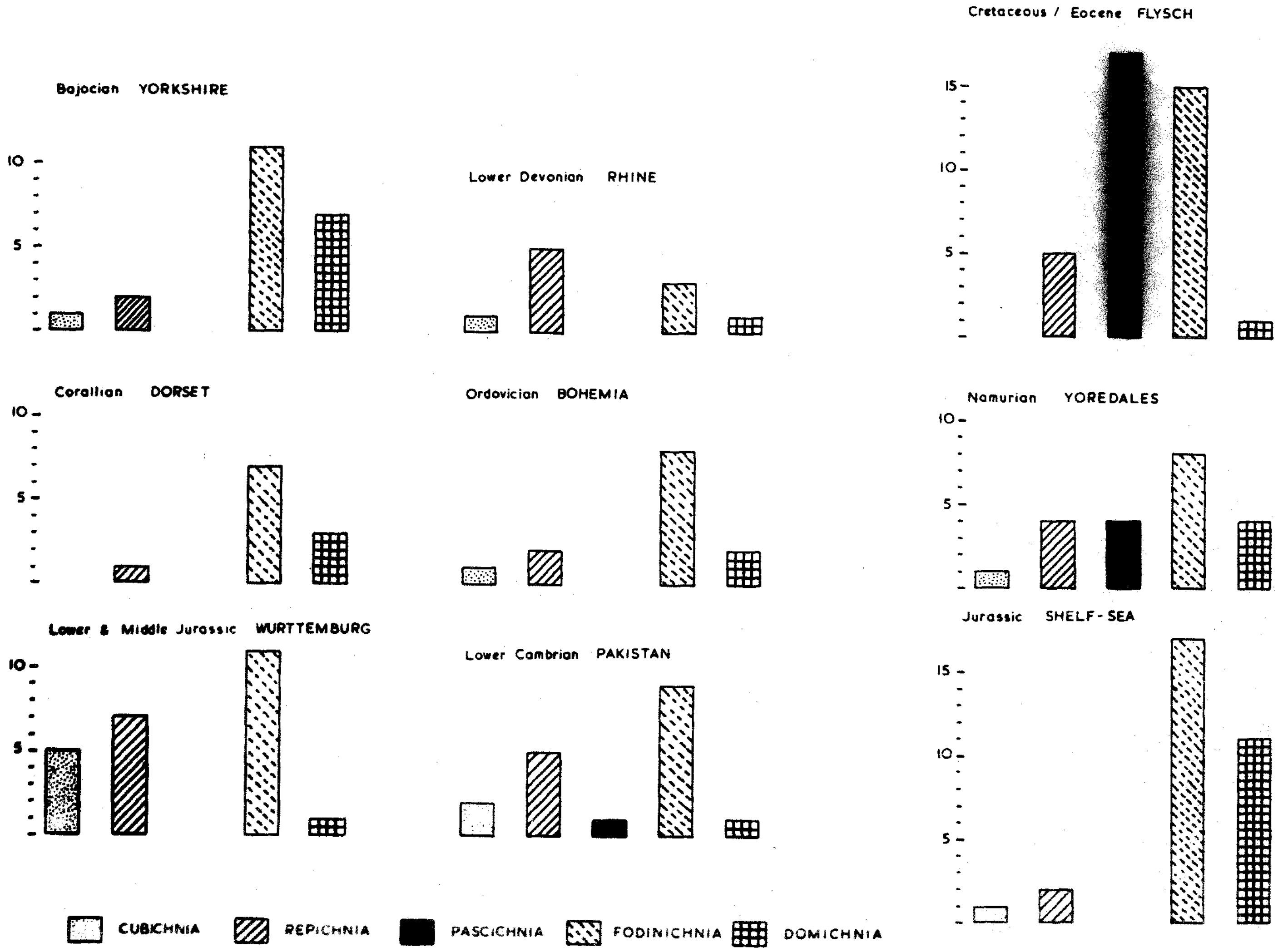
Text-figure 54A illustrates the trace-fossil assemblages which most closely compare with the English Jurassic. All are classic examples of the *Cruziana* Facies, and all

Text-figure 54.

A. Histograms comparing English Jurassic trace-fossil assemblages with those from other shelf-sea environments.

B. Histograms showing the contrasts in trace-fossil types between the shelf-sea Jurassic and the bathyal Flysch, and the enigmatic nature of the Namurian Yoredale trace fossils.

The vertical axis shows the number of different trace-fossil 'species'. The horizontal axis, their distribution among the five major 'orders' of Seilacher.


Bajocian YORKSHIRE
10
5
Lower Devonian RHINE
Cretaceous / Eocene FLYSCH
15
10
5
Corallian DORSET
10
5
Ordovician BOHEMIA
Namurian YOREDALES
10
5
Lower & Middle Jurassic WURTTEMBURG
10
5
Lower Cambrian PAKISTAN
Jurassic SHELF-SEA
15
10
5
CUBICHNIA
REPICHNIA
PASCICHNIA
FODINICHNIA
DOMICHNIA

were produced during Periods of widespread epicontinental seas.

The shelf-sea environment is characterised by an abundance of feeding burrows (Fodinichnia), while in the nearshore regions the Domichnia are dominant.
A high ratio of Domichnia : Fodinichnia indicates a littoral environment ; a low ratio, a sub-littoral or neritic environment, depending on the associated sedimentary structures (Table 17).

Thus the Bajocian of Yorkshire and the Corallian of Dorset differ markedly from the Lower and Middle Jurassic of Wurttemberg in their relatively greater preponderance of Domichnia over Fodinichnia (Text-fig. 54 & Table 18), ratios being 1:1.6, 1:2.3 and 1:11.0 respectively.

The inference is that the English Jurassic as a whole was deposited much nearer shore than the German Jurassic. How much nearer shore is shown by the great difference in ratios, and also by the occurrence of the Zoophycos facies in Wurttemberg, which is unknown in England.

It is also noticeable that resting trails (Cubichnia) and Repichnia are very much more abundant in Germany than in England (12 'species', compared with 3). These two

TABLE EIGHTEEN. ENGLISH JURASSIC TRACE-FOSSIL ASSEMBLAGES COMPARED WITH THOSE OF OTHER SYSTEMS.

	CUBICHNIA	REPICHNIA	PASCICHNIA	FODINICHNIA	DOMICHNIA
Yorkshire M.Jur.	1	2	-	11	7
Dorset Corallian	-	1	-	7	3
Wurttemberg L.&M.Jur.	5	7	-	11	1
German Muschelkalk	-	3	-	4	3
Rhine L.Devonian	1	5	-	3	1
Bohemian Ordovician	1	2	-	8	2
Pakistan L.Cambrian	2	5	1	9	1
swiss Cret/Eoc.Flysch	-	5	17	15	1
Northumberland Namurian	1	4	4	8	3
English Jurassic	1	2	-	17	11

Data chiefly from sEILACHER (1955) and the author's notes

groups stand little chance of being preserved in littoral sediments since they are formed very close to the sediment/water interface. Their presence in quantity in the German sequence again demonstrates quieter, offshore sedimentation.

Similarly the lower Devonian of the Rhine and the lower Cambrian of the Salt Range, Pakistan, contain fewer Domichnia and more Repichnia than the English Jurassic, and essentially indicate a sub-littoral, offshore environment.

On the basis of facies comparison by trace-fossil analysis, the system which most strongly resembles the English Jurassic is the Bohemian Ordovician, comparing very closely with the histogram for the Dorset Corallian.

Comparing geological systems on the basis of four universal trace-fossil facies is excellent for generalised comparisons, though such comparisons can invariably be made on more simple sedimentological and stratigraphic grounds. It is evident that the Cruziana Facies in particular is too broad, and does not enable the recognition of more precisely defined facies within epi-continental and deltaic sequences.

In this context the trace-fossil facies formulated from an analysis of the Jurassic rocks of England (Text-figures 51, 52 & 53) enable such a subdivision to be undertaken. More detailed comparisons may then be made between suites of trace fossils from various horizons within a geological system.
Such comparisons are rendered more meaningful when the trace-fossil facies are related to the "regime" of sedimentation.

FUTURE RESEARCH.

Although trace fossils provide much interesting palaeoecological data, particularly concerning the bathymetry of ancient seas and the degree of exposure of ancient environments, they nevertheless reflect only one facet of the complete palaeoecological picture.

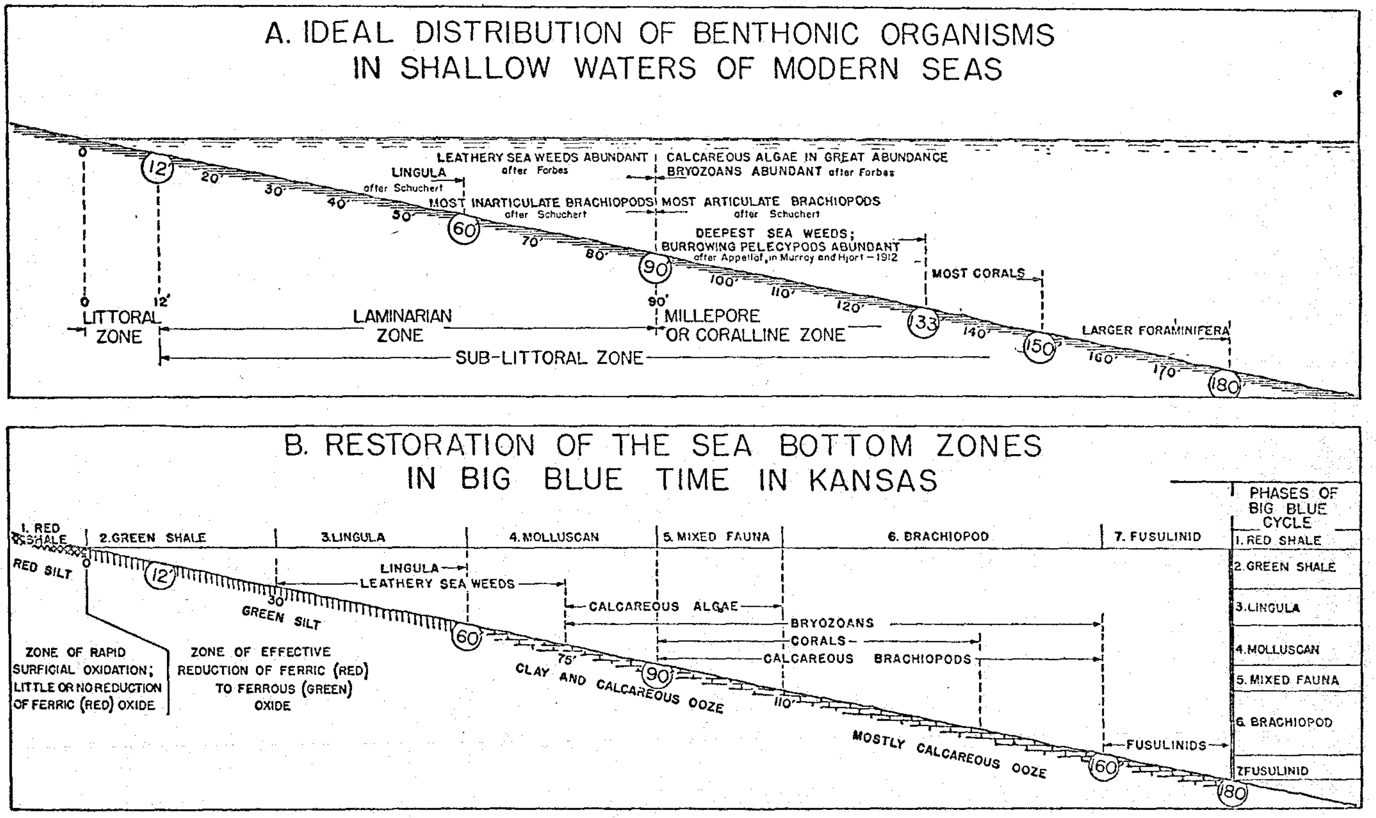
The possibility of establishing bathymetric zones based on the macrofauna has received remarkably little attention, in spite of the promising results of ELIAS (1937; Text-fig.55) on the Lower Permian Big Blue sediments. It would be most instructive to construct a system of bathymetric zones for the English Jurassic based on the shelly fauna. The relative merits of the two series of zones, one based on trace fossils and the other on shelly fossils, could then be investigated.

I suspect that the reluctance to use the shelly macrofauna, especially in nearshore marine environments, stems from an over-awareness of the possibility of post-mortem transport. One should first ascertain from Recent ecological studies whether this factor is of major importance, especially where highly disturbed, current-swept sea-floors are involved.

It should be comforting for palaeoecologists to read that a very detailed study (HOLME 1961) of the shelly fauna

Text-Figure 55.

System of bathymetric zones based on the Lower Permian macrofauna of the Big Blue sediments of Kansas (after ELIAS 1937).



By Maxim K Elias, 1935-1936

FIGURE 3.—*Sea-bottom zones in modern and in Big Blue seas*

A.—Ideal distribution of benthonic organisms in shallow waters of modern seas.
B.—Restoration of the sea bottom zones in Big Blue time in Kansas.

of the English Channel, an area intensely scoured by bottom currents, revealed (*op.cit.*, p.443):-

> " There is no evidence that dead shells are transported any appreciable distance from the areas in which they originally lived."

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The work has been forwarded considerably by the forebearance, and enduring assistance, of the author's wife, for which no written acknowledgment is adequate.

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APPENDIX I : GLOSSARY OF ESSENTIAL TERMS.

"bioturbation" = disturbance of sedimentary laminae by animals.
"churned" = an expression used by sedimentologists for an horizon which been nearly 100% re-worked by animals.
"ichnofacies" = a recurring association of trace fossils.
"innenspuren" = a trace fossil constructed within the seafloor.
"littoral" = between the tide-marks.
"mottling" = process by which burrowing animals impart a striking colour change to sediments; aided by diagenesis.
"neritic" = offshore region, beneath wave-base.
"sole trail" = trace fossil occurring at the base of a unit.
"sub-littoral" = nearshore region, from wave-base to the level of the lowest tides.

"Spreite" /"Septum" /"Festoons" = scratches or laminae arranged as though draped from two limbs.

Other terms, which are not as equivocal as those listed above, will be found at the back of AGER (1963).

APPENDIX V : DETAILED STRATIGRAPHY OF THE BLACK HEAD.

		ft.	ins.
12.	Nodular rubbly limestone Base : clay/oolite interdigitations.	Seen	
11.	Cross-bedded grey-white oolite with much comminuted shell débris, marl lenses and clay-galls along erosion planes.	1	3
10.	Grey clay with ironshot oolite lens 9" from base	3	0
9.	b) Pure white oolite with low angle XB: shell débris no clay-galls 1ft 2ins *Skolithos* *Thalassinoides* a) Grey, marly limestone, sparsely oolitic appears "churned" due to high burrowing activity. 10ins	2	0
8.	Light grey clay with cementstone nodules	6	6
7.	j) Light-brown oolitic limestone 1st Tier 1ft 2ins i) 2nd Tier 5 h) Marcasite nodules at top 3rd Tier 1 2 g) Greyer, passing down into 4th Tier 10 f) clay seam 6 e) Coarse oolite, extensive bioturbation 5th Tier 1 6 d) Phosphatic nodules at base 6th Tier 9 c) Nodular mottled marl 7th Tier 1 0 b) Diplocraterion Ophiomorpha 1 0	8	7

OSMINGTON OOLITE SERIES, DORSET.
RINGSTEAD - OSMINGTON HILLS.

	ft.	ins.
Nodular rubbly limestone Base : clay/oolite interdigitations	11	0
Clay with laminae of fissile white oolita with small *ostrea*	1	0
Grey clay, lower part oolitic	3	3
False bedded oolite, upper part solid. *Skolithos*.	2	0
Clay, with three bands of nodular white mudstone in highest 4 feet.	8	3
Marl and soft rubbly marlstone, in several bands, strongly oolitic, with fucoidal markings: *Exogyra nana* *Chlamys qualicosta*.	5	9

				ft.	ins.
6.	Solid white oolite with large-scale XB dipping west, *ophiomorpha* at top	10ft	0ins	13	4
	Marly limestone	1	8		
	Interdigitated marly limestone/oolite XB, dipping west with *skolithos*	1	8		
	Clay with nodular limestone and *Teichichnus* 2' from top	5'	0	13	2
	Marly limestone with oolitic streaks, *Teichichnus*		8		
5.	Clay with two bands of nodular limestone 2' and 1'3" from top with good *Teichichnus*.	7'	6		
4.	Pisolite with phosphatic nodules.		11		

Bed nos. 12-4 inclusive TOTAL 60ft. 9ins.

	ft.	ins
Marly limestone, top 2' oolitic	10	0
Clay with bands of nodular white mudstone.	12	6
Pisolite, coarse, purplish-grey	1	6
TOTAL	55ft.	3ins.