The British Lithostrotiontidae

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THE BRITISH LITHOSTROTIONTIDAE

by John R. Nudds

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PLATE 1 (Frontispiece)

Lithostrotion sive Basaltes minimus striatus et stellatus. Reproduced from the 1760 'Editio altera' edition of 'Lithophylacii Britannici Ichnographia' by Edward Lhwyd (First edition 1699). This is the earliest illustration of Lithostrotion and the first designation of a scientific name to this group of corals, albeit pre-Linnaen. Lhwyd states that the coral came from Wales. Parkinson (1808) states that it is from Giltar Point, Tenby, Pembrokeshire (S2 Zone). A visit to Giltar Point proved unsuccessful for no specimens of cerioid Lithostrotion could be found at this locality. It is possible that Parkinson was mistaken in suggesting this locality for Lhwyd's coral. Alternatively the species may be rare in this area and industrious palaeontologists, following Parkinson's directions, may have collected the few that were present.

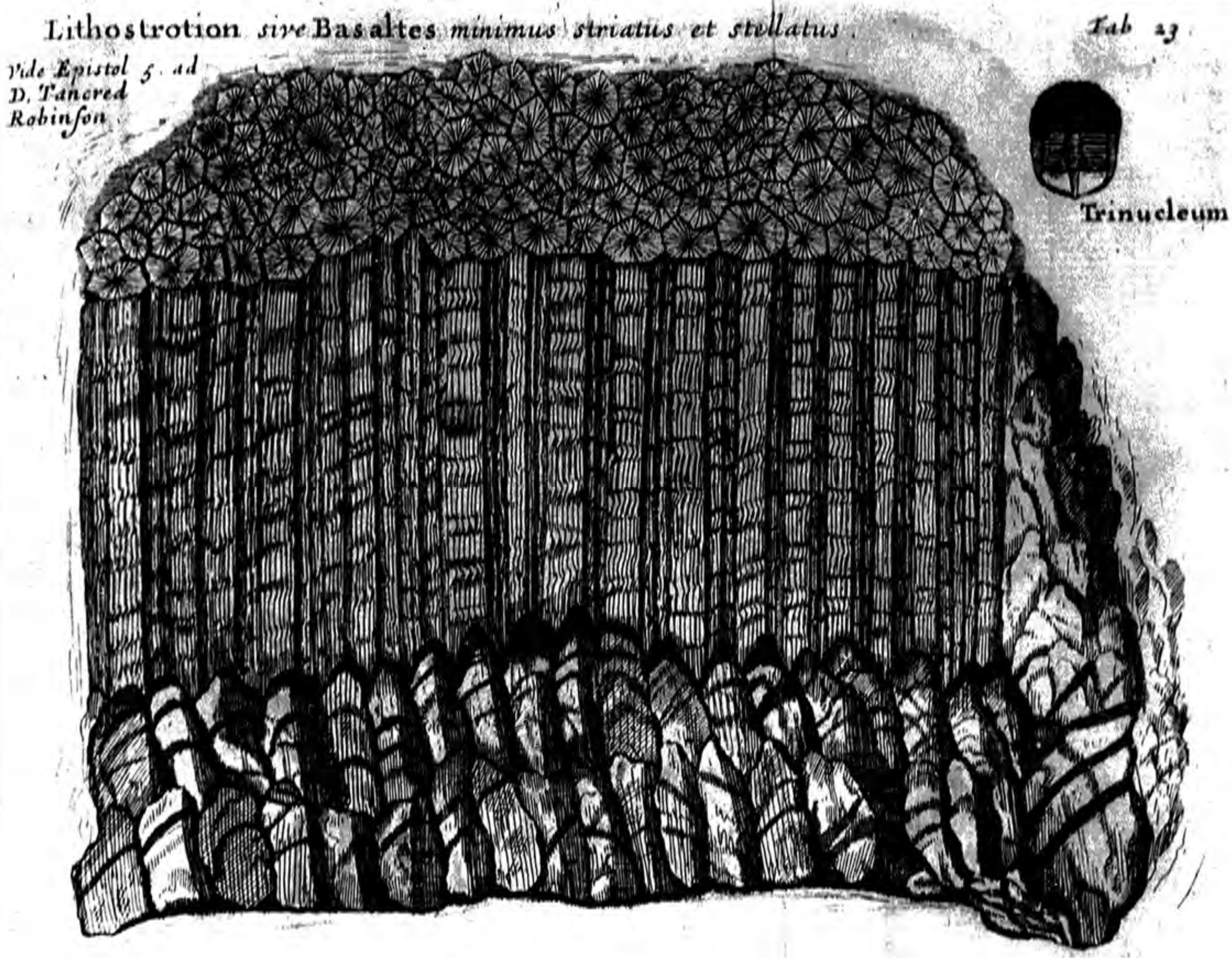

Plate I. Frontispiece

ABSTRACT

A revision and systematic study of the British species of the Carboniferous rugose coral family *Lithostrotiontidae* is described. No revision of this group has appeared since the middle of the last century. Results show that 15 described cerioid species of *Lithostrotion* can be lumped into four species. In addition *L. decipiens depressum subsp. nov.* is described in this group. The fasciculate species of *Lithostrotion* have been extended by the separation of *L. variabile sp. nov.*, *L. scaleberense sp. nov.*, *L. junceum communicatum subsp. nov.*, *L. martini praenuntium subsp. nov.* and *L. martini simplex subsp. nov.*

The genus *Diphyphyllum* is shown to be polyphyletically derived and its species are referred back to *Lithostrotion.* The monospecific genus *Nemistium* is considered synonymous with *Lithostrotion* and removed. Its one species is an evolutionary intermediate between two species of *Lithostrotion*. The genus *Orionastraea* is reviewed and *O. sera sp. nov.* is described. Two species of *Orionastraea* are referred to *Hudsonia gen. nov.* which, though similar morphologically to *Orionastraea*, has a different ancestral species. *H. matura sp. nov.* is described in this genus.

The genus *Aulina* is excluded from the *Lithostrotiontidae* as it is thought to have different ancestors. It is restricted to include only forms with massive coralla and *A. botanica sp. nov.* and *A. rotiformis aphroidia subsp. nov.* are described. Fasciculate species of *Aulina* are referred to *Fascicaulina gen. nov.* as they are apparently unrelated to *Aulina sensu stricto*.

The phylogeny of the *Lithostrotiontidae* is described and shown to proceed by following certain evolutionary trends which lead to an increasing level of coloniality within the group. The evolutionary centre and therefore the palaeomigration directions of the *Lithostrotiontidae* are shown to change during the phylogeny and this is related to the global palaeogeography of the Carboniferous period. Discovery of well preserved material has allowed the skeletal changes during the hystero-ontogeny of *L. martini* to

be determined.

This revision has led to a better understanding of the species in the Lithostrotiontidae so that their value as statigraphical zonal indices has been increased.

ACKNOWLEDGEMENTS

The author is indebted to numerous persons and organisations for help freely given in pursuit of this research. First, I am indebted to Professors G.M. Brown and M.H.P.Bott of the University of Durham for allowing me to use the facilities in the Department of Geological Sciences. Secondly, special thanks are due to Dr. G.A.L. Johnson for originally suggesting the topic of this research, for his supervision of the work and for his constant enthusiastic encouragement during the past three years. I am also grateful to Drs. G.P. Larwood and J.R. Senior for helpful palaeontological discussion and to the former especially for his help with taxonomic problems.

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CONTENTS

LIST OF FIGURES

EXPLANATION OF PLATES

LIST OF TABLES

PART 1

INTRODUCTION

CHAPTER 1

INTRODUCTION

The subject of this thesis is a complete revision of the species of the extinct Carboniferous coral family Lithostrotiontidae. A revision of the systematics of the group and a determination of the evolutionary history is the main theme but also such factors as ecological effects on morphology, methods of asexual reproduction (budding), palaeomigration directions, development of colonialism in the group and the use of such fossils as geochronometers are described and discussed. The research has been carried out in the three years from October 1972 to July 1975 at the University of Durham.

The project was undertaken for two main reasons, First, apart from a short period in the 1920's when Dr. Stanley Smith published a series of papers on this family, little work has been carried out on these fossils, since they were first described by the early palaeontologists viz Parkinson, Edwards and Haime, McCoy, Fleming, Phillips and Lonsdale. In those days (1800-1850) many species were described, a large proportion being erected on characters not nowadays regarded as being specifically important. Also the total variation of a species was not studied so carefully with the result that many species described were merely varieties of an earlier named form. Moreover, with the poorer communications of those times, the same species was often given more than one name, and, to add to the confusion The Rules of Zoological Nomenclature were not strictly applied and many of the early workers simply ignored an earlier name and published a new one of their own. The result of these contributing factors was that a state of confusion developed in the group with too many specific names and a large proportion of them being ill-defined. As a result of this muddle some names have survived with time while others rightly or wrongly have been dropped. This project has therefore been undertaken with the object of re-defining all of the species erected in the family *Lithostrotiontidae* and to determine their total variation. This has enabled first, synonymy to be worked out, secondly, lumping together of those species which show a continuous variation of characters between them and thirdly, to erect any new species which may be useful biologically or stratigraphically.

Another and more important reason~~s~~ for needing a fuller understanding of these corals is that the different species, once redefined, may be useful as zonal indicators within the Carboniferous System. They are an important group of corals for such work as they are relatively common as fossils, they are widely distributed geographically and they evolved fairly quickly so that the different species in the group are restricted to quite narrow ranges in the Carboniferous sequence. Historically the stratigraphic use of the group was lost in the muddle that existed prior to this research.

The five pre-existing genera of the family have been revised, namely *Lithostrotion*, Fleming 1828, *Diphyphyllum*, Lonsdale 1845, *Orionastraea*, Smith 1916, *Aulina*, Smith 1916, and *Nemistium*, Smith 1928. A majority of the specimens studied during the revision have been collected by the author from the following regions in the North of England; the area around Kirkby-Stephen, Cumbria, the Yorkshire dales of Swaledale, Wensleydale, Nidderdale, etc., the Tyne Valley, Northumberland and the Carboniferous Limestone of West Cumbria. Also some species not represented in these areas have also been collected from Derbyshire and Scotland. Altogether a total of 462 different colonies have been collected from which 1385 thin sections have been cut and examined by the author. The proportions of the different species represented in these figures are set out in table 1 .

The revision of the species has been carried out in the following manner. External morphological characters have been examined on hand specimens which have been prepared by a variety of laboratory techniques. The external epithecal surface and the calicular pit, where preserved, have been stripped clean of matrix by washing in the ultra-sonic tank and by use of

TABLE 1

Table showing the number of colonies collected and thin sections prepared for the species studied in this thesis. L.= *Lithostrotion*, O.= *Orionastraea*, A.= *Aulina*, H.= *Hudsonia gen. nov.*, F.= *Fascicaulina gen. nov.*

SPECIES	No. of Colonies Collected	No. of Thin Sections Prepared
L.junceum junceum	62	145
L.junceum communicatum subsp. nov.	2	1
L.pauciradiale	30	34
L.irregulare	33	131
L.variabile sp. nov.	21	73
L.martini praenuntium subsp. nov.	6	14
L.martini martini	43	282
L.martini simplex subsp. nov.	1	15
L.sociale	11	38
L.scaleberense sp. nov.	2	12
L.affine	0	0
L.maccoyanum	10	11
L.decipiens decipiens	50	79
L.decipiens depressum subsp. nov.	17	
L.vorticale	24	56
L.aranea	11	36
L.lateseptatum	17	59
L.furcatum	25	104
L.fasciculatum	16	76
L.gracile	29	110
L.edmondsi	3	4
O.ensifer	0	0
O.phillipsi	1	0
O.tuberosa	0	0
O.placenta placenta	9	32
O.placenta garwoodi	9	11
O.sera sp. nov.	1	3
O.rete	9	25
O.edmondsi	0	0
O.indivisa	2	6
H.matura sp. nov.	0	0
H.magna	1	1
A.senex	1	0
A.botanica sp. nov.	3	7
A.rotiformis rotiformis	9	11
A.rotiformis aphroidia subsp. nov.	4	9
F.horsfieldi	0	0
F.hibernica	0	0
F.furcata	0	0
TOTAL	462	1385

Table 1.

the 'vibrotool'. Some silicified specimens have had their exterior revealed by dissolving the calcareous matrix in a hydrochloric acid bath. Internal morphological characters have been examined by use of polished specimens, acetate peels and thin sections. All significant morphological characters (Chapter 3) have then been measured and compared (p. 94).

In addition to this detailed examination of newly collected material, the original type material of the primary authors has been traced and examined. In this way it has been possible to assess accurately the total variation of each species described and thence to work out synonymy and erect new species. In this way I have arrived at a new list of valid species in the family *Lithostrotiontidae*. A full list of the species names, within the *Lithostrotiontidae*, both those in current use and those that had lapsed prior to this revision is given in table 2 .

TABLE 2

Lists of species considered in this thesis.
Column 'a'. Species names in current use prior to this revision.
Column 'b'. Species names that had lapsed prior to this revision.
Column 'c'. Species names used in this revision.
Column 'd'. Species names lapsed in this revision.
The species in column 'b' were considered junior synonyms of the corresponding species in column 'a'.
The species in column 'd' are here considered junior synonyms of the corresponding species in column 'c'.
L.= *Lithostrotion*, O.= *Orionastraea*, A.= *Aulina*,
H.= *Hudsonia gen. nov.*, F.= *Fascicaulina gen. nov.*

a) Names in current use before revision	b) Names lapsed before revision
L.junceum	L.coarctatum L.sexdecimale
L.pauciradiale	L.aggregatum L.irregulare
L.carpathicum	
L.martini	L.phillipsi
L.caswellense	
L.scoticum	
L.sociale	L.longiconicum
L.affine	L.proliferum
L.maccoyanum	
L.portlocki	L.decipiens L.clissioides L.derbiense
L.minus	
L.basaltiforme	L.kendalense L.verticale L.striatum L.flemingi
L.aranea	
L.bristoliense	
L.clavaticum	
L.arachnoideum	L.hexagona L.septosum L.major
D.lateseptatum	D.concinnum D.approximatum D.lateseptatum var. giganteum D.lateseptatum var. interruptum
D.smithi	
D.ingens	
D.furcatum	
D.fasciculatum	D.interruptum D.Blackwoodi var. approximatum D.Blackwoodi D.cylindricum
D.gracile	
N.edmondsi	
O.ensifer	
O.ensifer var. matura	
O.phillipsi	O.tuberosa
O.placenta	
O.garwoodi	
O.garwoodi var. sera	
O.garwoodi var. pristina	
O.prerete	
O.rete	
O.edmondsi	
O.edmondsi var. laciniosa	
O.indivisa	
O.magna	
A.senex	
A.rotiformis	
A.horsfieldi	
A.hibernica	
A.furcata	

Table 2 (cont. overleaf).

c) Names used in revision	d) Names lapsed in revision
L.junceum junceum	L.coarctatum L.sexdecimale
L.junceum communicatum subsp. nov.	
L.pauciradiale	L.carpathicum L.aggregatum
L.irregulare	
L.variabile sp. nov.	
L.martini praenuntium subsp. nov.	
L.martini martini	L.caswellense L.scoticum L.phillipsi D.smithi
L.martini simplex subsp. nov.	
L.sociale	L.longiconicum
L.scaleberense sp. nov.	
L.affine	L.proliferum
L.maccoyanum	
L.decipiens decipiens	L.derbiense L.clissioides
L.decipiens depressum subsp. nov.	
L.vorticale	L.portlocki L.minus L.basaltiforme L.clavaticum L.kendalense L.striatum L.flemingi L.bristoliense
L.aranea	L.hexagona L.arachnoideum L.septosum L.major
L.lateseptatum	D.concinnum D.approximatum D.lateseptatum var. giganteum D.lateseptatum var. interruptum D.ingens
L.furcatum	
L.fasciculatum	D.interruptum D.Blackwoodi D.Blackwoodi var. approximatum D.cylindricum
L.gracile	
L.edmondsi	
O.ensifer	
O.phillipsi	
O.tuberosa	O.edmondsi var. laciniosa
O.placenta placenta	O.prerete O.garwoodi var. pristina
O.placenta garwoodi	
O.sera sp. nov.	
O.rete	
O.edmondsi	
O.indivisa	
H.matura sp. nov.	
H.magna	
A.senex	
A.botanica sp. nov.	
A.rotiformis rotiformis	
A.rotiformis aphroidia subsp. nov.	
F.horsfieldi	
F.hibernica	
F.furcata	

Table 2 (cont.).

CHAPTER 2

STRATIGRAPHY

The division of the Carboniferous rocks in England is a simplified threefold division based on lithology:

Upper Carboniferous.	Coal Measures.	(Westphalian)
	Millstone Grit.	(Namurian)
Lower Carboniferous.	Carboniferous Limestone Series.	(Dinantian)

The term 'Carboniferous Limestone' is a misnomer because only in the south is continuous limestone overlain directly by "Millstone Grit" facies; in most regions a varying amount of the top of the 'Limestone Series' is replaced by an alternation of rocks between the limestone and the "Millstone Grit" facies. This is the Yoredale Series, a rhythmic sequence of repeated limestone, shale, sandstone and seatearth. The term 'Millstone Grit' has been used for facies and for geological time and is now ambiguous. In this thesis 'Millstone Grit' will be used as a facies term and 'Namurian' for the central division of the period.

The fossil corals studied in this project were mainly collected from the Pennines and adjacent areas in the North of England which can be divided into the following structural regions, running from north to south (fig. 1).

1. Northumberland Trough (Tyne Valley including the Roman Wall district). Bounded on the south by the Stublick Faults.

2. Alston Block (Weardale, Teesdale, Cross Fell). Bounded on the south by the Stainmore Trough and on the west by the Pennine Faults.

3. Stainmore Trough (Brough, Kirkby-Stephen area including the Cotherstone Syncline around Botany).

4. Askrigg Block (Swaledale, Wensleydale, Nidderdale, Wharfedale, Ribblesdale). Bounded on the south by the Craven Faults and on the west by the Dent Faults.

5. Northern margin of the Craven Basin (District around Settle, Grassington, Greenhow and Malham).

FIGURE 1

Map illustrating the structural regions of the Northern Pennines. Heavy lines represent the faults which are the boundaries of the regions; dotted lines represent the County boundaries.

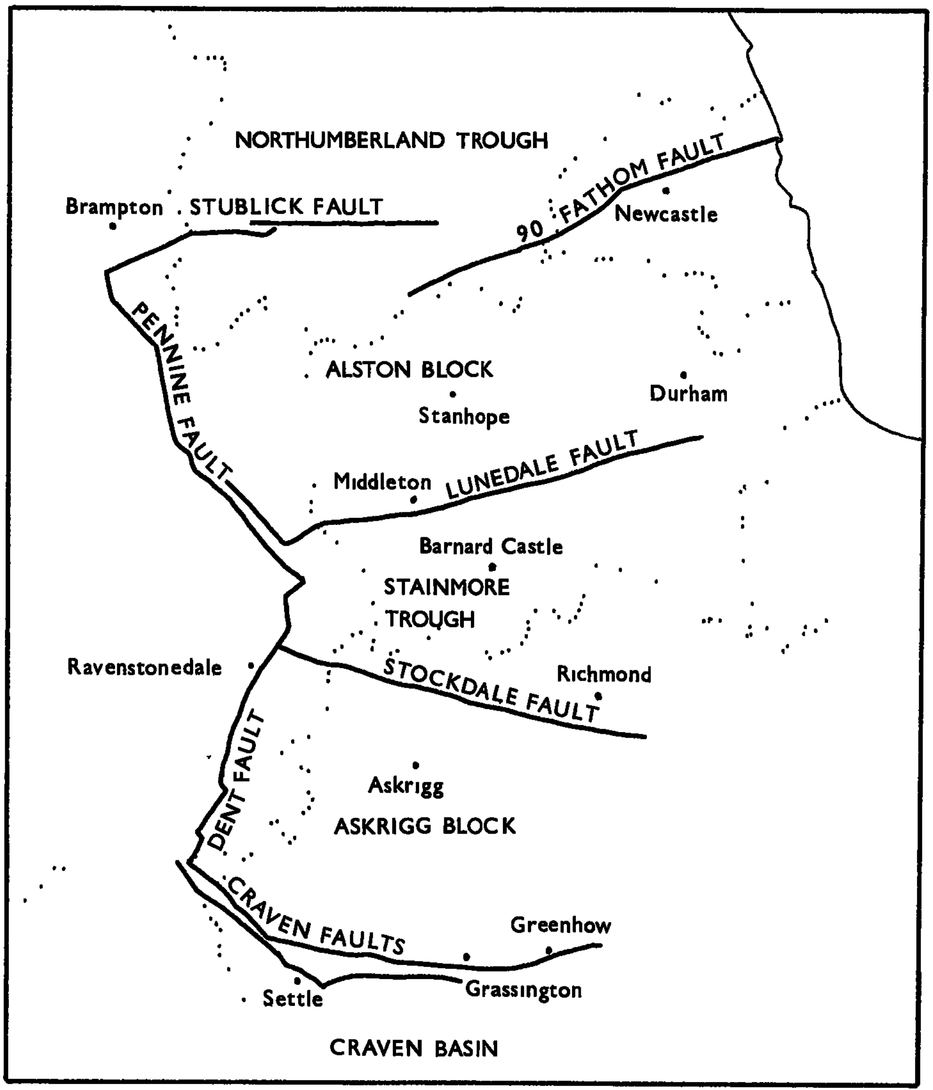

NORTHUMBERLAND TROUGH
Brampton
STUBLICK FAULT
90 FATHOM FAULT
Newcastle
PENNINE FAULT
ALSTON BLOCK
Stanhope
Durham
Middleton
LUNEDALE FAULT
Barnard Castle
STAINMORE TROUGH
Ravenstonedale
STOCKDALE FAULT
Richmond
DENT FAULT
Askrigg
ASKRIGG BLOCK
CRAVEN FAULTS
Greenhow
Settle
Grassington
CRAVEN BASIN

fig 1

In addition some specimens were collected from West Cumberland (Cleator Moor), Derbyshire (Castleton) and North Wales (Great Orme).

The palaeogeography of this area can thus be seen to consist of an alternating series of blocks or positive areas (often underlain by granite) and troughs. However, it must not be assumed that these conditions led to any great differences in sea depth during the Carboniferous, but rather that the troughs were areas that were sinking at a quicker rate than were the blocks, so that greater thicknesses of sediment were able to build up in the troughs. Not only are the sediments thinner on the blocks, they are also less complete. The blocks were not generally submerged until fairly late in the lower Carboniferous so that the earliest rocks are absent on the block regions.

The lithological succession of the Carboniferous sediments in these structural regions varies from area to area and this variation in lithology concerns the gradual replacement of Carboniferous Limestone by the Yoredales and is a result of the palaeogeographical history of the region. This history was one of large 'deltas' advancing slowly southwards from the north with the result that on reaching an area the steady deposition of standard limestone in that area ceased and conditions changed to thin beds of limestone separated by a rhythmic succession of shale, sandstone and seat-earth. At the top of the Carboniferous Limestone Series deposition of limestone generally stopped altogether and the sequence is then continual shale and sandstone, this being the Namurian.

As these deltas were moving in a southerly direction clearly the more northern regions were affected earlier by the deltas, and the more southern regions were not affected until quite late in the Carboniferous. Thus the continuous limestone of the Limestone Series is very thick in the Craven area, much thinner on the Alston Block and absent altogether in the Northumberland Trough. In Northumberland almost all of the true Carboniferous limestone is replaced by the Yoredale Series whereas south of the Craven area in Derbyshire no Yoredale Series is present at all because when the deltas reached this area the rhythmic sequence of the Yoredales failed.

Thus in Derbyshire continuous limestone is overlain directly by continuous Millstone Grit facies.

The correlation of these varying lithological successions in the different regions is shown in fig. 2 .Vaughan's coral/brachiopod Zones are shown in the column at the left.

Lithostrotiontid corals are common in all of these five plaeogeographic regions but perhaps more so in the central region, the Stainmore Trough (fig.2 , column D), where the very earliest Carboniferous sediments are present, and in considerable thickness. In the area around Ravenstonedale the basal Carboniferous beds, the Pinskey Gill Beds (shale, sandy-shale and limestone) rest unconformably on the Silurian. These are overlain by the Feldspathic Conglomerate Division which is followed by the Ravenstonedale Limestone in which the Lithostrotiontidae species first appear. This limestone has been described in detail by Johnson and Marshall (1971) who show that it passes upwards into the Ashfell Sandstone, "with the Brownber Pebble Bed forming a valuable lithological marker band". It is in the grey limestones just below the Brownber Pebble Bed that the first Lithostrotion species has been found in beds of C2 age. The term 'Ashfell Sandstone' is somewhat of a misnomer as these beds, which are roughly equivalent to Vaughan's S1 Subzone, consist of an alternating series of red and grey shales with calcareous sandstone and limestone bands. Above the Ashfell Sandstones is another extensive series of limestone in which Davidsonina carbonaria first appears, these limestones being equivalent to Vaughan's S2 Subzone. The Beehive Band at the top of these limestones is the base of the D1 Subzone which begins in this region with the thick Potts Beck Limestones followed continuously by the Melmerby Scar Limestones. Above this thick limestone an important change occurs with the rhythmic Yoredale Series beginning and no more extensive limestones occurring, but only thin bands of generally darker limestones separated by shale and sandstone. The first two such limestones, the Robinson and Peghorn limestones complete the D1 Subzone with similar thin limestones continuing above D1 to the top

FIGURE 2

Comparative sections of the Carboniferous successions in the various structural regions of Northern England. The base of the Namurian is taken as a datum line. The Dinantian strata are divided using Vaughan's coral/brachiopod zones, as shown on the left hand side of the diagram. All strata names refer to limestone unless otherwise stated.

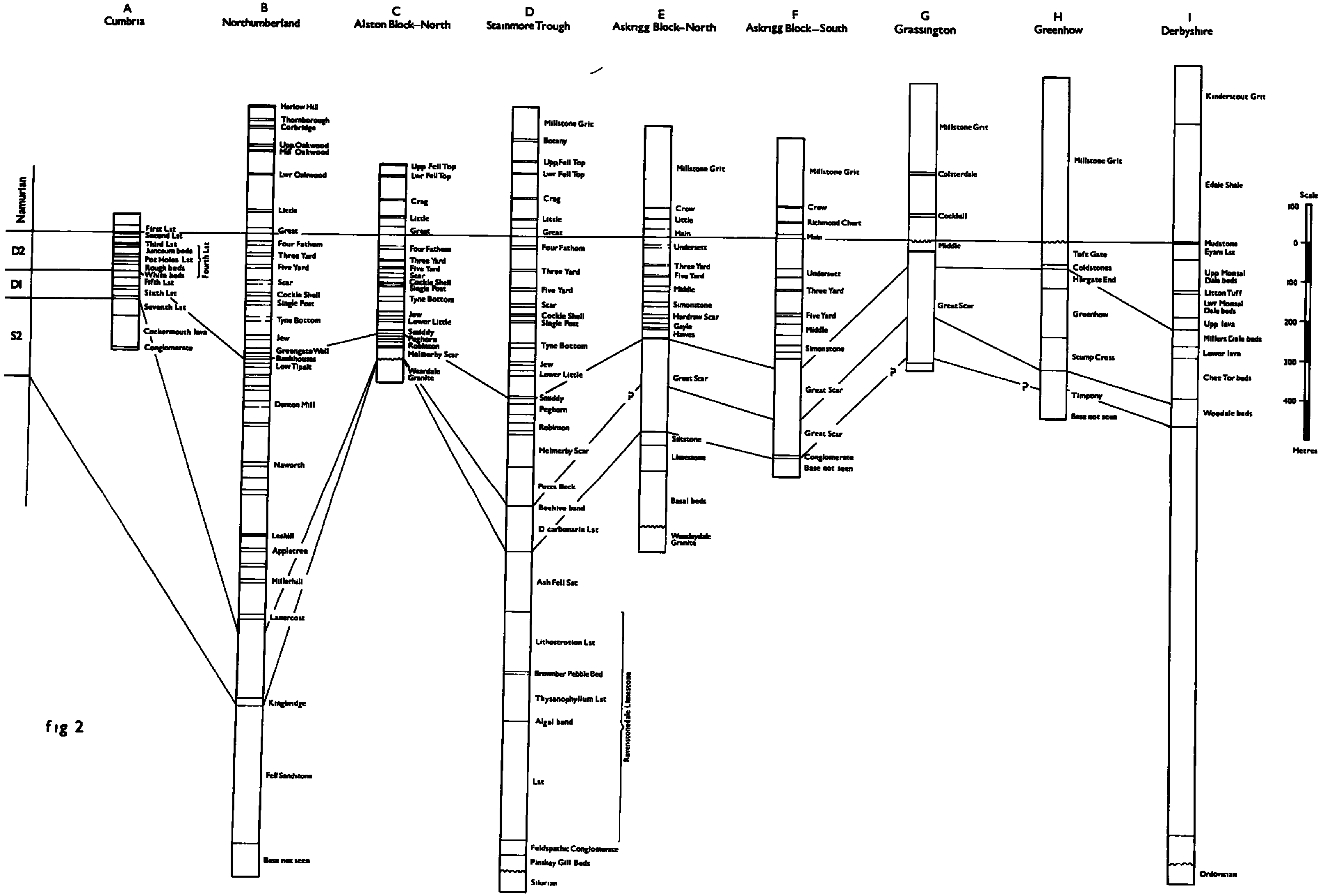

Namurian
D2
D1
S2
A
Cumbria
First Lst
Second Lst
Third Lst
Junceum beds
Pot Holes Lst
Rough beds
White beds
Fourth Lst
Fifth Lst
Sixth Lst
Seventh Lst
Cockermouth lava
Conglomerate
B
Northumberland
Harlow Hill
Thornborough
Corbridge
Upp Oakwood
Mid Oakwood
Lwr Oakwood
Little
Great
Four Fathom
Three Yard
Five Yard
Scar
Cockle Shell
Single Post
Tyne Bottom
Jew
Greengate Well
Bankhouses
Low Tipalt
Denton Mill
Naworth
Leahill
Appletree
Millerhill
Lanercost
Kingbridge
Fell Sandstone
Base not seen
C
Alston Block–North
Upp Fell Top
Lwr Fell Top
Crag
Little
Great
Four Fathom
Three Yard
Five Yard
Scar
Cockle Shell
Single Post
Tyne Bottom
Jew
Lower Little
Smiddy
Peghorn
Robinson
Melmerby Scar
Weardale
Granite
D
Stainmore Trough
Millstone Grit
Botany
Upp Fell Top
Lwr Fell Top
Crag
Little
Great
Four Fathom
Three Yard
Five Yard
Scar
Cockle Shell
Single Post
Tyne Bottom
Jew
Lower Little
Smiddy
Peghorn
Robinson
Melmerby Scar
Potts Beck
Beehive band
D carbonaria Lst
Ash Fell Sst
Lithostrotion Lst
Brownber Pebble Bed
Thysanophyllum Lst
Algal band
Lst
Ravenstonedale Limestone
Feldspathic Conglomerate
Pinskey Gill Beds
Silurian
E
Askrigg Block–North
Millstone Grit
Crow
Little
Main
Undersett
Three Yard
Five Yard
Middle
Simonstone
Hardraw Scar
Gayle
Hawes
Great Scar
Siltstone
Limestone
Basal beds
Wensleydale
Granite
?
F
Askrigg Block—South
Millstone Grit
Crow
Richmond Chert
Main
Undersett
Three Yard
Five Yard
Middle
Simonstone
Great Scar
Great Scar
Conglomerate
Base not seen
G
Grassington
Millstone Grit
Colsterdale
Cockhill
Middle
Great Scar
?
H
Greenhow
Millstone Grit
Toft Gate
Coldstones
Hargate End
Greenhow
Stump Cross
Timpony
Base not seen
?
I
Derbyshire
Kinderscout Grit
Edale Shale
Mudstone
Eyam Lst
Upp Monsal
Dale beds
Litton Tuff
Lwr Monsal
Dale beds
Upp lava
Millers Dale beds
Lower lava
Chee Tor beds
Woodale beds
Ordovician
Scale
100
0
100
200
300
400
Metres

fig 2

of the Viséan. The Namurian begins with the last of the important limestone bands, the Great Limestone, and above this horizon the marine phases become more scarce and the limestone beds thinner. The highest marine band of the Carboniferous in England however has been preserved in the Stainmore Trough in the Cotherstone Syncline (Reading, 1957) around the village of Botany, where the Botany Limestone is important in containing the highest species of the British Lithostrotiontidae.

To the south of the Trough, the Askrigg Block (fig.2 , column E) is also prolific in Lithostrotion fauna although the beds are generally thinner and the sequence less complete. The Carboniferous seas did not cover the block until the beginning of C2 times but the first limestone outcropping on the block is the thick D1 Great Scar Limestone. In the Northern part of the block, around Swaledale and Wensleydale, this limestone extends right to the top of the D1 Subzone, and is equivalent to the Potts Beck Limestone, the Melmerby Scar Limestone, the Robinson and the Peghorn Limestones of the Stainmore Trough. Having moved southwards therefore the continuous limestone extends to a higher level with the Yoredale sequence not beginning until D2 times with the Hawes and Gayle Limestones, etc. beginning the rhythmic sequence that again continues into the Namurian. Moving further south on the block to Wharfedale (fig.2 , column F) this same trend continues with the Great Scar Limestone now extending to the top of D2, the Hawes, Gayle and Hardraw Scar Limestones all having merged into it. Moving off the block into the Craven Fault district, the northern border of the Craven basin, we find that in the west of the area, around Malham and Settle (fig. 2, column C), the Great Scar Limestone attains vast thickness by this time incorporating the Simonstone Limestone so that the first true Yoredale Limestone here is the Middle Limestone. Having moved off the block the older beds are again present in this area. Garwood and Goodyear (1923) state that the age of the lowest beds exposed in the River Ribble at Settle Bridge is problematic but suggest that they should represent the Michelinia

Zone which is part of Vaughan's C Zone. The overlying beds consist of dark limestones and are equivalent to the Ashfell Sandstone beds (S1) of the Stainmore Trough. Above these are the dark grey *Nematophyllum minus* beds equivalent to the S2 *D. carbonaria* limestones of Stainmore and these extend up into the D1 Great Scar Limestone although the S/D boundary is difficult to trace.

In the east of the Craven Fault district at Greenhow again younger beds are present (fig. 2, column H). The lowest beds of the Carboniferous the Timpony Limestones have been shown by Dunham and Stubblefield (1945) to contain a similar fauna to the S2 beds at Scalber near Settle and are thus assigned to this zone. These are overlain by the Stump Cross, Greenhow and Hargate End Limestones of the D1 Subzone followed by the Coldstones Limestone of D2. The succeeding Toft Gate Limestones are correlated on the basis of an *Orionastraea* species (see p.234), with the D2 Simonstone Limestone of the Askrigg Block. An unconformity at the top of the Toft Gate Limestone marks the top of the Viséan, the uppermost beds being missing.

On the other side of the Craven Basin in Derbyshire (fig. 2, column I) continuous limestones extend all the way to the top of the Viséan and thus in this region is the final expression of the trend of continual limestone becoming gradually thicker upwards and replacing the Yoredale Series.

Moving northwards from the Stainmore Trough the opposite trend occurs with the Yoredale Series entering gradually earlier and earlier. The situation on the Alston Block (fig. 2, column C) is similar to that of the Stainmore Trough except that at the base of the Melmerby Scar Limestone is a gap with the Potts Beck Limestones missing and the Melmerby Scar Limestone hence resting directly on pre-Carboniferous granite. The Yoredale Series begin above the Melmerby Scar Limestone as in Stainmore. However, in the Northumberland Trough (fig. 2, column B) still further to the north there is no true extensive Carboniferous Limestone at the base of the Carboniferous at all. This area being a low lying trough was submerged at the beginning of Carboniferous times and hence the earliest rocks are present and in parts of the trough these can be seen resting on Old Red Sandstone facies. However in the Brampton district, from where most of the Lithostrotiontid specimens have been collected, the base of the Carboniferous is not actually seen. Here the lowest rocks present are the Cementstone group of C1 age and in this area even this very early group consist of a succession of sandstones, limestones and shales. They are overlain by the extensive Fell Sandstone Group (C2S1) which although largely arenaceous does also show rhythmic sedimentation with thin limestones and shales. These continue upwards almost to the base of the S2 Subzone, the base of which is marked by the Kingbridge Limestone. This is overlain by a second extensive sandstone, the Craighill Sandstone group also containing marine limestones, and the base of the D1 Subzone is near the top of this sandstone. In the D1 Subzone the lithology changes from one of predominantly arenaceous character to a more 'normal' Yoredale sequence of marine limestones separated by thinner sandstones and shale. Thus immediately above the Craighill Sandstone is the first of these D1 limestones, the Lanercost Limestone which is approximately equivalent to the level of the Beehive Band in the Stainmore Trough. This is followed by the Millerhill Limestone, the Appletree Limestone, the Leahill Limestone and eventually the Naworth Limestone which is equivalent to the base of the Melmerby Scar Limestone in the Stainmore Trough and on the Alston Block. Thus the limestone, shale and sandstone succession between the Lanercost and Naworth Limestones are equivalent to the continuous Potts Beck Limestone of Stainmore (and equivalent to the gap in the succession on the Alston Block). Above the Naworth Limestone is the Denton Mill Limestone and then the Bankhouses Limestone which is equivalent to the Smiddy Limestone of the Alston Block, and the succession above this is similar to the Yoredale succession of the Alston Block. Thus in this northernmost trough the Yoredale type sequence begins almost from the base of the Carboniferous. Moreover, the Yoredale sequence continues to a very high level in this region, the highest limestone, the Harlow Hill bed, being equivalent to the Botany Limestone of the Stainmore Trough.

CHAPTER 3

SKELETAL MORPHOLOGY OF THE LITHOSTROTIONTIDAE

This chapter described the different morphological elements of the skeleton present in the Lithostrotiontidae and lists in capital letters the morphological terms used in this thesis. Most of the terms refer to all rugose corals, but only those applicable to the Lithostrotiontidae are included here. The skeletal elements described are illustrated in figs. 3 and 4 .

All of the species in the family are COMPOUND corals, that is they are all colonial corals growing by asexual reproduction. One species, Aulina simplex, described by Hill (1934, p.93) is a SIMPLE (solitary) coral, but this is now not thought to be a member of the Lithostrotiontidae family (p.242). The skeleton of a single individual within the colony is termed the CORALLITE, the soft tissue of the individual is termed the POLYP and the skeleton of the entire colony is the CORALLUM. The skeletal parts of the corallite are built of a calcareous tissue termed SCLERENCHYME and Hill (1935 p.483) drawing an analogy with living corals, assumes this to be laid down as an exoskeleton by the ectoderm cells (soft tissue) of the polyp.

The skeletal parts of the corallite can be divided into two groups; the VERTICAL ELEMENTS (those being secreted parallel to the upward growth of the corallum) and HORIZONTAL ELEMENTS (secreted at right angles to the vertical elements). The parts of the elements where growth began are the PROXIMAL parts while the last formed parts are termed DISTAL parts.

The most important vertical elements of the skeleton are the SEPTA, radially arranged plates extending from the proximal apex of the corallite to the top. In the Lithostrotiontidae these are divided into two orders, MAJOR and MINOR septa, alternating with each other. In some species (L. martini) a third or TERTIARY order of septa may be present, while in

FIGURE 3

Diagram illustrating the main skeletal features of the Lithostrotiontidae as seen in transverse section.

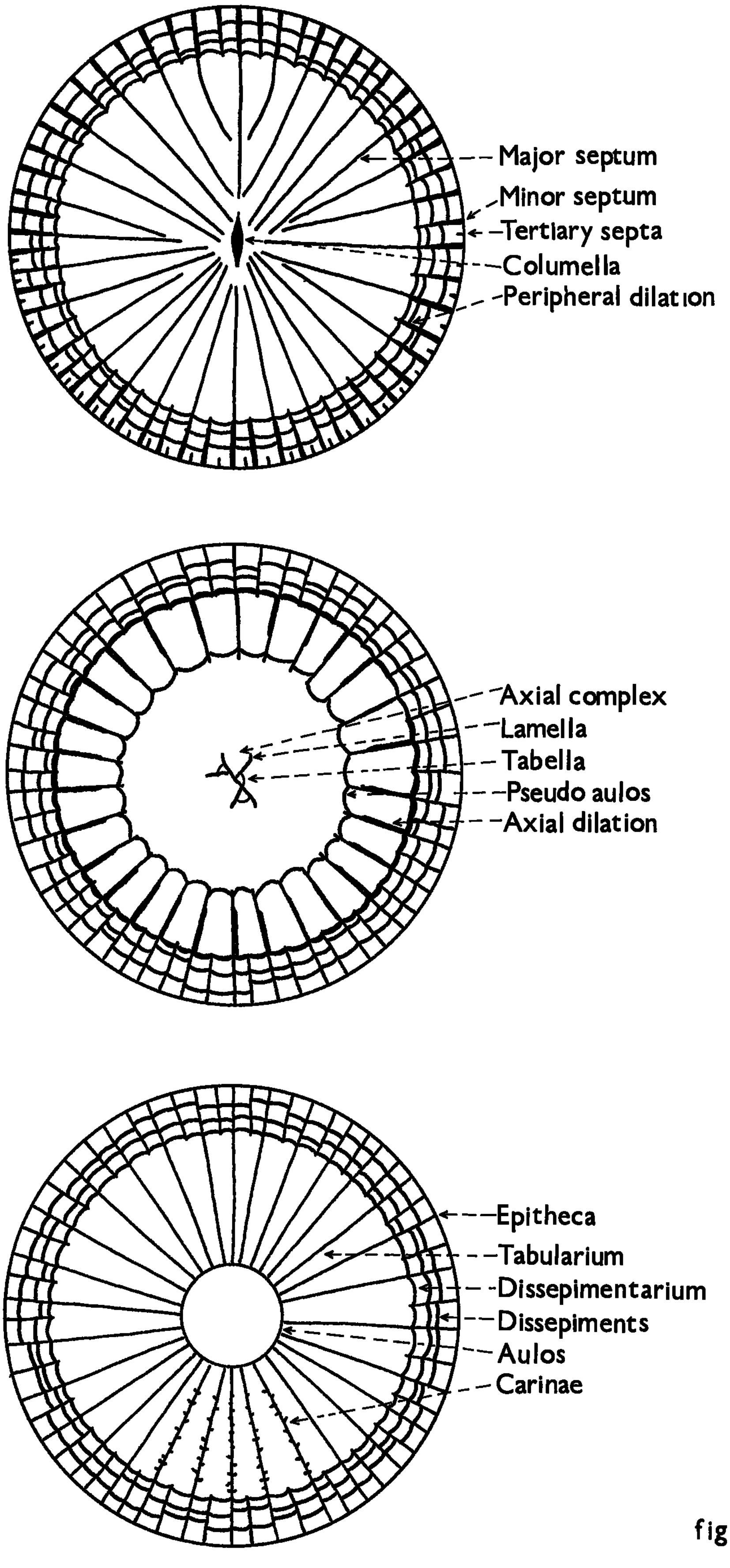

Major septum
Minor septum
Tertiary septa
Columella
Peripheral dilation
Axial complex
Lamella
Tabella
Pseudo aulos
Axial dilation
Epitheca
Tabularium
Dissepimentarium
Dissepiments
Aulos
Carinae

fig 3

others (L. junceum) only the major septa may be present. The space between two adjacent septa is an INTERSEPTAL LOCULUS. The three edges of the 'triangular' septa are also given different terms; the CALICULAR EDGE being its upper surface, the PERIPHERAL edge being the side attached to the corallite wall, and the AXIAL edge being the inner surface. Septa vary greatly in length, those in the columellate Lithostrotion and Orionastraea being LONG and reaching almost to the axis, while those of the diphyphylloid Lithostrotion species and Fascicaulina are generally SHORT. Septa are often dilated to a greater or lesser degree, the zone of dilation also varying. In the genus Lithostrotion the septa usually have a PERIPHERAL DILATION, while those of Orionastraea, Aulina and Hudsonia have an AXIAL DILATION. The sides of the septa of the Lithostrotiontidae are usually plane but they may be WAVY and rarely ZIG-ZAG in some of the ceroid species. Those of the genus Aulina and Fascicaulina are usually carinate bearing flanges or CARINAE. DISCONTINUOUS septa are common in the family and are of different kinds. First, those of the diphyphylloid species of Lithostrotion and some species of the columellate Lithostrotion are AMPLEXOID, being completely developed only on the upper surfaces of the tabulae. Secondly, some species of the columellate Lithostrotion and one species of the diphyphylloid Lithostrotion group may have LONSDALAEOID septa which do not extend all the way to the epithecae but become discontinuous in the dissepimentarium.

The second vertical skeletal element is the AXIAL structure. This may take several forms and in the Lithostrotiontidae four types are seen. Most common and occurring in the columellate Lithostrotion species and in two species of Orionastraea and one species of Hudsonia is a COLUMELLA, an axial rod, oval or lath shaped in cross section formed by the axial edges of some of the septa. In the columellate species of Lithostrotion, Orionastraea and Hudsonia it is a continuous structure running from the apex of the corallite to its growing edge, but in the diphyphylloid group of

FIGURE 4

Diagram illustrating the main skeletal features of the Lithostrotiontidae as seen in longitudinal section. d.=dissepimentarium, t.=tabularium, o.=outer series of tabulae, i.=inner series of tabulae.

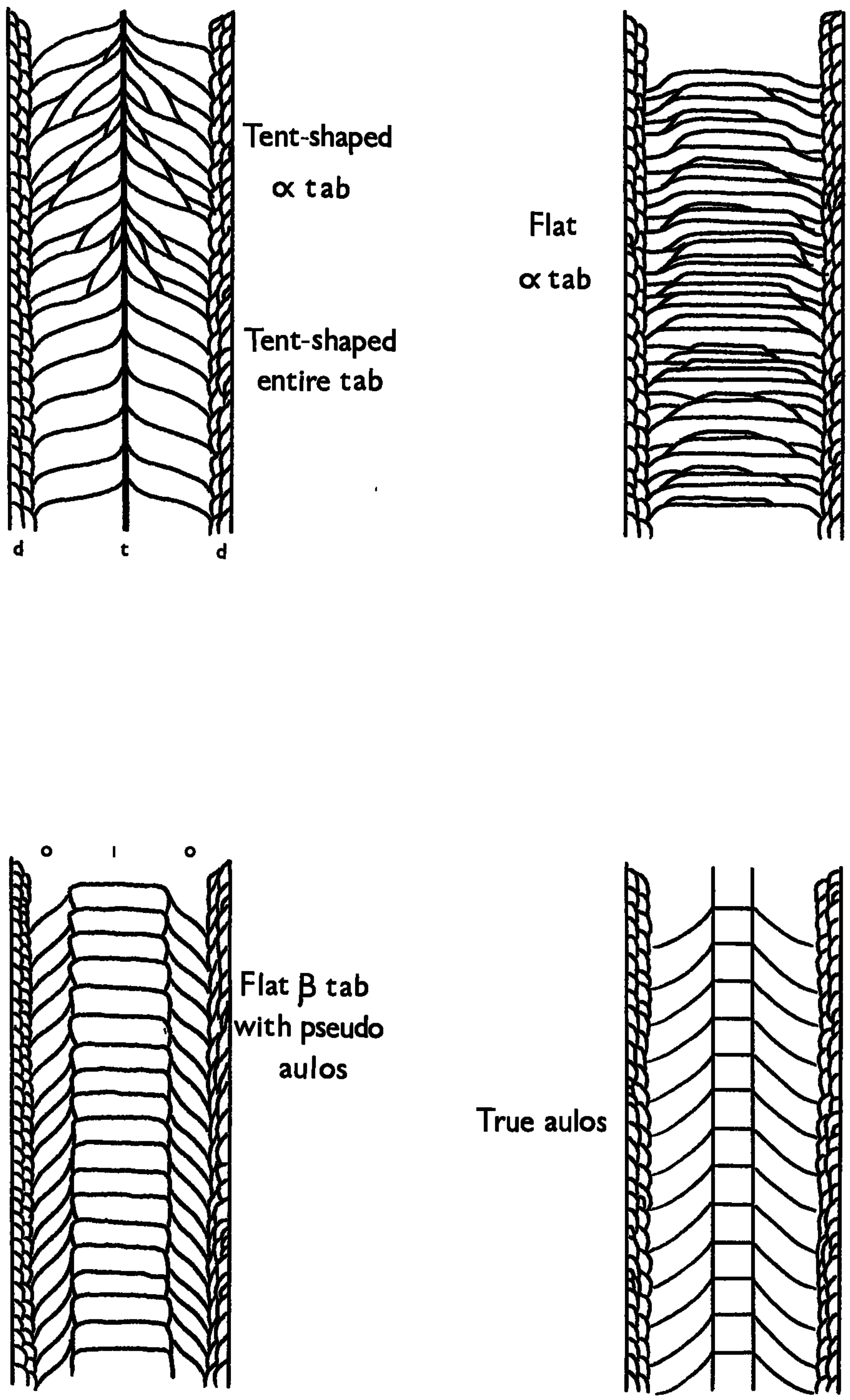

Tent-shaped
∝ tab
Tent-shaped
entire tab
d
t
d
Flat
∝ tab
o
I
o
Flat β tab
with pseudo
aulos
True aulos

fig 4

of *Lithostrotion* if it is present at all it is a discontinuous structure reduced to spines on the upper surfaces of successive tabulae. More commonly in the diphyphylloid group there is no axial structure at all. In the remaining species of *Orionastraea* and *Hudsonia* again the axial structure is absent, although often the counter septa does extend into the axial region and appears at first sight to be a columella but this is never dilated as a true columella always is. Another common axial structure seen in these corals is an AULOS, present in all the species of the genera *Aulina* and *Fascicaulina*. An aulos is a hollow axial tube running continuously down the length of the corallite. A true aulos is formed by the axial edges of all the septa bending through 90° so as to meet with the adjacent septa and produce a solid wall that divides the tabulae into an inner and outer series. This is an advanced condition and many of the more primitive species especially those in the diphyphylloid group do show a structure which may be mistaken for an aulos, but in these cases the 'wall' is produced by the downturned edges of the tabulae resting on the tabulae beneath. This structure, produced by the horizontal elements rather than the vertical elements, is not a true aulos, and the new term PSEUDO-AULOS is intoduced here for this structure. It is probably an intermediate structure which may develop into a true aulos in some lineages. It is noteworthy that the diphyphylloid lineage develops a pseudo-aulos, but never a true aulos, whereas in some more primitive examples of *Aulina* a pseudo-aulos is present and may develop towards a true aulos (p.36).

Finally, in the Nemistioid group of *Lithostrotion* there is a loosely formed and irregular axial structure which according to Smith (1928 p.116) "in some instances persists throughout the corallites and in others arises from successive tabulae and does not reach the tabulae above". This axial structure consists of a slender, somewhat irregular medial plate, a few radiating LAMELLAE and some steeply inclined TABELLAE (small sub-horizontal plates in the central part of the corallite forming part of an incomplete tabulae).

The final vertical skeletal element is the EPITHECAE, a thin calcareous coating covering most of the corallite except for its open top. A consistent epitheca is present around the corallites of the fasciculate *Lithostrotion* and the ceroid *Lithostrotion* and an inconsistent epitheca is seen in one species of *Hudsonia* and *Orionastraea*, while it is absent in the remaining species of these latter two genera and in *Aulina*. In the ceroid colonies of *Lithostrotion* and in *Hudsonia*, *Orionastraea* and *Aulina* a common calcareous sheath is present on the external surface of the corallum but not surrounding the individual corallites. This is a HOLOTHECAE. The epithecae and the holotheca may show both vertical and horizontal ornament. Vertical ornament may be a fine or coarse striation and is related to the vertical elements, the septa. Each groove on the external epithecae corresponds to the position of an internal septum and is termed a SEPTAL GROOVE, while each ridge on the epithecae corresponds to an interseptal loculus and is termed an INTERSEPTAL RIDGE.

Horizontal ornament or annulation (Smith and Ryder 1926, p.153) is present on the wall in varying degrees, and is a result of the periodic nature of the growth of a colony (see **Reprint**). Calcium carbonate is secreted in diurnal layers resulting in a horizontal ornament of GROWTH INCREMENTS, bands of tissue, separated by GROWTH LINES, a line marking an abrupt change in the character of the tissue (Clark 1974, p.1). As well as these diurnal horizontal ornamentations, both monthly and annual ornamentations may also rarely be present (see **Reprint**).

Horizontal skeletal elements are two-fold. First, are the TABULAE which are horizontal platforms usually extending continuously across the corallite and representing successive positions of the floor of the calyx. In the *Lithostrotiontidae* they may take on a variety of forms. The most simple are seen in the columellate group of *Lithostrotion* when the tabulae run uninterrupted from the columella to the epitheca (as in *L. junceum*) or to the dissepimentarium if one is present (as in *L. martini*, *L. pauciradiale* etc.). In all the columellate species the tabulae rise in the centre upon meeting the columella and can therefore be described as TENT-SHAPED. Some species however show a slight complication in that the tabulae are not so complete but instead their edges turn sharply downwards to rest on the tabulae below, while a second series of smaller tabulae then runs from the downturned edge to the dissepimentarium. In these cases the tabulae can be divided into an INNER (or AXIAL) and an OUTER (or PERIPHERAL) series. This situation is seen in some examples of the species mentioned above and also in the cerioid species. When this condition is first seen the points of contact of the downturned tabulae onto the tabulae below is haphazardly arranged, a condition described by Smith (1928) as α tabulae, but as evolution progresses the points of contact gradually become aligned and the successive downturned edges of the inner series form a wall-like structure previously described as a PSEUDO-AULOS. This case, described by Smith (1928) as β tabulae, is most often seen in the species of the diphyphylloid group when due to the absence of any axial structure the inner tabulae are not tent-shaped but entirely flat, with the outer series still steeply inclined. In the species with a true aulos, i.e. *Aulina* and *Fascicaulina* the division between the inner and outer series is made even more clear as they are separated by the septal tube. In these cases the outer series also becomes horizontal.

The area of the corallite containing the tabulae is known as the TABULARIUM and this occupies the inner or axial region of the corallite. On the periphery of the corallite outside the tabularium is the DISSEPIMENTARIUM, the area containing the second horizontal skeletal element, the DISSEPIMENTS. These are much smaller arched plates built between adjacent septa and lining the interior of the epithecae. They are present in all the species of the *Lithostrotiontidae*, except for *L. junceum*, but they vary greatly in number from a single row, in the small fasciculate species, to eight or nine in some of the larger cerioid species. Almost invariably in the Lithostrotiontidae the innermost series of dissepiments is dilated to a certain degree. In most of the species the major and minor septa are continuous to the epithecae so that the sides of the dissepiments abut on to the sides of the septa. The dissepiments are then arranged in a CONCENTRIC manner. However in some specimens, especially of the cerioid species, the minor septa degenerate to setpal ridges only. The inner dissepiments then lose the concavity of their upper surface and meet at an angle on alternate sides of the loculus left between two major septa. As seen in transverse section this gives a HERRINGBONE pattern. A third type of dissepiment is seen when both the major and the minor septa become degenerate and do not extend all the way to the epithecae. In this case, seen only rarely in the Lithostrotiontidae a space is left between the peripheral edges of the septa and the epithecae which is filled entirely by large LONSDALAEOID dissepiments. In almost all the species of this family all the dissepiments are concave inwards and in every species the inner ring is always in this condition. However in some species of Orionastraea the outer series of dissepiments becomes convex inwards and when this happens these are often quite angular. In one species of Orionastraea these convex dissepiments break at this angle and turn to lie parallel to the septa lining the septal sides.

The final morphological character of a corallite is the CALICE. This is a depression at the distal end of a corallite bounded laterally by the walls of the corallite and at its base by the last formed tabula. This depression is subdivided by the axial edges of the septa. According to Hill (1935 p.495) "many calices show a central cavity corresponding to the tabularium the AXIAL or CALICULAR PIT which may, or may not, contain a CALICULAR BOSS corresponding to an axial structure. Forms with a calicular pit have a PERIPHERAL or CALICULAR PLATFORM between the pit and the periphery". In the fasciculate species the calice is quite deep. This is less so in the cerioid species and in *Orionastraea*, *Aulina* and *Hudsonia* it is quite flat.

In addition to these terms describing the corallite there are also some useful terms applicable to the corallum regarding the stage of colonialism within the colony. The most primitive type of colony seen in many *Lithostrotion* species is FASCICULATE where the individual corallites are independent and not in contact except at their bases. Fasciculate coralla may be DENDROID with spreading branches, as in the early *L. martini* colonies, or PHACELOID with almost parallel and more closely packed branches, as in *L. junceum*. Some phaceloid coralla may have their corallites joined by CONNECTING PROCESSES but this is only seen in one species of *Lithostrotion*, again *L. junceum*. However many phaceloid species of *Lithostrotion* do have connections from corallite to corallite when a phaceloid corallum becomes periodically cerioid. This is an intermediate stage of colony between the fasciculate colonies and the MASSIVE colonies. A massive corallum is one in which the neighbouring corallites are in contact with each other. Massive coralla may be CERIOID when each corallite is bounded by an epithecae as in *L. aranea*, *L. verticale*, *L. decipiens* etc., or PLOCOID when no epithecae is present between corallites as in *Orionastraea*, *Hudsonia* and *Aulina*. The species of the plocoid *Orionastraea* take on different forms; they may be ASTRAEOID when the corallites have continuous but not confluent septa, THAMNASTRAEOID when the corallites have continuous and confluent septa, APHROID, when the septa withdraw from the periphery and the neighbouring corallites are united by dissepiments only, or finally when the septa are absent altogether and the corallum is composed of tabulae and dissepiments only, the colony can be described by the new term INDIVISOID proposed here.

PART 2

PALAEONTOLOGICAL CONCLUSIONS

CHAPTER 1

PHYLOGENY

The Early Lineage

Little evidence has been given so far as to the ancestors of the *Lithostrotiontidae*. The earliest example of *Lithostrotion* found in Ravenstonedale, Cumbria occurs in the *Thysanophyllum* Limestone immediately below the Brownber Pebble Bed in the C2 Subzone. This species is *L. martini*, but it appears more simple than later colonies of the same species and has thus been described as a separate sub-species, *L. martini praenuntium* (p.173). It shows a number of primitive characters:

(a) Conical shape to the corallites.

(b) Widely spaced dendroid form of growth to the corallum.

(c) Closely spaced growth lines.

(d) Closely spaced tabulae.

The most important distinction between this form and later colonies of the species however is the high number of dissepiments seen in this sub-species; there may be up to six rows present. This fact, plus the closely spaced conical tabulae, means that any one section across such a corallite cuts across both a high number of dissepiments and tabulae and hence has the appearance of a closely spun web.

This subspecies is restricted to the *Thysanophyllum* Limestone and above the Brownber Pebble Bed in the Ravenstonedale Limestones it immediately evolves to the more usual *L. martini martini* with:

(a) Cylindrical corallites.

(b) Phaceloid growth habit.

(c) Wider spaced growth lines and tabulae.

(d) Fewer dissepiments (only three to four rows).

This common subspecies persists until the Jew Limestone (D2 Zone), but in the S2 *D. carbonaria* limestones it gives rise to a third subspecies,

FIGURE 5

Diagrammatic illustration of the early lineage of the Lithostrotiontidae with L.martini evolving by a reduction of dissepiments.

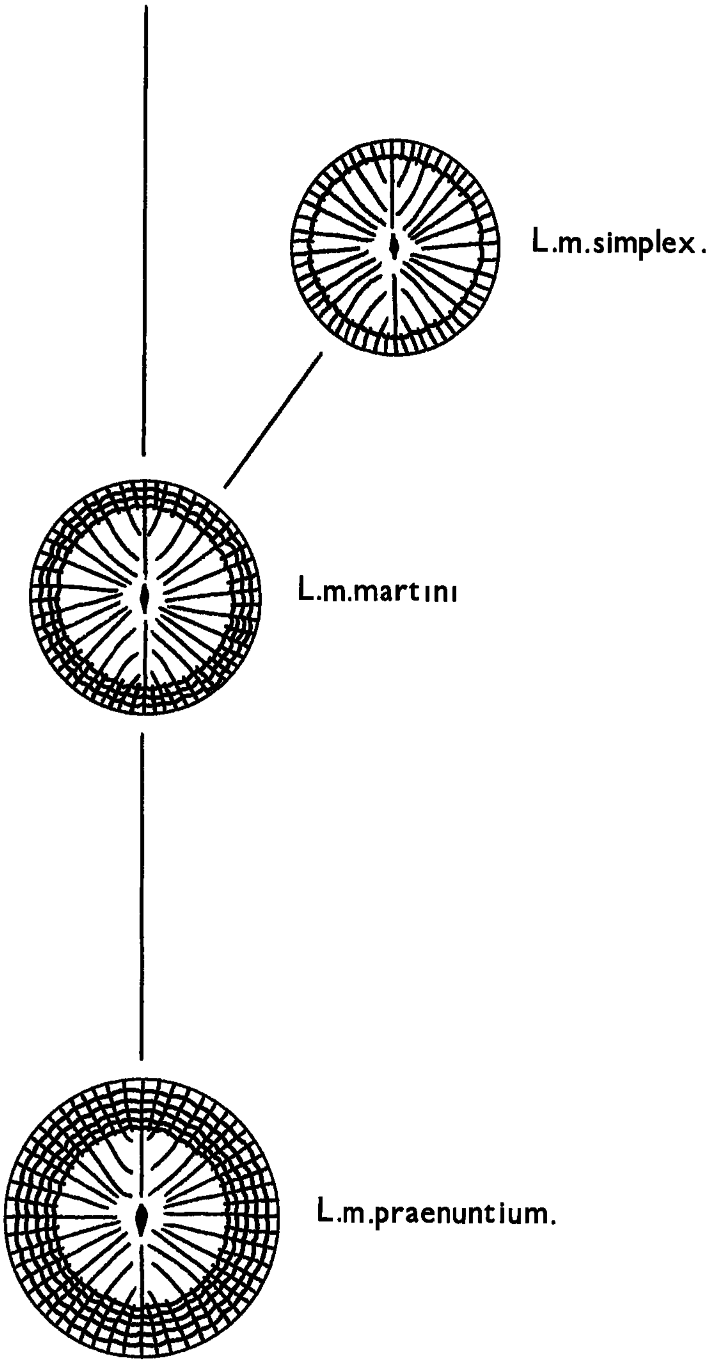


fig 5

L. martini simplex (fig. 5) which has just a single row of dissepiments. However this subspecies has a restricted range as it is found only in the S2 Subzone.

Characters constant in all subspecies of L. martini are septal number (26-28 maximum septa in a colony) and tabularium diameter (mean 5.7 mm.) and these can thus be considered as specific characters.

Primary Radiation

In the Seminula Zone the fasciculate lineage of L. martini begins to evolve along a number of definite 'trends'. First is a change in the growth habit of the lineage. The individual corallites of a colony cease to become laterally free from adjacent corallites, but instead are in contact on all sides with their neighbouring corallites and hence form a cerioid type of colony. Secondly there is a change in the method of budding in the colonies such that the non-parricidal lateral budding of L. martini is replaced by parricidal calicular budding. This change also involves the loss of the columella producing a diphyphylloid type of colony.

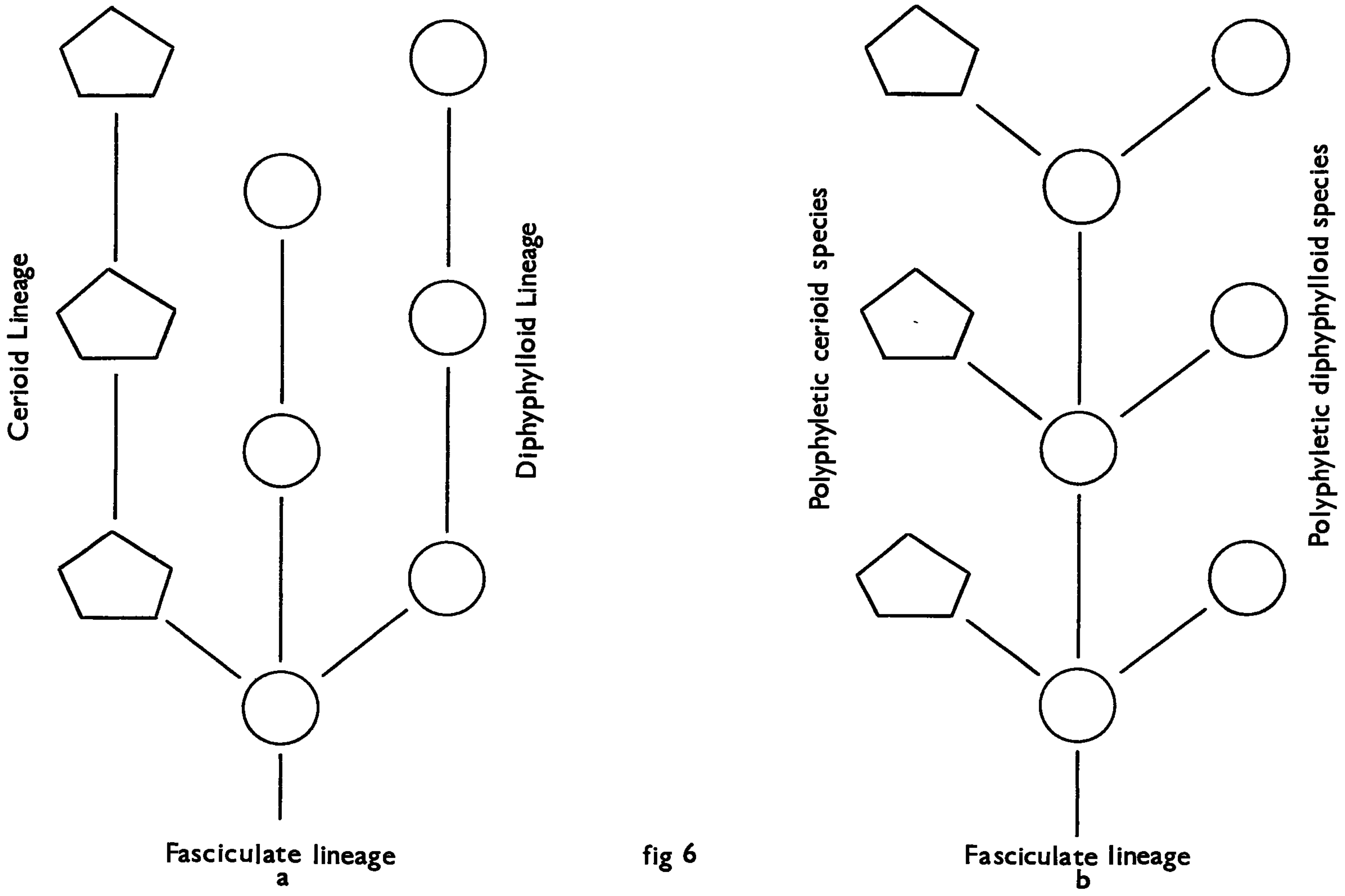
Concurrently the columellate fasciculate lineage of L. martini continues to evolve independently producing subsequent columellate fasciculate species. Previously it has been thought that evolution along those two trends represents separate lineages, i.e. a cerioid lineage and a diphyphylloid lineage. By this theory (fig. 6a) the trend would occur only once in the fasciculate columellate lineage producing, for example, an ancestral cerioid species which later gave rise to subsequent cerioid species. These supposed lineages were classed as genera or subgenera (e.g. Genus Diphyphyllum for the non-columellate group of species, and the subgenus Lithostrotion (Lithostrotion) for the cerioid species, as opposed to L. (Siphonodendron) for the fasciculate species). It is now thought however that the genetic ability to evolve along these two trends

FIGURE 6

Theories of evolution in the *Lithostrotiontidae*.

a. Diagram showing the 'standard' theory of evolution in the *Lithostrotiontidae*. The fasciculate lineage of *Lithostrotion(Siphonodendron)* was thought to give rise to a cerioid lineage of *Lithostrotion(Lithostrotion)* and to a non-columellate or diphyphylloid lineage of *Diphyphyllum*.

b. Diagram showing the polyphyletic evolution of the *Lithostrotiontidae* as described in this thesis, whereby each fasciculate columellate species gives rise to a cerioid species and a diphyphylloid species.



Fasciculate lineage
a

Fasciculate lineage
b

fig 6

is incorporated in the fasciculate lineage early on, and that each of the later fasciculate columellate species follows the same two trends. Thus each fasciculate columellate species has a cerioid and a diphyphylloid ancestor (fig. 6b).

There are two pieces of evidence for this; first, is the occurrence of intermediate coralla, i.e. at the correct stratigraphic position between each fasciculate species and its cerioid successor, are found partly fasciculate/partly cerioid coralla. Similarly, early members of each diphyphylloid species show a degenerate columella. Secondly is the similarity of all of the other characters between each fasciculate columellate species and its cerioid and diphyphylloid ancestors (see Table 3). Because these sub-genera and genera (e.g. Diphyphyllum) are polyphyletic they are abandoned in this thesis (p.119).

Thus the cerioid expression of L. martini martini is L. aranea S.S. (fig. 8) which is similar in all characters (septal number, diameter of tabularium) to L. m. martini except for its growth form. L. aranea evolves in the D. carbonaria limestones of the S2 Subzone, but intermediate colonies with partly cerioid and partly fasciculate corallites occur at the top of the S1 Subzone and at the base of S2 (see discussion in Chapter 3).

The diphyphylloid expression of L. m. martini is L. lateseptatum (fig. 8) which first appears in the Ashfell Sandstones (S1 Subzone). This differs from L. m. martini in having calicular budding as opposed to the lateral budding of L. m. martini and also in having no columella. Thus, as in all non-columellate species that have followed such a diphyphylloid trend the septa also tend to be shorter and the tabulae flatter than in its columellate ancestor. More important, the septal number also differs from L. m. martini, there being a maximum of anything up to 34 septa. However, this is not due to any additional genetic change controlling septal number, nor does it show a lack of relationship with L. m. martini, instead it is a direct result of the new method of

TABLE 3

Table showing the polyphyletic evolution of the cerioid group and the diphyphylloid group from the columellate/fasciculate group. Note the similarity of characters between each columellate/fasciculate species and its respective cerioid and diphyphylloid ancestors.
R.= range of maximum number of septa in a colony;
M.T.= mean tabularium.
The figures for the diphyphylloid species tend to be rather higher than their fasciculate ancestors due to the prevalence of calicular increase (see p.96).

Diphyphylloid Group	Columellate/Fasciculate Group	Cerioid Group
		L.maccoyanum R = 11-14 M.T. = 1.6
L.gracile R = 18-24 ← M.T. = 3.0	*L.pauciradiale* R = 18-20 → M.T. = 2.6	↑ *L.decipiens* R = 14-18 M.T. = 2.5
L.fasciculatum R = 22-29 ← M.T. = 4.2	↑ *L.irregulare* R = 21-26 — M.T. = 4.2	
L.furcatum R = 26-30 ← M.T. = 5.3	↑ *L.variabile* R = 22-26 → M.T. = 4.6	*L.vorticale* R = 19-24 M.T. = 4.2
L.lateseptatum R = 28-34 ← M.T.. = 6.9	↑ *L.martini* R = 26-28 → M.T. = 5.7	*L.aranea* R = 26-31 M.T. = 6.0

Table 3.

budding. It has been explained on p. 96 that any calicular budding species shows a sudden increase in the diameter and hence in septal number in its corallites immediately prior to splitting. It is only those corallites that are about to divide, i.e. the super mature corallites, that support the high number of septa, the majority of corallites (i.e. the mature corallites) having the same number of septa as the ancestral species *L. m. martini* (i.e. 26-28). Furthermore, *L. lateseptatum* must evolve from *L. martini* as this is the only other fasciculate species present at the time that *L. lateseptatum* evolves. Similarly the tabularium of *L. lateseptatum* tends to be rather larger than *L. martini*.

Also during this primary radiation, two important changes occur in the independently evolving fasciculate ~~evolving fasciculate~~ columellate lineage and these changes paradoxically occur in opposite directions. First, a much larger fasciculate columellate species evolves from *L. martini*, again, the evidence for this evolutionary link being that *L. martini* is the only species present from which it could have evolved. This new species, *L. scaleberense* (fig. 7) has 34-39 septa and a tabularium with a mean diameter of 11.8 mm. and has so far only been recorded from its type locality at Scaleber Quarry, near Settle, Yorkshire.

The second change seen in the fasciculate columellate lineage at this time is the appearance in the (S1) S2 Limestones around Kirkby-Stephen of a smaller species than *L. martini*. It has a mean tabularium diameter of only 4.6 mm. and usually has only 20-24 septa (although rare examples with 26 septa have been recorded) and retains the two to four rows of dissepiments of *L. martini*. This form has probably previously been recorded as *L. martini*, but even if there is continuous variation between this form and *L. martini* S.S. there is stratigraphic evidence to warrant the recognition of the smaller form as a new species as this smaller form does not appear before S2 (? or the top of S1). Thus it is described in this thesis as *L. variabile* (fig. 7). It is thought that the reason why

FIGURE 7

Diagrammatic illustration of the primary radiation of the *Lithostrotiontidae* lineage. *L.martini* gives rise to a larger species(*L.scaleberense*) and a smaller species (*L.variabile*).

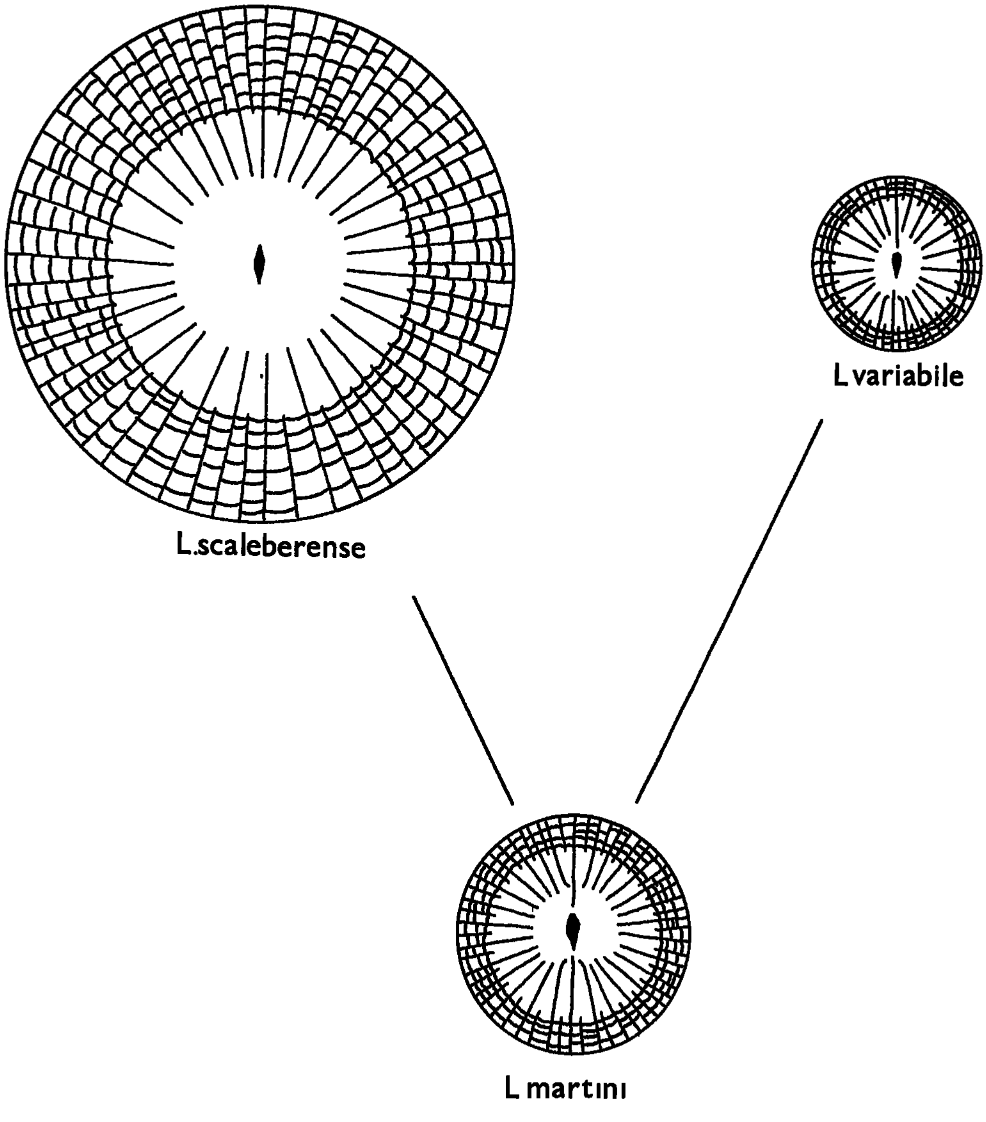


fig 7

L. martini evolves in opposite directions at the same time is that the two species evolved in different areas. The large *L. scaleberense* only occurs in South Yorkshire close to the reefs in what must be a more favourable area for coral growth, whereas the small *L. variabile* occurs more abundantly further to the north in less favourable conditions (i.e. darker limestones).

During the primary radiation *L. variabile* also follows the two evolutionary trends and a second piece of evidence for the recognition of *L. variabile* as a distinct species from *L. martini* is that a second cerioid species has long been recognised which bears the same relationship to *L. variabile* as *L. aranea* does to *L. martini*. The cerioid expression of *L. variabile* is *L. vorticale* (= *L. minus* = *L. basaltiforme* = *L. flemingi* = *L. striatum* = *L. clavaticum* = *L. portlocki* S.S.). *L. vorticale* (fig. 8) has a similar tabularium diameter (4.2 mm.) as *L. variabile* and has the same number of septa (20-24) and first appears in the S2 Subzone. Evidence for supposing that *L. vorticale* evolves from *L. variabile*, and not directly from the already cerioid species *L. aranea* by a reduction in size, is first, the similarity in septal counts and tabularium diameter between *L. variabile* and *L. vorticale*, and secondly the fact that partly cerioid colonies of *L. variabile* have been found as an intermediate stage. Thus the cerioid trend occurs for a second time in the fasciculate lineage and so *L. aranea* and *L. vorticale* are not members of a separate cerioid lineage but instead are independently evolved cerioid species from the fasciculate lineage.

Similarly the diphyphylloid trend expresses itself in *L. variabile*, the resulting new species being *L. furcatum* (fig. 8). Again this has a similar tabularium to *L. variabile* but differs in its lack of columella, its shorter septa, flatter tabulae and parricidal calicular method of budding. Also, as with *L. lateseptatum* it has a higher maximum number of septa (30) than its ancestor, but again the majority of the corallites do have only 20-24 septa. *L. furcatum* makes its first appearance in the

FIGURE 8

Diagrammatic illustration of the primary radiation of the Lithostrotiontidae lineage. L.martini evolves to L.variabile and both of these fasciculate columellate species give rise to a cerioid and diphyphylloid successor.

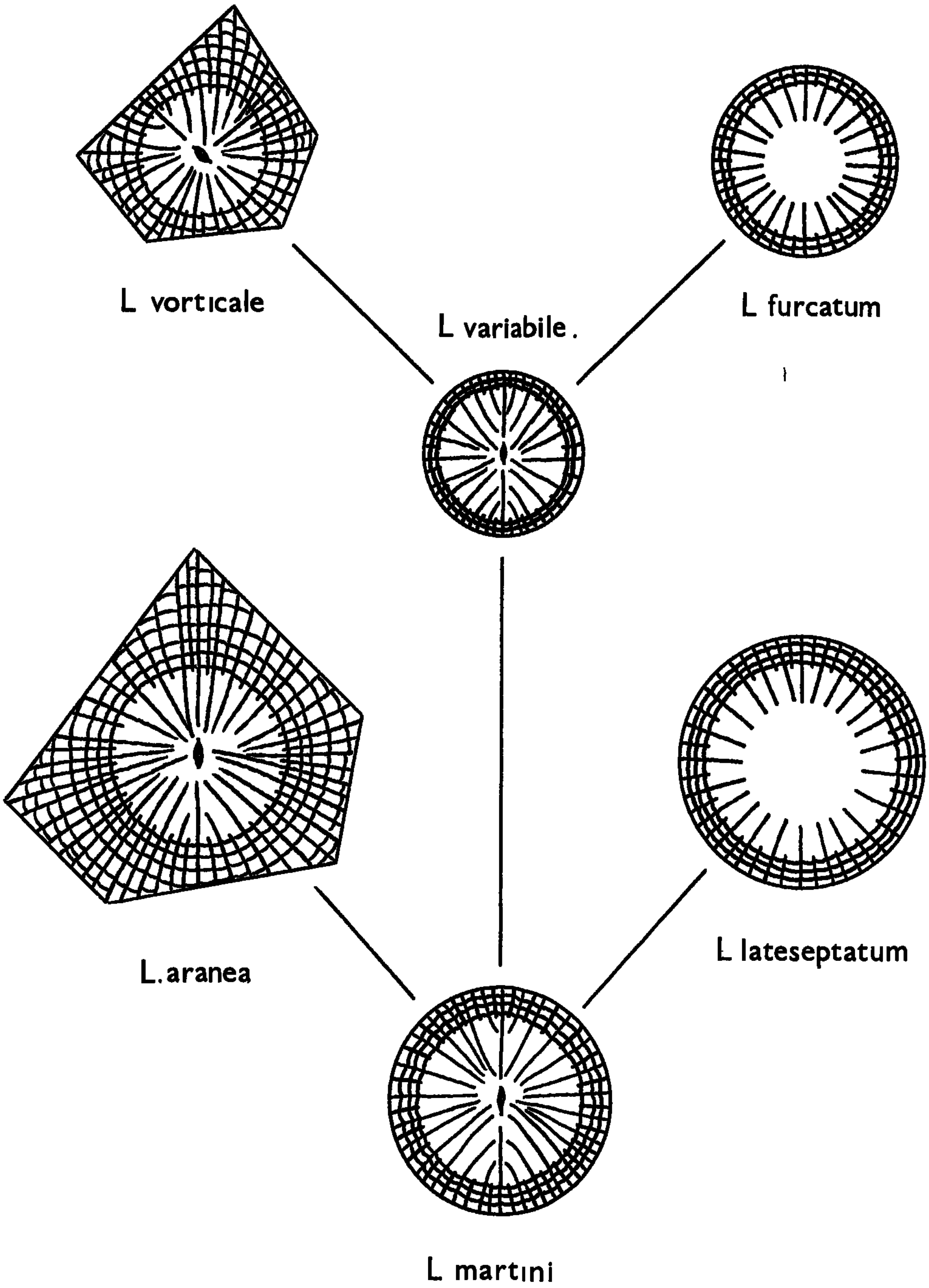

L vorticale
L variabile.
L furcatum
L.aranea
L lateseptatum
L martini

fig8

Great Scar Limestone (D1 Subzone).

Evidence for *L. furcatum* evolving from *L. variabile* and not direct from the diphyphylloid *L. lateseptatum* is first, similarity of all other characters, secondly that while they both show parricidal budding, the nature of the budding is different, being axial in *L. furcatum* and peripheral in *L. lateseptatum*, and finally some early colonies of *L. furcatum* do show a gradual degeneration of the columella, it being represented as spines on successive tabulae. If evolution of *L. furcatum* was direct from the non-columellate *L. lateseptatum* one would expect *L. furcatum* to be entirely free of a columella.

Second Radiation

L. variabile persists into the D2 Subzone, but in D1 a second major radiation occurs when it gives rise to three more fasciculate columellate species namely *L. irregulare*, having 21-24 (rarely 26) septa and one row of dissepiments, *L. pauciradiale* having 18-20 septa and one row of dissepiments, and *L. junceum* with 14-18 septa and no dissepiments (fig. 9).

These three species may in fact form a continuous variation series, but there is sufficient difference between the end members to warrant some sort of separation.

Also in this radiation a final fasciculate columellate species evolves from *L. martini*. This is *L. sociale* (fig. 9) which appears in the D1 Subzone. It is similar to *L. martini* but has a slightly larger tabularium diameter (mean 7.2 mm.) and more septa (29-32). Again as with *L. variabile* there is continuous variation in septal number between *L. martini* and *L. sociale* but the stratigraphic evidence warrants the recognition of this species as these larger forms with over 28 septa do not occur below the base of D1.

Some of these species are also affected by the cerioid and diphyphylloid trends almost as soon as they appear in this evolutionary radiation.

FIGURE 9

Diagrammatic illustration of the second radiation of the *Lithostrotiontidae* lineage. *L.variabile* gives rise to *L.irregulare*, *L.pauciradiale* and *L.junceum*, and *L.martini* gives rise to *L.sociale*.

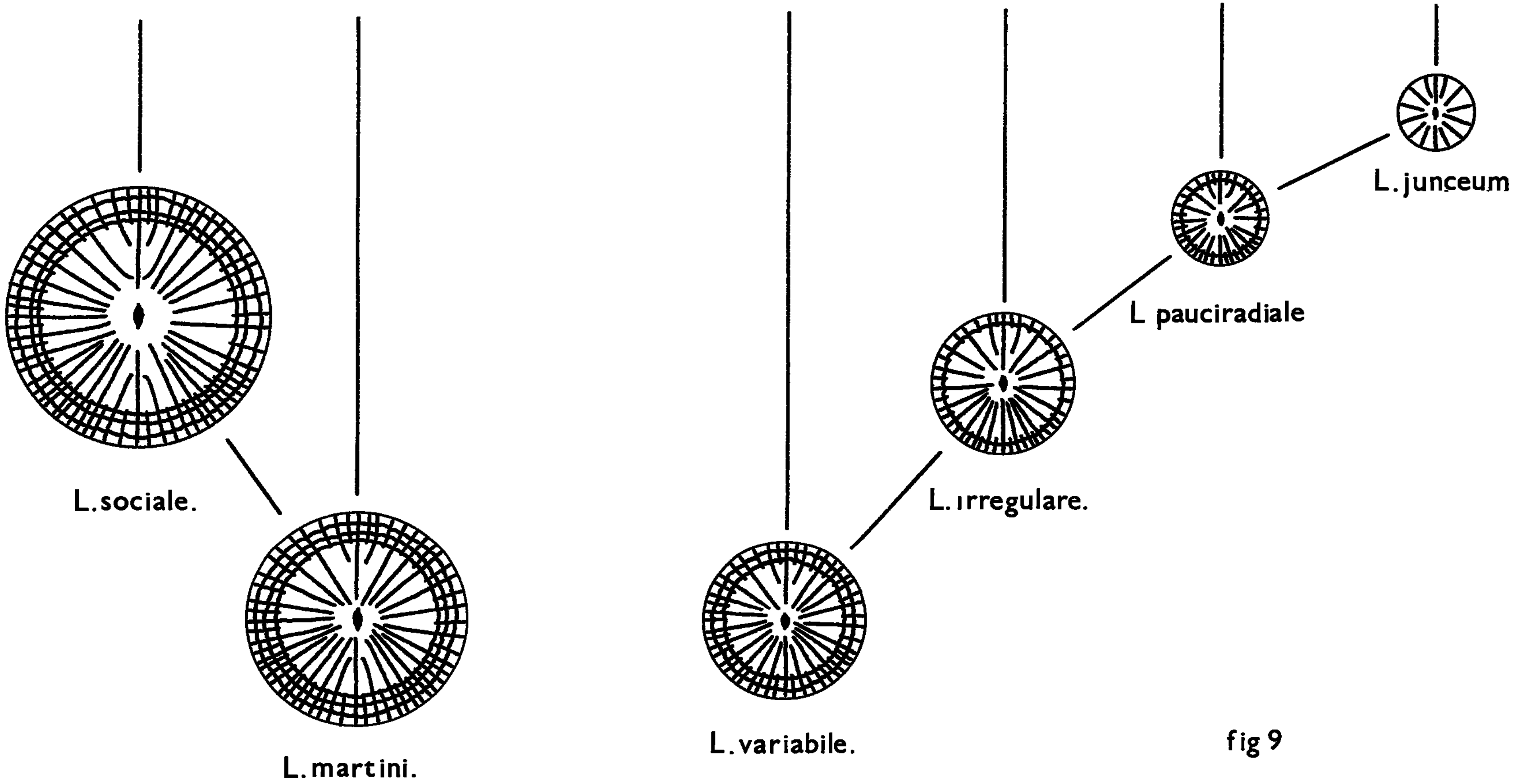

L.sociale.
L.martini.
L.variabile.
L.ırregulare.
L pauciradiale
L.junceum

fig 9

It is not known, however, whether L. irregulare has a cerioid descendant or not. The only difference between L. variabile and L. irregulare is in the number of dissepiments. When a species becomes cerioid the number of dissepiments ceases to be of any use as a distinguishing character as all cerioid species have a high number of dissepiments as it is the dissepimentarium that expands laterally when producing the cerioid growth habit. Thus there is no method of distinguishing between a cerioid descendant of L. irregulare and L. variabile as they would be identical in all respects including the number of dissepiments. Thus, some part of L. vorticale may have evolved from L. irregulare, it is not yet possible to separate this cerioid species.

L. pauciradiale on the other hand definitely does follow a cerioid trend (fig. 10) and produces the cerioid descendant L. decipiens (= L. clissioides = L. portlocki of Edwards and Haime but not L. portlocki S.S.). Again L. decipiens is identical to L. pauciradiale in every respect except for its growth habit, having a tabularium mean of 2.5 mm. and possessing 14-18 septa. However, it will be seen that the range of variation of the two species is dissimilar; while the larger examples of L. pauciradiale can have 19 or 20 septa and thus grade upwards into L. irregulare, L. decipiens never has more than 18 septa and is therefore exclusively distinct from L. vorticale there being discontinuous variation.

If L. pauciradiale and L. variabile were a continuously variable population then two distinct points on this continuous variation have followed the same cerioid trend, but in different geographical areas. Separation was such that initial interbreeding between the two was not possible and they did not migrate into the same area until after the point in time when interbreeding capacity had ceased. This is quite feasible because if there is a continuous interbreeding population between L. pauciradiale and L. variabile then it is likely that the different size orders of this variation were existing in different environments (the

FIGURE 10

Diagrammatic illustration of L.irregulare and L.pauciradiale giving rise to cerioid species in the second radiation of the Lithostrotiontidae lineage and to diphyphylloid species in the final radiation.

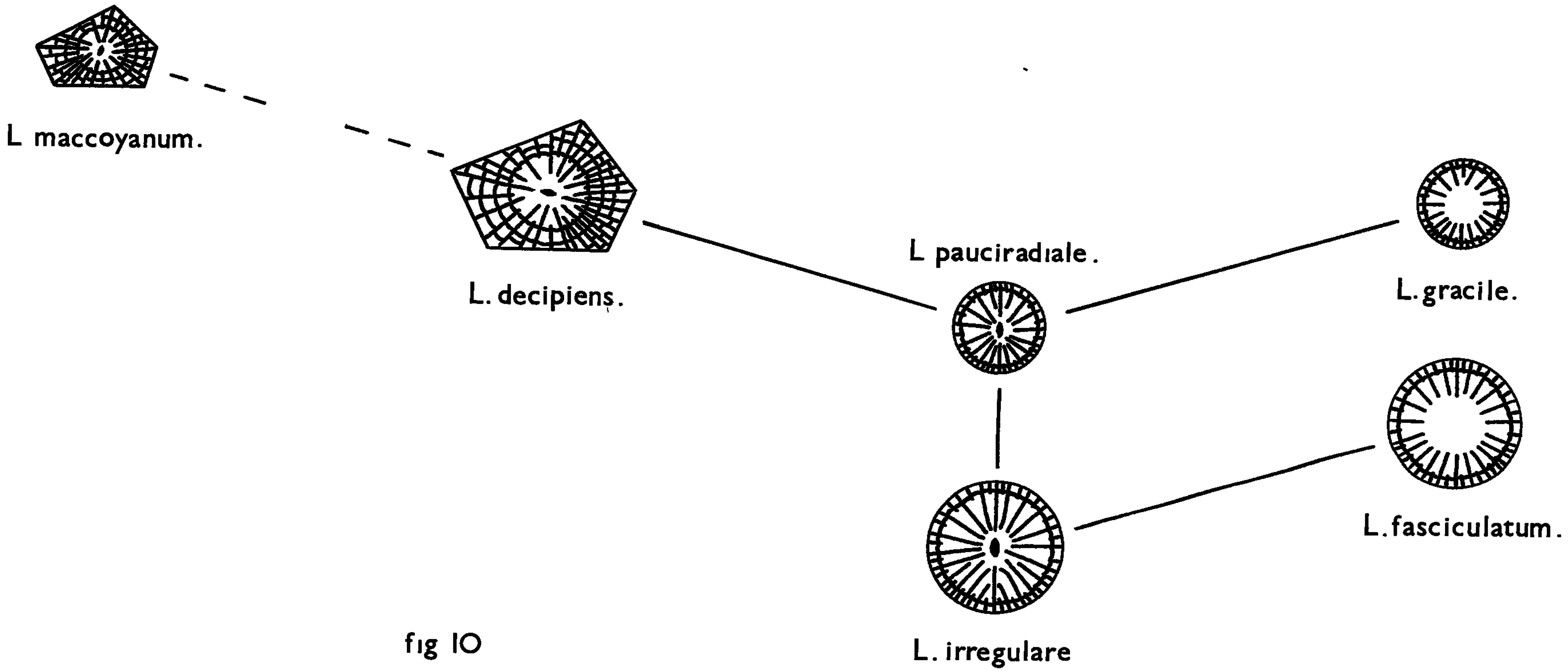

L maccoyanum.
L. decipiens.
L pauciradiale.
L. gracile.
L. fasciculatum.
L. irregulare

fig 10

smaller members being in the more adverse environments) and so they would have been geographically separated. At any rate the existence of a third cerioid species is extra evidence for recognising its ancestor *L. pauciradiale* as distinct from *L. irregulare* (p.161).

Again partly cerioid colonies intermediate between *L. pauciradiale* and *L. decipiens* have been found extensively low in the D1 Subzone just before *L. decipiens* appears.

L. junceum does not follow a cerioid trend and the reason for this may be that it has no dissepimentarium that could extend laterally to produce such a colony. This argument is strengthened by the fact that some sort of lateral connection between corallites appears to be advantageous to the coral and *L. junceum*, unable to do this by becoming cerioid, achieves the same end in a way seen in no other species of *Lithostrotiontidae*. In the Scar Limestone *L. junceum communicatum* is seen to achieve at least a temporary connection in the form of transverse connecting processes. This type of structure may not be formed to achieve any cellular connection, but instead may just be a skeletal strengthening to the colony (p. 67).

A fourth cerioid species, *L. maccoyanum*, does occur, appearing in the D1 Subzone. While this has 14 septa the same as *L. junceum* and is of similar dimensions, it is doubtful if it evolves from *L. junceum* because *L. junceum* has no dissepiments. Specimens of *L. maccoyanum* have not been found with partly fasciculate coralla and so this species may not evolve from a fasciculate ancestor, but may descend directly from a larger cerioid species, e.g. *L. decipiens* (see also p.153).

Final Radiation

In the D2 Subzone a final radiation occurs and many new species appear. Both *L. irregulare* and *L. pauciradiale* follow the diphyphylloid trend and their diphymorph descendants *L. fasciculatum* and *L. gracile* respectively bear the same relationship to each other as do their ancestors in that there is continuous variation between them (fig. 10). *L. gracile* can have mature corallites with 16-20 septa but super mature corallites with 21-24 septa, while *L. fasciculatum* has mature corallites with 21-24 septa and super mature corallites with 25-28 septa. However the great difference between the end members does warrant some sort of separation of the two forms. Also the fact that the variation between *L. fasciculatum* and *L. gracile* is identical to the variation between *L. irregulare* and *L. pauciradiale* is good evidence that these diphyphylloid species do evolve from the respective columellate ancestors and not from *L. furcatum*. Again they are identical in all other characters and not only can the gradual degeneration of the columella be followed in both *L. fasciculatum* and *L. gracile*, but also a gradual change in the tabulae of *L. irregulare* and *L. pauciradiale* can be seen towards the type of tabulae in *L. fasciculatum* and *L. gracile* (p. 58).

There is additional evidence that *L. fasciculatum* evolves from *L. irregulare* provided by a further species which appears in this final radiation. This species, called *Nemistium edmondsi* by Smith (1928), is restricted to the Jew Limestone, and is morphologically intermediate between *L. irregulare* and *L. fasciculatum*. Like these two species it has 21 - 24 septa and one dissepiment, but it differs in its axial structure. Smith (1928) describes this axial structure as consisting of lamellae and tabellae, but these are never well developed and in reality the axial structure is more of a degenerate columella rather than a true axial complex. If this is true then *N. edmondsi* is an intermediate evolutionary link between *L. irregulare* and *L. fasciculatum*. This is backed up by stratigraphic evidence as *N. edmondsi* appears in the Jew Limestone and *L. fasciculatum* appears in the succeeding Tyne Bottom Limestone. This also rejects Smith's theory that *N. edmondsi* developed from *L. fasciculatum* by reforming the axial complex. If *N. edmondsi* is intermediate between *L. irregulare* and *L. fasciculatum* then the genus *Nemistium* must be abandoned.

One further trend affects the *Lithostrotiontidae* and again the resulting species have previously all been grouped into one genus assuming that the trend affected only one initial species. This trend is the loss of the dividing wall between corallites producing a plocoid type of colony. Again evidence is forthcoming that this trend affects two parent species and therefore that the resulting plocoid species should be divided into two genera. This trend begins to occur lower down in D1, but it is during the final radiation of D2 that the majority of species appear. The first stage that is seen in this trend is a change in the shape of the colony of *L. decipiens*. While the early colonies of this species are tall and bun-shaped, later colonies are flat and spreading. This type of colony has been described as *L. decipiens depressum* and this subspecies may give rise to *Orionastreae ensifer* when the epithecae dividing the corallites becomes thin and inconsistent. However there is some doubt regarding this evolutionary link as *L. decipiens depressum* has so far not been recorded from lower than the Tyne Bottom Limestone and yet *O. ensifer* appears in the top of D1. If *O. ensifer* does not evolve from *L. decipiens depressum*, then it evolves from *L. d. decipiens* and *L. d. depressum* marks the evolution of a flat type of colony for a second time in the same lineage. *O. ensifer* is identical in all other respects to *L. decipiens*. *O. ensifer* evolves to *O. phillipsi* when the wall disappears completely and so *O. phillipsi* is the first truly plocoid species. *O. phillipsi* then evolves to *O. tuberosa* by losing its columella. These first three *Orionastraea* species all retain many of the morphological characteristics of *L. decipiens* including a tabularium diameter of 2.5 mm. and septal counts of 15 - 18 major septa (30 - 36 total septa.) However, almost as soon as *O. tuberosa* appears a change occurs in the range of the number of septa, some of these non-columellate individuals having only 20 - 28 septa. Although initially there is a continuous series of variation between *O. tuberosa* and the smaller form, above the base of the Tyne Bottom Limestone it is only the smaller types that occur; no forms above this horizon occur with over 30 septa. On this stratigraphic evidence therefore these two size orders have been described

FIGURE 11

Diagrammatic illustration of the evolution of the genus *Orionastraea* from *L. decipiens*.

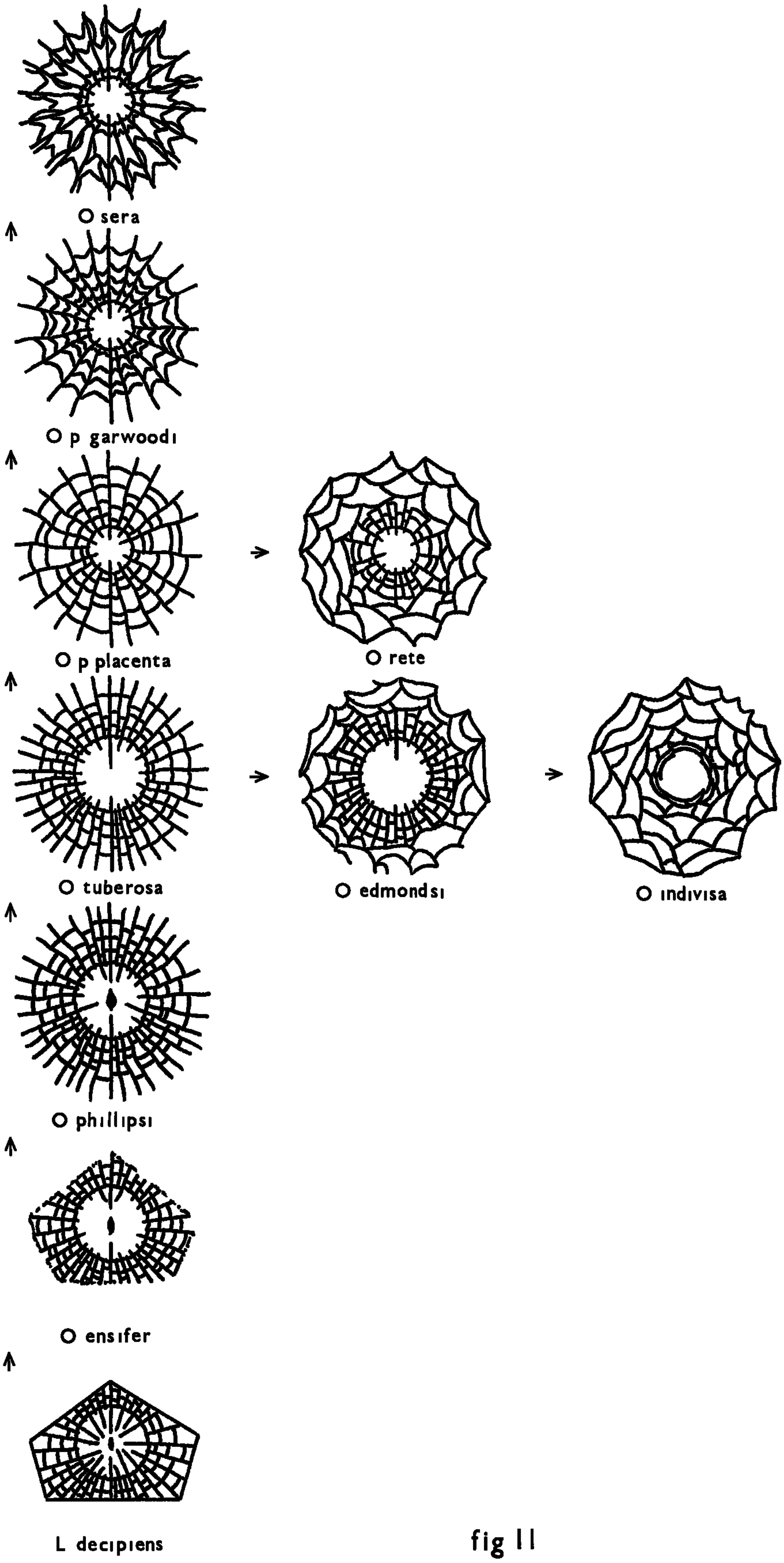

O sera
O p garwoodi
O p placenta
O rete
O tuberosa
O edmondsi
O indivisa
O phillipsi
O ensifer
L decipiens

fig 11

as separate species, the smaller form being *O. placenta* and having 20-28 septa.

All of these *Orionastraea* species are thamnastraeoid or astraeoid, i.e. their septa are continuous to the adjacent corallite. However soon after both *O. tuberosa* and *O. placenta* appear they are both affected by a trend of peripheral retreat of the septa so that an aphroid type of colony is produced. *O. tuberosa* gives rise to *O. edmondsi* in the Jew Limestone and *O. placenta* gives rise to *O. rete* in the Middle Limestone. *O. edmondsi* is identical in all other respects to *O. tuberosa* (36 septa) and *O. rete* is identical in all other respects to *O. placenta* (28 septa). The fact that these two aphroid species appear at different points in the stratigraphic column is again good evidence that both they and their astraeoid ancestors should be separated.

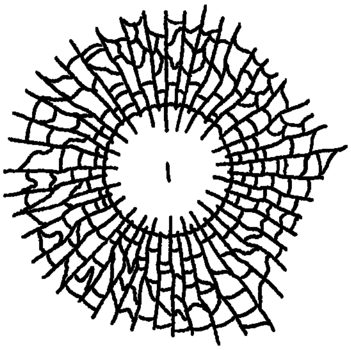
When *O. placenta* first evolves from *O. tuberosa* it has the normal ancestral 'Lithostrotion' type of dissepimentarium, i.e. concave towards the axis of the corallite. Some individuals develop dissepiments that are sharply convex towards the axis. This condition was described as *O. garwoodi* by Hudson in 1930, but as every intermediate condition of dissepiments is found it is considered in this thesis to be a sub-species of *O. placenta* and is therefore described as *O. placenta garwoodi*. However it is an important sub-species as it is the sub-specific stage between *O. placenta placenta* and *O. sera*, a further species that evolves in the Middle Limestone, in which the convex dissepiments break at the angle of the convexity and turn to run parallel to the septa, lining their edges.

The final species of *Orionastraea* evolves in the Simonstone Limestone from *O. edmondsi* by a further retreat of the septa until in *O. indivisa* the septa are completely absent. Thus in *O. indivisa* the corallum is composed of dissepiments and tabulae only and the corallum is indivisoid.

This plocoid trend also affects one of the other cerioid species, that of *L. vorticale*. Again the wall dividing the corallites gradually thins

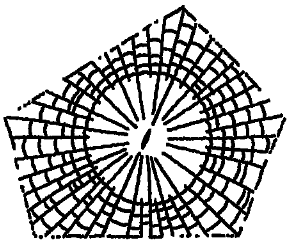
FIGURE 12

Diagrammatic illustration of the evolution of the genus *Hudsonia* from *L.vorticale*.



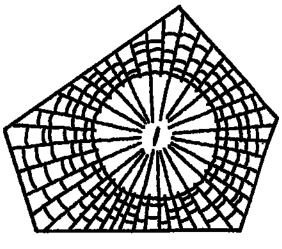
H. magna

↑



H. matura.

↑



L. vorticale.

fig 12

and becomes inconsistent. Because the plocoid species evolving from *L. vorticale* have a different ancestor to the *Orionastraea* species they should be split from the genus *Orionastraea*. In this thesis they are placed in the new genus *Hudsonia* (p.235). Thus *L. vorticale* gives rise to *Hudsonia matura* with an inconsistent wall. This differs from *O. ensifer* in having 43 septa (in total) the same as *L. vorticale* (20-24). *H. matura* then gives rise to the first truly plocoid species of *Hudsonia* when the wall disappears completely in *H. magna*. The phylogeny of *Orionastraea* and *Hudsonia* is shown in figs. 11, 12 and 14.

The Aulate Genera

There have been many conflicting theories on the evolution of the genus *Aulina* (p.242). Smith changed his mind three times on the subject, first suggesting that the plocoid species evolved from *P. radiata*, secondly that the plocoid species evolved from the fasciculate species and thirdly that the plocoid and the fasciculate species were polyphyletically derived from *L. maccoyanum* and *Diphyphyllum* respectively.

At the beginning of this research the present author was in more or less agreement with Smith's final theory but modifying this slightly supposing first that the plocoid species evolved from the plocoid *Orionastraea placenta* as this seemed more nearly related in growth form than *L. maccoyanum* which is cerioid, and secondly that the three fasciculate species of *Aulina* evolved from three similar sized species of *Diphyphyllum*, the evidence being that these three species of *Diphyphyllum* all had developed a kind of pseudo-aulos by superimposition of domed tabulae (p. 13) and thus the only change required to change *Diphyphyllum* into *Aulina* would be for the septa to contribute towards the building of this pseudo-aulos to produce a true septal aulos (p. 13).

However, certain facts have since come to light that cast~~s~~ considerable doubt on such a theory. First, the palaeontological records show that *Aulina horsfieldi*, the largest of the fasciculate aulate species, occurs at a position in the stratigraphic column that is earlier, not only than *Diphyphyllum*, but also earlier than any other species in the family *Lithostrotiontidae*; *A. horsfieldi* occurring in the Upper Tournaisian (C1) (See Smith and Yu, 1943, p.50-51) while the first species of *Lithostrotion* (*L. martini*) does not appear until Viséan times (C2). It is obvious, therefore that the ancestors of the advanced species *A. horsfieldi* cannot be any member of the *Lithostrotiontidae*, but that *A. horsfieldi* is a late member of a much earlier stock.

This fact on its own does not put any doubt on the relationship of the other fasciculate species (*A. hibernica* and *A. furcata*) with the *Lithostrotiontidae* but another important piece of information that has hitherto escaped notice does throw some doubt on all three fasciculate species being allied to the *Lithostrotiontidae*. This is that all three fasciculate species of *Aulina* have obvious carinate septa. This structure is never found in the *Lithostrotiontidae* and Smith and Yu (1943) state that while carinae are by no means unknown in Carboniferous and Permian corals, they are much less common in these than they are in corals of Devonian age. Carinate septa have long been held to be an important hereditary character and hence important in classification as they show phylogenetic relationships. If we accept that carinae are such important structures (and all the evidence seems to suggest that they are) then we are led to the inevitable conclusion that neither *A. horsfieldi*, *A. hibernica* or *A. furcata* are members of the *Lithostrotiontidae*, but that they themselves represent a continuous lineage with *A. hibernica* and *A. furcata* evolving from the earlier *A. horsfieldi*, and that *A. horsfieldi* itself is derived from a late member of a Devonian stock of corals that possess carinate septa. Further evidence to back this up is that while the species of *Diphyphyllum* do possess a pseudo-aulos similar to the true aulos of *Aulina*, the pseudo-aulos of *Diphyphyllum* is always much larger in size than is the true aulos of the fasciculate *Aulina* species. Also while the inner row of dissepiments is always dilated and regular in every species of *Lithostrotion* and *Diphyphyllum*, it is never either dilated or regular in the fasciculate species of *Aulina*.

This conclusion leads us to re-consider the supposed phylogeny of the plocoid *Aulina* species from *Orionastraea* and it would again appear that this theory is erroneous for three reasons. First *A. rotiformis*, *A. senex* and *A. botanica* (p.249) also show prominant carinate septa which never occur in *Orionastraea*. Secondly, while the major and minor septa are easily distinguishable in the plocoid *Aulina* species, being of different lengths, in *Orionastraea* the septa are less easily divisible into two orders as they are normally of similar lengths. Finally while *A. rotiformis* is of similar size to *Orionastraea* the aphroid species of *Aulina*, *A. senex* and *A. botanica*, are much larger than any *Orionastraea* species and evolution would thus have to be from *Orionastraea* to *A. rotiformis* to *A. senex* which Smith in fact considered to be the case (1943, p.47-48). However, one can trace the gradual improvement of the aulos in this group with *A. senex* having a poorly developed aulos and *A. rotiformis* having a well developed tube. Evolution therefore must go from *A. senex* to *A. rotiformis*, and *A. senex* is too big to evolve from *Orionastraea*.

Thus the plocoid *Aulina* species must also be rejected from the family *Lithostrotiontidae* but we must now consider from where they do evolve. Is it possible that the plocoid *Aulina* species do, as Smith at one time considered, evolve from the fasciculate *Aulina* species, as they all have carinate septa. Again this is considered unlikely for many reasons. First, there is a considerable gap in time between the highest fasciculate *Aulina* species (*A. furcata* in D2) and the lowest plocoid *Aulina* species. Secondly there has never been described any cerioid aulate coral which must exist as an intermediate stage if the plocoid species evolve from the fasciculate species. (*Lithostrotionella tubifera* Hayasaka, previously included in the genus by Hill (1940, p.190) was rejected by Smith and Yu (1943, p.43). Although this species has an aulos and is cerioid, it has no carinae and it possesses a columella). Thirdly the fasciculate species differ from the plocoid species in that the aulos is much smaller in proportion to the tabularium diameter, the septa extending further to the centre in the fasciculate species before they bend to produce the aulos. Fourthly while the fasciculate species all show axial budding this has never been observed in the plocoid species. Fifthly, if the plocoid Aulina species evolved from the last fasciculate species A. furcata then one would expect all the plocoid species to have a perfect aulos as has A. furcata instead of which A. senex and A. botanica have a poorly developed aulos. In fact one can trace the gradual improvement of the aulos in both fasciculate and plocoid groups and so they must represent different lineages. The final piece of evidence is perhaps the most important. The author has shown (Chapter 5) that the three plocoid species of Aulina that occur in Britain (A. rotiformis, A. senex and A. botanica) all occur at the same quite limited horizon in the Namurian (E2 Zone). They are not introduced into this area (Northern England) from a European centre of evolution to the south, as are all the Viséan corals, but that the palaeomigration directions have changed in the Namurian and these three species arrive in this area from the east. In fact they have passed through the Mid-European Channel from their centre of evolution in China. We can predict that these species have their origins in China as this is the only other area in the world where they occur. Thus the three species that are represented in Britain are just a small part of a much larger Chinese stock of aulate corals which includes A. senex and A. rotiformis plus a host of exotic Chinese species such as A. carinata Yu (not Carruthers), A. carcer, A. puerilis, A. manchuriensis and A. cystoides. Moreover we can be sure that this group had its origins in China, and not in Britain, as they occur at a lower horizon in China being present in the Upper Viséan whereas they do not appear in Britain until the Namurian. It is therefore pointless looking for an ancestor for this stock in Britain as they do not appear in Britain until late in their evolutionary history. In my opinion their ancestors will be found in China. Now the critical argument is that while *A. horsfieldi*, *A. hibernica* and *A. furcata* are common in England, these fasciculate aulate species are entirely absent in China and thus cannot be the ancestral stock of the Chinese plocoid aulate group.

Thus we are led to the conclusion that first, neither the plocoid nor the fasciculate aulate species should be included in the family *Lithostrotiontidae*, and secondly that these two groups are not directly related to each other. Thus in this thesis (p.244) the genus *Aulina* has been split into two genera; *Aulina* now being restricted to the plocoid species, while the new genus *Fascicaulina* has been proposed to refer to the fasciculate aulate species (p.257).

The Fascicaulina Lineage

The genus *Fascicaulina* comprises three species all possessing carinate septa and an aulos in varying degrees of development. The first of these to appear is *F. horsfieldi* which is found in beds of C1 age (see Smith and Yu, 1943, p.50 for occurrence). This species has 28-32 septa and its aulos may either be poorly developed with a convex bend to the axial ends of the septa (fig.21b) or well developed with a concave bend to the septa and hence a circular aulos (fig.21c). This species evolves by a reduction of the septa to *F. hibernica* in the upper S2 Zone, *F. hibernica* being smaller and having only 24-27 septa. The development of the aulos of *F. hibernica* shows exactly the same wide variation as does the aulos of *F. horsfieldi*. However when *F. hibernica* evolves to *F. furcata* in the upper D1 Zone there is not only a further reduction in the number of septa (to 18-22) but also a change in the aulos.

F. furcata has an aulos which is always very well developed, all the septa contributing to it, and the aulos being almost a perfect circle in transverse section.

The ancestors of *Fascicaulina* are unknown but there are several possibilities. Tracing the evolution of this genus the species gradually become smaller in size. If this trend is reversed it follows that the ancestors were at least as large as *F. horsfieldi* and possibly larger. Secondly the earliest of the species of *Fascicaulina*, *F. horsfieldi*, shows an aulos that is in quite an advanced state of development. This structure has possibly evolved through a pseudo-aulos of the tabulae (p. 59) and therefore the ancestor should possess, if not a true septal aulos, some sort of pseudo-aulos. Finally it must have carinate septa.

A group of corals of similar structure to the *Lithostrotiontidae* and to *Fascicaulina* and of slightly larger dimensions is the Koninckophyllids. These range from the Z2 Zone to high in the Viséan. While these corals do not normally show carinate septa, some species do possess such structures, one such species being *K. echinatum*. This has been figured by Hill (1940, pl.IIII, figs 19-23) and she remarks on its great similarity to *Aulina* (i.e. *Fascicaulina*). This particular species however cannot itself be the ancestor of *Fascicaulina* as it does not appear until quite late in the Viséan, but the similarity of structure does suggest that *Fascicaulina* and *Koninckophyllum* may be related.

Secondly, the Devonian coral *Eridophyllum* possesses carinate septa and an aulos which may not always be perfectly developed and Smith and Yu (1943, p.41) state that *E. seriale* is an almost perfect homeomorph of *A. horsfieldi*. *Fascicaulina* therefore may be a relict of a Devonian fauna. It is obvious however that much more research is required to elucidate this problem.

The Aulina Lineage

The evolution of the plocoid genus *Aulina* is even more difficult to evaluate due to the paucity of material present in this country. Only three species have been recorded from Britain and these species are quite dissimilar. If the evolution of *Aulina* can be compared in general terms to that of *Lithostrotion*, *Orionastraea* and *Fascicaulina* then it may be assumed that the largest form evolved to the smallest and so *A. senex* gave rise to *A. rotiformis* through *A. botanica*. This is backed up by tracing the development of the aulos through these three species. In *A. senex* it is very poorly developed being produced only by the tabulae and hence is a pseudo-aulos. In *A. botanica* however the septa begin to contribute to its development but it is still a primitive structure, the septa having the convex bend to their axial ends (fig.21b). In *A. rotiformis* however the aulos is very well developed being often perfectly circular in outline.

However the state of development of the colony of these species suggests that this might not be true. *A. botanica* and *A. senex* have aphroid coralla which is a more advanced growth form than the astraeoid colony of *A. rotiformis*. *A. rotiformis* could not therefore evolve directly from *A. senex* or *A. botanica* but would have to had evolved from an astraeoid ancestor of one of these species and such corals have not been found. The growth forms in fact suggest a reverse order of evolution. In fact Smith and Yu did suggest that evolution progressed from *A. rotiformis* to *A. senex* by the features of *A. rotiformis* breaking down, but it seems unlikely that if the structures were breaking down at the end of a lineage, that that lineage would at the same time increase in size.

What may be more likely is that *A. rotiformis* is a member of a separate lineage from *A. senex* and *A. botanica*. If as has been suggested on p.148 *A. senex* evolves from the fasciculate *A. vesiculata* by this lonsdalaeoid fasciculate coral becoming massive then A. senex would be automatically aphroid without going through an astraeoid stage. In this case A. rotiformis could not be directly related to A. senex.

Again this problem can not be satisfactorily answered here as the majority of the species of this genus do not occur in this country. Detailod collecting in China and Japan is needed before a complete picture can be obtained. The ancestors of the genus Aulina, however, are not to be found in Britain as the genus occurs at an earlier horizon in China than it does in this country.

Conclusion

The complete phylogeny of the Lithostrotiontidae is shown in figs 13 and 14. It is seen that evolution proceeds in two main directions from the initial species L. martini. First a fasciculate lineage becomes progressively smaller as it evolves with occasional additional modifications to the form of the budding, and secondly is a continual change in the growth form of the colony from fasciculate through cerioid to thamnastraeoid, aphroid and indivisoid. Both lineages show different methods of a constant reduction in skeletal tissue, but the reasons are probably quite different. The appearance of progressively smaller species in the fasciculate lineage suggests that the larger species could not survive and that this lineage was gradually failing in an environment in which conditions were gradually worsening (i.e. the steady oncome of the sandy and shale facies with the limestones becoming darker up the succession) and in which competition for food and space was also increasing. The lineage involving colony form, however, shows a loss of skeletal plates in a way that is a gradual improvement of the efficiency of the species and also which leads to progressively higher levels of colonial integration (p. 62). This lineage is thus improving itself and becoming more specialised in the same worsening environment.

FIGURE 13

Illustration of the phylogeny of the genus *Lithostrotion* with stratigraphical boundaries marked. The stratigraphic sequence is taken from the Stainmore Trough. Correlation with other areas is shown in Fig.2. All strata names refer to limestone unless otherwise stated.

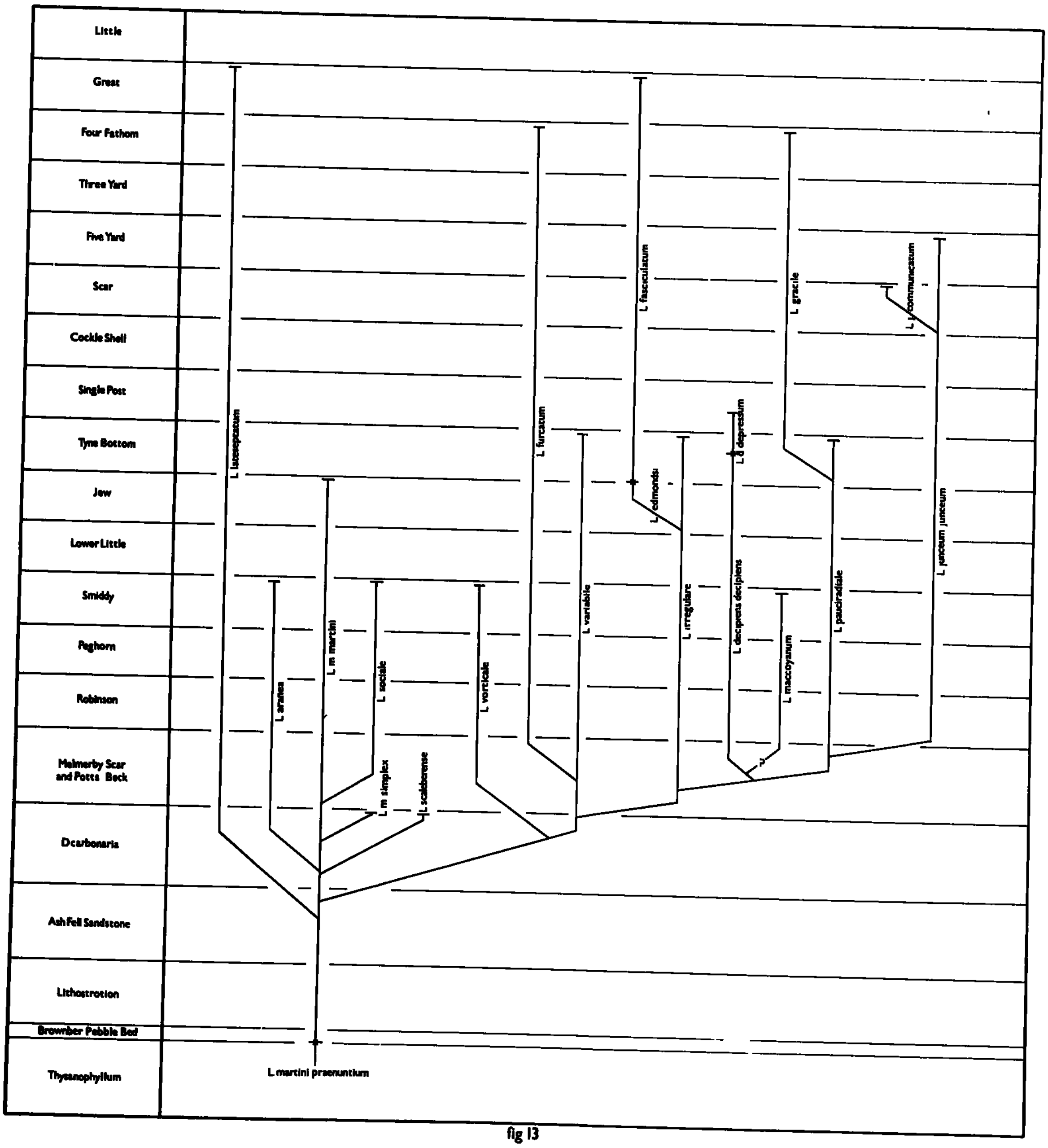

Little
Great
Four Fathom
Three Yard
Five Yard
Scar
Cockle Shell
Single Post
Tyne Bottom
Jew
Lower Little
Smiddy
Peghorn
Robinson
Melmerby Scar and Potts Beck
Dcarbonaria
Ash Fell Sandstone
Lithostrotion
Brownber Pebble Bed
Thysanophyllum
L latiseptatum
L aranea
L m martini
L sociale
L m simplex
L scaleberense
L verticale
L furcatum
L variabile
L fasciculatum
L edmondsi
L irregulare
L d depressum
L decipiens decipiens
L maccoyanum
L gracile
L pauciradiale
L j communicatum
L junceum junceum
L martini praenuntium

fig 13

Some idea of the ancestors of the *Lithostrotiontidae*, is obtained if these two trends are reversed from the initial *Lithostrotion* species. The result is a species with corallites larger than *L. martini* and with either a dendroid or a simple growth form to the colony and a similar morphology to the *Lithostrotiontidae* occurring in Tournaisian strata.

One group of corals that satisfies all these requirements is the genus *Koninkophyllum*, the species of which are usually larger than the *Lithostrotion* species and can be either simple or dendroid. They possess fine concentric dissepiments and a styliform columella as do the *Lithostrotion* species and the genus occurs both in the Tournaisian and Viséan of the British Isles and Belgium. This genus is thus a possible ancestor to the *Lithostrotiontidae* although more work is needed to verify this.

FIGURE 14

Illustration of the phylogeny of the genera *Hudsonia* and *Orionastraea* from *Lithostrotion* with stratigraphical boundaries marked. The stratigraphic sequence is taken from the Stainmore Trough. Correlation with other areas is shown in Fig.2. All strata names refer to limestone unless otherwise stated.

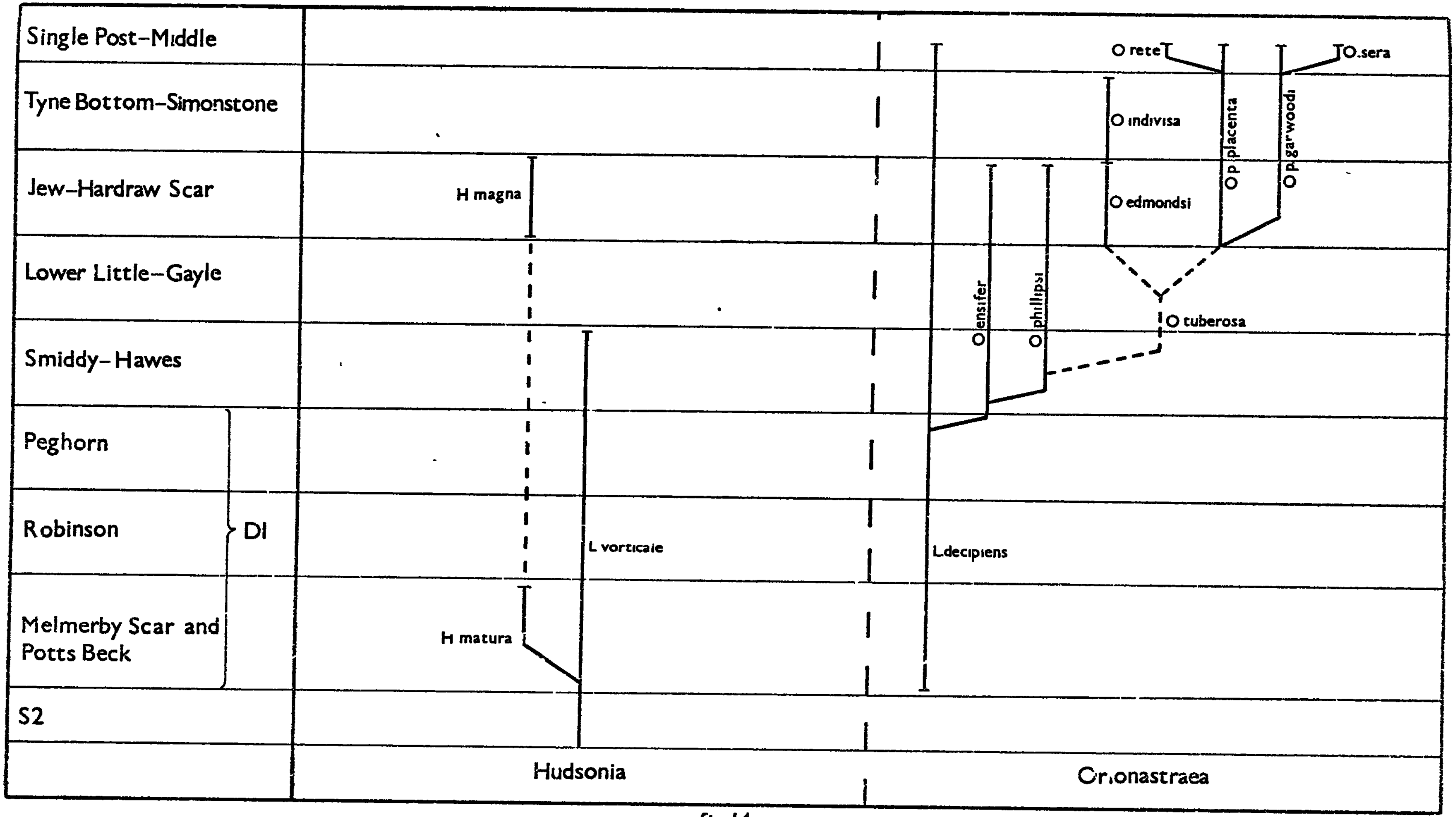

Single Post-Middle
Tyne Bottom-Simonstone
Jew-Hardraw Scar
Lower Little-Gayle
Smiddy-Hawes
Peghorn
Robinson
DI
Melmerby Scar and Potts Beck
S2
H magna
H matura
L vorticale
L.decipiens
O ensifer
O phillipsi
O rete
O indivisa
O edmondsi
O tuberosa
O p placenta
O p garwoodi
O.sera
Hudsonia
Orionastraea

fig 14

CHAPTER 2

STRATIGRAPHICAL RANGES OF THE SPECIES OF THE LITHOSTROTIONTIDAE

The stratigraphical ranges of the species of the Lithostrotiontidae are set out in figure 15. The Table shows that the range of the different species varies considerably. In the genera Lithostrotion and Orionastraea one species or species group persists for quite a considerable time forming the main stock of the lineage while the subsequent species, that evolve from these stocks in different directions, tend to have more limited ranges and are hence more useful as zonal indicators.

Thus L. martini and its successors in the fasciculate columellate group have extended ranges with the larger species both appearing and dying out earlier while the smaller species persist for longer. L. martini appears in the C2 Subzone and dies out in the Jew Limestone (= Hardraw Scar), L. variabile appears at the top of the S1 Subzone and dies out in the Tyne Bottom Limestone (= Simonstone), L. irregulare appears at the top of the S2 Subzone and dies out also in the Tyne Bottom Limestone, and L. pauciradiale appears in the D1 Subzone and again dies out in the Tyne Bottom Limestone. L. junceum junceum, the smallest of the fasciculate species has the longest range persisting until the shales above the Five Yard Limestone. The subspecies L. junceum communicatum is more useful stratigraphically however as it appears to be restricted to the Scar Limestone.

It should be pointed out here that L. m. martini has not been recorded from any horizon higher than the D1 Melmerby Scar Limestone in the Stainmore Trough, Alston Block or Northumberland Trough; it thus appears to die out earlier in the north than in the south. Secondly, while L. variabile, L. irregulare and L. pauciradiale appear in the S1, S2 and D1 Subzones respectively, these three species do not reach their peaks until the S2, D1 and D2 Subzones respectively. Also L. pauciradiale,

FIGURE 15

Diagram showing the stratigraphical ranges of the species of the Lithostrotiontidae. The stratigraphic sequence is taken from the Stainmore Trough. Correlation with other areas is given in Fig.2. All strata names refer to limestone unless otherwise stated.

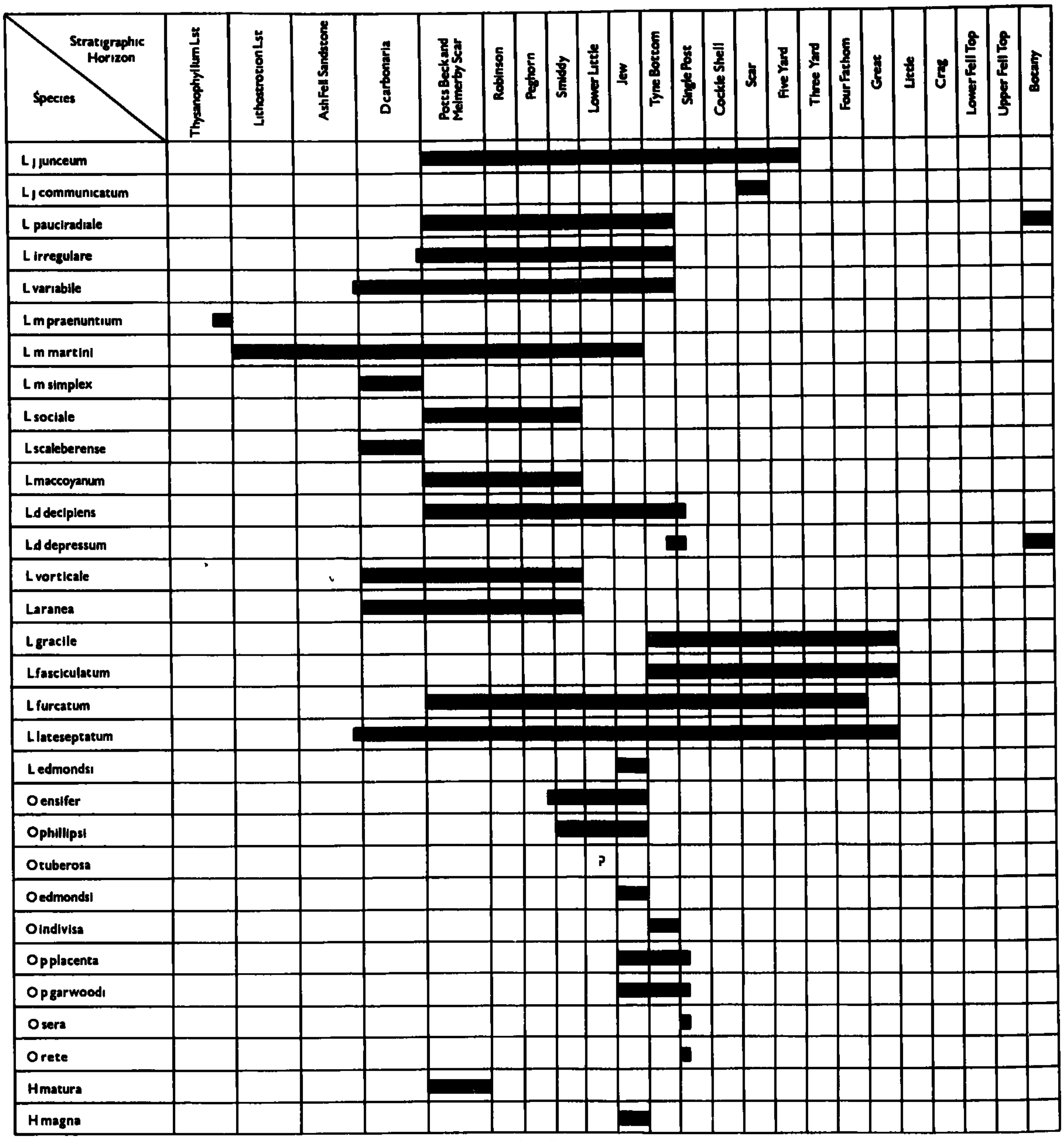

Stratigraphic Horizon
Species
Thysanophyllum Lst
Lithostrotion Lst
AshFell Sandstone
D carbonaria
Potts Beck and Melmerby Scar
Robinson
Peghorn
Smiddy
Lower Little
Jew
Tyne Bottom
Single Post
Cockle Shell
Scar
Five Yard
Three Yard
Four Fathom
Great
Little
Crag
Lower Fell Top
Upper Fell Top
Botany
L j junceum
L j communicatum
L pauciradiale
L irregulare
L variabile
L m praenuntium
L m martini
L m simplex
L sociale
L scaleberense
L maccoyanum
L d decipiens
L d depressum
L vorticale
L aranea
L gracile
L fasciculatum
L furcatum
L lateseptatum
L edmondsi
O ensifer
O phillipsi
O tuberosa
?
O edmondsi
O indivisa
O p placenta
O p garwoodi
O sera
O rete
H matura
H magna

fig 15

although becoming extinct in the Tyne Bottom Limestone, does reappear again in the E2 Botany Limestone (= Harlow Hill) after being completely absent in the intervening strata.

The subspecies of L. martini have a more limited vertical range; L. m. praenuntium has only been recorded from the limestone below the Brownber Pebble Bed, while L. m. simplex has only been found in beds of S2 age.

The larger species in the fasciculate columellate group are also more restricted in vertical distribution; L. scalberense only having been collected from its type locality in the ?S2 Subzone, while L. sociale is known only from the Great Scar Limestone (= Melmerby Scar) to the Smiddy (= Hawes) Limestone.

The four diphyphylloid species are of less use as zonal indicators as they all have quite long vertical ranges all extending up to the Great Limestone (= Main) which virtually marks the end of the Lithostrotiontidae. It should be pointed out here that while the range of L. lateseptatum is recorded as from the S1 Subzone (Ash Fell Sandstone) the only specimen collected from this zone is doubtful; the next lowest occurrence of this species is in the Peghorn Limestone.

The most interesting point here is that L. fasciculatum and L. gracile have identical ranges from the base of the Tyne Bottom Limestone to the Great Limestone indicating, as has been suggested, that they may form a continuous interbreeding series and be only morpho-species. The same is true for the columellate ancestors of these species, i.e. L. irregulare and L. pauciradiale. These also have similar ranges to each other and to L. variabile and so again as has been suggested (p. 48) these three 'species' may form one continuous series. (Although they appear in order of size they all die out together in the Tyne Bottom Limestone (= Simonstone). Also interesting is that L. fasciculatum and L. gracile appear just as L. irregulare and L. pauciradiale are dying out in the Tyne

Bottom Limestone. This is further evidence that the former two diphyphylloid species evolve from the latter two columellate species.

Similarly the four cerioid species have quite long ranges; *L. aranea* and *L. vorticale* extending from the S2 Subzone to the base of D2, and *L. decipiens decipiens* and *L. maccoyannum* extending from the base of D1 to the Single Post (= Middle) and Smiddy (= Hawes) respectively. *L. d. depressum* however, is more useful, having only been found so far in the Tyne Bottom Limestone (= Simonstone) and at the base of the Middle Limestone and its equivalent, the Single Post Limestone. This subspecies also reappears with *L. pauciradiale* in the Namurian E2 Botany Limestone.

Of greater use as zone fossils are the species of *Orionastraea* and *Hudsonia* and the nemistioid *Lithostrotion* species. *L. edmondsi* is restricted to the Jew Limestone and its equivalents. *H. Matura* is only found in the lower part of D1, while *H. magna* is restricted to the 'Orionastraea' Band in the Hardraw Scar (= Jew) Limestone.

In the genus *Orionastraea* the main stock is represented by *O. ensifer*, *O. phillipsi* and *O. tuberosa*. *O. ensifer* and *O. phillipsi* appear at the D1/D2 boundary (Hudson, 1929) and persist to the Fourth Limestone of Cumberland (= Jew Limestone). The range of *O. tuberosa* is as yet undetermined, but it is the species that evolve from *O. tuberosa* that are the most interesting. *O. edmondsi*, its aphroid successor, is restricted to the Jew (= Hardraw Scar) Limestone and *O. indivisa*, the indivisoid successor, is only found in the Tyne Bottom Limestone and its equivalent, the Simonstone and Toft Gate Limestones. The two subspecies of *O. placenta* have identical ranges from the Jew Limestone to the base of the Middle (= Single Post) Limestone, while the successors of this species, *O. rete* and *O. sera* are only found in the base of the Middle Limestone and its equivalents in Cumbria.

CHAPTER 3

EVOLUTIONARY TRENDS IN THE LITHOSTROTIONTIDAE

The phylogenetic history of the Lithostrotiontidae has been shown in Chapter 1 to be characterised by a number of evolutionary trends which occur repeatedly throughout the history of the group affecting different species in the same way. The end result of this parallel evolution is that a number of species show morphological similarities. In some cases these similar species have previously been grouped into separate genera. Because these trends affect different species in the same way the morphologically similar species are polyphyletic. Thus the generic grouping shows no real relationship and therefore has been abandoned (p.119). This Chapter reviews these evolutionary trends.

1. The 'Martini' Trend

The first evolutionary trend to affect the Lithostrotiontidae is a gradual loss of dissepiments in L. martini as it is traced up the stratigraphical column in that the earliest subspecies L. m. praenuntium has up to six rows, L. m. martini has three to four rows when it first appears and two to three rows later, and L. m. simplex develops only one row of dissepiments (fig. 5). Moreover this trend is exactly correlated to a second change in the same three subspecies leading to a gradual wider spacing of the tabulae and of the epithecal growth bands. Thus it appears that the growth rate of the species was gradually increasing as it evolved, i.e. the initial subspecies, L. m. praenuntium was slow growing. It has conical corallites which took a long time to mature and a dendroid colony. Now it may be that the number of dissepiments is also related to the growth rate, there being a high number in the slow growing subspecies as there was a greater time period at any one point in the growth of the corallite for the polyp to spread laterally and for dissepiments to be added. On the other hand it may be that as growth quickens there is less calcium carbonate available for secretion as dissepiments as it is all being put into a vertical building of the skeleton. At any rate as this species evolves its growth rate gradually quickens and its number of dissepiments decrease, thus the width of the dissepimentarium decreases and so does the overall diameter. Two questions therefore present themselves; first why does this change in the growth rate occur and secondly how is it possible genetically?

Advantages of the 'Martini' Trend and Genetic Considerations

Presumably as this species evolved in the shelf seas of the Lower Carboniferous there was continually increasing pressure from, and competition for, some factors such as space and food. Therefore those colonies which could grow quickly to the higher levels above the sea floor could both trap the food and utilise the space better than could the slow growing colonies. The quicker growing colonies were continually selected by the environment in this way. Assuming that growth rate is controlled by a number of different genes (a gene complex) it will be those gene complexes that accentuate the affect of a 'quick growing' mutant gene that were selected. As selection pressure increases the gene complexes selected will be those in which the mutant gene is more and more dominant. Thus the mutant gene will be made to become dominant in the gene pool of the species by the environment selecting as parents those individuals whose gene complexes accentuate the affect of that gene. The species therefore is gradually improved not necessarily by any additional mutations, but instead by only the more advantageous gene complexes being selected. It is possible, however, that a series of mutations takes place all in the same direction, a process described by Darlington (1969, p.25) as positive feedback.

2. Neoteny

The 'Martini' trend therefore involves a loss of dissepiments. A second trend that occurs in the evolution of L. martini to L. variabile and of L. variabile to L. irregulare, L. pauciradiale and L. junceum continues this loss of dissepiments, but also shows a loss of septa as well. Because this new factor is introduced it is thought that L. junceum, with no dissepiments, is not the final expression of the L. martini trend, but is the result of a second trend which has partly the same affects. It is due however to a different cause which has an entirely different mechanism. This is the trend of neoteny whereby later species show in their maturity an identical morphology to the immature stages of their ancestors. Thus Moore, Lalicker and Fischer (1952, p.28) state that "omission of normal adult characters and maturation in what are normally earlier stages is termed neoteny or paedomorphism". Thus L. variabile in its mature state represents an early stage of L. martini, and L. irregulare, L. pauciradiale and L. junceum all represent successively earlier stages of L. variable (fig.16).

Advantages of Neoteny and Genetics

The advantages of such a trend are obvious; first, less food and space are needed in a smaller species and less effort is required in the colony building. The interesting factor in this trend is the way in which these earlier stages appear. For instance in the Ash Fell Sandstone (S1 Subzone) is a repetitive sequence of shale and limestone bands. In the limestone bands normal colonies of L. martini occur with the mature corallites showing 28 septa. However in the shale bands colonies occur having some of their mature corallites with the normal 28 septa, but other corallites in which these normal adult characters never develop and possessing only 24 septa throughout their length. It seems therefore that these 'abnormal' corallites have been stunted by

FIGURE 16

Diagram illustrating the trend of Neoteny. The transverse section cut from the immature proximal end of a corallite of *L.martini* is identical to the mature stage of *L.variabile*. Similarly, successively earlier stages of *L.variabile* are identical to the mature stages of *L.irregulare* and *L.pauciradiale*.

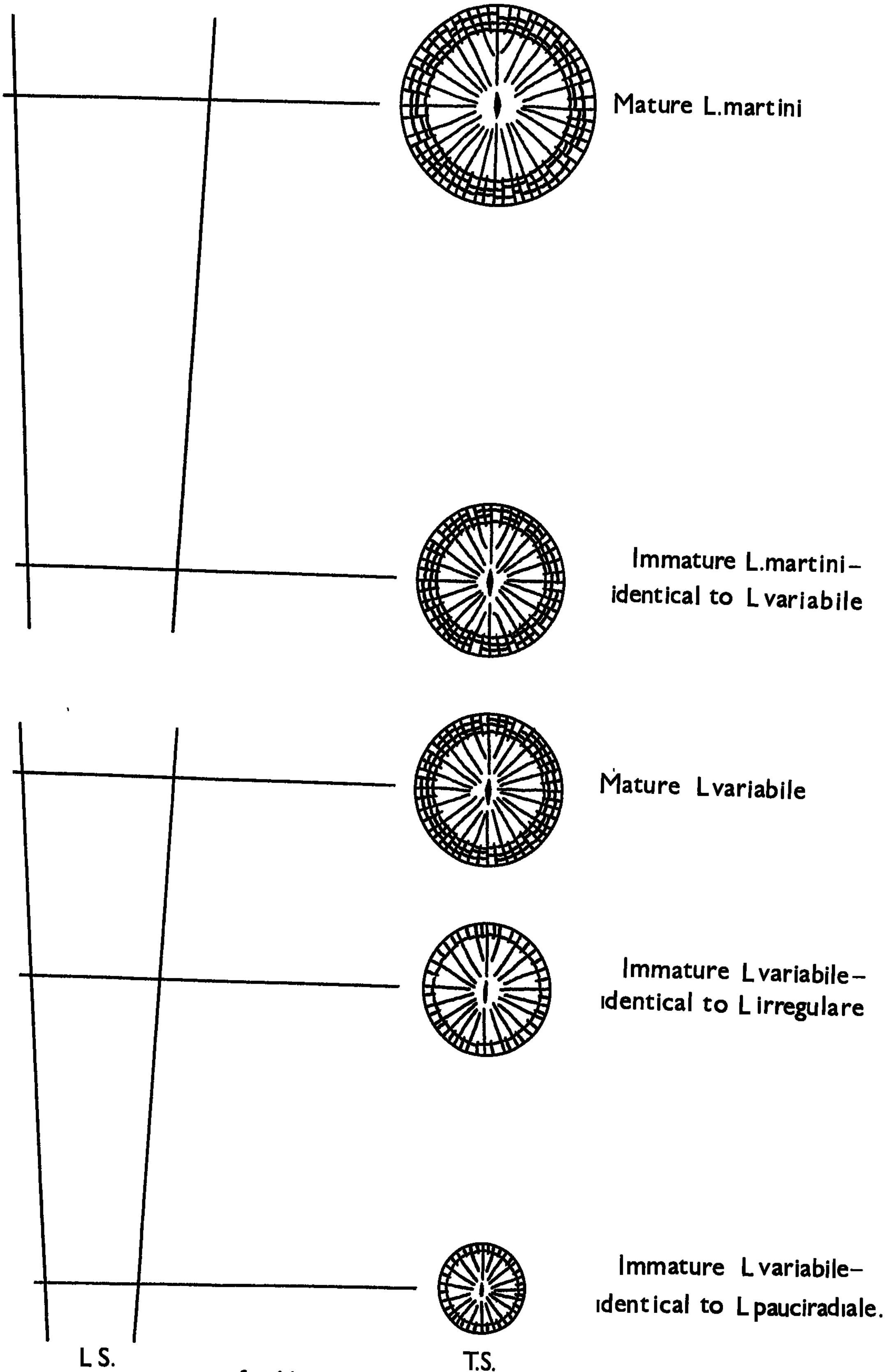

Mature L.martini
Immature L.martini-
identical to L.variabile
Mature L.variabile
Immature L.variabile-
identical to L.irregulare
Immature L.variabile-
identical to L.pauciradiale.
L.S.
T.S.

fig 16

the adverse environment of the shale, but the interesting point is that they are identical in all respects to the corallites of L. variabile which first appears in the succeeding S2 Limestone.

Similarly, almost as soon as L. variabile appears, interesting and important changes are seen in some colonies. In these colonies there is a sudden vast variation in the appearance of the member corallites of any one colony, the like of which is never seen in any other species of the Lithostrotiontidae. While some of the corallites are of the 'normal' dimensions and appearance, others stay the same diameter, but have only a single row of dissepiments, others are much smaller, being only half the maximum diameter, while still retaining the single row of dissepiments. Others even lose their dissepiments so that the diameter is only the width of the tabularium (p. 186). In fact there is a continuous variation from the largest down to the smallest, but they can arbitrarily be divided into these four 'types'. The important significance of these different types of corallites is that the three 'abnormal' types of corallite are exactly identical to the three subsequent species of the fasciculate columellate lineage that eventually evolve in the D1 Subzone soon after this initial variation in L. variabile first appears, viz, L. irregulare, L. pauciradiale and L. junceum respectively.

The question that must be answered is, do these different types of corallite within the same colony of L. variabile have any significance in the later evolution of the three subsequent species ? The first point that must be emphasised is that there can be no genetic difference between these different types of corallite; reproduction being asexual and all corallites therefore being genetically identical, and somatic mutations being comparatively rare (Wilson, 1963, p.87). Neither is this variation entirely ontogenetic because while the smaller corallites do represent the early stages of the larger corallites, the reverse is not true in that the smaller corallites never increase in size, but stay 'immature' throughout the length. Thus this variation is phenotypic in character; due to some environmental cause the smaller corallites have not been allowed to advance beyond an immature state. In other words they have been stunted by some adverse environmental character, the variation in size being due to stunting at various stages of the ontogeny. Can any such phenotypic variation have any bearing on the later evolution of the three subsequent species or is the similarity merely coincidental?

One important observation that has been made is that in the variable colonies the smaller corallites never give rise by budding to a larger, more mature type of corallite, but always to a corallite of similar size or even smaller, presumably because a small corallite could not support a larger offset. Now, if the very first corallite of a newly settling coral larva, after a period of sexual reproduction, was stunted by the adverse environment to a small size it therefore follows that every succeeding corallite in the colony would be small. However while this would produce an entirely small colony, identical to a colony of one of the subsequent species, this would only be effective for one generation. When next this colony reproduced sexually its larva would still have the genetic potential to produce a larger corallite type of colony once again; the new species obviously cannot be formed in this way. Romer (1960, p.19) states that "an animal may refuse to grow up and, except that its reproductive organs mature, remain a larva all its life - a situation termed 'paedogenesis'. If this condition long persists in the race, the potentiality of ever assuming adult form may disappear from its germ plasm - the animal has, so to speak, forgotten how to grow up". However in the case described by Romer the static immaturity was always caused in the first place by a genetic change (mutation) and not by a phenotypic cause. The point at which the potentiality of maturation disappears from the germ plasm is when the mutant becomes reproductively isolated from its parent species. In the immature colonies of L. variabile if the immaturity was phenotypic then even if they became reproductively isolated from L. variabile they would still have the genetic potential of reaching mature dimensions again.

Thus, what is more likely to have happened is that a straight mutation has occurred, unrelated to the stunting in L. variabile and the resulting mutants happen to be identical to the stunted corallites. This is perhaps not so much of a coincidence as it first appears; the fact that the corallites of L. variabile were stunted at all points first to the fact that the larger corallites of this species were becoming unstable in a worsening environment and could not survive, and secondly that the smaller stunted corallites were able to be successful. The fact that a subsequent mutation exactly reproduced the form of the stunted corallites is not surprising considering the simplicity of the morphology of the coral skeleton; the number of mutations likely from such a simple morphology is low anyway.

There are in fact two possible methods that the three subsequent species were produced. Either L. variabile underwent one drastic mutation that produced the very smallest form, but that this smallest form retained its interbreeding capacity with L. variabile and hence produced the intermediate forms. If this is the case then L. variabile and the three other species are in fact a completely continuous population and the division into four species is purely arbitrary. Alternatively there may have been a series of mutations in the same direction (i.e. L. variabile mutated to L. irregulare, L. irregulare mutated to L. pauciradiale and L. pauciradiale mutated to L. junceum). This is probably unlikely as all three species appear more or less contemporaneously. What is likely however is that a combination of these two possibilities occurred, i.e. that L. variabile, L. irregulare and L. pauciradiale are an interbreeding continuous population, while L. junceum is a separate mutation and a true biological species. This seems quite likely first, as the division between L. irregulare and L. pauciradiale is purely arbitrary anyway (p.162), secondly the division between L. variabile and L. irregulare is only a matter of number of dissepiments and thirdly, on the other hand, L. junceum does seem to be distinct from the other species in that not only are the dissepiments absent altogether, but also the method of budding is entirely different (p. 91). Thus L. junceum is probably a true biological species, the others may not be biological species, but instead are morphospecies, arbitrarily divided units of an interbreeding population, but the enormous difference between the two end members does warrant some sort of separation.

Whether or not the stunted corallites of L. variabile play any part in the later evolution of the three subsequent species, the presence of morphologically identical corallites to L. irregulare within the colonies of L. variabile does suggest that L. irregulare evolves from L. variabile and not from L. martini simplex which is also intermediate between L. martini and L. irregulare.

A third case of neoteny is seen in the genus Orionastraea in the evolution of O. placenta from O. tuberosa, but in this case the smaller corallites do not appear as stunted individuals in the colonies of O. tuberosa.

3. The Cerioid Trend

The cerioid trend expresses itself in four different fasciculate species producing similar end products. It involves the change of the growth habit of the colony from phaceloid, when the individual corallites are cylindrical, and free from their neighbours, to cerioid, when the corallites are polygonal and in contact with the surrounding corallites.

The actual procedure of this change in growth habit is very interesting. It has often been thought to be the result of compaction (obviously not external squashing), but internal pressure for space, i.e. as new buds appear there is no room for their circular outline and therefore they are forced into a polygonal shape. However if this was so one would expect three results to occur; first, the corallites would have a smaller diameter as there was not room for full development, secondly one would expect the dissepimentarium to be distorted in the same manner as the epithecae and thus be polygonal in outline. Finally one would expect some space, at least temporarily, between corallites as there would be nothing to bind adjacent corallites so closely together. However none of these occur; the diameter is even larger in cerioid species than in their fasciculate ancestors, the dissepimentarium retains its circular outline and there is never space between adjacent epithecae. Thus this process must occur by some other procedure and many colonies have thus been serially sectioned in order to discover this process.

First, a colony was found in the C2S1 Limestones in which the corallites show a much exagerated diameter and no minor septa. It was noticed that some corallites show this larger diameter only in one direction and moreover that it was in this area of increased diameter that the minor septa were absent or at least inconsistent. The area of increased diameter was always on the side of the corallite that was nearest to a neighbouring corallite, as if it were growing out towards the adjacent corallite (fig.17a). In areas of the colony where density of corallites is high and neighbouring corallites surround the corallite in question closely on all sides, then the diameter increased in all directions and produced a larger diameter overall. Thus it seems as though the cerioid habit is not due to lack of space, as space is plentiful in these colonies. Instead the corallites 'want' to come together and they therefore grow laterally towards each other, rather than having to come together. This method of cerioid colony formation may be called 'lateral extension'. In the succeeding limestone, the S2 D. carbonaria limestone, just before the

FIGURE 17

Diagram illustrating the first stages in the Cerioid trend.

a. Transverse section of corallites from the C2S1 limestones in which the diameter of the corallites has increased towards the adjacent corallite. The corallites are growing towards one another.

b. Transverse section of a colony from the S2 limestones in which adjacent corallites have extended laterally and come into contact so that the epithecae of the adjacent corallites is confluent.

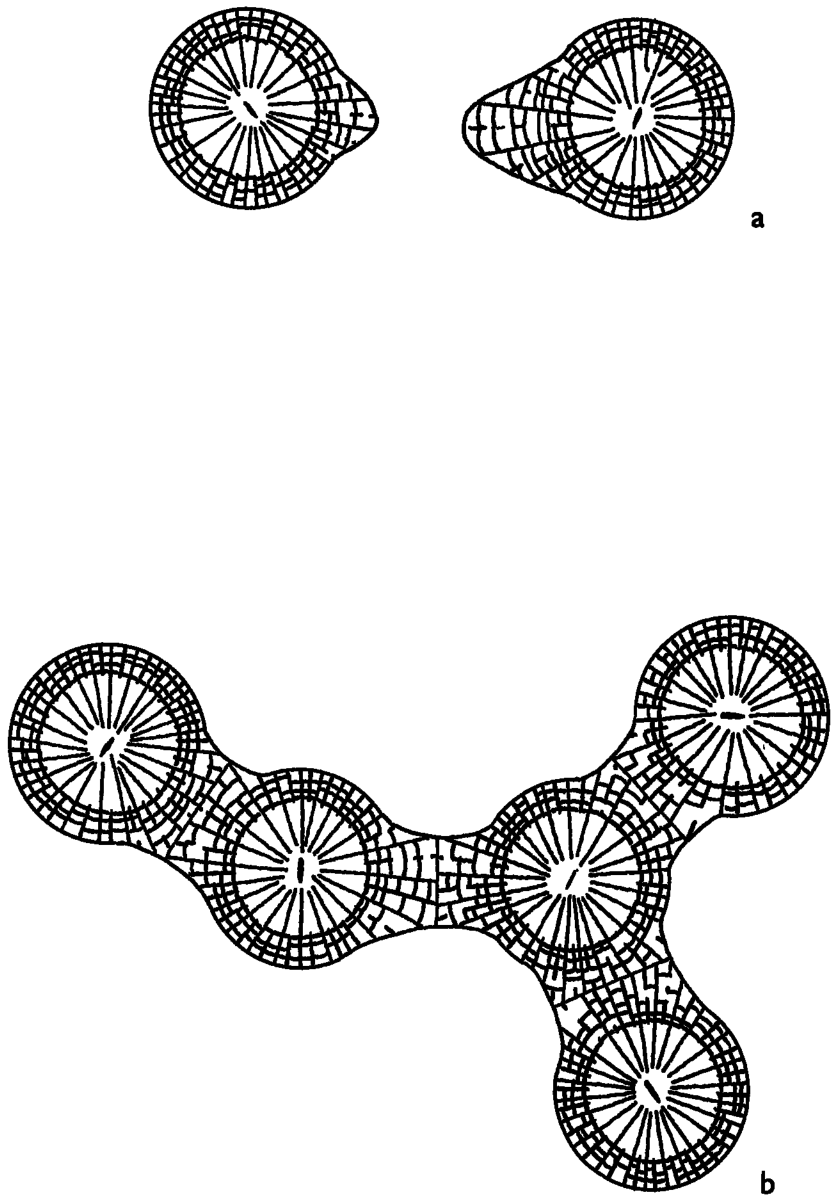


fig 17

first true cerioid colony appears, colonies have been collected in which the corallite epithecaes not only grow towards one another, but the epithecaes were actually joined at least in parts of the colony (fig.17b) and this seemed at first sight to be the next stage of the lateral extension process. However by this method a colony affected by such a process will be more cerioid at its top than at the base of the colony and yet some colonies in the S2 limestones show the reverse of this being cerioid at the base and phacelloid at the top. If the corallites do not then come together by this method then a second alternative hypothetical process is that they never divide from their parents after budding. This hypothetical process can be called 'incomplete fission'. When a bud first appears the adult and daughter are connected to each other. As the bud matures this connection is eventually lost as fasciculate corallites are separated after the budding stage. Competition for survival leads to the coral taking advantage of the one point in its life when it is in contact with its neighbour (i.e. budding) by not breaking off from its parent completely and remaining therefore connected by an extension of the dissepimentarium. Now, once the process of incomplete fission is introduced in the lineage, if it appears right at the base of a colony then the whole colony will immediately become cerioid. This cannot be the case as many colonies are only partly cerioid. However if the point at which incomplete fission starts in the life of a colony (i.e. ontogeny) changes as the lineage evolves (i.e. phylogeny) then partly cerioid colonies can be produced by this method. For example if when incomplete fission first appears in the lineage it takes effect right at the base of the colony but is only effective for a short period, i.e. sooner or later the buds do separate, but separation is delayed and if, as the lineage evolves, it is effective for a longer and longer period, then not only can a completely cerioid colony eventually be produced by this method, but also early stages will result in a colony cerioid at the base and phacelloid at the

FIGURE 18

Diagram illustrating later stages in the Cerioid trend by serial sections of a colony from the S2 limestones. The colony exhibits alternate cerioid and phaceloid stages due to lateral extension and lateral retreat.

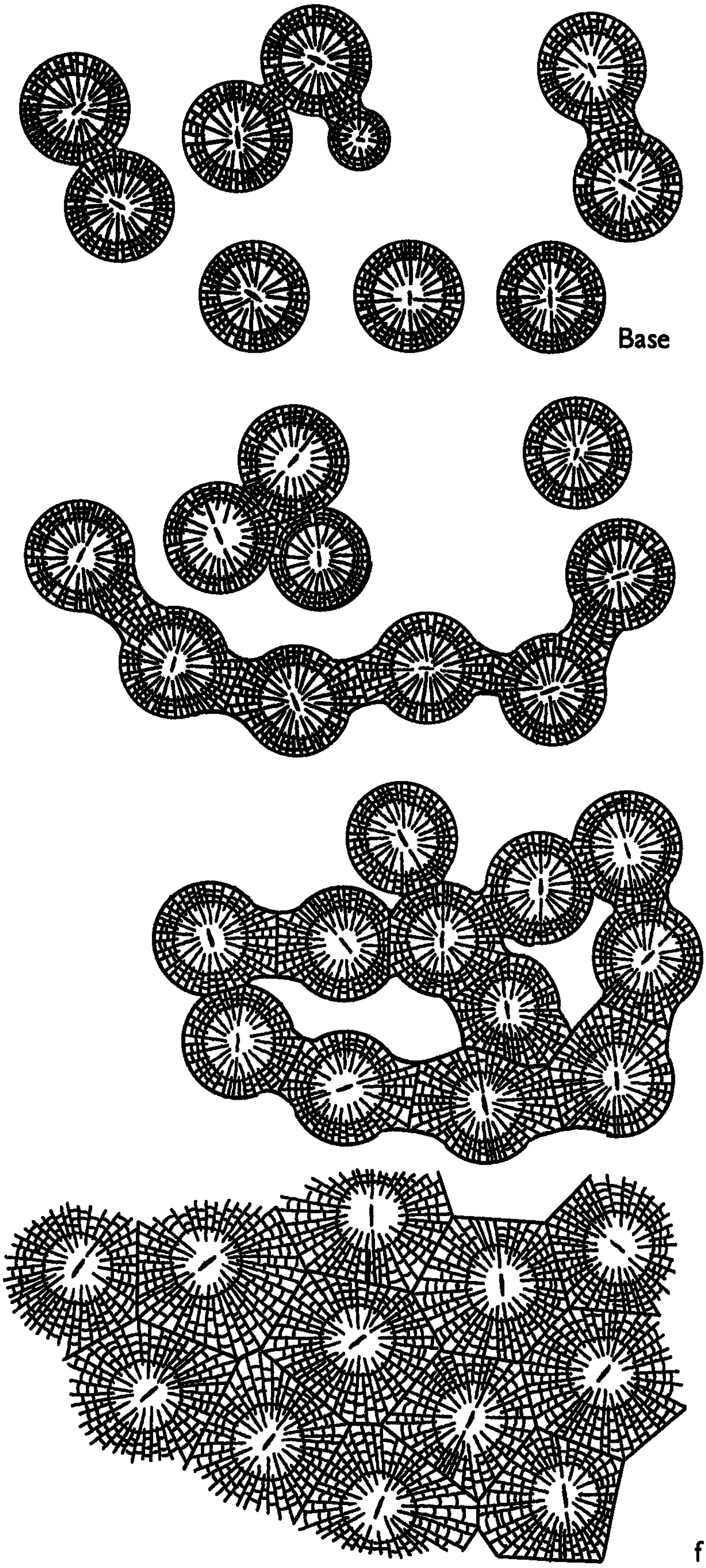


fig 18a

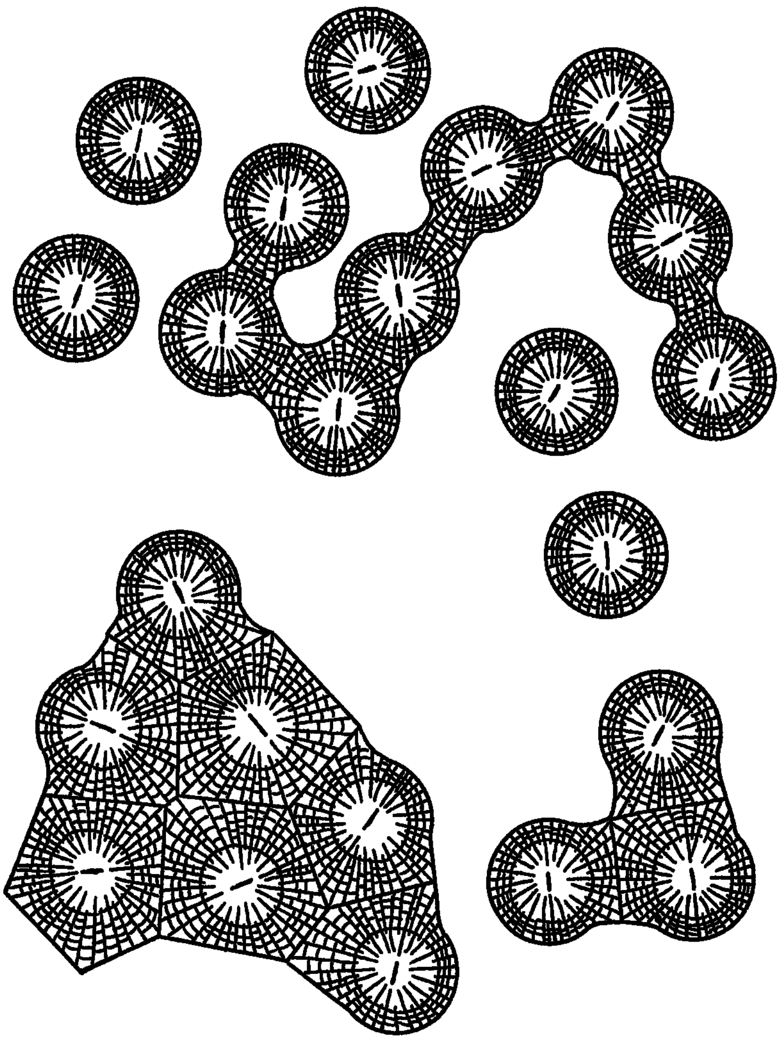


fig 18b

top as in the colonies from the S2 Limestones. This method of cerioid colony formation also explains the increased diameter of the cerioid species as when a bud forms in a fasciculate colony the diameter of the adult is greater than usual in the direction of the bud. Now, when the partly cerioid corallites of the S2 colonies were serially sectioned towards their proximal ends some of these connected corallites were found to merge back into a parent corallite and so incomplete fission is to some extent responsible for the formation of a cerioid colony. However when the complete colony was serially sectioned towards its distal end it was found not to be simply phacelloid at its top and cerioid at its base, but instead to be alternately phacelloid and cerioid throughout its height (fig. 18). Thus if a colony can become cerioid after having been phacelloid (i.e. after fission has occurred) then while incomplete fission may play a small part in the formation of a cerioid colony it is lateral extension which is having the greater effect.

Advantages of the Cerioid Trend

If, as has been postulated, there was at this time increasing competition for food and space then the advantages of a cerioid colony are many. Growing laterally to join with neighbouring corallites is an alternative method of improving the species to growing quickly vertically as the fasciculate species were doing. First, such a connection between all corallites utilises all the available space and secondly such a reduction in the space between the corallites of a colony ensures that no food particles fall between the corallites, but instead that it is all trapped by the corallites. Furthermore there is reason to believe (p. 63) that not only are the corallites in contact, but there is also a cellular connection in which case nourishment could be transferred from one corallite to another across the colony. Finally such a cerioid colony is not only a more economical type of colony to build, it also would be stronger and more stable in areas of water currents.

Genetics of the Cerioid Trend

Now, considering the genetic changes that take place to produce a cerioid colony it obviously cannot be a simple mendelian gene that controls growth habit because if this were the case then once that mutant gene (to produce a cerioid growth habit) was present in an individual, then that individual would be entirely cerioid and no intermediate colonies would occur. Instead there must be a gene complex controlling the growth habit. As interbreeding occurs the mutant gene will assume varying degrees of importance in the gene complexes of the individuals and so partly cerioid colonies will be produced. Moreover as the cerioid growth habit was advantageous to the coral, the environment would select as parents of the next generations those individuals whose gene complexes accentuated the effect of the cerioid gene so that those gene complexes were made to become dominant in the gene pool of the species. Eventually a gene complex would arise in which the mutant gene had total effect and the colony will therefore be entirely cerioid. However it will be noted that in those colonies which are partly cerioid and partly phacelloid, the individuals do not all show the same degree of lateral extension and yet all the corallites are genetically identical. Thus the actual amount of lateral extension shown by any one corallite must be a phenotypic expression induced by some factor of the environment. Obviously therefore the feature that is controlled genetically is the ability to extend laterally; the extent to which the corallites do so is phenotypically controlled by the environment. However, when the mutant gene becomes completely dominant in the gene complex then the colony will be cerioid whatever the environment.

We are now faced with the problem of how can the environment induce a colony to become cerioid, and there seem to be two possibilities. It may be that in times of strong water currents the corallites connect themselves laterally for added support, or, if in a cerioid colony there is a cellular, as well as a skeletal, connection, then it may be that in times of low food supply the corallites will connect cellularly so that nourishment can be transferred across the colony via the adjoining cells. Also when normal food supply was restored the corallites cease to need lateral connection and so a phase of lateral retreat occurs causing the alternately cerioid and phacelloid colonies.

4. The Astraeoid Trend

With the cerioid habit well established a further trend in the growth form of the colony affects two such cerioid species, *L. verticale* and *L. decipiens*. This is the loss of the dividing wall between the corallites so that the colony becomes plocoid in nature. Initially it may be thamnastraeoid when the septa of adjacent corallites become confluent, or astraeoid if the septa do not become confluent. To understand the significance of this loss of wall it will be well to examine the series of changes that take place. The epithecae of both *L. verticale* and *L. decipiens* gradually thins until it begins to be inconsistent and at this stage *Hudsonia matura* and *Orionastraea ensifer* respectively have evolved (fig.12). Eventually it disappears altogether in *H. magna* and *O. phillipsi*. At the same time there seems to be also a gradual shallowing of the calicular pits of these species. Now most of the vertical skeletal plates of a corallite are secreted by the soft tissue underneath a point in which there is a sharp upfold in that tissue (Kato, 1963, p.581). It may be that as the calices shallow the upfold in the peripheral tissue of adjacent corallites at the point at which it is cellularly connected, becomes gradually flatter so that less calcium carbonate is deposited and the wall will therefore become thinner (fig. 19).

FIGURE 19

Diagrammatic illustration of the gradual shallowing of the calicular pits in species following the astraeoid trend, with a corresponding thinning of the dividing wall.

a. shows the situation in L.decipiens and L.vorticale with a deep calice and a strong wall.

b. shows the situation in O.ensifer and H.matura which have a shallow calice and an inconsistent wall.

c. shows the situation in O.phillipsi and H.magna in which there is virtually no calicular pit and no traces of wall.

Stipple represents areas of concentration of calcium carbonate secretion by the polyp tissue.

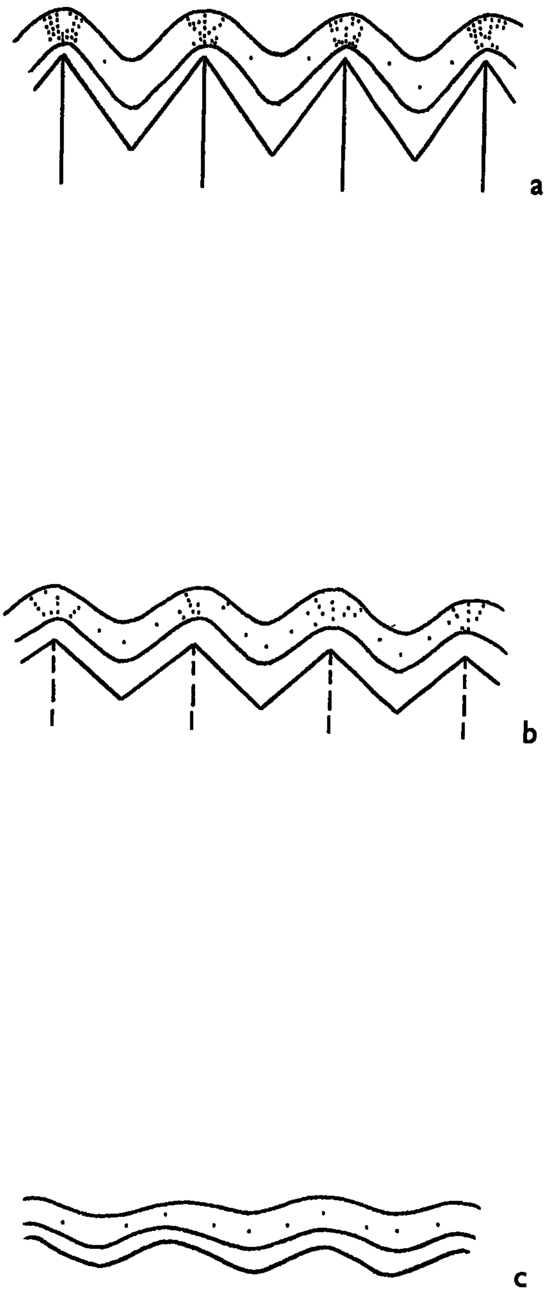


fig 19

Advantages of the Astraeoid Trend

The advantages of a plocoid colony over a cerioid colony are many. First, any dividing wall between the corallites of a cerioid colony is a useless feature; if the polyps are cellularly connected there is no point in having a wall. It has never had any purpose in a cerioid colony but is merely a vestigial feature derived from the fasciculate ancestors. Thus its loss will mean less energy involved in colony building and more calcium carbonate available for secretion elsewhere, without any loss of strength to the colony. Secondly as the calice becomes shallower and its wall thins there will be a greater cellular connection between adjacent corallites. (In a cerioid colony although the polyps are joined at their edges, the calice is still quite deep and so the proximal soft parts are still well separated).

The loss of wall is related to a complete change of emphasis from the individual corallites to the colony as a whole. First, the epithecae defining the boundary of the corallites is replaced by a holothecae defining the boundaries of the colony. Secondly, there is a change of emphasis from the edges of the corallites (their boundaries) to the centres of the corallites as the boundaries become less important. Thus as the wall disappears the zone of dilation of the septa moves from the dissepimentarium in the cerioid species to the tabularium in the plocoid species.

Genetics of the Astraeoid Trend

Because such a change is advantageous to the colony again the environment will select as parents those individuals whose gene complexes produce shallower calices and thinner walls and so this feature gradually becomes dominant. It is important to realise however that once a gene complex occurs which produces a completely plocoid colony then this gene complex must become reproductively isolated from the main gene pool so that it can eventually lose its interbreeding capacity with that gene pool. Only in this way can the two species, cerioid and plocoid, exist together and remain distinct. Finally as with the transitionary stage between phacelloid and cerioid, those corallites in colonies with thin and inconsistent walls will show a variation in the actual thickness of the walls. Thus while the maximum potential thickness of the wall is reduced genetically, the actual thickness will be controlled phenotypically, i.e. by how much calcium carbonate each corallite has available for secretion.

5. The Aphroid Trend

Once the astraeoid/thamnastraeoid species are established a final trend in the growth form of the colony takes place. This trend, which can be called the aphroid trend, is seen to develop in the evolution of *O. tuberosa* to *O. edmondsi* and from *O. placenta* to *O. rete*, when the septa retreat peripherally so that the space between adjacent corallites is filled with dissepiments only. The final expression of this trend, when the septa disappear completely, is seen in the evolution of *O. edmondsi* to *O. indivisa* when the colony is composed of tabulae and dissepiments only (fig.11).

Advantages and Genetics of the Aphroid Trend

As with the wall in the cerioid colonies the extrathecal septa ceased to have any real function and therefore any individual that ceases to secrete them may be in an advantageous position as more energy and more calcium carbonate can be put into colony building elsewhere, i.e. in a vertical direction.

The method by which this change is seen to take place is not a sudden retreat of the septa, instead every intermediate type of colony can be found in which the corallites will have some of their septa retreated while others are still continuous. However all corallites are genetically identical and so, as with the loss of wall in the cerioid colonies, while the extrathecal tissue will be overall flattened genetically, the actual amount of CaCO3 secretion of extrathecal septa will be phenotypically controlled by the micro-environment of the individual. Again gene complexes accentuating this affect will gradually be made to become dominant by selection.

In the case of O. edmondsi evolving to O. indivisa selection continues in the same direction until no septa at all are secreted. It is possible that a species with no septa may have developed a new feeding mechanism so that mesenteries and tentacles no longer existed, but it seems dangerous to assume that absence of hard parts points to a similar absence of the soft tissue that secretes those hard parts. It is unlikely that such a big change as this in the feeding methods would take place in a species almost at the end of its lineage; it is more likely that the mesenterial tissue ceased secreting septa, finding that the colony could be successful without such plates. A second possibility suggested by Mitchell (pers. comm. 1974) is that the development of aphroid tendencies in a number of plocoid species at horizons high in the Viséan or low in the Namurian (e.g. Palaeosmilia, Aulina) may be a feature of old age in the lineage as the genes in the germ plasm are breaking down.

6. 'Garwoodi' Trend

One further minor trend does occur in the thamnastraeoid species O. tuberosa and O. placenta and it involves a change in the character of the extrathecal dissepiments. O. tuberosa has its outer dissepiments secreted in a similar manner to the inner dissepiments, that is concave towards the axis. However when O. placenta evolves from O. tuberosa, while a majority of individuals retain the concave dissepiments, other individuals occur in which the outer dissepiments are convex towards the axis, a condition described by Hudson in 1929 as O. garwoodi (fig.11).

In this thesis, however, the two forms are regarded as only subspecies of O. placenta (p.223) i.e. O. p. placenta and O. p. garwoodi are two end members of a variable gene pool. However O. p. garwoodi is nevertheless an important subspecies as it was successful and the trend continued in the same direction until the dissepiments actually broke at the angle of the convexity and ran parallel to the septa lining their sides. Such a situation is seen in the new species O. sera (fig.11).

Advantages and Genetics of the 'Garwoodi' Trend

The advantages of this trend may be that the convex dissepiments of O. p. garwoodi gave extra support to the septa. Selection continued in the same direction to O. sera and again dissepiments lining the septal sides would probably strengthen the septa more than would transverse plates. So again the species is improving itself by the gene producing convex dissepiments becoming dominant in the gene complex controlling curvature of the dissepiments. There may be no additional mutation.

7. The Diphyphylloid Trend

Another trend that expresses itself at least four times in different species of the Lithostrotiontidae, and which takes its name from this group of corals, is the diphyphylloid trend. This is a common trend in other groups of corals and is usually regarded basically as being merely a loss of the columella with a resulting flattening of the tabulae and a shortening of the septa. However every species in the Lithostrotiontidae that follows this trend also shows the development of a further important character; that of calicular parricidal budding, instead of the lateral budding of the columellate parent species. At first sight it may seem a coincidence that every species that follows this trend also produces the same type of budding (i.e. that two characters are always affected in the same way.) One might be tempted to suppose that the four non-columellate species have not all followed the trend individually, but instead that they have evolved from each other along a non-columellate lineage, and thus all possess the same two characters. However this can be explained if, perhaps, the basis of the trend is not the loss of the columella, but instead is the development of calicular budding and that any calicular budding requires the loss of the columella. After all axial budding does involve the extension of one septa across the middle of the corallite and it might be that this cannot take place if a columella is in the way in the axis of a corallite. If this is so then it is possible that there is a genetic link between these two characters and that they are both controlled by the same gene and therefore that if this gene does mutate then both characters are simultaneously affected.

The first change to occur in the development of this trend happens long before the disappearance of the columella and involves a change in the tabulae of the parent columellate species. Smith described two types of tabulae (1928, p.114) as α and β tabulae (p.15), the α tabulae having the downturned edges of the inner series resting on the tabulae below, but not in any regular manner, and the β tabulae having the downturned edges aligned to form a tube, or pseudo-aulos, running down the length of the corallite (p. 15). Now the tabulae of the parent columellate species, when they first appear, are of the α type, but as these species evolve the points of contact of the downturned edges of the inner tabulae, on to the tabulae below gradually become more and more aligned. Eventually when these points of contact are all in the same plane, the downturned edges produce the tube running the length of the corallite (β tabulae), a kind of structure which has been described in this thesis as a pseudo-aulos (fig.20).

Advantages and Genetics of the Diphyphylloid Trend

A corallite with such a structure will clearly be much stronger than a corallite with α tabulae. The species is thus becoming more advanced

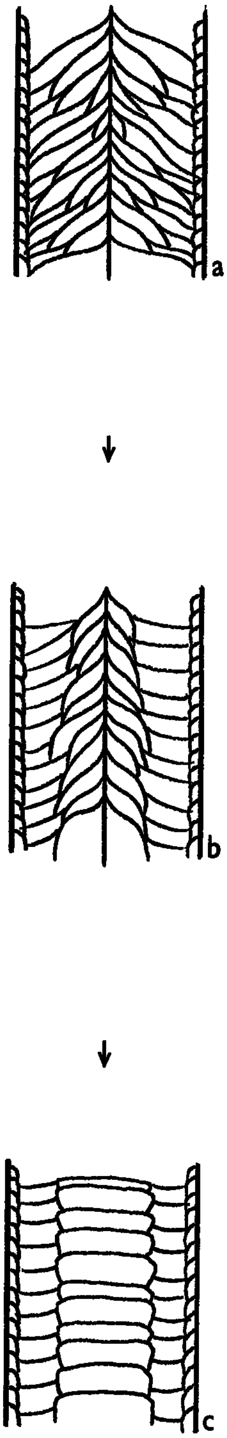
FIGURE 20

Diagram illustrating the Diphyphylloid trend in longitudinal section.

a. Early stage of the ancestral columellate species with α tabulae when the points of contact of the inner tabulae onto the outer tabulae are haphazardly arranged.

b. Later stage in the ancestral columellate species when the points of contact gradually become aligned (α/β tabulae).

c. The diphyphylloid(non-columellate) species with β tabulae when the points of contact are so well aligned that the downturned sides of the inner tabulae form a continuous tube or pseudo aulos.



α tabulae.

$\alpha-\beta$ tabulae

β tabulae with pseudo aulos

fig 20

by using its past skeleton more efficiently so that its structure is more useful in the day to day existence of the polyp. Genetically the species is improving itself again by selecting only those types whose gene complexes produce this kind of structure. Now, if it is true that this structure produces a strengthening to the corallite, and assuming also that the columella is a strengthening structure, then once this pseudo-aulos is developed, any mutations involving the loss of the columella can now be successful as the corallites will have an alternative method of support. Such mutations occurring in a corallite with α tabulae could possibly not survive. Thus the trend involving a mutation to produce calicular budding can only be successful once the species has developed an alternative method of support as this mutation also involves the loss of the species original strengthening structure. Such a mutation would be advantageous to the coral as a calicular budding polyp can give rise to a greater number of individuals at any one time than can a laterally budding polyp, so that greater proliferation can be achieved. This is only a hypothetical theory that can never be proved, but at least it offers one possible explanation for the chain of events.

8. The Aulate Trend

The development of a pseudo-aulos seems to be an intermediate stage in the trend towards a true septal aulos. The diphyphylloid lineages do not persist for long enough to develop a true septal aulos, but the species of *Aulina* and *Fascicaulina*, which show a septal aulos in various stages of development, do seem to suggest that they were developed from ancestors with a pseudo-aulos.

The development of this structure is in three stages shown by the three plocoid species of *Aulina*. In *A. senex* the tube is really no more than a pseudo-aulos built by the tabulae with virtually no septal contribution. In *A. botanica* the tube is still built mainly by the tabulae but some septa do begin to contribute towards it by bending at their axial ends and merging with the downturned edges of the tabulae, but this bend to the septa is always convex inwards producing an irregular shaped aulos in cross section (fig.21). However in A. rotiformis all of the septa contribute to the aulos and when this happens the inner tabulae cease to be downturned at their periphery, but become simply horizontal as successive platforms within the septal tube. Moreover in A. rotiformis the axial bend to the septa is now concave inwards so that the aulos is circular in cross section and therefore a stronger structure.

Advantages and Genetics of the Aulate Trend

The advantages of such a structure are the same as those for a pseudo-aulos, i.e. it gives the corallite additional support and presumably the continuous vertical structure of a septal aulos is better in this respect than the more discontinuous tube built by successive horizontal tabulae. If the septal aulos is developed from a pseudo-aulos then selection pressure clearly continued in the same direction on this strengthening structure. There may have been an additional mutation causing the septa to contribute towards this tube.

The development of this structure is also seen in the genus Fascicaulina. In F. horsfieldi and F. hibernica the aulos is produced by septa, but the bend to the septa while usually convex inwards is occasionally concave and so the structure is quite variable in these species. In F. furcata on the other hand, it is always concave. Initially those individuals with the mutated gene were still interbreeding with the main stock causing the great variation in the development of the aulos as seen in F. horsfieldi. When F. horsfieldi evolved to F. hibernica it passed on the completely variable gene pool as regards the development of the aulos as F. hibernica has an aulos in just as variable a state. Thus selection pressure on the state of development of the aulos had not begun until

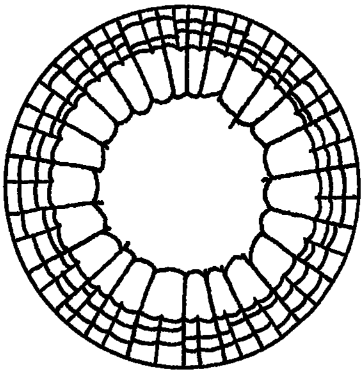
FIGURE 21

Diagram illustrating the Aulate trend in transverse section.

a. Pseudo aulos built by the tabulae only. Some of the septa extend through this structure showing that they do not contribute towards it.

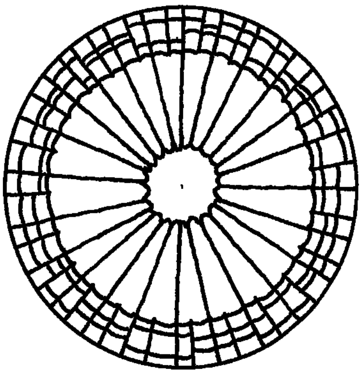
b. Primitive aulos built by the septa, but with a convex bend at their axial ends.

c. Well developed aulos with the septa bending in a concave manner so that the aulos is circular in cross section.



Pseudo aulos

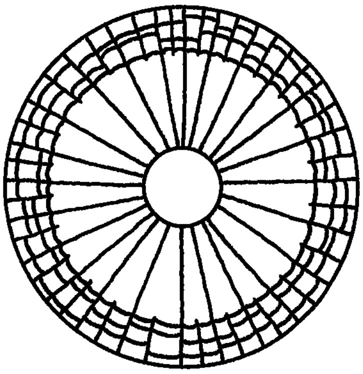
a



Convex aulos.

b

c



Concave aulos

fig 21

after *F. hibernica* had evolved otherwise only those geno complexes producing a well developed concave aulos would have been passed on from the gene pool of *F. horsfieldi*. By the time *F. furcata* evolved from *F. hibernica* selection pressure was acting on the type of aulos and only those gene complexes producing a well developed aulos were passed on to *F. furcata*.

CHAPTER 4

DEVELOPMENT OF COLONIALITY IN THE LITHOSTROTIONTIDAE

The Lithostrotiontidae lineage evolves in an overall trend of increasing coloniality. It evolves from fasciculate through cerioid to astraeoid and thamnastraeoid and finally to aphroid and indivisoid. We are now concerned not with the actual changes that take place, but with the significance of those changes in the light of soft part morphology and perfection of the colonial habit. We must look at the boundaries between the different types of colony and estimate the significance of changes that take place as the different types of colony evolve.

Simple to Fasciculate (Dendroid and Phaceloid) Colonies

There is no solitary coral representative of the Lithostrotiontidae, but an unknown solitary ancestor will have occurred in the distant past, so it is important to look at this boundary. The fasciculate type of colony is not an important type of coloniality as every individual is entirely independent. The polyps are not connected by any soft tissue, but only at their proximal ends by previously deposited skeleton (fig.22a). This type of colony is little different from a number of solitary corals attached to the same block of substrate in that the individuals do not rely or depend on each other at all.. Coates and Oliver (1971, p.11) state that if there is any co-operation between such polyps it is only that which results from extrinsic factors acting upon a cluster of polyps and not from any biological integration. However the fasciculate habit is important as it marks the beginning of asexual reproduction, a factor which is vital to colonial growth. Boardman et al. (1971, p.vii) state that solitary corals can reproduce asexually but a colonial coral has developed the ability to prevent its asexual buds from separating from the parent skeleton. Thus the important change from simple to fasciculate corals is not only the development of the ability to reproduce asexually, but also the continued adherence of the buds to the parent after reproduction has taken place. Once the asexual daughter polyps appear, although they remain connected to the parent by a fused skeleton, they separate cellularly and are entirely independent biologically. The main advantage of this type of colony is that each new individual polyp that is produced does not have to find hard ground substrate to initiate the process of skeleton building. It continues the skeleton of earlier individuals. As Coates and Oliver state (loc. cit., p.24) all coralla tend to lift polyps away from the substrate and up into the water column. A second significant point is that as every individual polyp in the colony was produced asexually from the same protocorallite then every individual will be genetically identical. Thus the polyps at this stage develop the potential to become cellularly fused with their neighbours. This feature can only occur when the fusing cells contain identical genetic make up. It is therefore the essential genetic feature of the cerioid and more complex colonial corals.

There is little difference between dendroid and phaceloid coralla in the level of colonial integration, but the close packing of the corallites in the phaceloid colony does indicate a move towards a higher level of integration.

Fasciculate to Cerioid Colonies

The skeletal change occurring at this stage is the fusion of the hard parts at their distal ends instead of just proximally, i.e. fused epithecae~~s~~ (fig.22c). In the discussion of the cerioid trend (p.51) it was postulated that such fusion of hard parts may point to a similar fusion of the soft tissue that was secreting those hard parts and that, at this stage, the polyps may have realised the potential for fusion that was present in the fasciculate colony. Oliver and Coates (loc. cit.,

FIGURE 22

Levels of coloniality in Phaceloid and Cerioid colonies.

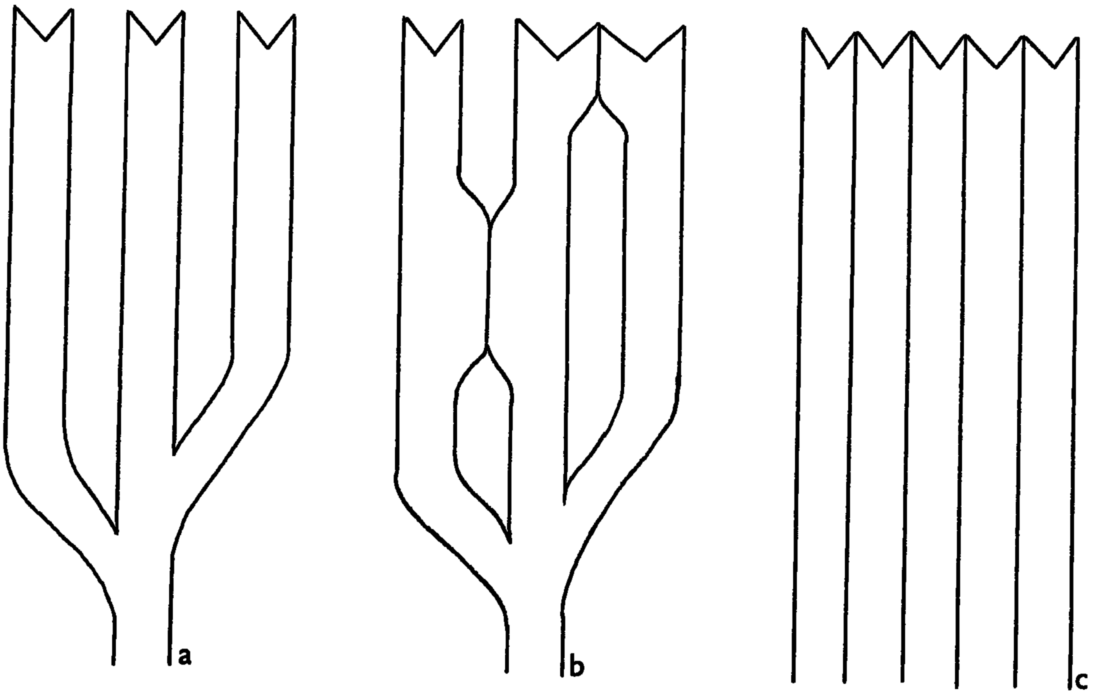
a. Phaceloid colony with the corallites only connected at their proximal ends by previously deposited skeleton.

b. Colony intermediate between phaceloid and cerioid with intermittent fusion of corallites at their distal ends by temporary lateral connections.

c. Cerioid colony with corallites connected at their distal ends by fusion of the epithecae.

d. Hypothetical illustration of the fusion of soft tissue in a cerioid colony. The gastrovascular cavities may not be continuous between corallites due to the high epithecal wall. Possibly only the outer cells of the endoderm are in contact. The colonies intermediate between phaceloid and cerioid will show such fusion of tissue intermittently.

gvc.= gastrovascular cavities, ec.= ectoderm,
en.= endoderm, sk.= skeleton of corallite.



Phaceloid Phaceloid-cerioid Cerioid

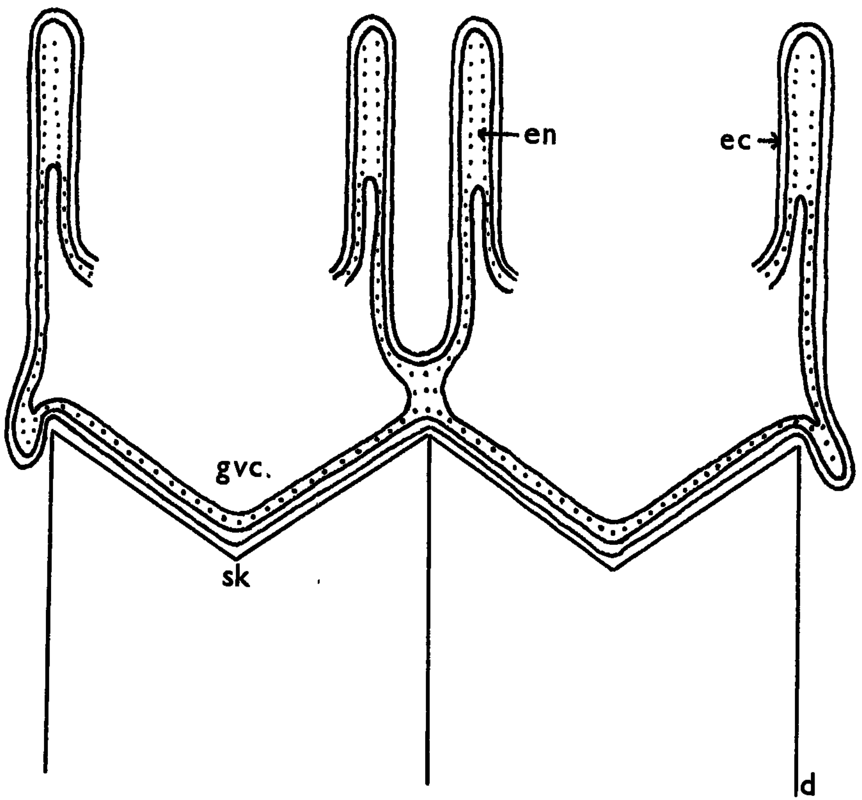


fig 22

p.11), however, believe that because each adjacent polyp is still secreting its own wall, then although these walls are fused, this fusion of soft parts does not occur until the change from cerioid to astraeoid. To throw some light on this problem the cerioid colony may be compared to fasciculate corallites at the stage when an offshoot appears from its parent. At the first stage of appearance of the fasciculate bud, the bud must be cellularly connected to its parent as it was asexually derived from the cells of the parent. Using this analogy at what point does the bud lose cellular connection with its parent; when the daughter and adult are separated by a wall (fig.23) or when they are totally separated by space (fig.23)? If the first case is true then a cerioid colony has no cellular connection of corallites and the cerioid condition is only a continuation of the close packing of the phaceloid stage and is quite distinct from the astraeoid and later types of colony. This case has been put forward by Coates and Oliver (loc. cit., p.11) who say that as the polyps of a cerioid colony are separated by a wall, they are not in cellular connection and that cerioid coralla are little more than a compact phaceloid colony, i.e. the reason why the corallites grow so close together is that there is no space for them to grow separated.

Before examining this argument we must review some of the terms employed in the description of the polyp's soft tissue. Vaughan and Wells (1943, p.16-17) state, "the coenosarc is that part of a polyp in a colony that lies outside the thecae or skeletal wall. The edge zone is that part that lies over the free portions of the corallite ... The edge zone is then simply a horizontal fold of the column wall over the column wall itself. Within the fold is a continuation of the gastro-vascular cavity."

Now, Coates and Oliver (loc. cit., p.11) point out that the epitheca is deposited by the outer margin of the edge zone, so corallites that are separated from each other by epithecae were not occupied by

FIGURE 23

Longitudinal and transverse sections of a fasciculate corallite in the budding stage. Section '1' shows the adult and daughter corallites separated by the daughter's wall, but still in contact by an extended branch of the adult dissepimentarium. Section '3' shows the adult and daughter growing completely separated, but with the extended branch of the dissepimentarium now being deposited by the daughter corallite.

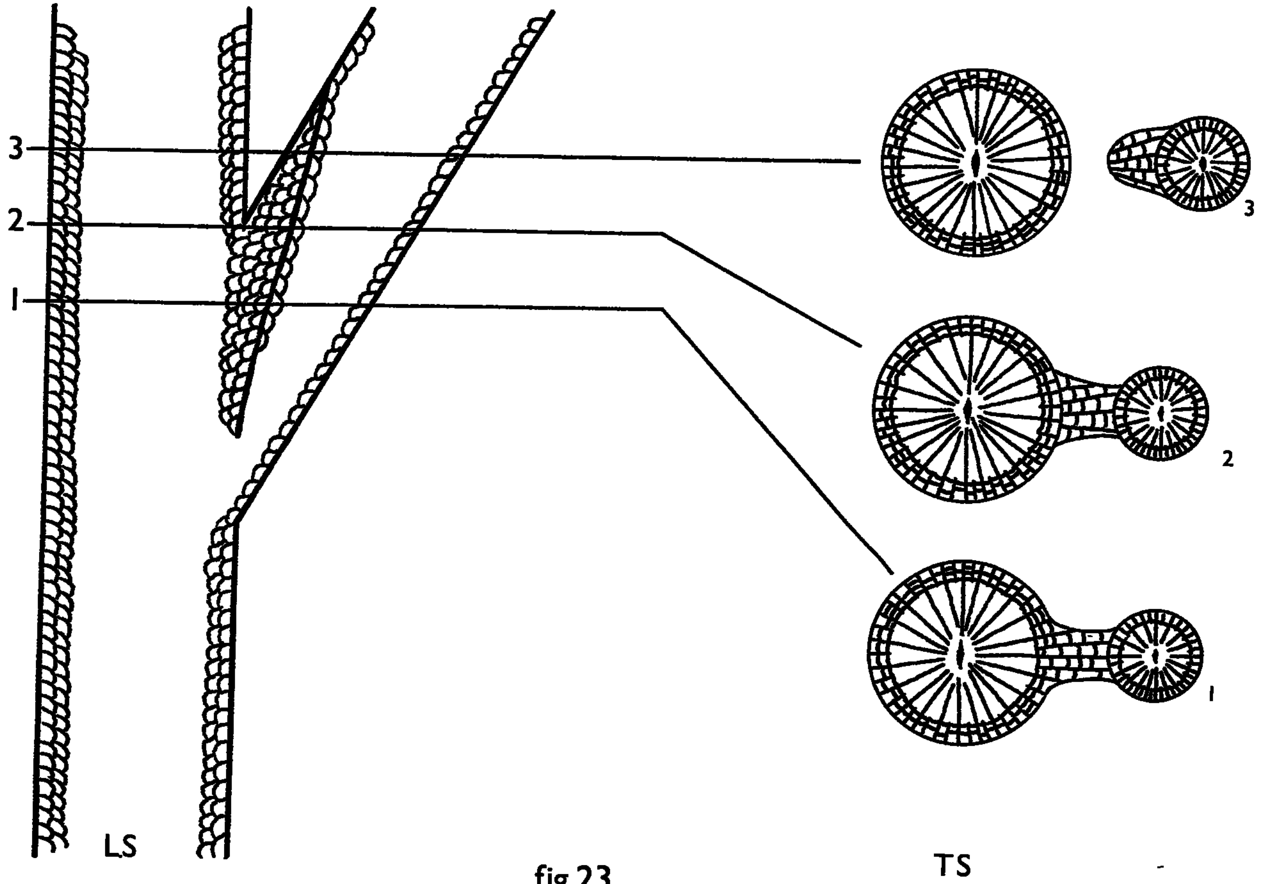


fig 23

polyps connected to each other by edge zone or coenosarc. They state that most likely the polyps were separate individuals, although in physical contact with other polyps on all sides. However, it seems to me that if the polyps were in physical contact and still depositing a wall, then there is no reason whey those cells that are in contact should not be cellularly connected.

Returning to the analogy of the fasciculate offset, if cellular connection ceases when a wall is formed between parent and offset, why does the daughter continue to grow in skeletal connection with the parent for a period after the wall is produced? In a fasciculate colony it is not lack of space that is keeping the parent and the offset side by side as spreading space is available in such a corallum; there must be some other factor holding the two corallites together. Examination of a transverse section of a budding corallite of *L. martini* from the Ash Fell Sandstones, of Cumbria (No. 3c) throws light on this problem. After the formation of the daughter's wall (fig.23.1) the adult continues to extend a branch of its dissepimentarium towards the daughter. The tissue secreting this branch is shown by fig.23.1 to belong to the adult as no wall divides this branch from the main body of the adult. However when the adult and daughter break, this tissue is seen to adhere to the daughter corallite, and the daughter continues to secrete this dissepimentarium for a period after it has broken from its parent corallite (fig.23.3). Now if Coates and Oliver are correct and cellular connection between adult and daughter ceases when the daughter's wall is formed, this situation would be impossible as the extended tissue would first be cellularly disconnected from the daughter in fig.23.1 and therefore could not be later secreted by the daughter in fig. 23.3.

This example shows that the adult and daughter corallites, although separated by a wall, are still in cellular connection. Therefore, the outer margin of the edge zones (of the daughter and parent) that are secreting the wall are cellularly connected. There is no reason why this should not also be the case in the cerioid coralla.

The alternative hypothesis is that cellular connection does not take place until the transition to astraeoid colonies when there is no wall dividing the corallites. However, although the corallites of a cerioid colony are separated by a wall, and although each adjacent corallite was secreting its own part of that wall (cerioid epithecae can be separated into two halves with a dark line running down the middle) the two parts are so strongly fused together that it seems that the cells that were secreting the wall were also fused in the same manner. If there was no such connection between adjacent polyps one would expect at least some small temporary space to occur periodically between the two halves of the epithecae and such spaces are never seen. Moreover, if there was no cellular connection it would be difficult to explain why two corallites should grow towards each other in partly cerioid colonies. It seems unlikely that they were merely touching together with no additional connection. It seems likely therefore that cellular connection does occur at this stage and presumably the polyps could pass nourishment across the colony.

McCoy (1851) in his classification of the cerioid species suggested that a far more important change occurred in the colony at this stage. He divided the cerioid species into two groups, viz, Nematophyllum, for those species whose individual corallites could not be split along the epithecal walls, and Stylaxis, for those species whose corallites could be separated from each other. If this was a valid classification the reason behind it would seem to be that Stylaxis had a double wall with adjacent corallites secreting their own wall, whereas the species of Nematophyllum did not split as the adjacent corallites shared a common wall. If this was correct then the Nematophyllum species will have reached an advanced stage of coloniality as two individuals would be secreting a common structure. However examination at high magnification of all the species of Stylaxis and Nematophyllum shows that this is not true. Instead all the species do have a double wall and thus the ability to split is probably controlled by a factor of preservation, dependent on diagenesis and weathering.

While it is suggested that there is some sort of cellular connection between the polyps of a cerioid colony it is not possible to evaluate whether this was a simple fusion of the outer cells of the edge zone or whether there was a higher level of integration and that within the fused zone there was a continuation of the gastrovascular cavity over the dividing epithecae. This is perhaps unlikely as the epitheca is quite a high ridge and there would have been little depth to the fusion of the cells (fig.22d). The proximal soft parts would not become fused until the calice shallowed and the epithecae became reduced in the plocoid coralla (p.68).

Some phaceloid coralla show temporary lateral connections that are extensions of the dissepimentarium. These coralla appear to be intermediate between phaceloid and cerioid coralla and therefore temporarily possess the higher integration of a cerioid corallum (fig.22b).

One phaceloid species of the Lithostrotiontidae (L. junceum) possesses temporary lateral connection of a different kind. Hollow transverse connecting tubes are developed between corallites (fig.24b). The lack of dividing walls in these structures indicates a higher level of integration than in a cerioid corallum. Certainly there was temporary cellular connections as the construction of the tubes involves the co-operation of two polyps, and probably these tubes connected the gastrovascular cavities. However, such a connection was only temporary as the tubes must have been vacated by the polyps when the polyp continued to build its skeleton vertically (fig.24a).

If, as is usually assumed, such connection processes in phaceloid coralla are equivalent to mural pores in a cerioid corallum, then it

FIGURE 24

Level of coloniality in Phaceloid colonies with connecting processes.

a. Connecting processes between adjacent corallites as in L. junceum.

b. Hypothetical illustration of the soft tissue in L. junceum with the connecting processes allowing connection of the gastrovascular cavities of adjacent corallites.

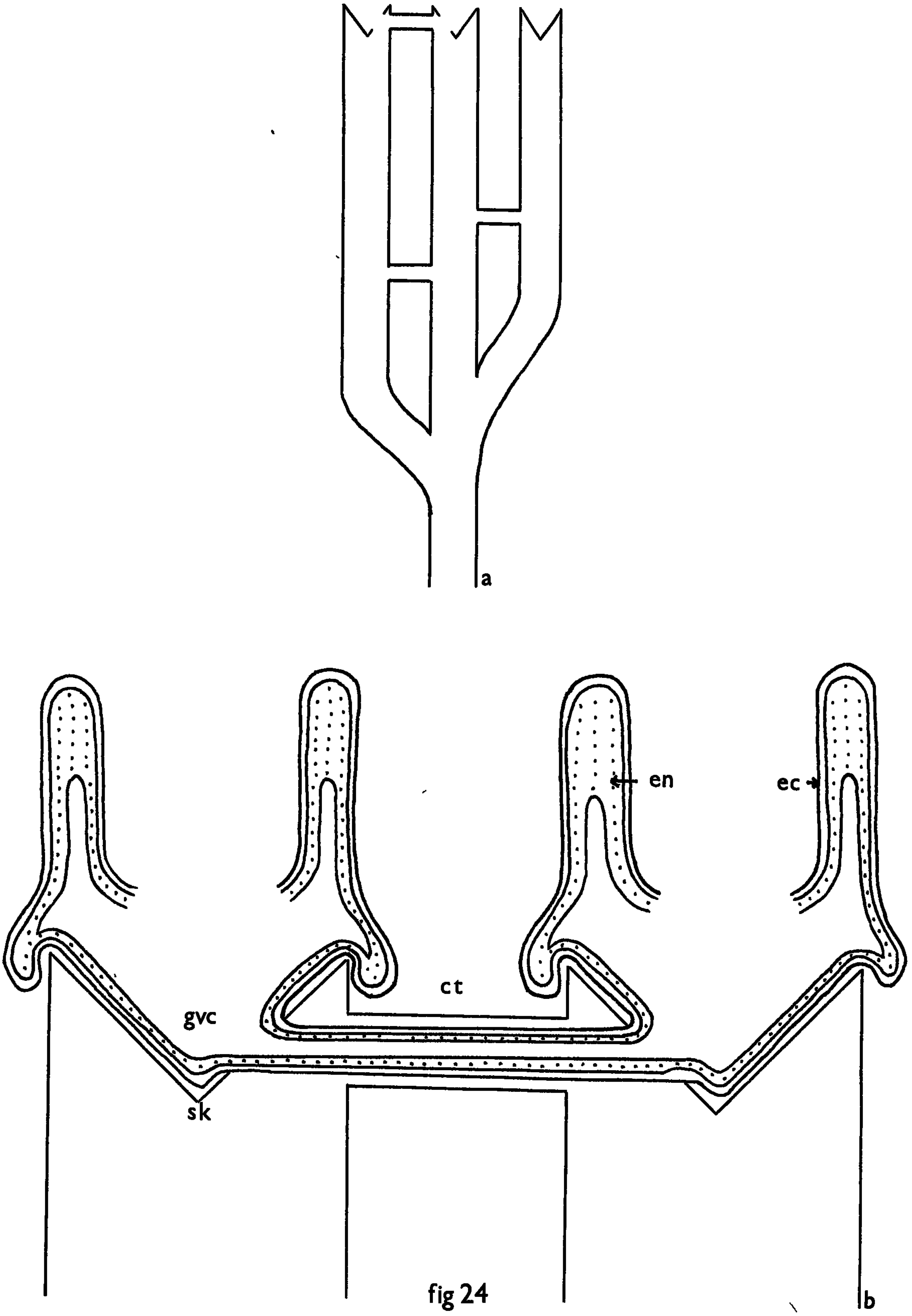


fig 24

seems that mural pores in a cerioid corallum also enabled connection of the gastrovascular cavities. If this is correct then again it seems likely that a cerioid corallum without mural pores (e.g. the cerioid Lithostrotion species) had no such connection of gastrovascular cavities.

Cerioid to Astraeoid and Thamnastraeoid Colonies

With the change from cerioid to thamnastraeoid and astraeoid the calices become shallower and so the proximal soft parts become more and more fused. Thus as there is a greater depth to the fusion of cells it is likely that in this stage the gastrovascular cavity of adjacent corallites becomes continuous; a move towards a higher lever of integration (fig.25). Indeed in those coralla that are thamnastraeoid the septa of adjacent corallites are confluent and therefore so are the mesenteries of the gastrovascular cavity. Coates and Oliver (loc. cit., p.18) state that as in astraeoid colonies the septa are not confluent this suggests that the mesentaries were not continuous and that the gastrovascular cavities were not communicate. However, while it is true that the mesentaries of an astraeoid coralla are not continuous this does not mean that the gastrovascular cavities are not continuous. Continuation of the gastrovascular cavity can easily occur at a level above the mesentery folds in the basal body wall. If this is correct then the soft part morphology would agree with the hard part morphology (p.217) that there is little significant difference between astraeoid and thamnastraeoid coralla at least in the Lithostrotiontidae. However, the thamnastraeoid coralla are slightly more integrated as they would have had a greater continuity of the gastrovascular cavity than would the astraeoid coralla.

As McCoy's epithecal wall theory is not substantiated by detailed study this stage in colony development is important for another reason. First the epithecal boundaries disappear and this is related to a change

FIGURE 25

Hypothetical illustration of the soft tissue of a plocoid colony with shallow calices and gastrovascular cavities continuing from one corallite to another.
gvc.= gastrovascular cavities, ec.= ectoderm,
en.= endoderm, sk.= skeleton of corallite.

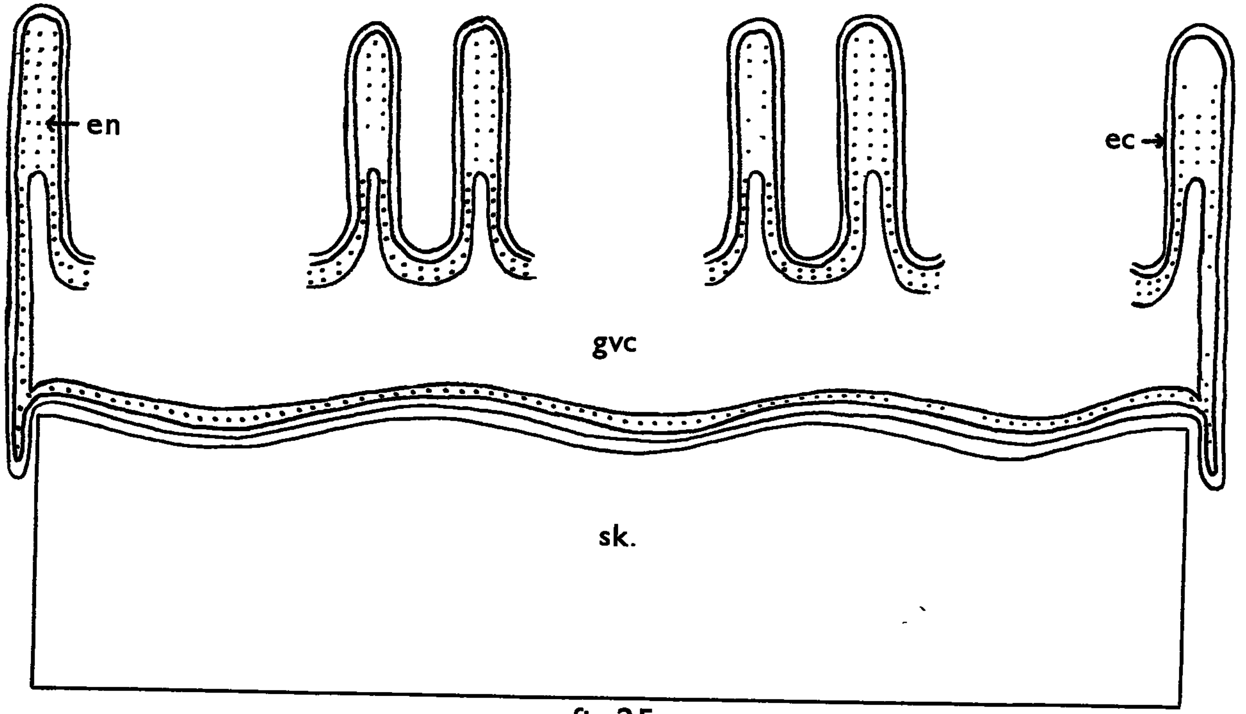


fig 25

of emphasis from the individual to the colony as a whole. More important, it means that it is at this stage that two adjacent corallites begin to share common hard parts. The septa of adjacent corallites are confluent (in thamnastraeoid coralla) and while at the centres of these corallites the septa can be attributed to a certain individual, somewhere between the centres of the two corallites the septa will be shared by both corallites. If the hard parts express exactly the nature of the soft tissue then one can assume also that some tissue between the two individuals will be common tissue, i.e. not attributable to any one individual. Coates and Oliver (loc. cit., p.18) suggest correctly that the development of this extrazooidal tissue marks the development of coloniality in a further direction. However they suggest that such extrazooidal tissue does not begin to occur until the aphroid coralla develop. Detailed study of one particular colony of the thamnastraeoid Orionastraea placenta (No. 172c) from the Middle Limestone of Coverdale throws light on this problem. This colony does not exhibit continuous growth, but in longitudinal section (fig. 26) is seen to be composed of discontinuous masses of colony growth with a mud matrix in the resulting spaces. An influx of mud has invaded the colony and completely covered the soft tissue (fig.26a). However, certain parts of the colony, the centres of the individuals, have protruded through the mud and carried on growing (fig.26b). Eventually these centres have extended laterally and joined up once more to produce a continuous layer of soft tissue, trapping the mud as lenses in the skeleton below (fig.26c).

Considering the implications on the soft part morphology of the polyps it is most probably the tentacular ring and the stomach region that has protruded through the mud, and as it is only the tabularia that are protruding the tentacles must be situated above the inner ring of dissepiments defining the tabularium. The tissue that does not protrude through the mud, but is reformed above it, is thus extratentacular tissue.

FIGURE 26

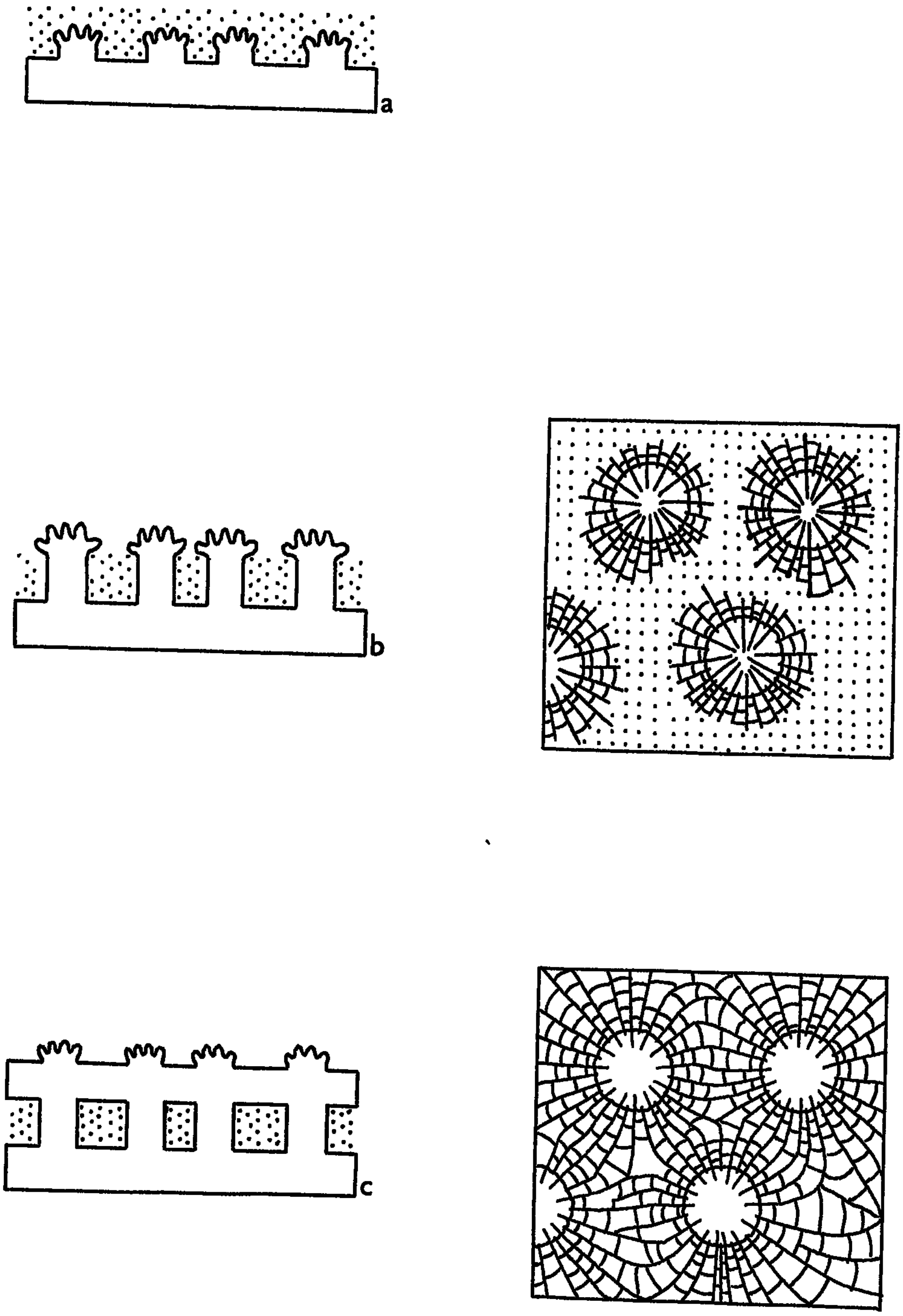
Diagrammatic illustration of the peculiar growth of a colony of O.placenta (No. JN 172c) from the Middle Limestone of Wharfedale.

a. Influx of mud invades the growing polyps on the surface of the corallum.

b. Individual polyps continue to grow and protrude through the mud while the tissue between the polyps does not survive the mud influx.

c. The polyps extend laterally and connect once more trapping the mud as lenses in the skeleton below.

L.S.= Longitudinal section, T.S.= Transverse section. Stipple indicates mud matrix.



LS

TS

fig 26

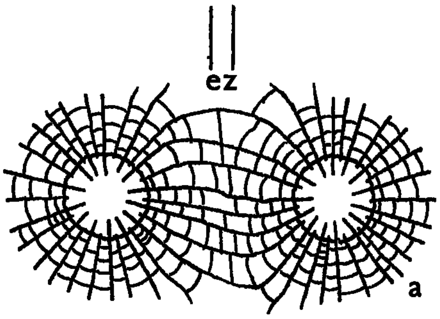
It is usually assumed (Coates and Oliver, loc. cit. p.18) that is is in the aphroid corals that extrazooidal tissue first develops (i.e. that tissue above the periphery of the corallite where the septa have retreated). However, the extratentacular tissue of a thamnastraeoid colony only differs from the extrazooidal tissue of an aphroid colony in that it secretes septa. There is no more reason to believe that the peripheral tissue of an aphroid colony is extrazooidal than there is to believe that the peripheral tissue of a thamnastraeoid colony is extrazooidal. After all, the central parts of the individual confluent septa cannot be attributed to any given corallite any more than can the peripheral dissepiments of an aphroid colony (fig. 27). Moreover, the Coverdale colony shows that the individual corallites can survive without this extratentacular tissue as this is periodically destroyed by the mud. Thus the extratentacular tissue of the thamnastraeoid (and astraeoid) colony seems to be extrazooidal also.

Thamnastraeoid to Aphroid to Indivisoid Colonies

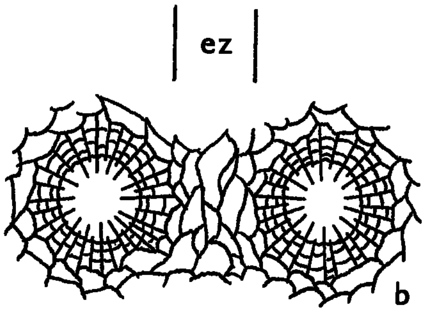
In the development of an aphroid colony Coates and Oliver (loc. cit., p.18) point out that as the septa are lacking in the peripheral parts, direct evidence of polyp integration is lacking. However in the Lithostrotiontidae the aphroid species clearly evolved from thamnastraeoid ancestors and so we can assume that they also had gastrovascular cavities intercommunicated. Coates and Oliver also consider that the aphroid colony marks the beginning of extrazooidal sclerenchyme and coenosarc, but this probably occurs in thamnastraeoid and astraeoid coralla as has been shown above. Thus the development of an aphroid coralla (and eventually the indivisoid coralla) merely marks a change in the nature of this tissue in that the basal body tissue flattens out peripherally and ceases to be upfolded into mesentaries. This is interesting however in that it means that the endodermal tissue must show a reduction in total

FIGURE 27

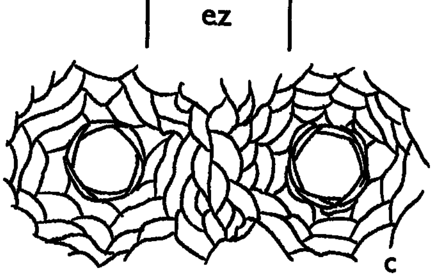
Illustration of the increase in extrazooidal tissue from thamnastraeoid to astraeoid to aphroid coralla.
ez.= extrazooidal tissue.



Thamnastraeoid



Aphroid



Indivisoid

fig 27

surface area and therefore in capacity of digestion. However it has the advantage that the interior of the polyp is more open and in indivisoid coralla is completely open, and that the colony in effect has one large gastrovascular cavity.

The aphroid and indivisoid coralla also show an increase in the amount of extrazooidal tissue (fig. 27) as less of the skeletal plates can be attributed to any one individual. A high state of coloniality is reached when a daughter corallite, that appears within this extrazooidal tissue, can not be attributed to any one parent, but only to the colony as a whole.

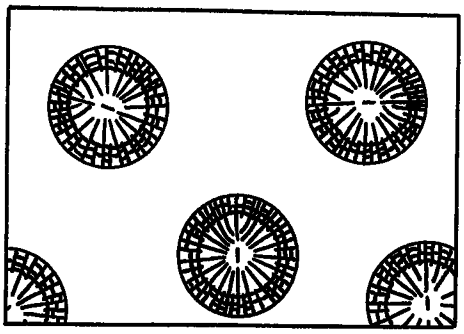
Summary

The following table shows the opinion of Coates and Oliver and the opinions of the present author regarding the level of coloniality of the different types of coralla. Generally the author regards each successive stage of colony development to be rather more integrated than do Coates and Oliver.

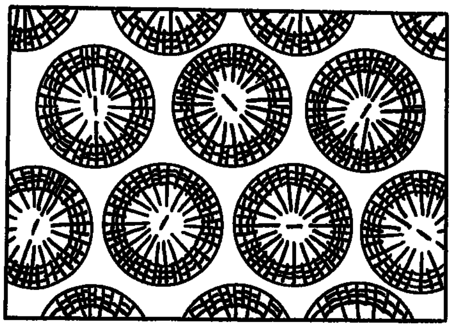
	Coates and Oliver (1971)	Lithostrotiontidae Thesis
Polyps separated in space	Fasciculate	Fasciculate
Polyp walls in apposition	Cerioid	
Fusion of tissue	Astraeoid	Cerioid
Confluent body cavities	Thamnastraeoid	Astraeoid Thamnastaeoid Aphroid Indivisoid
Extrazooidal tissue	Aphroid	

FIGURE 28

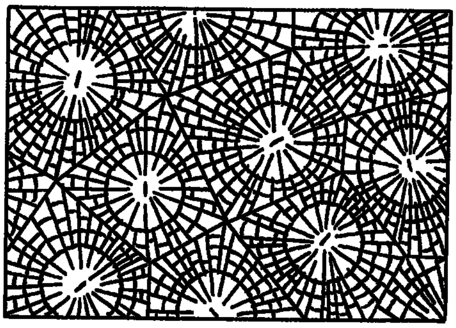
Diagram showing the increasing level of coloniality in the different types of corallum seen in the Lithostrotiontidae.



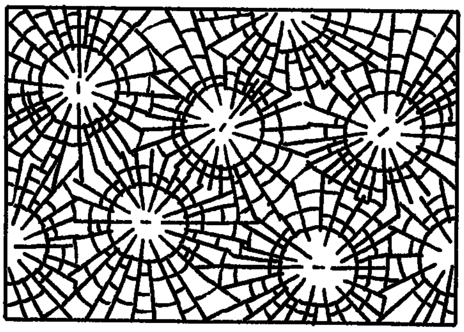
Dendroid



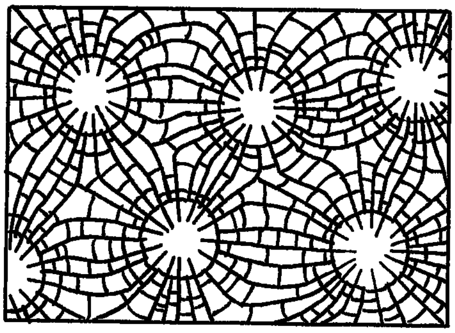
Phaceloid



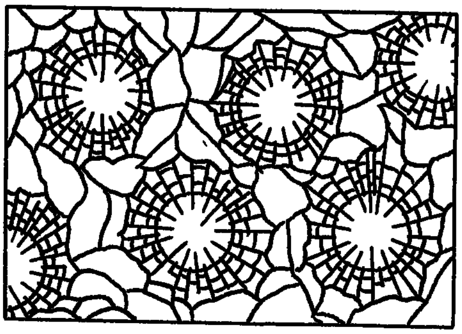
Cerioid



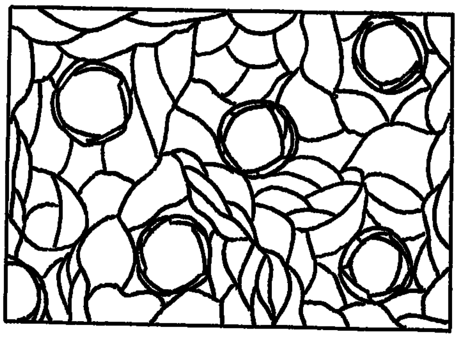
Astraeoid



Thamnastraeoid



Aphroid



Indivisoid

fig 28

CHAPTER 5

PALAEOMIGRATION DIRECTIONS OF THE LITHOSTROTIONTIDAE FAUNA IN THE NORTH OF ENGLAND

Introduction

In collecting and examining coral faunas from the limestone bands of a repetitive sequence such as the Yoredale Series in the North of England the fact that the same coral faunas do not occur in the intervening sandstone and shale beds between the limestones is taken for granted. The obvious explanation is that at the end of every limestone phase the coral fauna becomes temporarily exterminated from the particular area in question. Moreover as the same coral fauna usually reappears in the succeeding limestone band it is clear that this fauna has re-entered the area in question and that it has come from an adjacent area in which limestone deposition and coral growth continued, uninterrupted by detrital phases, throughout the time period. The establishment of the whereabouts of such areas of continuous favourable conditions for coral growth is important as it gives first, an indication of the direction that the corals have migrated, and secondly it may point to the centre of evolution of the lineage. These areas might be immediately adjacent or quite distant.

The Viséan Lithostrotion fauna

When considering the palaeomigration directions of the Lithostrotiontidae species from the Viséan Yoredales and the earliest Namurian, i.e. all the Yoredale limestones up to andincluding the Great Limestone, the area from which the species are migrating into the successive limestone bands is possibly the Derbyshire dome area to the south. In this region (see Chapter 2) there is continuous deposition of limestone and therefore the possibility of continuous coral growth almost to the top of the P2 Subzone, that is almost to the horizon of the base of the Great Limestone. Moreover when the limestone deposition of the Derbyshire area does eventually cease at the top of P2, and is replaced by the non-coral bearing Edale Shales (E Zone) the coral fauna is permanently eliminated from Derbyshire and at the same time no more Lithostrotiontid corals are found in the North of England above this horizon even though limestone bands are present in the north in the E Zone (i.e. no Lithostrotiontid corals in the Little Limestone or the Crow Limestone, immediately above the Great Limestone).

Thus the corals found in all these Yoredale Limestones could have migrated from the south, northwards to the North of England, most probably from a European centre of evolution. This centre of evolution may possibly have been around the margins of the St. George's Land/Brabant Massif land mass that existed in Carboniferous times to the south of the Derbyshire dome (fig.29). The shelf seas peripheral to this massif were present throughout the Dinantian and every type of ecological niche must have been represented in such conditions, producing the varied Lithostrotiontid fauna found in Britain. This European fauna (including L. martini, L. junceum etc.) did find its way to America and Asia during the Viséan and was therefore cosmopolitan, but at the same time independent evolution was occurring in these areas producing differentiated American and Asian faunas which were geographically restricted (p. 83).

The Namurian Lithostrotiontid fauna

At a much higher horizon, near to the top of the E2 Subzone of Northern England, a limestone band occurs which once more contains a reef coral fauna, a significant portion of which is made up of the Lithostrotiontidae. This limestone outcrops in the Cotherstone Syncline, Stainmore Trough, between the Alston and Askrigg blocks on Hunderthwaite Moor, where it was described by Garwood (1912, p.542) as the Botany Limestone, and also in Northumberland, near Harlow Hill and Newton, where it was originally described by Smith (1911, p.629) as the Fell Top Limestone, but is now better known as the Harlow Hill Limestone or the Newton Limestone. These three limestones were later correlated by Smith (1916, p.293-4) on the

FIGURE 29

Outline map showing palaeogeographical conditions in Europe during the Viséan. Northern and southern forelands are separated by the Mid-European Channel which is flanked by shelf seas.
'o' marks the Askrigg/Alston Block region of Northern England, the area of the Viséan Yoredale sequence and intermittant coral growth.
'x' marks the Derbyshire Dome area of continual Viséan limestone deposition and continuous coral growth.
'SGL' is the St. George's Land/Brabant Massif land mass which persisted throughout the Viséan so that the shelf seas that surrounded it provided a stable environment for a long period of time. This would have constituted an ideal centre for evolution.
Arrows indicate direction of migration of coral faunas.

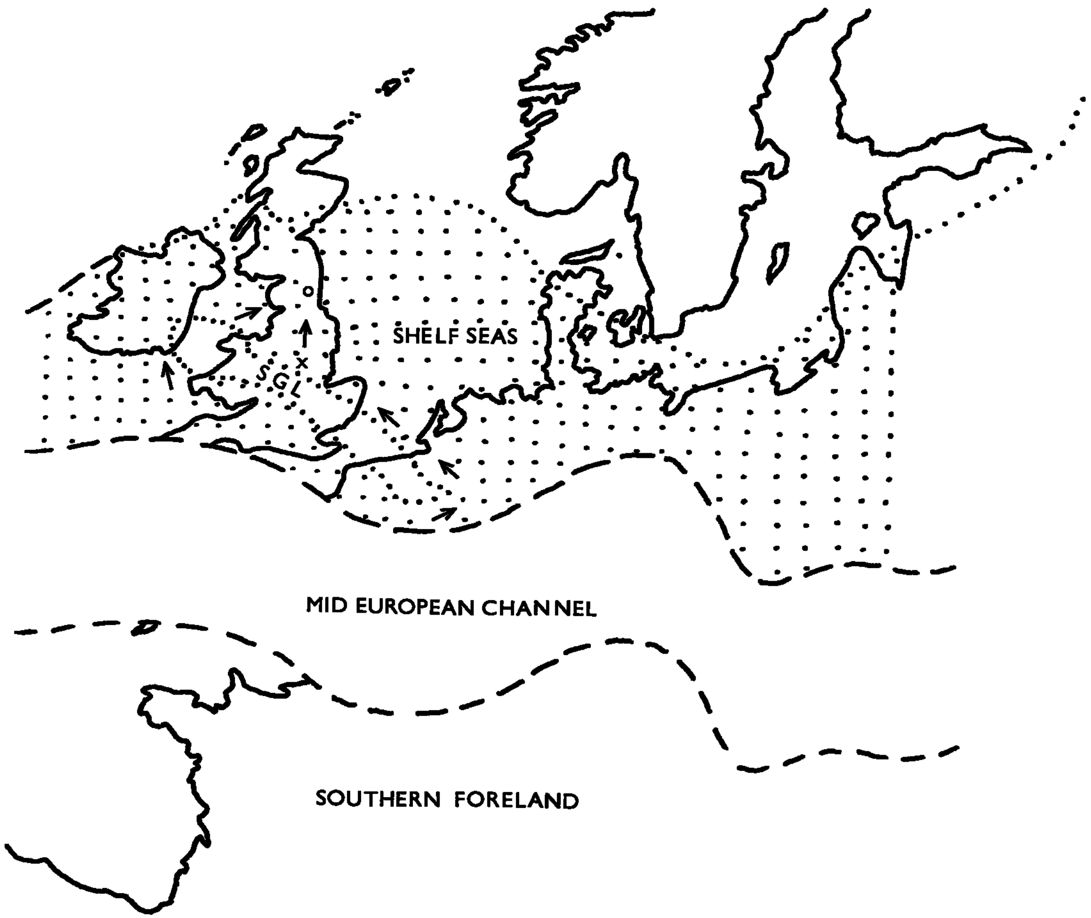


fig 29

evidence of similar stratigraphical position, sequence and faunal content. All of these limestones contain a similar Lithostrotion fauna with L. pauciradiale, L. decipiens and Aulina rotiformis. The latter species was attributed by Smith to the Lithostrotiontidae, but in this thesis it is rejected from the family (p.100). The Newton Limestone also contains A. senex which has not as yet been found in the Botany Limestone and the Botany Limestone contains A. botanica (p.249).

Certain anomalies in the elements of this fauna suggest that these corals, occurring at this high horizon, may have completely different origins from the Lithostrotiontid fauna of the Viséan Yoredales. First, L. decipiens and L. pauciradiale become extinct in the North of England in the Middle and Simonstone Limestones respectively some 450 metres below, and yet now suddenly reappear after being absent in the coral-bearing Five Yard, Three Yard, Four Fathom and Great Limestones. Secondly, the species of Aulina are all highly evolved forms which must represent the end of a long lineage and yet neither they nor their ancestors have been found elsewhere in the British Viséan or Namurian, suggesting that they did not evolve in this region. Thus the Botany-Harlow Hill fauna is quite distinct from the underlying Viséan fauna. Finally there is the long time gap between the E2 fauna of Lithostrotion and the preceding Viséan Lithostrotion fauna, and furthermore we know that this fauna could not have migrated from the southern evolution centre as coral growth was eliminated in that region at the end of Viséan times. We must look therefore for a second source area for this high Namurian exotic Lithostrotion fauna; an area of continual limestone deposition into the E Zone is required where all four elements of the fauna occur.

The Aulina-Lithostrotion fauna has been recorded by Hill (1940, p.192-3) from the Linn Spout Limestone (Upper Limestone Series) of Dalry in Scotland, again in the E2 Subzone, but this cannot be regarded as a source area as again there is not continual limestone deposition beneath the Linn Spout Limestone. The Linn Spout Limestone therefore represents an extension of the same sea that was depositing the Harlow Hill and Botany

Limestones. We must look elsewhere for the true source area.

Garwood realised this problem and in 1912 (p.543) stated, "the fauna cannot be considered as a remnant of the local Yoredale fauna that collected here before being completely exterminated; for not only is the fauna as a whole not characteristic of the underlying beds, but the arenaceous character of the deposit immediately below makes this hypothesis untenable". Garwood considered these deposits must have resulted from a local depression which carried the sea floor temporarily beyond the area of mechanical deposition and which was connected by a communicating channel with the deeper sea. He suggested that this deeper sea from which the corals migrated was to the west as in that direction erosion has removed all the upper beds of the D Zone and the Millstone Grit. So he considered that the Botany and Harlow Hill Limestones could previously have extended in that direction. However this appears to the author to be rather negative evidence and moreover neither the Aulina fauna of Botany nor its ancestors have ever been recorded from any area to the west of Northern England.

In an easterly direction, however, albeit after a considerable distance, we find two distinct areas, one in Russia and the other in China and Japan, where not only the identical fauna of A. rotiformis, A. senex, L. decipiens and L. pauciradiale occurs, but also a number of other species of Aulina, some of which appear more primitive, and from which the British species may probably have evolved.

It has been supposed that the Aulina species in China were a part of the European fauna that migrated eastwards with the other European species that are common to both regions. Smith (1943, p. 61) considered, that the Aulina species evolved independently in these two widely separated areas from the same ancestor by following the same trend of development of the aulos. These possibilities seem unlikely as first, the European fauna of China is Viséan and not Namurian in age, and secondly it seems too great a coincidence for parallel evolution to produce such identical and species. It is however possible that Aulina could have had its origins in China and migrated to England, either direct or via the Russian Platform, or that it had its origins on the Russian Platform and migrated eastwards to China and westwards to Britain. In other words that it is a part of Asian fauna that has migrated to Europe thus reversing the trend of the Viséan coral migration.

To test this hypothesis and discover which of the two areas supplied the fauna to Britain it is useful to discuss the stratigraphy of the occurrence of this genus in these two areas.

The Lithostrotion-Aulina fauna in China and Russia

In China the Lower Carboniferous or Fenginian Series is divided into two stages, the Lower Aikuanian Stage (approximately equivalent to the Tournaisian) and the Upper Tantangian Stage (corresponding, according to Yang and Wu, 1964, p.853, to the Viséan). The Tantangian is subdivided into a Lower Thysanophyllum Zone and an Upper Yuanophyllum Zone (fig.30). In China Aulina has been recorded from several localities. In North China A. rotiformis occurs in the Kansu Province in the Choniukou Formation in the Yuanophyllum Zone and in Chilienshan in the Huaitoutala Group also of the Yuanophyllum Zone. In Central China the same species is found in the Anhuei Province in the Hochow Limestone again in the Choniukou Formation. It is in South China however that the genus is most abundant. Here A. rotiformis occurs in the Kiangsu Province again in the Hochow Limestone, but most important in Hunan Province where it occurs with A. carcer in the Tzemanchiao Limestone of the Yuanophyllum Zone and with A. puerilis in the Shihtengtze Formation at the very base of the Yuanophyllum Zone. Also in Kwangsi Province of South China A. senex occurs in the Yengtze Series also of the Yuanophyllum Zone. All of these species are present throughout the whole of the Yuanophyllum Zone appearing at the base and persisting to the very top.

The detailed stratigraphy of the Tantangian Stage in these areas does vary, but it is predominantly a continuous limestone succession right to the top of the Fenginian and so it can safely be considered as a possible

FIGURE 30

Lower Carboniferous stratigraphical divisions in China and comparative sections of the Lower Carboniferous strata in some of the Chinese Provinces. Hunan, Kweichow and Singkiang from Yu (1964).
G.= Gastrioceras, H.= Homoceras, E.= Eumorphoceras.

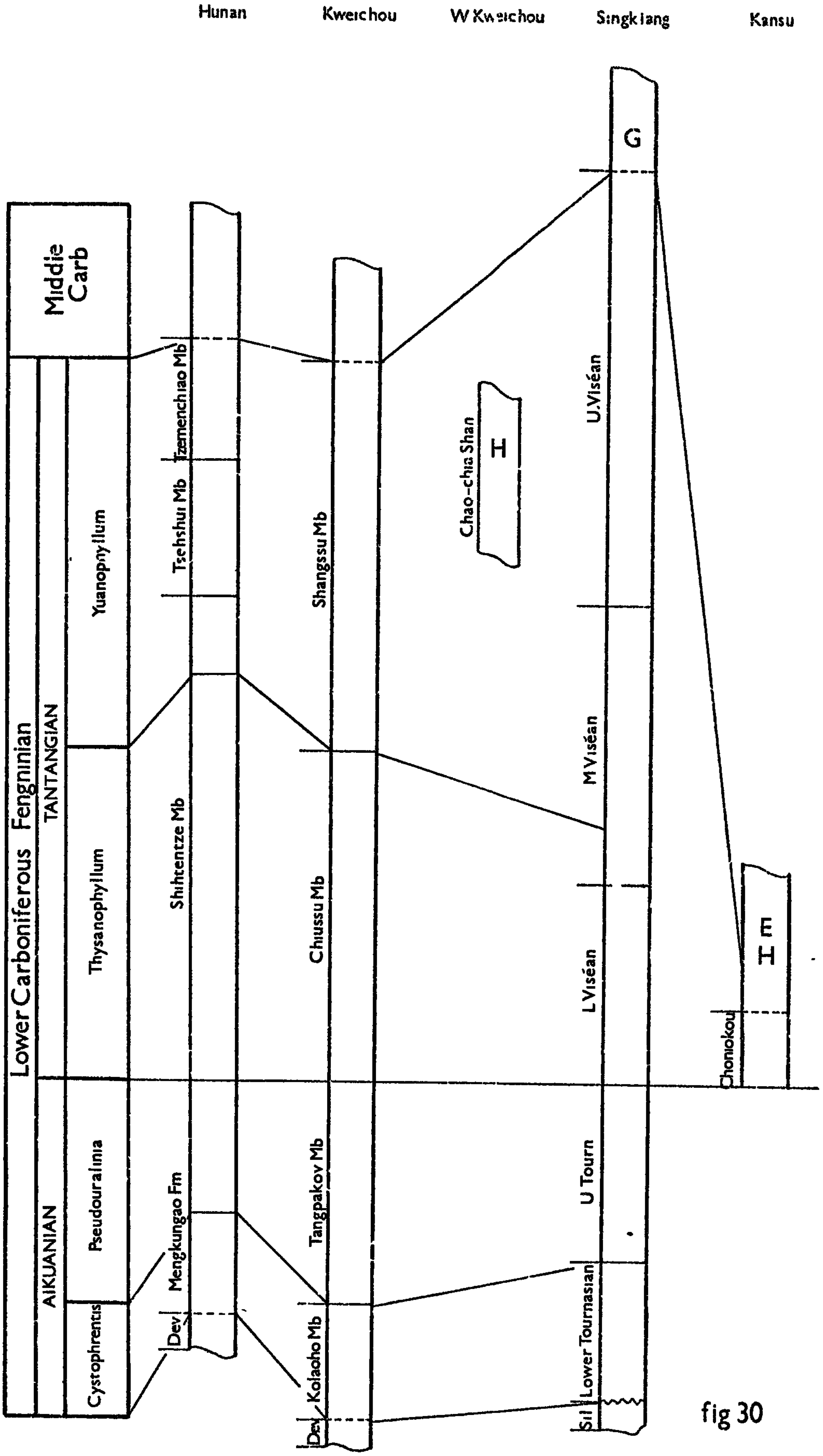

Hunan
Kweichou
W Kweichou
Singkiang
Kansu
Middle Carb
Lower Carboniferous Fengninian
TANTANGIAN
AIKUANIAN
Yuanophyllum
Thysanophyllum
Pseudouralinia
Cystophrentis
Tzemenchiao Mb
Tsehshui Mb
Shihtentze Mb
Mengkungao Fm
Dev
Shangssu Mb
Chiussu Mb
Tangpakov Mb
Kolaoho Mb
Dev
Chao-chia Shan
H
G
U.Viséan
M Viséan
L Viséan
U Tourn
Lower Tournasian
Sil
E
H
Chonlokou

fig 30

source area.

According to the correlations of Yu (1933, p.27) and Yang and Wu (1964, p.853) the Yuanophyllum Zone is equivalent to the Upper Viséan beds of England. If this is to be accepted completely then it will be seen that the Aulina fauna first occurs at a lower horizon in China than in Britain again suggesting its probability as a source area for these corals, i.e. they evolved in China long before migrating to Britain. Moreover it will be seen that they not only appear earlier in China, but they also die out earlier as they do not persist into the Middle Carboniferous (= Namurian). Does this mean that they could not have migrated direct from China to Britain in the Namurian, but that they came to Britain from the Russian Namurian? One of the pieces of evidence on which Yu based his correlation was the fact that Garwood and Goodyear (1924, p.252) recorded A. rotiformis from Viséan strata in Wharfedale and so Yu considered that the Chinese Aulina fauna was of the same age and therefore that the Fenginian was Viséan in age. However Hill (1940, p.192) considered that this specimen needed further confirmation and that it was probably Orionastraea. If Hill is correct then Yu's correlation was based on a misconception and the top of the Yuanophyllum Zone may be younger than previously supposed and equivalent to the Namurian E2 Zone. Yu (pers. comm. 1975) rejects this hypothesis with the evidence that Yuanophyllum itself is restricted to Viséan rocks, secondly that no Namurian goniatites have ever been found in the Yuanophyllum Zone, and thirdly that the top of the Shangssu Member (at the top of the Yuanophyllum Zone) is overlain disconformably by the Middle Carboniferous strata.

It appears to me that these arguments are inconclusive. First, the range of Yuanophyllum has only been tested in China. Secondly while it is true that the top of the Yuanophyllum Zone is overlain disconformably by Middle Carboniferous strata, as far as I am aware the actual horizon of these Middle Carboniferous beds is only known accurately by goniatite evidence in two localities. In the first of these, the Singkiang

Province, the top of the Yuanophyllum Zone is overlain disconformably by the Middle Carboniferous Yumansu beds containing only Gastrioceras and no Eumorphoceras, Homoceras or Reticuloceras. Therefore it is possible that the disconformity represents the R and H Zones only and that the top of the Yuanophyllum Zone is still E Zone in age (fig. 30). The second of these areas is Kansu Province and here the Middle Carboniferous Yanghoukou beds above the disconformity contain Eumorphoceras and Homoceras. At first sight it may seem that if the Yuanophyllum Zone is overlain disconformably by E Zone then the Yuanophyllum Zone must be younger than the E Zone. However according to the correlation diagram of Yang and Wu (1964, Tab.2) the disconformity is at a level well below the top of the Yuanophyllum Zone, i.e. within the Yuanophyllum Zone. According to this diagram the lower portion of the Yanghoukou Member containing the Eumorphoceras and Homoceras are of Yuanophyllum Zone age and if this is correct then the top of the Yuanophyllum Zone could well be E or H Zone in age (fig.30). Finally Dr. Yu has communicated to me a further piece of evidence that has recently come to light. Some geologists have reported that examples of Homoceras have been found in the Chao-chia-shan Member of W. Kueichou Province with L. portlocki (= L. decipiens) and L. irregulare var. asiatica (= L. pauciradiale). As regards the geological age they insisted that the Chao-chia-shan Member was equivalent to the upper part of the Shangssu Member (fig.30) i.e. the upper part of the Yuanophyllum Zone.

Whether or not this is correct, L. decipiens and L. pauciradiale definitely persist into the Namurian in China and if the Shangssu Member is Namurian in age then the Aulina species could have migrated direct from China to Britain in the Namurian. This does not mean that Aulina does not occur in Viséan rocks at all in China, as the occurrence of A. rotiformis in the Shihtengtze Formation in Hunan is in the very lowest Yuanophyllum Zone which is definitely Viséan in age.

In Russia A. rotiformis occurs with A. parasenex at the very top of the Viséan of the Donetz Basin (Vassiljuk, 1960) and in the Serpukhovskii

Substage of the Russian Platform (Dobrolyubova, 1958) which is either Upper Viséan or Namurian E Zone. It isknown to persist into the Namurian of the Donetz Basin occurring in the C_1^na Zone in the River Berestovja (Vassiljuk, 1964). Also a fasciculate species *A. vesiculata* occurs in the Tournaisian C_1^ttd-C_1^tntz Zone of the Kutznetz Basin (Dobrolyubova et al. 1966).

In summary therefore the plocoid species of *Aulina* appear in the early Upper Viséan (Lower *Yuanophyllum* Zone, Shihtentze Series) of China and persist definitely to the top of the Viséan (i.e. top of *Yuanophyllum* Zone) and may persist into the Namurian. In Russia however they do not appear until the top of the Upper Viséan but definitely persist into the Namurian.

It seems probable therefore that the *Aulina* lineage initially evolved in China. First, it appears earlier in China than in Russia, and secondly it is much more prolific. Also it seems that China was supplying the fauna to Britain for three reasons. First, *A. senex* that occurs in Scotland and at Newton has not yet been found in Russia. Secondly, *A. botanica sp. nov.* from Botany is very closely related to a further Chinese species *A. manchuriensis* (Yabe and Minato 1944, p.148) from the Upper Viséan, which also does not seem to occur in Russia. Finally conclusive evidence can be drawn from the two species of *Lithostrotion*, *L. decipiens* and *L. pauciradiale* that migrated to Northern England with the *Aulina* spedies. As has been already stated these two species both die out in Northern England in the Middle and Simonstone Limestones, well below the base of the Viséan and yet reappear again in E2. In Russia these two species have not actually been described but the cerioid *L. columellata*, *L. laminacolumellata* and *L. acolumellata* and the fasciculate *L. rossicum* (Dobrolyubova 1958, p.300-326) which seem to be varieties of *L. decipiens* and *L. pauciradiale* respectively, do not persist higher than the Steshevskii Zone which is approximately equivalent to D2. Thus the *Lithostrotion* species could not have migrated to Britain in the Namurian from Russia. However in China *L. portlocki* (= *L. decipiens*) and *L.*

irregulare var. asiatica (= L. pauciradiale) not only occur right to the top of the Yuanophyllum Zone (Yu, 1964, p.870) and are found in common association with Aulina as at Harlow Hill, but also as we have stated, these two species have been found in rocks containing Homoceras and therefore definitely persist into the Namurian. L. decipiens and L. pauciradiale must have migrated to Britain in the Namurian from China and not from Russia and so it is likely that Aulina also migrated from China in the Namurian, if the Shangssu Member is Namurian in age.

Palaeogeography

Further evidence can be obtained by studying the palaeogeography of these areas in Carboniferous times. Smith, Briden and Drury (1973, fig.11) show a reconstruction of the continents in the Mid-Carboniferous and this was modified by Johnson (1973, fig.3b) who included a Mid-European plate suture. Figs 31 and 32 show this reconstruction for the Viséan and Namurian respectively, with land masses and major ocean currents added from Ramsbottom (1971 and 1973). The first point that appears from this is that the dominant westerly movement of the ocean currents, as postulated by Ramsbottom assuming that the earth rotated in the same direction as today, suggests that migration from Russia to China would be difficult as the currents would be carrying coral larvae in a westerly direction. Thus again it seems that China is more likely to be the area where the lineage first evolved.

From the figures it can be seen that at this time the majority of Asia including China and Japan was separated from Europe by the Eurasian or Uralide sea along a line now represented by the Ural Mountains. The Donetz and Kutznetz Basins are on the west of this sea on the European plate, while the Chinese localities are on the east, on the Asian plate. Thus to migrate from China to Russia and Britain the coral larvae would have to cross the Eurasian sea, but this sea was closing during the Upper Viséan and Namurian times (figs 31 and 32) and had closed completely by

FIGURE 31

Outline map showing a reconstruction of the continents and palaeogeographical conditions during the Viséan. From: Smith, Briden and Drury (1973) and Johnson (1973) with Viséan land masses added from Ramsbottom (1973). Heavy lines show plate sutures, finer lines show outline of present day land masses, stipple represents Viséan land masses. The Eurasian Sea and the Mid-European Channel are both wide at this time.

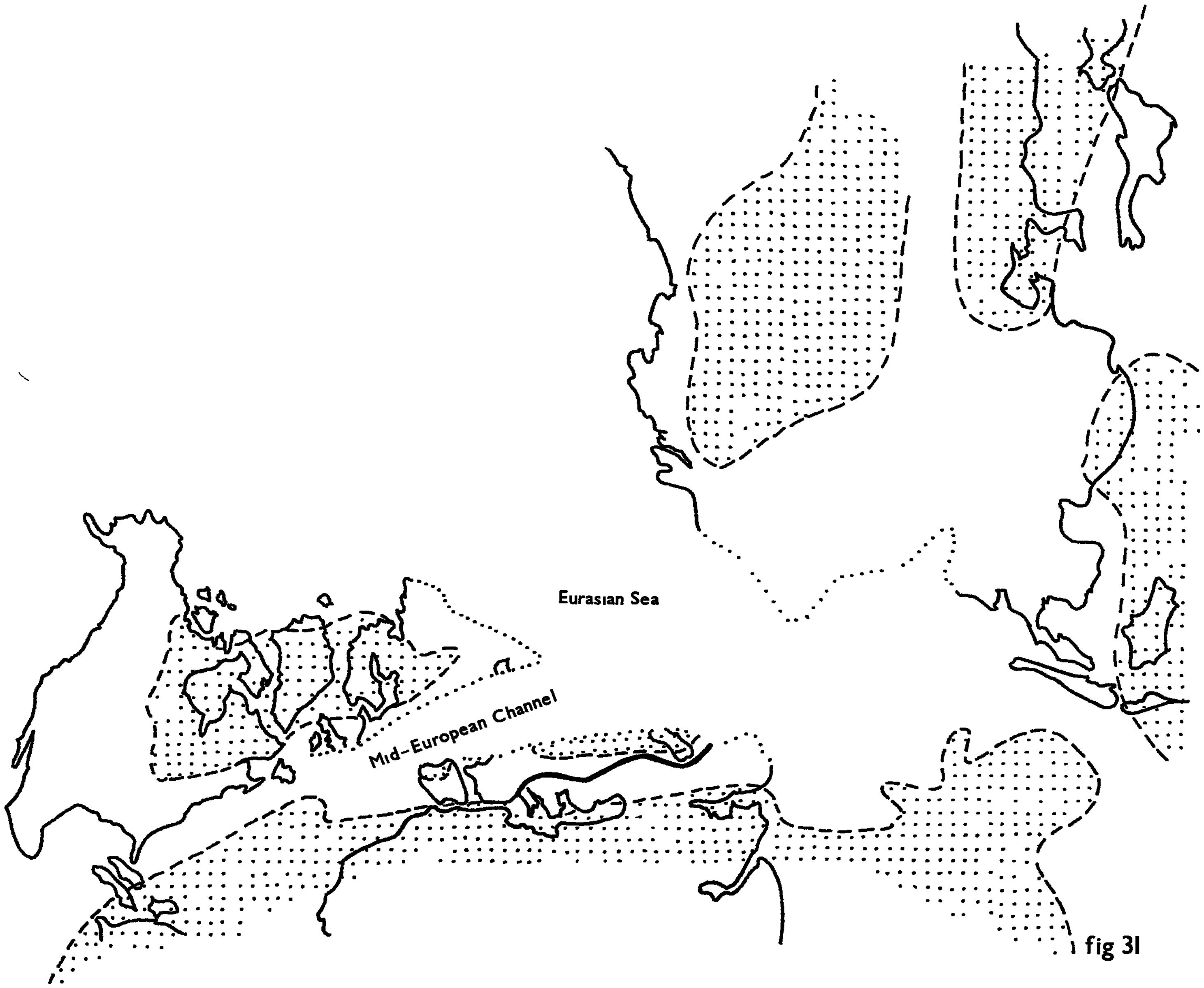


fig 31

FIGURE 32

Outline map showing a reconstruction of the continents and palaeogeographical conditions during the Namurian. From: Smith, Briden and Drury (1973) and Johnson (1973) with Namurian land masses and ocean current directions added from Ramsbottom (1971). Solid lines represent the outline of the present day land masses, stipple represents Namurian land masses, crosses show the areas of the *Aulina*- *Lithostrotion* fauna, arrows indicate the dominant direction of the Namurian ocean currents. The Eurasian Sea and the Mid-European Channel are both becoming narrower.

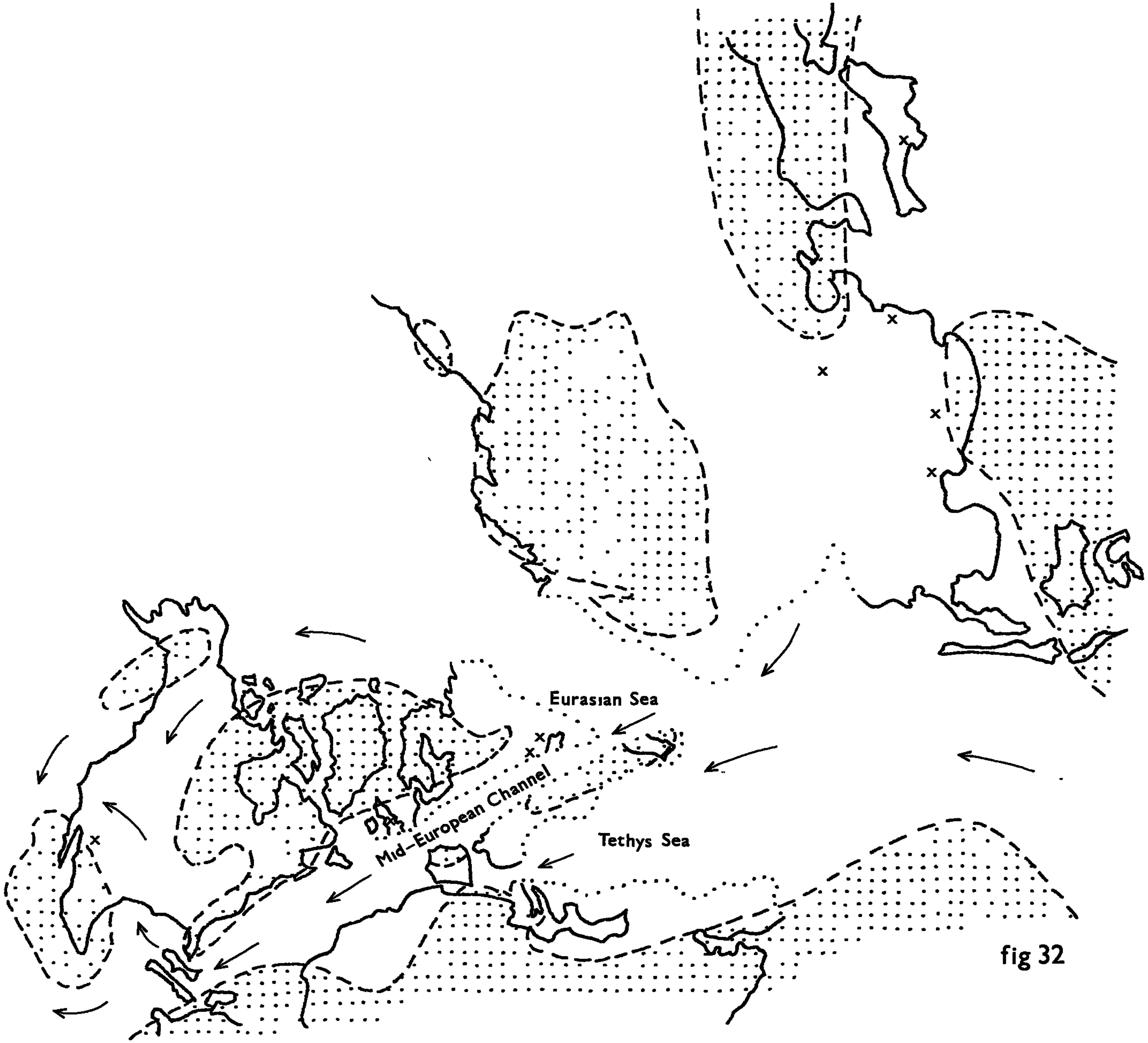


fig 32

the Permian and so its extent would not be too great. Europe at this time was divided into two plates separated by a channel, the Mid-European Sea or Rheic Sea (Johnson, 1973; Whittington and Hughes, 1972). This sea, connecting the Eurasian Sea with the seas covering Britain thus provided the channel to the east of Britain necessary to supply the exotic Asian coral fauna to Northern England. Ramsbottom (1971) shows this seaway, but at that time it was not known that a plate suture existed in this region. He shows that Viséan goniatites had passed through this channel so that goniatite faunas in the Viséan were sosmopolitan, but that the seaway was closed in Namurian times so that Namurian goniatite faunas were more differentiated. Ramsbottom supposed that the sea closed as a result of being choked with sediment but it is now clear that the sea was closed by the Mid-European plate moving northwards. The need for such a seaway in E2 times to allow the Chinese coral faunas to reach Britain shows that the closure of the Mid-European Ocean did not occur until after E2 times.

Aulina fauna in America

Two plocoid species of Aulina also occur in North America (Sando, 1963). While these species (A. semimuralis and A. occidentalis) appear closely related to the Asian species (cf. A. senex) they are so far exclusive to America suggesting that they had the same ancestors as the Asian forms but have evolved independently. This is quite likely as migration from Asia to North America involves a considerable distance either through the Mid-European Ocean and into America from the south, or through the Eurasian Sea into America from the north. An eastward migration from China to America is possible, but unlikely as it is against the postulated water currents. It is clear that some coral larvae must have reached North America from Asia, but the migration was so restricted that the North American stock evolved independently and produced two new species. It is impossible to tell whether this particular migration occurred in the Viséan or was part of the same migration that reached

Britain in the Namurian as the deposit in which the Aulina species occurs is a residual chert and its age is therefore doubtful. (Had the limestone conditions in Northern England persisted longer then the British species might also have evolved differently from the Chinese stock instead of which they were exterminated soon after they arrived by the oncome of arenaceous conditions at the end of the deposition of the Botany Limestone).

Conclusion

Thus in conclusion there has been a change in the evolution centre of the Lithostrotiontidae during their phylogeny. In Viséan times when the shelf seas of Europe were widespread this was the main supply area of the Lithostrotion species. This European fauna, however, did find its way to America and Asia and considering that the dominant ocean currents were westerly then this fauna must have migrated westwards from Europe to America and westwards from America to Asia. At the same time in the Lower Viséan an Asian fauna including Aulina was evolving independently, but this fauna did not appear in Europe in the Lower Viséan. The reason for this may have been that migration would again have to be in a westerly direction and such a migration from China to Europe in Lower Viséan times would have involved crossing a Eurasian Sea which in these times was very wide and probably too wide for the faunas to cross. At the end of Viséan times when the shelf seas of Europe were replaced by arenaceous conditions it was the independently evolving fauna of Asia that became the main centre of evolution in the Namurian. In Upper Viséan times the Asian plate moving westwards was closing the Eurasian Sea and so the Asian fauna was able to cross it and began to appear in Russia in the Upper Viséan. In the Namurian the Eurasian Sea was now closed sufficiently for the Asian fauna to migrate from China to Europe (Northern England). In other words as the sea closed the Asian fauna gradually was able to migrate further west.

Thus Viséan European faunas are cosmopolitan as they travelled west and therefore did not have to cross the Eurasian Sea. Lower Viséan Asian faunas are restricted as they could not cross the sea as it is too wide at this time. Upper Viséan and Namurian Asian faunas are cosmopolitan again as the sea is now closed sufficiently for a westerly migration from Asia to Europe to occur.

CHAPTER 6

ASEXUAL REPRODUCTION IN THE LITHOSTROTIONTIDAE

Introduction

An account of the ontogeny of a protocorallite, the first skeleton formed by the settling larva after a period of sexual reproduction, cannot be given in the Lithostrotiontidae since the preservation of a colony with its protocorallite intact is unknown. The weight of the colony as it grows may be sufficient to crush the protocorallite during the life of the colony. Ontogenetic studies are therefore confined to the development of asexual hysterocorallites which nevertheless are interesting, and variation in this feature may in some cases be of specific importance.

Two main types of increase occur in the rugose corals and these are both seen in the Lithostrotiontidae. First, calicular increase, which is always parricidal, involves the splitting of the parent corallite into two, three or four daughter corallites. This may be either axial, when the splitting occurs through the axis of the parent, or peripheral, when the splitting occurs at the periphery of the parent corallite.

The second, and most common, method of increase in the Lithostrotiontidae, occurring exclusively in almost all of the columellate fasciculate and cerioid species, is lateral increase, which is non-parricidal, involving the formation of one or more daughter corallites in the peripheral parts of the calice.

References to increase in Lithostrotion have been made by many workers, but exact details were not discussed until Dobrolyubova (1958) described the hystero-ontogeny of some species from the Russian Platform using thin sections. Following this lead, Jull (1965) used a more accurate serial sectioning technique taking acetate peels at closely spaced intervals and described the increase of ten species of the genus

Lithostrotion.

Methods

In general the conclusions of Jull (1965) have been borne out by the present studies and thus it is not proposed to describe in detail every type of increase in the Lithostrotiontidae. However, it is considered that his methods were suspect and thus that while his general conclusions on the different types of budding may be sound, his precise details of the skeletal changes taking place are not completely accurate.

Hysterocorallite ontogeny is studied by chosing specimens which show a well developed, and intact, lateral offshoot. This must be attached by resin to a 'Croft' grinder which grinds the corallite down in parallel stages of 1/100 mm. Acetate peels are then taken at various intervals to show the changes in the adult and daughter corallites. It is imperative to keep each section and each peel parallel to the position of the floor of the calice at the stage in the growth being studied. This ensures that the section represents a static point in time of the growth history. The peels must therefore be taken at right angles to the direction of growth. This direction can be inferred to be parallel to the internal tabulae and the external growth lines. At later stages in the growth of the daughter corallite the direction of growth will be parallel to the growth of the parent, as both daughter and parent eventually grow parallel. However, in the early stages of a daughter corallite's life, the daughter offshoots from the wall of the parent at an angle of about 45° to the direction of growth of the parent (fig.33a). This has two consequences; first, the direction of growth of the daughter is initially not parallel to the direction of growth of the parent, and secondly, in the later stages when the two corallites do become parallel, the daughter corallite must change its direction of growth turning back through an angle of 45° to become parallel to its parent.

Hence when studying the hysterocorallite ontogeny by continually

FIGURE 33

Diagram illustrating the technique of serial sectioning lateral offshoots.

a. Diagrammatic illustration of the differing directions of growth of the parent and daughter corallites. Arrows represent the direction of growth.

b. Position of the serial sections of the parent and daughter corallites keeping the sections parallel to the direction of growth of both corallites. In stages 'G' and 'F' both corallites are sectioned in one plane. In stages 'E', 'D' and 'C' the sections of the daughter are turned through 45°.

c. Serial sections of the parent and daughter corallites with the daughter corallite always sectioned in the plane of the parent section. The section across the daughter corallite in stage '4' will represent a time interval - i.e. the period of time between stages 'D' and 'E' in fig.2b. In this section the daughter corallite is more developed on its far side(E) than on the side in contact with the parent(D).

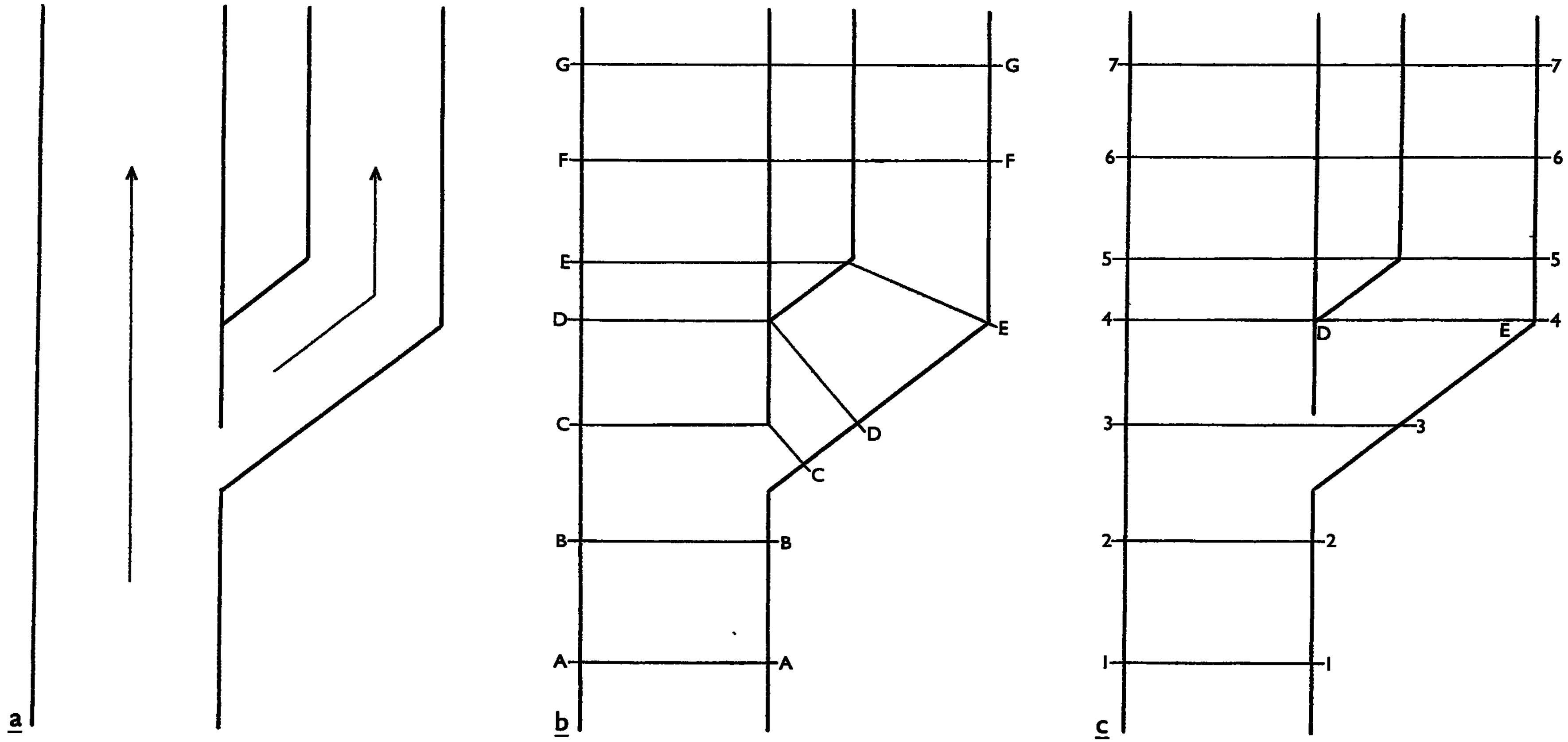


fig 33

rubbing down the distal end of a daughter corallite, when the very earliest stages are reached, the sections must gradually be turned through 45° (fig.33b). If this rule is not followed and sections of the daughter are always taken parallel to the calice of the parent, then in the early stages of the offshoot a line drawn across the offshoot in the plane of the section will represent a passage of time - a time interval (fig.33c). The offshoot will inevitably be more developed on the far side than it is at the point of contact to the parent. It appears that this is the method that Jull was using.

Using the latter method (fig.33c) Jull found that a rather irrggular series of changes took place in the formation of a daughter corallite, all stages being characterised by the septa, at the side of the daughter corallite that was in contact with the parent, being much shorter and less developed than those on the free side of the daughter corallite. This seems to be due to the fact that Jull's section was not parallel to the direction of growth of the daughter corallite and the free side of the daughter corallite, at any point in Jull's growth series, represents a much later stage in the growth history than does the side in contact with the parent.

Hence to get an accurate picture of the successive stages in the ontogeny of the offshoots two separate surfaces must be sectioned. It is impossible to take thin sections and difficult to take acetate peels, as two facets must be studied at the same time. The only method is to grind the two facets down and draw the structure at each stage. This has the disadvantage that the actual record is destroyed; only a pictoral record, the drawer's interpretation, remains. Using the standard mounting block supplied with the 'Croft' Grinder it is impossible to serial section in this way for two reasons. First, having cemented the corallite to the mounting block only one surface can be ground, i.e. that surface parallel to the surface of the block. Secondly, the surface of the daughter can never be turned through the necessary 45° angle as the grinder always grinds absolutely parallel.

To overcome this difficulty a new graduated tilting mounting block attachment has been designed and manufactured for the 'Croft' Grinder. It consists of the basic mounting attachment on which is a raised platform that can be turned through 90° as marked on a graduated scale (Pl.2). Mounting the corallite on this platform enables the parent corallite to be ground down a given distance and then by altering the setting of the platform the daughter can be ground the same distance. Moreover, when the daughter begins to turn its growth direction through 45° this can be followed accurately in the grinding again by alteration of the angle of the platform (Pl.2).

The hystero-ontogeny of the daughter corallite should be studied in reverse order by continually grinding down the distal end of the corallite. The section of the adult should be ground down at parallel intervals, while the section of the daughter must gradually be turned through 45° and then kept at that angle. The final stage seen by this method is when the daughter disappears completely and only the circular outline of the parent remains. Thus a re-study of the types of budding in the various species of the <u>Lithostrotiontidae</u> is needed to obtain a more accurate picture of the chain of events.

<u>Lateral budding in Lithostrotion martini</u>

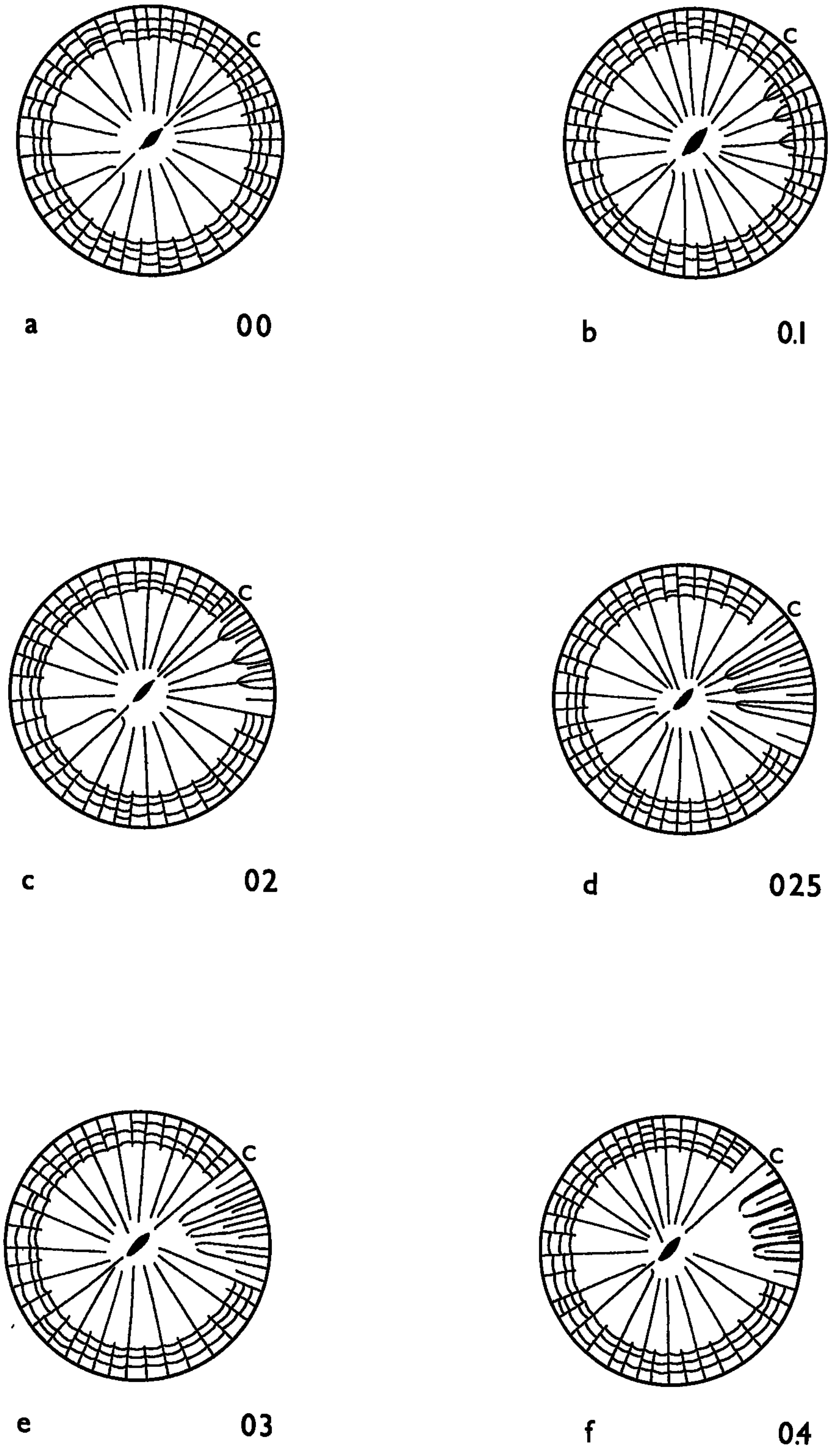
Ontogeny in <u>L. martini</u> was studied using separated corallites from Ash Fell Edge, Cumbria, mounted on the tilting stage. The first change seen in the adult in the preparation for a daughter corallite is the modification of some of the adult major septa. Usually three major septa are involved, although sometimes a fourth may be modified also. However, modification of a fourth septa is usually suppressed again at a later stage and is not involved in the daughter. The three major septa are modified by two new short septa appearing on either side of the major septa. It appears that this modification can affect any of the adult septa, but there is definitely a strong preference for modification to affect the septa including or adjacent to the cardinal septum. Initially these new septa only reach to the dissepimentarium (fig.34b) and do not extend to the epithecae. However, almost as soon as they appear the dissepiments in this region fail completely and when this happens the new septa extend completely to the epithecae (fig.34c). The next stage is the gradual suppression of the original three major septa and of their minor septa. In fig.34h the minor septa disappear and in fig.34i the major septa disappear. At stage 34j the six new septa, and also one of the major and minor septa adjacent to these six new septa become very dilated (fig. 34j & k). Eventually the six new septa take on the role of three new major and three new minor septa so that the number of adult septa is maintained. The corallite has an oval outline at this stage, due to a bulge in the epithecae in the area of septal modification. Thus the modified septa are longer than normal in this region. The next stage is the gradual coalescence of the ends of the dilated septa to form a new continuous daughter wall (fig. 34k & l).

At this point (fig.34l) the new corallite is formed and at this first stage the appearance of the daughter is one of an oval outline with these four major septa and four minor septa inherited from the parent reaching the daughter and extending right the way across the daughter corallite to the far wall in a series of sub-parallel 'septal bars' (fig.34m). The story of the continued development of the daughter is one of gradual splitting of these bars in the centre to form two new major septa (one on each side of the corallite) and the rotation of these parallel septa into a radial pattern (fig.34n). Thus the daughter inherits six or seven septal bars which will eventually form twelve to fourteen major daughter septa from the major and minor septa of its parent. At this stage there are no minor septa or dissepiments in the daughter and also in the adult dissepiments are missing from the region in contact with the daughter.

Of the three parent major septa that are included in the daughter the centre septa takes on the role of the axial septa. This will

FIGURE 34

a-x. Successive serial sections of a corallite of Lithostrotion martini from the Ash Fell Sandstone, Ash Fell, Cumbria, showing the development of a lateral offshoot.
C.= Cardinal septum in the adult corallite, c.= cardinal septum in the daughter corallite. Intervals between figures are in mm's.



a 00

b 0.1

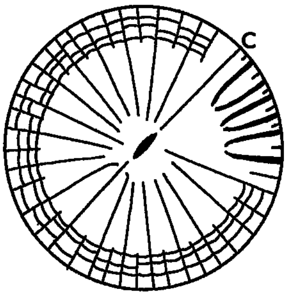
c 02

d 025

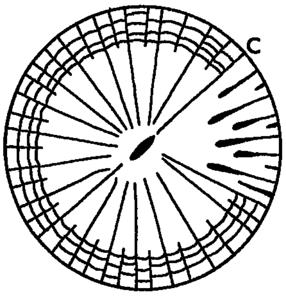
e 03

f 0.4

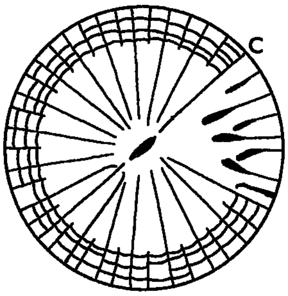
fig 34



g 05



h 06



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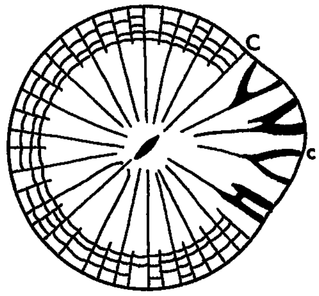

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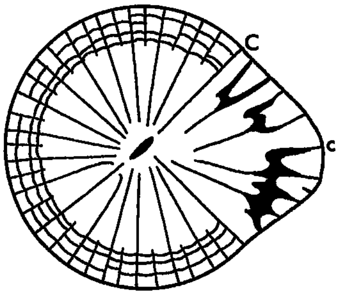
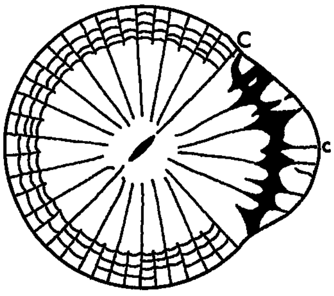
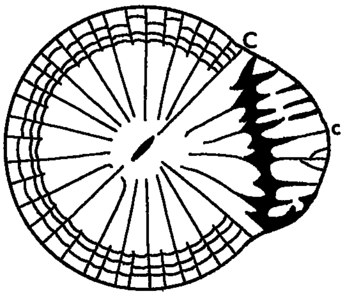


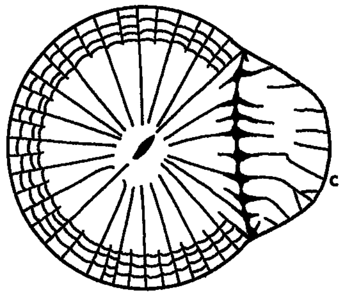
k 09



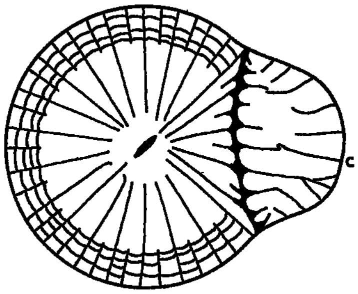
l 10



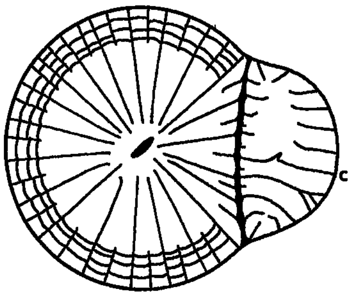
m 11



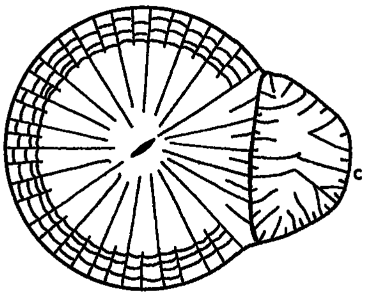
n 1.3



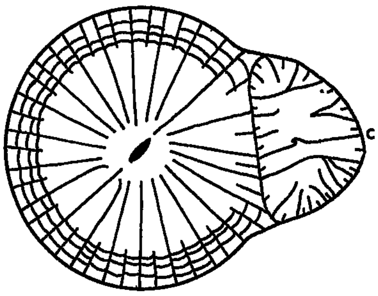
o 145



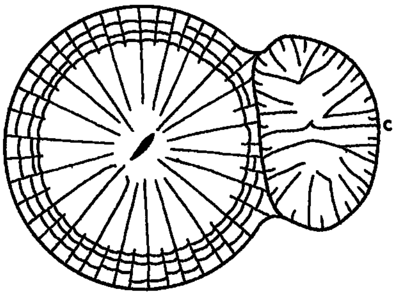
p 16



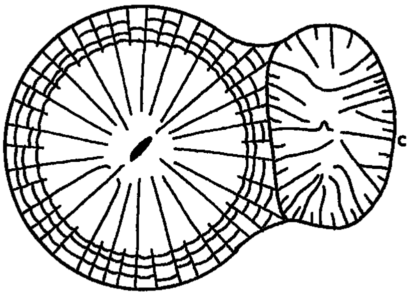
q 18



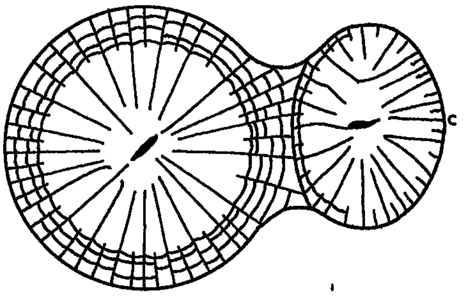
r 1.95



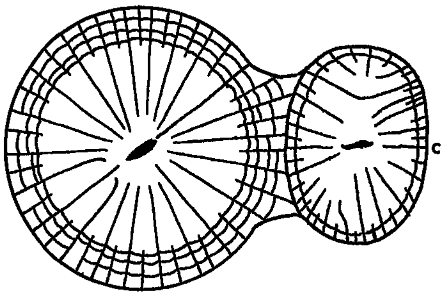
s 21



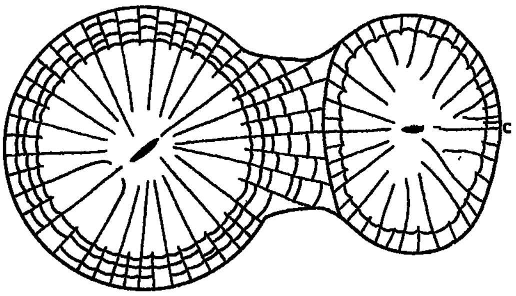
t 2.35



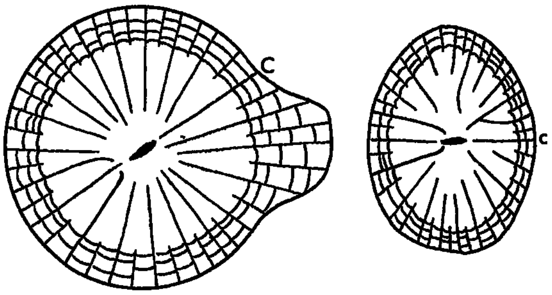
u 25



v 265



w 285



x 30

eventually split in the middle to form the cardinal and counter-cardinal septa. From Jull's interpretation of the process he recognises the introduction of the new septa and to some extent his diagrams show the suppression of the original major and minor septa, but from this point onwards his interpretation becomes exceedingly complex and lacks any uniform procedure. This appears to be due to the fact that his serial sectioning technique was tangential to the daughter corallite as has been explained.

At the initial stage there are thus fourteen or so potential major septa and no minor septa. Insertion of metasepta takes place quite quickly and appears to be by two methods. Fig.34n shows a new septum inserted and it appears one one side of the daughter corallite only, i.e. it is not a new septal bar. This will lead to there being more septa in the cardinal quadrant as opposed to the counter quadrant, i.e. a form of increased septal insertion. This type of metasepta insertion is seen also in a second specimen studied (fig.35 , septum x) and also in this specimen insertion takes place by a second method. Here a second metasepta is inserted which appears at one end of the oval shaped corallite and extends right the way across the corallite as a new 'metaseptal bar' (fig. 35, septum y). It is not known if this metasepta appears by simple insertion or if it appears by a hypothetical process termed 'inclusion', whereby the wall of the daughter growing upwards includes in it a further major septa of the adult. The fact that it is a septal bar and not a separate septum, and the fact that the corresponding septum in the adult of this specimen was dilated suggests that inclusion could occur. After a short distance a further modification to the septal plan of this specimen occurs. Here one of the original septal bars (one of those inherited from the parent) retreats across the daughter corallite so that it eventually only appears on the far side of the daughter, i.e. the same side as the newly inserted septum x (fig. 35, septum z). This also has the effect of producing accelerated insertion

FIGURE 35

Different methods of metaseptal insertion in a lateral offshoot of a second corallite of L.martini from Ash Fell, Cumbria. In stage 'b' a metaseptum (x) is inserted on the cardinal side only, and a metaseptal bar (y) is included, extending right across the corallite. In stage 'c' one of the original septal bars (z) retreats to the cardinal side. The insertion of 'x' and the retreat of 'z' maintain bilateral symmetry, but lead to increased insertion on the cardinal side.

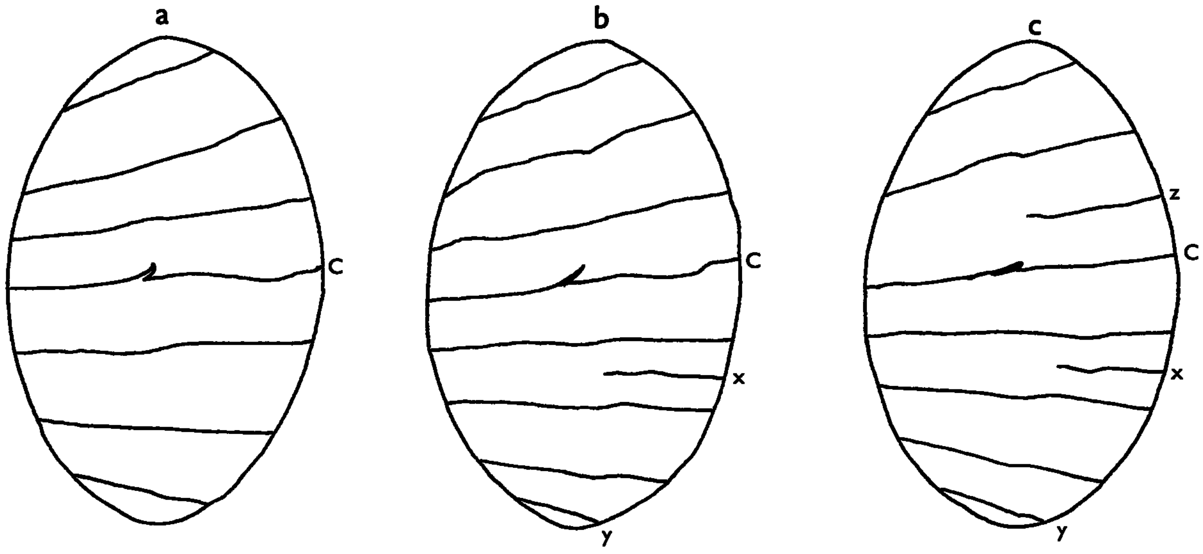


fig 35

in cardinal quadrants and may in fact be in response to the insertion of the metasepta on this side to maintain bilateral symmetry.

In fig.34o splitting of the septal bars in the centre is underway and at the same time the septa begin to rotate to form a radial pattern. Also at this stage although the daughter is still united to the parent by the common wall the daughter is able to rotate independently of the adult so that the septal bars of the daughter may no longer be continuous with the septa of the adult. In fig.34p minor septa begin to appear in the daughter. They are inserted first on the side of the daughter that is adjoining the parent, but in fig.34q they appear all round the daughter. As the daughter develops splitting continues, but new metasepta can still be inserted in the daughter once it has begun. In fig.34r a marked 'notch' is formed in the centre of the axial septa and this is the rudimentary beginnings of the columella. At this time there are about 20 major septa developed and this number persists for a considerable time, even into the adult stages. In fig.34s dissepiments appear in the adult in the region of contact and almost as soon as these adult dissepiments appear the first signs of dissepiments in the daughter also appear, first on the side joined to the adult (fig.34u) and finally all the way round (fig.34v). At this stage the daughter takes on a more round outline and the radial plan of the septa becomes more evident. By fig.34w the daughter begins to separate itself from the adult by beginning to form a branch, but the adult extends her epithecal wall towards the daughter to aid support to the branch. As the daughter moves further away from the parent so the parental wall is extended further away from the parent to embrace the young. In this region of extended adult wall dissepiments are numerous and may be up to four rows. Eventually when the daughter is about 4.5 mm. in diameter the break is made and the daughter continues in her independent way. At this stage the adult is 6 mm. in diameter and has 24 major septa.

Variation in budding in Lithostrotiontid species

Jull's studies of increase in Lithostrotion led him to the conclusion that four main types of lateral increase occurred; first, increase in L. junceum is characterised by the daughter corallite forming almost entirely external to the parent calice and having an aseptate early stage, secondly in species having a narrow dissepimentarium (L. pauciradiale, L. irregulare) the new corallite arises almost at the periphery of the calice and typically does not inherit septa from the parent, thirdly in species having a wide dissepimentarium (L. variabile, L. martini, L. sociale) the daughter corallite inherits its initial septa from the ends of the parent septa, and finally in cerioid coralla (L. maccoyanum, L. decipiens, L. vorticale, L. aranea) increase is similar to those fasciculate species with a wide dissepimentarium except that the daughter does not grow laterally free of the parent.

Calicular increase is rare in the columellate fasciculate and cerioid species of Lithostrotion; axial increase having only been recorded by Dobrolyubova (1958) in three species from the Russian Platform, and peripheral increase has only been recorded in Lithostrotion sp. by Jull (1965) and in L. affine (= L. proliferum) by Hill (1940).

In the diphyphylloid and nemistioid species of Lithostrotion calicular increase exclusively occurs. In these species increase is axial in L. gracile, L. fasciculatum and L. furcatum and peripheral in L. lateseptatum and L. edmondsi. In the genus Orionastraea increase is most often lateral when the daughter appears in the peripheral parts of the skeletal tissue of the corallum. However, I have observed axial increase in a specimen of O. phillipsi (I.G.S. Leeds Collection, No.2710) and so both types of increase may occur in this genus.

Lateral increase in the dissepimentarium appears to be the most primitive method of increase as it occurs only in the early members of the lineage and gives rise to calicular increase in later species. It would appear that peripheral increase is more primitive than axial increase. The reason for this is that peripheral increase is more similar to lateral increase as it also takes place in the dissepimentarium. Thus there is a progression from lateral increase in the dissepimentarium, to calicular increase in the dissepimentarium (peripheral), to calicular increase at the axis. This progression is seen in the evolution of L. irregulare (lateral) to L. edmondsi (peripheral) to L. fasciculatum (axial). Also, as the various diphyphylloid species appear successively from the columellate species of Lithostrotion, it is interesting to note the progressive evolutionary advancement of these successive end members. For example when L. lateseptatum evolves from L. martini it develops the more primitive peripheral increase. When L. fasciculatum evolves from L. irregulare it develops axial increase, but through the intermediate stage of L. edmondsi which has peripheral increase. Finally, when L. furcatum and L. gracile evolve from L. variabile and L. pauciradiale respectively they develop immediately the more advanced axial increase.

Time has not been available during the present study to describe in detail these different methods of increase in all the different species, but it is hoped that this may be completed in the future.

PART 3

SYSTEMATICS

METHOD OF STUDY

The characters of the coral skeleton can be divided into two types; those that are measurable (diameter, width of dissepimentarium, width of tabularium, number of septa) and those that are not measurable (type of axial structure, growth habit of colony, type of septa, method of budding etc.). In most cases it is the non-measurable type of character that has been useful in distinguishing the species and thus, while the data collected from the recording of the measurable characters has been plotted as a means of describing the total variation of the species, these results have not been subjected to any intense statistical tests as generally it has been possible to distinguish the species on other characters without needing statistical procedures.

Now, in measuring the characters of a colonial organism it is easy to distinguish between genetic variation and phenotypic variation as all the corallites in one colony are genetically identical and so variation within colonies is phenotypic whereas variation between colonies ~~is~~ can be genetic. Thus it is more useful to measure a few individuals in a lot of colonies rather than to measure a lot of individuals in a few colonies.

With the measurable characters it has been observed that of greatest use in distinguishing between species is the number of septa. Now, differences in the number of septa within one colony reflects only ontogenetic and phenotypic variation. Each colony will have a maximum number of septa that it can potentially support which is controlled genetically. While ontogeny and phenotypic effects may reduce this number in some corallites, presumably this number can never be exceeded and so it is the maximum number of septa in a colony that is the genetic character that is useful as a specific character. Measurement of means of septa in a colony only shows the amount of immature or phenotypically affected individuals and so these are not plotted on a frequency distribution. Thus for each colony the maximum number of septa counted is the important character and for each species a range of the maximum number of septa counted in the member colonies of that species is quoted as the important specific character (R). This figure is additionally useful as it is a discontinuous type of character and so arbitrary divisions can be drawn between morphospecies and chronospecies using this character.

With the other measurable characters (tabularium, dissepimentarium and diameter) the maximum genetic potential of maturity in a given colony can not be evaluated in this way as these characters are continuously variable and so for these a mean value is taken for each colony, and then for the species as a whole, but counting only mature individuals. Maturity is evaluated on the basis of the corallite possessing either the maximum number of septa or almost the maximum number of septa.

It has been observed that in the species with a simple dissepimentarium (either no dissepiments or just one row of dissepiments) that this character is quite constant, but that in species with a complex dissepimentarium (over one row) that the actual number of dissepiments is immensely variable within each species and even within one colony. This means that diameter is also a very variable character as it is directly dependent on the dissepimentarium. In fact diameter is so variable that when trying to distinguish species on a size basis the diameters of larger and smaller species overlap, so that a small species with a large dissepimentarium is larger than a large species with a small dissepimentarium. In fact on the basis of diameter a continuous series is formed between the species of some (cerioid) lineages. However it has been observed that the tabularium of any one species is quite a constant character even when the diameter varies considerably. The tabularium is a far more useful character to distinguish species on the basis of size as there is less overlap than with diameter.

Thus for each species a mean diameter (MD) and mean tabularium (MT) is quoted, with the standard deviations of the mean, and the maximum and minimum adult propertions (max D, max T, etc.) plus the range of maximum septa (N). Such figures are only given when sufficient material has been collected to render such statistical results significant. It should also be stressed at this point that diameter curves are not given for the cerioid species as this feature is continuously variable between these species and so is of little use in distinguishing them.

However there is a problem in measuring these characters in the four diphyphylloid species due to the fact that this group possesses a parricidal calicular method of increase. The result of this method of increase is that in all the species the different corallites of any one colony will show a great variation in diameter (and hence in all other characters) due to the fact that any corallite, once mature, does not stay in that mature state, but instead no sooner is it mature than it divides again into 2, 3 or 4 new immature corallites. Thus any one transverse section of such a colony will show only a few individuals in a mature state, the majority being in various stages of immaturity. The actual amount of variation in size itself varies at different positions in any one colony and also from species to species. The variation within one colony depends on what point of ontogeny of the colony the section is taken. At an early stage in the growth of the colony increase will be numerous, asexual reproduction occurring quickly so that the colony quickly expands. There comes a point however in the life of the colony when its optium size is reached, then increase slows down, and a section taken at the top of a colony will show little variation in diameter as most of the corallites are static in their mature state. The amount of variation in diameter also varies from species to species as the corallites of different species reach maturity at different rates.

The number of septa is similarly variable. Moreover it is difficult to give a precise figure for the maximum number of septa in a colony, as can be done with the laterally budding species, for the following reasons. Immediately before axially dividing a corallite shows a sudden increase in diameter to accommodate the new individuals. This means there is a corresponding increase in the number of septa, but this increase is not constant in any one species as it depends on whether the corallite is splitting into 2, 3 or 4 buds. A colony that only exhibits bipartite increase has a lower maximum number of septa than does a colony that shows tripartite or quadripartite increase. Thus there is a greater variation in the maximum number of septa in any one axially increasing species. This means there are problems in distinguishing these diphyphylloid species. With the columellate laterally increasing species it is easy to distinguish the species on the maximum number of septa as the ranges of these figures do not overlap for the different species. It is difficult to do this with the diphyphylloid species as the ranges of maximum number of septa are now greater for each species and this has the effect that the ranges of maximum septa now overlap in the axially increasing species. (For example see discussion of L. lateseptatum). Thus one has to use a different character, the mean number of septa, to separate the species.

The number of septa immediately prior to the sudden increase in diameter is the same as the ancestral number of septa of the lineage (i.e. the number of septa in the laterally budding ancestor of the axially budding species in question). We can thus assume this to be the 'mature' number of septa, while the higher number of septa seen after the sudden increase is thus a 'supermature' number of septa. The mean number of septa will include both of these figures and enables distinction (see p.191).

Because of these problems it is also difficult to measure only adult corallites, when measuring the tabularium and the diameter, as the majority of corallites are in various stages of immaturity or supermaturity. Thus for the diphyphylloid species the figure given (mean tabularium and diameter) represent an average of all corallites in a colony (including immature and supermature). Due to the considerable increase in size in the supermature state these figures tend to be rather higher than in the corresponding laterally budding species and so this should be taken into account when comparing the figures for the laterally budding species and their axially budding successors.

SYSTEMATICS OF THE LITHOSTROTIONTIDAE

Family *LITHOSTROTIONTIDAE* D'Orbigny

1828 *Tubiporadae* Fleming, *partim*, p.529.
1828 *Lamelliferae* Fleming, *partim*, p.508.
1830 *Tubiporidae* Woodward, *partim*, p.5.
1830 *Lamelliferae* Woodward, *partim*, p.5.
1851b *Cyathophyllidae* McCoy, *partim*, p.85.
1851b *Nematophyllinae* McCoy, *partim*, p.97.
1851b *Astraeidae* McCoy, *partim*, p.109.
1851 *Cyathophyllinae* Milne-Edwards and Haime, *partim*, p.167.
1851 *Axophyllinae* Milne-Edwards and Haime, *partim*, p.173.
1852 *Lithostrotionidae* D'Orbigny, *partim*, p.184.
1852 *Lithodendroninae* Milne-Edwards and Haime, *partim*, p.LXXI.
1861 *Stylaxiniens* De Fromentel, *partim*, p.313.
1861 *Eridophylliens* De Fromentel, *partim*, p.301.
1873 *Axophylloidae* Dybowski, p.331.
1873 *Diphyphyllinae* Dybowski, p.456.
1916 *Lithostrotiontidae* Smith, p.294.
1921 *Stylaxinidae* Gerth, p.
1929 *Lithostrotiontidae* Hudson, p.441.
1930 *Lithostrotiontidae* Hudson, p.96.
1931 *Lithostrotiontidae* Chi, p.25.
1933 *Lithostrotiontidae* Yu, p.89.
1933 *Diphyphyllidae* Yu, p.82.
1940 *Lithostrotiontidae* Hill, *partim*, p.164.
1955 *Lithostrotiontidae* Minato, *partim*, p.71.
1958 *Lithostrotiontidae* Dobrolyubova, *partim*, p.257.
1961 *Lithostrotiontidae* Fontaine, *partim*, p.106.
1963 *Lithostrotiontidae* Sando, *partim*, p.1075.
1964 *Lithostrotiontidae* Vassiljuk, *partim*, p.88.
1970 *Lithostrotiontidae* Kato and Mitchell, p.47.

Type Genus: *Lithostrotion* Fleming, 1828.

Diagnosis: Compound rugose corals, either fasciculate, cerioid or plocoid, with or without a columella or with a weak axial structure, with major and minor septa usually continuous in the dissepimentarium.

Distribution: Viséan (C2) to Namurian (E2) of Europe, Asia and North America.

Discussion: The family *Lithostrotiontidae* was first proposed by Alcide D'Orbigny (1852, p.184) in his "Cours Elementaire de Paleontologie et de

Geologie Stratigraphiques, Vol.2, fasc.1". (Although most copies of this work bear the date '1851' the book was not published until 1852).

In the family he included the genus *Lithostrotion* Fleming, 1828, and many other unrelated genera. However, at this time he included only the cerioid species of *Lithostrotion*; the fasciculate species he placed in the genus *Diphyphyllum* Lonsdale, which he referred to the family *Cyathophyllidae* (*loc. cit.*, p.183) although Lonsdale had strictly intended *Diphyphyllum* to include only the non-columellate fasciculate species.

In the same year Edwards and Haime placed both the cerioid and fasciculate species in the genus *Lithostrotion* including both the columellate fasciculate species and also the non-columellate species, considering *Diphyphyllum* *S.S.* to be synonymous with *Lithostrotion*. Thus the genus *Diphyphyllum* was first admitted to the family in synonymy with *Lithostrotion*, but later authors have continued to use *Diphyphyllum* for the non-columellate fasciculate species.

Smith published the following genera and included them also in the *Lithostrotiontidae*; *Orionastraea* (1916), *Nemistium* (1928) and *Aulina* (published in 1916, included in the family in 1925).

In this thesis the genus *Aulina* has been rejected from the family as it is thought to have entirely different ancestore to the *Lithostrotiontidae*. Secondly, *Nemistium* and *Diphyphyllum* have been merged back into the parent genus *Lithostrotion* for the following reasons. The genus *Diphyphyllum* was found to be polyphyletic to such an extent that practically every species in the genus represents a separate lineage. *Nemistium* *edmondsi*, the only species in this genus, was found to be an evolutionary link between two species of *Lithostrotion* and so *Nemistium* is not a true biological genus.

Thirdly, the new genus *Hudsonia* has been proposed, similar to *Orionastraea*, but evolving from a different ancestral species of *Lithostrotion*.

Thus the family now contains three genera; *Lithostrotion*, *Orionastraea* and *Hudsonia*. It will be seen that the genus *Lithostrotion* now includes a wide variety of species which can be divided into four morphological groups, corresponding to the old genera, as follows; the cerioid group, the fasciculate group, the diphyphylloid group and the nemistioid group. It should be stressed here that these groups have no systematic value whatsoever, but are merely groups of species that have evolved a similar structure along different lineages. The division of these groups thus cut across the phylogenetic lineages within the genus.

The taxonomic history of the *Lithostrotiontidae* is summarised in the following pages under these groupings.

TAXONOMIC HISTORY OF THE *LITHOSTROTIONTIDAE*

Genus *Lithostrotion*

Cerioid Group

The first description of *Lithostrotion* was in 1699 in the pre-Linnean days prior to the system of binomial nomenclature. In that year Edward Lhwyd (Lhuyd, Luidi, Luid, Luidius, Ludwig) described in his 'Lithophylacii Britannici Ichnographia' a cerioid coral which he named *Lithostrotion sive Basaltes minimus striatus et stellatus* after the basaltic columns of the Giant's Causeway in Ireland (1699, p.122, pl.xxiii). This description is repeated in the 'Editio altera' of Lhwyd's original text (1760, p.125, pl.xxiii). His specimen is now lost and from his figure it is impossible to be sure which species he was referring to, but fortunately in the years immediately succeeding Lhwyd several other authors made reference to his description and in their works the species is better defined. Volkmann (1720, p.120) for example called this species *Corallium arachnion*, *astroites arachnoides*, *s. telis quasi araneis obtextus*, *pentagonus*, *astroites verticalis* after the appearance of the calicular surface to the web of a spider and after the figures used to illustrate the vortices of Descartes. Then Da Costa (1757, p.246) gives a long description of this species under the name of *Marmoroides columnaris stellatus*, *lithostrotion dictus* and gives a diameter of ¼- ½ inch for this species. Most important perhaps of these subsequent authors was Parkinson who in his 'Organic Remains of a Former World', vol.II, Zoophytes, gave the first binomial name to Lhwyd's coral as *Madrepora vorticalis* (1808, p.45, pl.v, figs 3 & 6). Lhwyd's coral came from Wales, but from his text it is impossible to say where in Wales, however, Parkinson, quoting Woodward, states that it is, "found on the rocky cliffs about two miles from Tenby, towards Milford in Pembrokeshire". The next reference to Lhwyd's coral was by Conybeare and Phillips (1822, p.359) who removed it from the broad genus *Madrepora* and called it *Astraea basaltiforme*.

An important step occurred in 1828 when Fleming in his 'History of British Animals' proposed the genus *Lithostrotion* with four genosyntypes, one of which was Lhwyd's coral, but called by Fleming *Lithostrotion striatum* (1828, p.508). Fleming's original specimen was until recently preserved in the Royal Scottish Museum at Edinburgh, but it has since been lost. Fortunately however this specimen was figured by Thomson (1887, p.387, pl.xii, fig.1) and his description and figure are good enough for us to recognise that this is a cerioid species with 20-24 major septa.

One of Fleming's other genosyntypes in his genus *Lithostrotion* was *L. floriformis*, a coral we now know as *Lonsdaleia floriformis*. Lonsdale (1845, p.602) recognised that this species differed from *L. striatum* sufficiently to warrant the erection of a separate genus, but unfortunately selected *L. floriformis* as the genotype of *Lithostrotion* and proposed the new name of *Stylastraea* to refer to Lhwyd's coral calling it *Stylastraea vorticalis*. Fortunately most later authors did not follow Lonsdale's selection and continued to interpret *Lithostrotion* on Lhwyd's coral (see p.117).

However, McCoy (1849, p.9) did follow Lonsdale's selection and described *Stylastraea irregularis* (= *Astraea irregularis* McCoy 1844, p.187, non Defrance), a smaller cerioid coral than Lhwyd's with only 18 septa.

Now, Lonsdale in his original definition of *Stylastraea* defined it on a misapprehension that Lhwyd's coral had no columella. McCoy, in describing *Stylastraea irregularis* had thought that the genus had a columella, but on discovering Lonsdale's definition he proposed a further new genus, *Stylaxis*, McCoy (1849, p.119) for those cerioid species with a columella that would include Lhwyd's coral. In this genus he described *S. flemingi* (*loc. cit.*, p.121) which he stated was *L. striatum* of Fleming (i.e. Lhwyd's coral), *S. major* (*loc. cit.*, p.120), a larger species than Lhwyd's coral with 28-30 septa, and he also re-named *Stylastraea irregularis* as *Stylaxis irregularis* (1851, p.101).

McCoy continued to use *Stylastraea* as distinct from *Stylaxis* for those cerioid species that had no columella. He placed *Astraea basaltiforme* Conybeare and Phillips in *Stylastraea* and described *Stylastraea basaltiformis* (McCoy, 1851, p.107), not realising that *Astraea basaltiforme* was also based on Lhwyd's coral and must therefore have a columella. In fact he deposited a 'holotype' of this species in the Sedgwick Museum, Cambridge, which had no columella, but this cannot be accepted as a holotype as McCoy was not the author of the species and his 'holotype' did not agree with Conybeare and Phillips' description.

McCoy also recognised that while some of the cerioid corals were composed of corallites that were easily separable from the main mass into individual columns, other colonies showed no such tendencies, being composed of united tubes. Regarding this factor to be of generic importance he erected the new genus *Nemaphyllum* (1849, p.15) for the colonies with inseparable corallites. (He later amended this to *Nematophyllum* (1851, p.97).) Thus he described *N. minus* with 20-24 septa (1849, p.17), *N. aranea* (= *Astraea aranea* McCoy 1844, p.187) with 28-30 septa, *N. septosum* with 28-30 septa, but an open inner zone (1849, p.19), *N. arachnoideum* also with 28-30 septa (*loc. cit.*, p.16) and *N. decipiens* loc. cit., p.18) and *N. clisioides* (*loc. cit.*, p.18) both with 18 septa, but of different diameters.

Edwards and Haime placed all these species in the genus *Lithostrotion* in 1851 including *S. irregularis* and in doing so were faced with the problem of having two species, one fasciculate (*Siphonodendron irregulare*) and one cerioid (*Stylaxis irregularis*) in the same genus and bearing the same trivial name. Thus they re-named the later *Stylaxis irregularis* as *Lithostrotion derbiense* (1851, p.445).

They also included in the genus *L. portlocki* (= *Astraea portlocki* Bronn 1848, p.128, = *A. irregularis* Portlock 1843, p.333, non Defrance, non McCoy) and published one new cerioid species, *L. maccoyanum* (1851, p.444), smaller than all the other cerioid species with only 14 septa.

Edwards and Haime also added two further species to the genus Stylaxis, viz, S. portlocki (1851, p.453) and S. m'coyana (loc. cit., p.453). They used this genus as they wrongly considered Stylaxis to possess a complex axial structure. On realising their mistake and discovering that Stylaxis was synonymous with Lithostrotion they referred these two new species to their new genus Petalaxis (1852, p.204).

Thomson described a cerioid species from Scotland with 20-24 septa as L. clavatica (1883, p.401) which he re-figured in 1887 (p.385, pl.xi, fig.6) as L. clavaticum.

Vaughan described L. basaltiforme var. bristoliense also with 20-24 septa (1903, p.106) which has since been quoted by several later authors as a separate species.

Schindewolf (1927) proposed the genus Cystistrotion from the Upper Viséan cerioid species asserting that they differed from the Lower Viséan Lithostrotion in having incomplete tabulae.

Finally Smith and Lang (1930, p.184) realising that Lonsdale had erred in defining Stylastraea to have no columella (as it was based on Lhwyd's coral which is columellate) proposed Diphystrotion for such non-columellate cerioid corals. They redescribed McCoy's 'holotype' of Stylastraea basaltiformis as D. kendalense giving the new species name as McCoy had erred in thinking A. basaltiformis Conybeare and Phillips to be non-columellate.

Fasciculate Group

The first reference to a specimen of fasciculate Lithostrotion appears to have been by Robert Plot in his 'Natural History of Staffordshire' where he figured a corallite under the name of 'Screw Stone' (1686, p.195, pl.xii, fig.3). However, it was over a century later before a true biological name was applied to a species in this group, when Ure in his 'History of Rutherglen' described Juncei lapidei, a much smaller species than Plot's 'Screw Stone' (1793; p.327, pl.xix, fig.12). This was soon followed by Martin who described two larger species by the names of *Erismolithus* (*Madreporae cespitosae*) (1793; 1809, pl.xvii, amended in the (Addenda et Corrigenda' to '*Erismatolithus*') and the still larger *Erismatolithus Madreporites* (*affinis*) (1793; 1809, pl.xxxi, fig.3).

Fleming (1828) realising the affinities of these four species placed them all in the genus *Caryophyllia*, calling Ure's species *C. juncea* (*loc. cit.*, p.508), Martin's *E. Madreporites* (*affinis*) by the name of *C. affinis* (*loc. cit.*, p.509) and Martin's *E.* (*Madreporae cespitosae*) by the name of *C. fasciculata* (*loc. cit.*, p.509). The name *C. fasciculata* was interpreted very widely at this time; Fleming's type specimen in fact is a diphyphylloid species, but as this original description was prior to Lonsdale's publication of the genus *Diphyphyllum* no significance was attached to the presence or absence of a columella. Thus this name was used for any fasciculate *Lithostrotion* with or without a columella that was intermediate in size between *C. juncea* and *C. affinis*, and thus it also initially included Plot's 'Screw Stone'. For example De Blainville in 1830 described a specimen which is similar to Plot's 'Screw Stone' by this name.

The next important step was in the years of 1834-6 when the species were placed in the genus *Lithodendron* (published by Schweigger in 1819) and thus removed from the broad genus *Caryophyllia*. Thus Kerferstein described *Lithodendron junceum* (1834, p.785) and *Lithodendron affinis* (1834, p.785) and Phillips described *Lithodendron fasciculatum* (1836, p.202, pl.ii, figs 16 and 17) but, meaning it to refer only to Martin's *E.* (*Madreporae cespitosae*). In this same publication Phillips, realising that Plot's 'Screw Stone' should be distinguished on its smaller size from *E.* (*M. cespitosae*) called this species *Lithodendron irregulare* (1836, p.202, pl.ii, figs 14 and 15). He also described the new species *L. sexdedimale* (p.203, pl.ii, figs 11, 12 and 13), *L. sociale* (p.203, pl.ii, fig.19) and *L. longiconicum* (p.203, pl.ii, fig.18).

Portlock added further to the genus when he described *Lithodendron coarctatum* (1843, p.336, pl.xxii, fig.5). In the following year McCoy described *Lithodendron pauciradiale* (1844, p.189) which is similar to Phillips *L. irregulare*, but smaller and with fewer septa.

In 1849 McCoy founded the genus *Siphonodendron* to refer exclusively to the species dealt with here and described in the years immediately following, *S. pauciradiale* (1849, p.135), *S. fasciculatum* (1851, p.108) and *S. sexdecimale* (*loc. cit.*, p.109). He later changed the specific name of *S. pauciradiale* to *S. aggregatum* (*loc. cit.*, p.108) as he had been misled in considering the species to have a paucity of septa, but according to the Rules of Nomenclature, the first name of *S. pauciradiale*, however inappropriate, must take precedence. However this generic division has not been followed as at about the same time Edwards and Haime finally placed all these species in Fleming's genus *Lithostrotion* which had hitherto only been applied to the cerioid species. Thus they described *Lithostrotion junceum* (1851, p.435; 1852, p.197), *Lithostrotion affine* (1851, p.437; 1852, p.200), *Lithostrotion irregulare* (1851, p.436; 1852, p.199), *Lithostrotion pauciradiale* (1851, p.439) and *L. martini* (1851, p.436; 1852, p.197), a new name for Martin's *E.* (*M. cespitosae*) distinguishing it from *C. fasciculata* as by this time Lonsdale's genus *Diphyphyllum* had been published, and the non-columellate and columellate forms were thus separated.

Edwards and Haime also described *L. phillipsi* (1851, p.439; 1852, p.201), *L. harmodites* (1851, p.440) and *L. stokesi* (1851, p.440) which Hill (1940, p.168) considered may be *Aulina*. However Easton (1957) showed that Edwards and Haime had erred in considering *L. harmodites* to be a Carboniferous coral and that it was in fact a Silurian coral probably *Synaptophyllum multicaule* (Billings). The same situation seems to apply to *L. stokesi*.

More recently Hill has described the Scottish *L. scoticum* (1940, p.173).

Finally Schindewolf proposed the genus *Cystidendron* (1927, p.149) for Upper Viséan fasciculate *Lithostrotion* species asserting that they differed from the Lower Viséan species by having incomplete tabulae.

Similarly Chi proposed *Stylostrotion* (1935, p.20) which differs from *Lithostrotion* by the greater tendency to diphymorphism of the former.

Diphyphylloid Group

The first record of a species in this group may have been by Martin in his, 'Figures and Descriptions of Petrifactions collected in Derbyshire'. Here he described *Erismatolithus* (*Madreporae cespitosae*) (1793, pl.xvii) which has since been re-collected by Hill (1940, p.185) from Martin's locality. She considers it to be a diphyphylloid species, but Martin's figure shows it to have a columella and thus it is not diphyphylloid, but probably, as Edwards and Haime stated (1852, p.197) a specimen of *L. martini*. Hill also noted the columella in the figure and thus did concede that *E.* (*M. cespitosae*) was only in partim a diphyphylloid species, i.e. that which she collected from the type locality. However, merely collecting from Martin's locality is not sufficient evidence on which to base the species especially as the collection was not made in situ, and so *E.* (*M. cespitosae*) should be considered as *L. martini*.

Martin figures this species again in his later publication, 'Petrificata Derbiensia' (1809, pl.xvii) where he also described and figured *Erismatolithus Madreporites* (*affinis*) (*loc. cit.*, pl.xxxi). Hill (1940, p.185) considered this to be identical to *E.* (*M. cespitosae*) and thus that was also a diphyphylloid species, but Martin's figure again shows it to have a columella and thus it is probably *L. affine* (Fleming).

In 1828 Fleming described *Caryophyllea fasciculata* (*loc. cit.*, p.509) and this is definitely non-columellate and can therefore be regarded as the first description of a species of this group.

In 1845 Lonsdale published the genus *Diphyphyllum* (*loc. cit.*, p.622) to include such non-columellate species of the *Lithostrotiontidae*, but included in it only one species, *D. concinnum* (*loc. cit.*, p.624) a larger species than Fleming's *Caryophyllea fasciculata*. Lonsdale did not at this stage include Fleming's species in his new genus, and thus *D. concinnum* must be considered the genotype. Unfortunately few authors following Lonsdale recognised his genus, most of them agreeing with Edwards and Haime who considered the absence of a columella to be an accident of preservation. What they did not consider was that this was not the only character upon which Lonsdale based the genus. He also recognised that these non-columellate species reproduced asexually by parricidal gemmation whereas budding in *Lithostrotion* was non-parricidal.

One of the few authors who did recognise Lonsdale's genus was McCoy who described two new species in the genus. McCoy described *D. lateseptatum* (1849, p.8) which he distinguished from *D. concinnum* on the greater proportional width of the transverse medial plates. He also described a species smaller even than *C. fasciculatum* by the name of *D. gracile* (1851, p.168).

In 1887 Thompson offered evidence in favour of the recognition of the genus and published further new species and varieties although his conception of specific characters was rather narrow. He described *D. blackwoodi* (1887, p.36), *D. blackwoodi* var. *approximatum* (*loc. cit.*, p.36), *D. cylindricum* (*loc. cit.*, p.36), *D. lateseptatum* var. *giganteum* (*loc. cit.*, p.37), *D. lateseptatum* var *interruptum* (*loc. cit.*, p.37) and finally *D. concinnum* var. *furcatum* (*loc. cit.*, p.36), intermediate in size between *D. concinnum* and *C. fasciculatum*. This variety was considered by Hill to be a distinct species from *D. concinnum* (= *D. lateseptatum*) and was described by her as *D. furcatum* (1940, p.185), raising Thompson's variety to specific level. It is this species that she considered to be synonymous with Martin's *E.* (*M. cespitosae*). Fortunately she used Thompson's name in preference to Martin's as there were no type specimens for Martin's coral. It was fortuitous that she did this as the International Commission of Zoological Nomenclature officially rejected

Martin's works from nomenclatorial purpose (Opinion 231, 1948) as Martin did not employ binomial nomenclature and thus his species became unavailable.

The next contribution to the genus was by Smith and Lang. They finally placed Fleming's *C. fasciculatum* in the genus *Diphyphyllum* (1930, p.183). They also suggested that as the type of *D. concinnum* was lost, the genus should now be based on *D. lateseptatum* which is probably conspecific with *D. concinnum*. Smith and Lang also introduced a new concept to Linnaen nomenclature in the same paper, the genomorph concept, to use in connection with the genus *Diphyphyllum*. This has however not been generally followed and is re-evalued by Wilson (1963).

Finally Hill also described two new species of *Diphyphyllum*, first *D. smithi* (1940, p.181) and secondly *D. ingens* (1940, p.186).

Nemistioid Group

The genus *Nemistium* was published by Smith in 1928 to include those corals similar to *Diphyphyllum* in most internal structures, "but differing from these in having a loosely formed and irregular axial structure which in some instances persists through the corallites and in other instances arises from successive tabulae and does not reach the tabulae above". Smith described only one species, *N. edmondsi* (1928, p.116) and the genus has remained monospecific to the present day.

Genus *Orionastraea*

The earliest record of a species in the present day genus *Orionastraea* was by William Martin in 1809 ('Petrificata Derbiensia', pl.xviii, figs. 2 and 3). Martin described the specimen under the name *Erismatolithus tubiporites* (*radiatus*) and said that the coral consisted of "straight tubes connected by transverse dissepiments or partitions". John Fleming in his 'History of British Animals' (1828, p.529) recorded Martins species as '*Tubipora radiata*'. Smith (1916) points out that, "this citation appears to have been overlooked hitherto, and those palaeontologists who refuse to acknowledge Martin's claims to the authorship of the species which he named, on the grounds that his terminology did not conform to the laws of Linnaen nomenclature, credit the trivial name '*radiata*' to Samuel Woodward" (1830, p.5).

John Phillips in his, 'Figures and Descriptions of the Palaeozoic Fossils of Cornwall etc.' gave a description of the Devonian coral, originally described by Lonsdale as *Astraea hennahi*, which he illustrated with drawings (1841, p.12, pl.vi, figs 16αa, 16βb, 16βc, and pl.vii, fig.15D). Plate vi, fig.16, is indeed that Devonian coral, however pl.vii, fig.15D was of a coral which Phillips found in the Carboniferous limestone of Flintshire and which although Phillips believed it to be allied to *A. hennahi*, actually belonged to the same genus as Martin's *T. radiata*. Unfortunately this figure has been the cause of much subsequent confusion because Alcide D'Orbigny in his 'Note sur des Polypiers Fossiles' (1849, p.12) introduced the generic name *Phillipsastraea* for this Devonian group and in his later publication, 'Prodrome de Paleontologie' he based this new genus on *A. hennahi* (1850, p.106-107) as figured by Phillips including Phillips' figure 15D. Edwards and Haime (1851, p.447; 1852, p.203) realising that the genus *Phillipsastraea* was based on a figure that contained unrelated Devonian and Carboniferous forms, decided correctly to erect a new genus so that the Devonian and Carboniferous corals could be split. However, they unfortunately based *Phillipsastraea* upon Phillips' Carboniferous specimen, fig.15D, and erected a new genus, *Smithia* (1851, p.421) for the Devonian corals based on Lonsdale's *A. hennahi*.

Smith (1916) challenged Edwards and Haime's use of the name *Phillipsastraea* stating that, "although the figure of the Carboniferous species was quoted by D' Orbigny he clearly intended the name *Phillipsastraea* to be applied to the Devonian species". Thus Smith published the new name of *Orionastraea* (1916, p.294) to include the Carboniferous forms including Martin's species and Phillips' figure 15D.

In 1849 McCoy described three species of '*Orionastraea*' under the generic name of *Sarcinula* (a genus proposed by Lamarck for recent coral species). The first of these *S. phillipsi* (1849, p.125) had a distinct dilated columella of the '*Lithostrotion*' type and McCoy correctly identified this with Phillips' Carboniferous specimen of fig.15D. The second *S. placenta* (*loc. cit.*, p.124) was similar but had no columella, and the third, *S. tuberosa* (*loc. cit.*, p.124) was distinguished by McCoy from the others, by its upper (calicular) surface being "covered with irregular tuberose projections".

Edwards and Haime (1851, p.448-9; 1852, p.203) considered these species, but under the generic name of *Phillipsastraea* for the reasons already given. They considered *S. phillipsi* to be synonymous with *S. placenta* as they paid no attention to the presence or absence of a columella, thinking its absence was only due to imperfect preservation. They called this species *P. radiata* using Martin's original name, but this is unwise as it is difficult to be sure to which species Martin's figured specimon actually belongs. Edwards and Haime also retained McCoy's *S. tuberosa* as distinct, by its peculiar surface, calling this *P. tuberosa*. In his paper publishing the new name of *Orionastraea* for these species Smith (1916) on the other hand cut sections of the three specimens and decided, that the peculiar surface of *O. tuberosa* was not of specific importance but merely an extreme growth form of the colony. He thought that *O. tuberosa* had a columella and therefore merged *O. tuberosa* with *O. phillipsi*, keeping *O. placenta* a distinct species as it had no columella.

In tho same paper Smith added a fourth species to the genus *Orionastraea*, that of *O. ensifer* (*loc. cit.*, p.301). This species was originally described by Edwards and Haime (1851, p.442; 1852, p.193) as *Lithostrotion cusifer* as it does show a very thin epithecal wall. In fact as Smith pointed out it forms the ideal passage from *Lithostrotion* to *Orionastraea* and could in reality be included in either genus.

The next substantial contribution to the research on *Orionastraea* was by Hudson in two papers published in 1926 and 1929. In the first of these he published a new species, that of *O. indivisa* (1926, p.144) which could be distinguished from all the others on the basis that it had no septa, but only tabulae separated by a mass of dissepimental tissue (*loc. cit.*, p.147, figs 1 and 2).

In his 1929 publication Hudson studied *Orionastraea* from the Yoredale Series of Northern England and showed that they differed from the forms described by McCoy from the older Carboniferous rocks. Thus he proposed four new species and four new varieties. Hudson considered the evolution of *Orionastraea* to be polyphyletic and therefore divided the nine species and four varieties into several species groups which he considered represented separate lineages. The first of these groups contained *O. phillipsi* (*loc. cit.*, p.444), *O. ensifer* (*loc. cit.*, p.445) and a new variety *O. ensifer* var. *matura* (*loc. cit.*, p.445) similar in all respects to *O. ensifer* except in its larger tabularium and greater number of septa.

Hudson's second species group included *O. indivisa* (*loc. cit.*, p.446) and a new species *O. edmondsi* (*loc. cit.*, p.446) and its variety *O. edmondsi* var. *laciniosa* (*loc. cit.*, p.447). *O. edmondsi* is distinguished on its being aphroid, the septa retreating from the periphery and the intervening space between corallites being filled with dissepiments. It has a high number of septa (30-34). *O. edmondsi* var. *laciniosa* is similar but is not in an aphroid condition.

His third species group contained his new species *O. garwoodi* (*loc. cit.*, p.449) and its varieties *O. garwoodi* var. *pristina* (*loc. cit.*, p.451) and *O. garwoodi* var. *sera* (*loc. cit.*, p.450). *O. garwoodi* has under thirty continuous septa and is thus similar to *O. placenta*, which Hudson did not describe, but he distinguishes it on account of it having its outer series of dissepiments convex inwards. *O. garwoodi* var. *pristina* is similar, but the convexity of the dissepiments is not so marked, and *O. garwoodi* var. *sera* has its dissepiments even more convex so that some of them run parallel to the septa, lining their sides.

Hudson's final species group contains *O. tuberosa* (*loc. cit.*, p.447) defined correctly by Hudson as having 30-34 septa, and Hudson like Smith considered it to possess a columella. Hudson thus distinguished it from *O. phillipsi* on the fact that the septa of *O. tuberosa* were not confluent. This species group also contained a new species *O. prerete* (*loc. cit.*, p.448) which Hudson again defined as having non-confluent septa, but septa only numbering 24. Hudson considered this to have evolved from *O. tuberosa*, by a reduction of septa, on the basis of the two species having non-confluent septa.

Hudson's last new species in this group is *O. rete* (*loc. cit.*, p.448) again with 24 septa, but differing in being in the aphroid state. Hudson regarded it as developing from *O. prerete*. *O. rete* differs from *O. edmondsi* which is also aphroid in having only 24 septa, as opposed to *O. edmondsi*'s 30 septa.

The most recent addition to the revision of the genus *Orionastraea* was by Kato and Mitchell when they revised a form originally described by Garwood and Goodyear (1924, p.219, 227 and 232) as "an exceptionally large variety of *Orionastraea phillipsi*". Kato and Mitchell regarded this to be a separate species on account of its size and published it as *O. magna* (1970, p.49).

Genus *Lithostrotion* Fleming

1808 *Madrepora*, Parkinson, *partim*, p.45. (Not *Madrepora* L.).
1822 *Astraea*, Conybeare and Phillips, *partim*, p.359. (Not *Astraea* Lamarck).
1828 *Lithostrotion*, Fleming, *partim*, p.508.
1828 *Caryophyllia*, Fleming, *partim*, p.509. (Not *Caryophyllia* Lamarck).
1830 *Caryophyllia*, De Blainville, *partim*, p.311. (Not *Caryophyllia* Lam.)
1830 *Columnaria*, De Blainville, *partim*, p.316. (Not *Columnaria* Gold.)
1830 *Lithostrotion*, Woodward, p.6.
1834 *Lithodendron*, Kerferstein, *partim*, p.785. (Not *Lithodendron* Schweigger).
1836 *Lithodendron*, Phillips, *partim*, p.202. (Not *Lithodendron* Schweigger).
1836 *Cyathophyllum*, Phillips, *partim*, p.202. (Not *Cyathophyllum* Gold.)
1836 *Columnaria*, Milne-Edwards, *partim*, p.343. (Not *Columnaria* Gold.)
1842 *Caryophyllia*, De Koninck, *partim*, p.17. (Not *Caryophyllia* Lam.)
1843 *Astraea*, Portlock, p.332. (Not *Astraea* Lam.)
1843 *Lithodendron*, Portlock, p.336. (Not *Lithodendron* Schweigger).
1843 *Cladocora*, Morris, *partim*, p.33. (Not *Cladocora* Etheridge).
1844 *Lithostrotion*, McCoy, p.188.
1844 *Lithodendron*, McCoy, p.188. (Not *Lithodendron* Schweigger).
1844 *Astraea*, McCoy, p.187. (Not *Astraea* Lam.)
1845 *Stylastraea*, Lonsdale, p.619.
1845 *Lithodendron*, Lonsdale, p.600. (Not *Lithodendron* Schweigger).
1845 *Diphyphyllum*, Lonsdale, p.622.
1846 *Cladocora*, Geinitz, *partim*, p.570. (Not *Cladocora* Etheridge).
1846 *Lithostrotion*, Keyserling, p.156.
1848 *Astraea*, Bronn, *partim*, p.128. (Not *Astraea* Lam.)
1849 *Nemaphyllum*, McCoy, p.15.
1849 *Stylastraea*, McCoy, p.9.
1849 *Stylaxis*, McCoy, p.119.
1849 *Siphonodendron*, McCoy, p.127.
1849 *Diphyphyllum*, McCoy, p.8.
1849 *Lasmocyathus*, D'Orbigny, p.12.
1850 *Lithostrotion*, D'Orbigny, p.159.
1850 *Lasmocyathus*, D'Orbigny, p.160.
1850 *Diphyphyllum*, D'Orbigny, p.159.
1851a *Diphyphyllum*, McCoy, p.168.
1851b *Stylaxis*, McCoy, p.100.
1851b *Siphonodendron*, McCoy, p.107.
1851b *Nematophyllum*, McCoy, p.97.
1851b *Stylastraea*, McCoy, p.107.
1851b *Diphyphyllum*, McCoy, p.87.
1851 *Lithostrotion*, Milne-Edwards and Haime, *partim*, p.432.
1851 *Stylaxis*, Milne-Edwards and Haime, p.452.
1852 *Lithostrotion*, D'Orbigny, p.184.
1852 *Lasmocyathus*, D'Orbigny, p.185.
1852 *Diphyphyllum*, D'Orbigny, p.183.
1852 *Lithostrotion*, Milne-Edwards and Haime, p.190.
1852 *Petalaxis*, Milne-Edwards and Haime, p.204.
1876 *Koninckophyllum*, Thomson and Nicholson, *partim*, p.297.
1876 *Lithostrotion*, Thomson and Nicholson p. .
1876 *Diphyphyllum*, Thomson and Nicholson, p.70.

1883 *Lithostrotion*, Thomspn, p.397.
1883 *Diphyphyllum*, Thomson, p.381.
1887a *Diphyphyllum*, Thomson, p.33.
1887b *Lithostrotion*, Thomson, p.377.
1903 *Lithostrotion*, Vaughan, p.106.
1920 *Lithostrotion*, Smith, p.56.
1927 *Cystidendron*, Schindewolf, p.149.
1927 *Cystistrotion*, Schindewolf, p.149.
1928 *Nemistium*, Smith, p.114.
1928 *Diphyphyllum*, Smith, p.113.
1929 *Lithostrotion*, Hudson, p.454.
1930 *Lithostrotion*, Hudson, p.97.
1930 *Lithostrotion* (*Diphyphyllum*), Smith and Lang, p.178.
1931 *Siphonodendron*, Chi, p.26.
1933 *Lithostrotion*, Yu, p.89.
1933 *Diphyphyllum*, Yu, p.82.
1933 *Depasophyllum*, Yu, p.85.
1934 *Lithostrotion*, Hill, p.81.
1935 *Stylostrotion*, Chi, p.20.
1935 *Lithostrotion*, Heritsch, p.142.
1937 *Lithostrotion*, Yu, p.37.
1940 *Lithostrotion*, Hill, p.165.
1940 *Diphyphyllum*, Hill, p.180.
1955 *Lithostrotion*, Minato, p.77.
1955 *Siphonodendron*, Minato, p.77.
1955 *Diphyphyllum*, Minato, p.80.
1955 *Depasophyllum*, Minato, p.84.
1971 *Siphonodendron*, Kato, p.85.
1972 *Lithostrotion*, Mitchell, p.105.

But Not:
1845 *Lithostrotion*, Lonsdale, p.602.

Diagnosis: Phaceloid and cerioid rugose corals, with or without a columella, or with a weak axial structure. Large inner tabulae, usually supplemented by smaller outer tabulae. Concentric dissepiments usually developed with major septa continuous in the dissepimentarium.

Genotype: *Lithostrotion striatum* Fleming 1828 (although this should be known as *L. vorticale* Parkinson 1808). See explanation below.

Discussion: Fleming proposed *Lithostrotion* in 1828 with four genosyntypes as follows:- (1) *Lithostrotion striatus* = *Lithostrotion sive Basaltes minimus striatus et stellatus* Lhwyd, 1699, (2) *Lithostrotion floriformis* = *Erismatolithus floriformis* Martin, 1809, (3) *Lithostrotion oblongum* = *Coralloidia oblonga pentaedra* Woodward, (4) *Lithostrotion marginatum sp. nov.*

Lonsdale (1845, p.602) selected *Lithostrotion floriformis* as the genotype of *Lithostrotion* and selected Lhwyd's coral (= *L. striatum*) as the genotype of his new genus *Stylastraea*. However most later authors have continued to base *Lithostrotion* on Lhwyd's coral. However as Hill (1940, p.166) states, "to insist on applying the Rules of Nomenclature here would mean calling the corals we now know as *Lonsdaleia* by the name *Lithostrotion*, losing the name *Lonsdaleia* altogether, and calling the corals we now call *Lithostrotion* by the name *Stylastraea*". At the instance of Smith and Lang (1930, p.178) the International Commission of Zoological Nomenclature has standardised *Lithostrotion* under suspension of the Rules with *L. striatum* as genotype and *Lonsdaleia* and *Lithostrotion* are used with their tranditional meanings. However, *L. striatum* had already been called *Madrepora vorticalis* by Parkinson in 1808 (see p.102) and so the genotype should be known as *L. vorticale*.

Smith and Lang (1930, p.178) have shown that *Stylastraea* is an objective synonym of *Lithostrotion* as Lonsdale based it on Lhwyd's coral.

The genus *Siphonodendron* with genosyntypes *Lithodendron pauciradialis* McCoy 1844, (p.189), *Lithodendron fasciculatum* Phillips 1836 (p.202) and *Lithodendron sexdecimale* Phillips 1836 (p.202) was proposed by McCoy for the fasciculate species of *Lithostrotion*, but Edwards and Haime did not recognise this division, regarding *Siphonodendron* as a subjective synonym of *Lithostrotion*. This ruling is followed in this thesis because such a separation of the fasciculate species from *Lithostrotion* would have rendered *Lithostrotion* a polyphylletic genus as the different cerioid species evolved from the various fasciculate species (p. 21).

McCoy's genus *Nemaphyllum* (later emended to *Nematophyllum*) erected for those cerioid colonies with non-separable corallites was considered by Edwards and Haime (1859, p.192) to be a subjective synonym of *Lithostrotion* as the separability of corallites is chiefly a matter of fossilisation. Edwards and Haime chose *N. arachnoideum* as the genolectotype of the genus.

McCoy's genus *Stylaxis* (with genosyntypes *S. flemingi* McCoy 1849 and S. major McCoy 1849) erected for those cerioid colonies with separable corallites was also considered by Edwards and Haime (1851) and Hill (1940) to be a subjective synonym for the same reason. It should be stressed here that Stylaxis is in fact an objective synonym of Lithostrotion as it is based on S. flemingi which McCoy states is L. striatum (= L. vorticale) of Fleming, the genotype of Lithostrotion.

Petalaxis was proposed by Edwards and Haime (1852, p.204) for cerioid Lithostrotionids with a complex axial structure. However, examination of the type specimens of the genosyntypes P. portlocki and P. m'coyana shows that they have no such axial structure. Petalaxis became a synonym of Lithostrotion by Hill's choosing (1940, p.167) of P. portlocki as the genolectotype. P. portlocki has no such complex axial structure and is probably L. decipiens.

Schindewolf proposed Cystistrotion (genotype C. paeckelmanni) and Cystidendron (genotype C. kleffense) for Upper Viséan cerioid and fasciculate Lithostrotion respectively as he thought that they differed from the Lower Viséan Lithostrotion by having incomplete, instead of complete, tabulae. However, Hill (1940, p.167) suggested that these genera were subjective synonyms of Lithostrotion as this seemed insufficient reason for generic separation. This argument is followed in this thesis.

Similarly Stylostrotion proposed by Chi (1935, p.20) is similar to Lithostrotion only differing in the greater tendency to diphymorphism of the latter. Hill (1940, p.167) again considers this genus a subjective synonym of Lithostrotion as the distinguishing character is only a matter of degree.

Diphyphyllum was proposed by Lonsdale (1845, p.624) with genotype D. concinnum for those fasciculate Lithostrotion species with no axial structure. When the type of D. concinnum was lost Smith and Lang (1930, p.180) based Diphyphyllum on D. lateseptatum which is probably conspecific with D. concinnum. However as it is shown on p. 21 the various species of *Diphyphyllum* are derived polyphyletically from the species of *Lithostrotion* and so *Diphyphyllum* is not a true biological genus. If we accept that the absence of a columella and the presence of parricidal gemmation are characters worthy of generic separation we are led to the inevitable conclusion that each species of *Diphyphyllum* must be placed into a new monospecific genus. However, this would lead to an unwieldy system of nomenclature, with a host of monospecific genera, that would be unacceptable to other workers. We are thus forced to the reverse procedure of placing *Diphyphyllum* back into the parent genus *Lithostrotion*. *Diphyphyllum* is here considered a subjective synonym of *Lithostrotion*.

Grabau (1922, p.   ) proposed the genus *Depasophyllum* for those species of *Diphyphyllum* having, according to Smith (1928, p.114), tabulae (p. 15). Hill (1940, p.167) has shown that Lonsdale's figure of the genotype of *Diphyphyllum* belongs to this group and so *Depasophyllum* is an objective synonym of *Lithostrotion*.

Smith and Lang (1930, p.184) proposed *Diphystrotion* for cerioid *Lithostrotion* species that were affected by the diphyphylloid trend, but the present author considers this only to be an ecological affect and so *Diphystrotion* is considered a subjective synonym of *Lithostrotion*.

Smith (1928, p.114) proposed *Nemistium* for those fasciculate species of *Lithostrotion* possessing a weak axial structure (genotype *N. edmondsi*). However the present author has shown that this cannot be a true biological genus (p. 27) so *Nemistium* is also considered a subjective synonym of *Lithostrotion*.

It is interesting to note, regarding *Nemistium* and *Diphyphyllum*, that Smith (1928, p.119) stated, "When this group is revised it may be found practicable to merge *Nemistium* and *Diphyphyllum* in *Lithostrotion*".

The genus *Lithostrotion* has been divided into four morphological groups (p.101) and the species are discussed under these groupings.

Stratigraphical Range: The genus appears in the C2 Subzone and persists just into the Namurian.

Lithostrotion maccoyannum Edwards and Haime
(Plates 3 and 4.)

1851 *Lithostrotion maccoyanum* Milne-Edwards and Haime; Pol. Foss. der Terr. Pal., p.441.
1852 *Lithostrotion maccoyanum* Milne-Edwards and Haime; 'Mon. of the Brit. Foss. Corals', Pal. Soc., p.195, pl.XLII, figs 2, 2a, 2b.
But Not:
1887b *Lithostrotion maccoyanum* Milne-Edwards and Haime, Thomson, Trans. Edinb. Geol. Soc., vol.5, p.385, pl.XI, fig.5, which is *L. decipiens*.

Diagnosis: Small diameter cerioid *Lithostrotion* with 12-14 septa tending to extend to a dilated columella. Dissepiments variable from 1-3 rows; tabularium under 2 mm. in diameter.

Type Material: Specimen GSM 36900 (Leeds Geological Survey Collection) was figured by Yu (1937, p.108, pl.11, figs 4a and b) as the syntype of *L. maccoyanum*. Also in this series of syntypes are specimen nos 36901 and 36902. Slides PF687-8 have been cut from specimen 36900a, and slides PF689-90 have been cut from specimen 36900. (From 'D Zone, Oswestry, Shropshire').

Mitchell (pers. comm.) informs me that these specimens were in the Survey Collection when Edwards and Haime would have examined them and so were probably seen by Edwards and Haime. Thus they can indeed be considered syntypes.

However, Semenoff-Tian-Chansky (pers. comm.) informs me that he has recently turned up a specimen of *L. maccoyanum* (No. 787 bis a) in the Milne-Edwards and Haime Collection in the Museum National D'Histoire Naturelle in Paris which compares with Edwards and Haime's figure of this species (1852, pl.XLII, fig.2A). This specimen is also worthy of recognition as a syntype of *L. maccoyanum* and is here chosen as lectotype of the species so that the Leeds specimens become paralectotypes.

Material: Melmerby Scar Limestone, Hartley Quarry, Kirkby-Stephen, Cumbria; Bankhouses Limestone, Tipalt Burn, Greenhead, Northumberland; Bankhouses Limestone, S. of Halleypike Lough, Northumberland.

Description: External Characters; The corallum is massive and cerioid, generally 'bun-shaped' and quite flat, although growth is predominantly in a vertical direction as opposed to the horizontally spreading tabular type of colony. The proximal surface is covered by an external holothecae which shows concentric growth bands and the distal surface shows relatively deep calices with a prominent columella.
Internal Characters; The septa are of two orders, major and minor and these are easily distinguishable in most colonies. Generally the major septa either extend to the columella or abut onto the neighbouring septa. Minor septa are variable in length, they always just extend into the tabularium and therefore their length is directly proportional to the width of the dissepimentarium which itself is very variable. Both orders of septa are dilated in the dissepimentarium and thinner in the tabularium at their axial ends. In a few corallites of one of the syntypes (Slide PF689) the septa are discontinuous peripherally and the dissepimentarium is therefore lonsdalaeoid but usually septa extend to the epithecae. The maximum number of septa in a colony varies from 12-14. There is usually a prominent columella although 'diphymorphs' may occur.

The tabularium of this species is very small and is a good diagnostic feature. It varies in adult corallites from 1.2 - 2.2 mm. and the mean tabularium diameter is 1.6 mm. The dissepimentarium on the other hand varies greatly in width. In the colonies from Greenhead, Northumberland, there is only one row of dissepiments and the dissepimentarium is only 0.2 mm. wide; thus the diameter is small and the minor septa are short. In the syntype however there are three rows of dissepiments and the dissepimentarium is 0.6 mm. wide; thus the diameter is much larger and the minor septa longer.

The inner row of dissepiments is dilated and regular whereas the outer dissepiments, if present, are finer and more irregular. All dissepiments are concave towards the axis.

The diameter of this species is variable due to changes in the width of the dissepimentarium. It ranges in adult corallites from 2.4 mm. (in the Greenhead specimen) to 4.0 mm. in the syntype.

The corallites are bounded by a distinct epithecae which is usually thin, but is nevertheless a double-walled structure. The tabulae are usually entire and slope gently towards the dissepimentarium. Occasionally a second incomplete series is developed in the periphery of the tabularium.

Discussion: This species can be distinguished from *L. aranea* and *L. verticale* by only having up to 14 septa. It can be distinguished from *L. decipiens*, which may also have 14 septa, by the small size of the tabularium. However, *L. maccoyanum* and *L. decipiens* cannot be distinguished on the basis of corallite diameter. The reason for this is the great variability in the dissepimentarium of both species, so that *L. decipiens* with a small dissepimentarium may be smaller in diameter than *L. maccoyanum* with a large dissepimentarium (fig. 40). Many early workers tried to use diameter as a distinguishing feature with the result that many records of *L. maccoyanum* in the literature refer to *L. decipiens*.

Statistical Results:

R. = 12 - 14

MD. = 3.24 mm.
S.D. = 0.512 mm.
max.D. = 4.0 mm.
min.D. = 2.4 mm.

MT. = 1.66 mm.
S.D. = 0.316 mm.
max.T. = 2.2 mm.
min.T. = 1.2 mm.

Stratigraphical Range: Base of D1 to base of D2 (Smiddy Limestone).

FIGURE 36

Plot of tabularium diameter against percentage frequency in *L. maccoyanum*. Intervals in mm's.

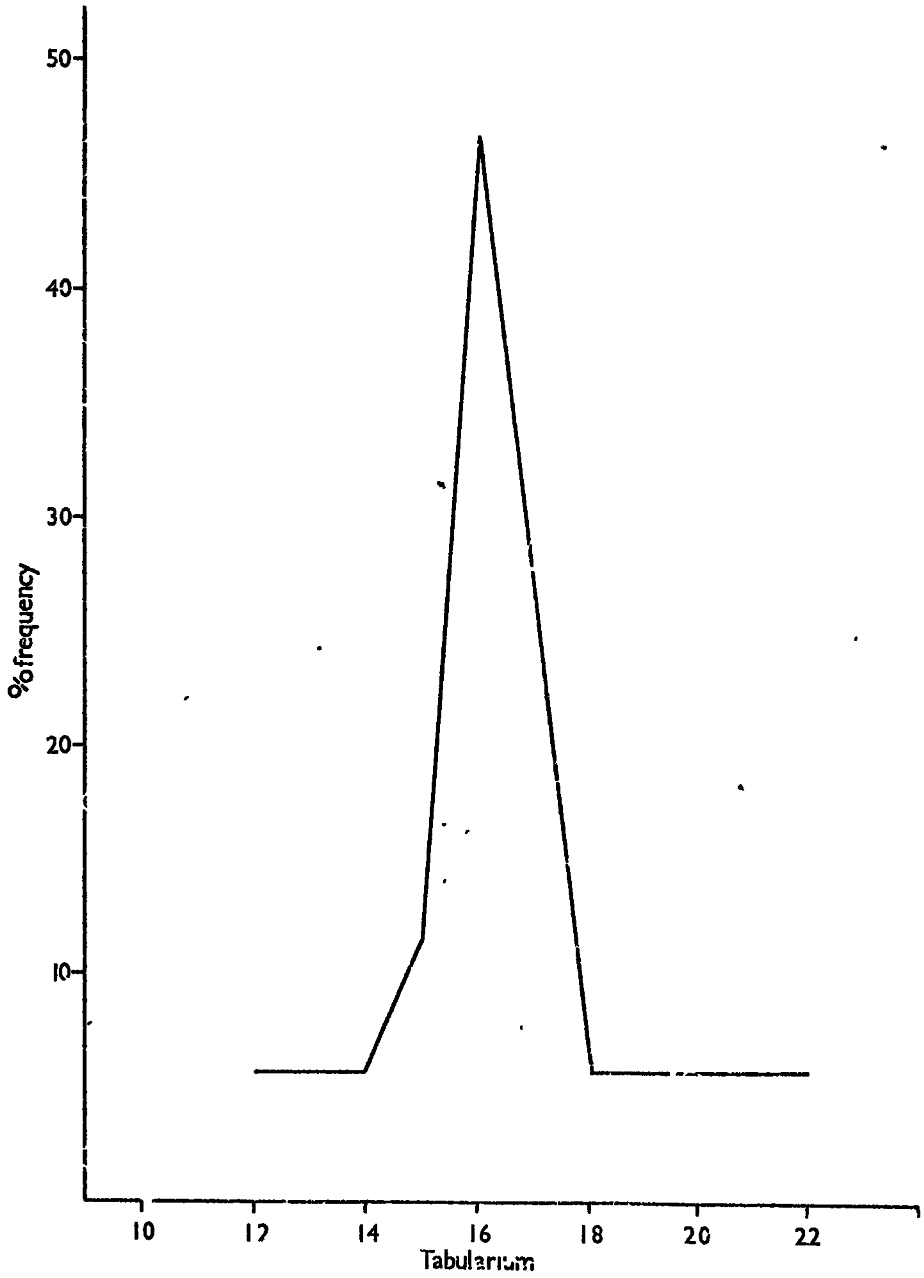


fig 36

Lithostrotion decipiens decipiens (McCoy)

(Plates 5 - 9.)

1843 *Astraea irregularis* var. *minor* Portlock, 'Geol. Rep. Lond. and Tyrone', p.333, pl.XXIII, fig.4 (Not *A. irregularis* S.S. Portlock).

1844 *Astraea irregularis* McCoy, Syn. Carb. Foss. of Ireland, p.187 (Not *A. irregularis* Defrance).

1849 *Stylastraea irregularis* McCoy, Ann. Mag. Nat. Hist., ser.2, vol.III, p.9.

1849 *Nemaphyllum decipiens* McCoy, *Ibid.*, ser.2, vol.III, p.18.

1849 *Nemaphyllum clissioides* McCoy, *Ibid.*, ser.2, vol.III, p.18.

1851 *Stylaxis irregularis* McCoy, 'Brit. Pal. Fossils', p.101, pl.IIIA, fig.5.

1851 *Nematophyllum decipiens* McCoy, *Ibid.*, p.99.

1851 *Nematophyllum clissioides* McCoy, *Ibid.*, p.98, pl.IIIB, fig.2.

1851 *Lithostrotion derbiense* Milne-Edwards and Haime, 'Pol. Foss. der Terr. Pal., p.445.

1851 *Lithostrotion decipiens* (McCoy), Milne-Edwards and Haime, *Ibid.*, p.441.

1851 *Lithostrotion portlocki* (Bronn), partim, Milne-Edwards and Haime, *Ibid.*, p.443, (Not *L. portlocki* (Bronn)).

1851 *Stylaxis portlocki* Milne-Edwards and Haime, *Ibid.*, p.453.

1852 *Lithostrotion derbiense* Milne-Edwards and Haime, 'Mon. of Brit. Foss. Corals', Pal. Soc., p.201.

1852 *Lithostrotion decipiens* (McCoy), Milne-Edwards and Haime, *Ibid.*, p.196.

1852 *Lithostrotion portlocki* (Bronn), partim, Milne-Edwards and Haime, *Ibid.*, p.194, pl.XLII, figs 1a-1g. (Not *L. portlocki* (Bronn)).

1852 *Petalaxis portlocki* Milne-Edwards and Haime, *Ibid.*, p.204, pl. XXXVIII, figs 4 and 4a.

1883 *Lithostrotion portlocki* (Bronn), Thomson, Proc. R. Phil. Soc. Glasg., vol.XIV, p.402. (Not *L. portlocki* (Bronn)).

1883 *Lithostrotion maccoyanum* Edwards and Haime, Thomson, *Ibid.*, vol.XIV, p.402. (Not *L. maccoyanum* Edwards and Haime).

1887b *Lithostrotion portlocki* (Bronn), Thomson, Trans. Edinb. Geol. Soc., vol.5, pt.3, p.384, pl.XI, figs 3 and 3a. (Not *L. portlocki* (Bronn)).

1887b *Lithostrotion clissioides* (McCoy), Thomson, *Ibid.*, vol.5, pt.3, p.384, pl.XI, fig.4.

1887b *Lithostrotion maccoyanum* Milne-Edwards and Haime, Thomson, *Ibid.*, vol.5, pt.3, p.385, pl.XI, fig.5. (Not *L. maccoyanum* Edwards and Haime).

1929 *Lithostrotion portlocki* var. *vesiculifer* Hudson, Proc. Leeds Phil. Soc., vol.I, pt.IX, p.454.

1940 *Lithostrotion decipiens* (McCoy), Hill, 'Mon. Carb. Rug. Corals of Scot.', Pal. Soc., p.178, pl.X, figs 2-4.

Diagnosis: Cerioid *Lithostrotion* with 14-18 septa, mostly extending to a columella. Tabularium 2.0 - 3.5 mm. in diameter; dissepimentarium variable in width. Corallum tall rather than depressed.

Type Material: Lectotype of *L. decipiens* is specimen no.SMA2077a, b (and slides A2077c and d) in Sedgwick Museum, Cambridge. From 'Carb. limestone, Derbyshire'.

Syntypes of *N. clissioides* include specimen no.SMA2072, A2070a-c and A2071a-d(+ e-h slides) in Sedgwick Museum.

Holotype of *L. derbiense* is specimen no.SMA2398 in Sedgwick Museum (includes slide A2398a-b cut from it). From 'Carb. limestone, Derbyshire'.

Material: Potts Beck Limestone, Ashfell Edge, Cumbria; Potts Beck Limestone, Potts Beck, Orton, Cumbria; Melmerby Scar Limestone, Hartley Quarry, Kirkby-Stephen, Cumbria; Great Scar Limestone, Askrigg, Wensleydale; Base of Middle Limestone, Arn Gill, Askrigg, Wensleydale; Middle Limestone, West Burton, Wensleydale; Middle Limestone, The Mount, Wensley, Wensleydale; Simonstone Limestone, Haw Bank, Woodhall, Wensleydale; Base of Middle Limestone, Sargill Gate, Askrigg, Wensleydale; Gayle Limestone, Mill Gill, Askrigg, Wensleydale; Simonstone Limestone, Middlesmoor Pasture, Kettlewell, Wharfedale; Simonstone Limestone, Whernside Pasture, Kettlewell, Wharfedale; Great Scar Limestone, Cow Gill, Malham, Yorkshire; Moulds Meaburn Limestone, Moulds Meaburn, Cumbria; Upper Monsal Dale Beds, Litton Mills, Millers Dale, Derbyshire; Upper Monsal Dale Beds, Intake Dale, Derbyshire; Upper Monsal Dale Beds, valley off Intake Dale, Derbyshire.

Description: External Characters; The corallum is massive and cerioid. Unlike *L. decipiens depressus* the corallum is tall, its vertical extent being greater than its horizontal extent, the direction of growth being predominantly in a vertical direction. The specimen from Whernside Pasture, Kettlewell shows its distal surface to consist of polygonal calices with a central circular depression surrounded by a flat peripheral platform. A columella is present in the calicular depression. The sides of the corallum consist of polygonal columns showing both horizontal transverse growth bands and vertical inter-septal ridges and septal grooves. The proximal base of the corallum has not been seen.

Internal Characters; The major and minor septa are easily distinguishable, most of the major septa extending to the centre where they meet the columella or abut onto the neighbouring major septa. Minor septa on the other hand only just reach the inner row of dissepiments just penetrating the tabularium. The length of the minor septa is therefore variable depending on the width of the dissepimentarium. Both orders of septa are dilated in the dissepimentarium and thinner in the tabularium. Rarely there is some proximal retreat of both major and minor septa with the outer dissepiments becoming lonsdalaeoid. This occurs in the specimen from the Gayle Limestone of Askrigg and when this occurs some of the minor septa may fail to develop.

The maximum number of septa in a colony varies from 14 - 18. A columella is usually present and diphymorphs are rare but do occur. The columella may be a stout dilated rod or may only be a thin plate.

The tabularium of this species varies from 2.0 mm. - 3.5 mm. in adult corallites with a mean of 2.52 mm., and is quite a constant character. The dissepimentarium on the other hand is immensely variable and thus the diameters of different examples of this species can be very different. For example a specimen from the Melmerby Scar Limestone of Hartley Quarry, Kirkby-Stephen, has a dissepimentarium only 0.2 mm. wide with just one row of dissepiments. A specimen from the Great Scar Limestone of Askrigg however has a dissepimentarium 1.9 mm. wide with up to eight rows of dissepiments. The diameters of the tabularia of these specimens is identical but their diameters vary from 3.0 mm. - 6.4 mm. Diameters can be as much as 8.8 mm. when the dissepimentarium is exceptionally wide.

Dissepiments are concave inwards and quite regular and concentric, but as already mentioned vary in number from a single row to up to ten rows. The innermost row is usually slightly dilated and more vertically inclined than the outer rows.

The corallites are polygonal, from four to eight sided and are bounded by an epithecae which is thin but nevertheless double-walled.

The tabulae are tent-shaped; rising to meet the axis, more horizontal peripheral to the axis and then sloping down to the dissepimentarium. They are usually incomplete and rest on the tabulae beneath in which case a second series is developed. The points of contact of the downturned edges onto the tabulae beneath are not aligned vertically and so the tabulae are of the α type (p. 15).

Discussion: A specimen that belongs to this species was first described by McCoy (1844, p.187) using Defrance's name of *Astraea irregularis*. Later (1849, p.9) realising that his specimen differed from Defrance's species McCoy placed it in the genus *Stylastraea* (as he was following Lonsdale's selection of *L. floriformis* as the genotype of *Lithostrotion*), but retained the same trivial name for his new species and placed a holotype in the Sedgwick Museum, Cambridge. Subsequently (1851, p.101) when he wrongly considered *Stylastraea* to be a non-columellate genus he removed the species to his new genus *Stylaxis* which he proposed for those cerioid species allied to Lhwyd's coral that had separable corallites. In 1849 he also proposed the new genus *Nemaphyllum* (later amended to *Nematophyllum* in 1851) to refer to related cerioid species, but with non-separable corallites. In this genus he described *N. decipiens* and *N. clissioides*.

Edwards and Haime placed all these species into the genus *Lithostrotion* in 1851 and in doing so were faced with the problem of having two species one fasciculate (*Siphonodendron irregulare*) and one cerioid (*Stylaxis irregularis*) in the same genus and bearing the same trivial name. Thus they renamed the later *Stylaxis irregularis* of McCoy as *Lithostrotion derbiense* with *L. irregulare* now referring to the fasciculate species.

Edwards and Haime considered *L. derbiense* (= *S. irregularis*), *L. decipiens* and *L. clissioides* to be separate species because of the different diameters of these three species.

For example the lectotype of *L. decipiens* (slide SMA2077c) shows rather large corallites often 5 - 6 mm. in diameter. The greater part of this diameter is made up of a dissepimentarium containing up to seven rows of dissepiments. The tabularium is only 2.5 - 3.00 mm. in diameter and there are up to 18 septa of both orders.

The lectotype of *N. clissioides* (slide SMA2071h) has much smaller corallites, often only 3 - 4 mm. in diameter. However the tabularium is of identical proportions to *L. decipiens* again being 2.5 - 3.0 mm. wide, and again there are 17 septa.

The holotype of *L. derbiense* (slide SMA2398b) has even smaller corallites only 3 mm. at the maximum and yet the tabularium is still 2.5 mm. wide in these corallites and again the mature corallites support 17 septa.

Thus all these species have the same septal counts (14 - 18) and similar tabularium diameters and only differ in the width of the dissepimentarium. Moreover, every intermediate diameter between these three species has been found and so they are here all considered to be synonymous.

The first published name for this species is *S. irregularis* McCoy, but this must be rejected as this name now applies to the fasciculate species. Portlock (1843) described *A. irregularis* var. *minor* which is also probably this species. His variety name could be raised to specific level, but according to Mayr *et al.* (1953, p.256) all variety names proposed prior to 1951 are invalid under the Rules. The names *N. clissioides* and *N. decipiens* were published in the same paper and so neither of them assumes priority, but Hill (1940, p.179) chose to use *L. decipiens* as the corallites are more fully grown in the type specimen.

In 1843 Portlock also described a similar species again using Defrance's name of *A. irregularis*. Bronn (1848, p.128), realising that Portlock's species also differed from Defrance's and from McCoy's, renamed this species *A. portlocki*.

Unfortunately Edwards and Haime considered *A. portlocki* Bronn to be synonymous with *N. clissioides* (= *L. decipiens*) and so they called this species *Lithostrotion portlocki*. However, *L. portlocki* is a larger species than *L. decipiens* as Portlock states it to have 40 septa (in total) and *L. decipiens* never has more than 18 (36 total). Close examination of the type of *L. portlocki* (slide PF685) does show it to have corallites up to 7 mm. in diameter, a tabularium up to 4 mm. diameter and possessing 20 septa of both orders. Thus it is a larger species than *L. decipiens* and is probably *L. verticale*.

Many later authors have followed Edwards and Haime in applying the name of *L. portlocki* to this species and so many records of *L. portlocki* in the literature, in fact refer to *L. decipiens*.

See p.118 for note on the synonymy of *Petalaxis portlocki*.

This species can be distinguished from *L. vorticale* and *L. aranea* by it never having more than 18 septa. Specimens of *L. decipiens* with 15 - 18 septa can be distinguished easily from *L. maccoyanum* which never has more than 14, but some specimens of *L. decipiens* also have 14 septa in which case it can be distinguished by its larger tabularium.

It is important to realise the great variation in diameter of this species. Some examples (e.g. the holotype of *L. derbiense*) may be as small as *L. maccoyanum* while others may be as large as *L. vorticale*, but the septal counts and tabularium diameter are always constant (see fig. 40).

Statistical Results:

R. = 14 - 18

MD. = 5.84 mm.
S.D. = 1.02 mm.
max.D. = 8.8 mm.
min.D. = 3.0 mm.

MT. = 2.52 mm.
S.D. = 0.33 mm.
max.T. = 3.5 mm.
min.T. = 2.0 mm.

Stratigraphical Range: Base of D1 to Single Post Limestone.

FIGURE 37

Plot of tabularium diameter against percentage frequency in *L. decipiens*. Intervals in mm's.

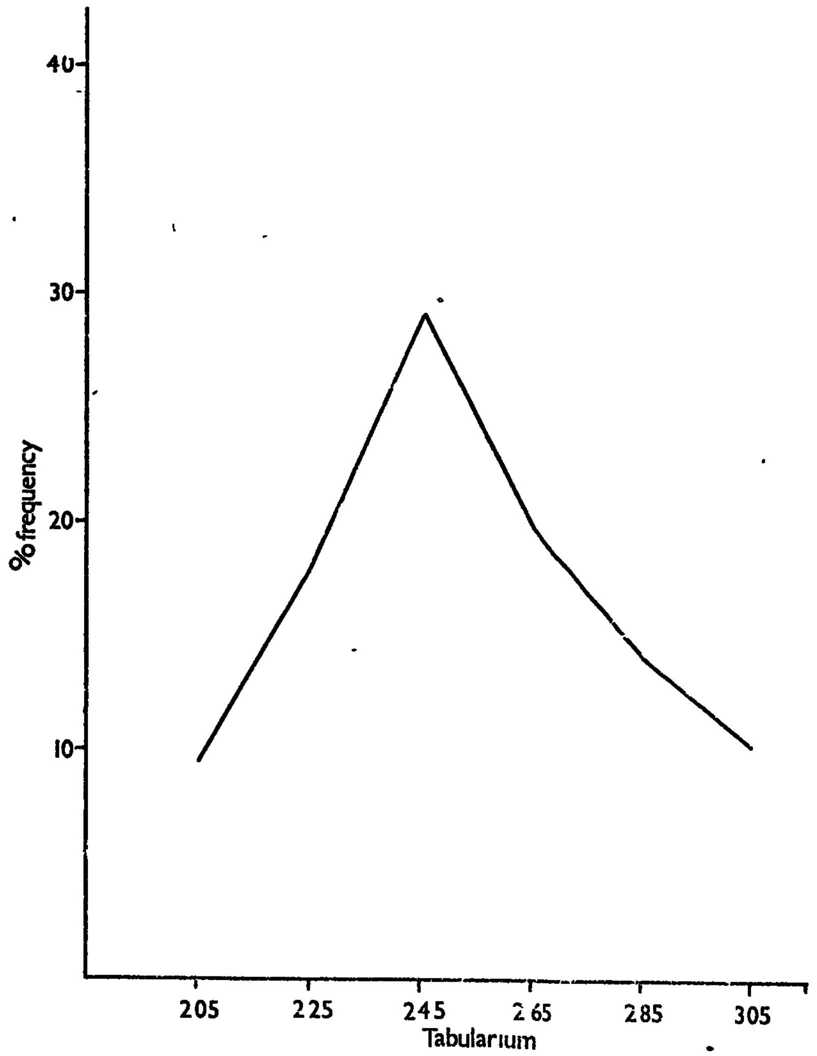


fig 37

Lithostrotion decipiens depressum subsp. nov.

Diagnosis: Cerioid Lithostrotion with 14-18 septa mostly extending to the columella. Tabularium 2.0 - 3.5 mm. in diameter; dissepimentarium variable in width. Corallum depressed and tabular.

Type Material: Holotype is specimen 17d, in the author's collection, University of Durham. From Harlow Hill Limestone, Harlow Hill, Northumberland.

Material: Harlow Hill Limestone, Harlow Hill, Northumberland; Coral band at base of Single-Post Limestone, Tipalt Burn, Northumberland; Single-Post Limestone, Longcleugh No.2 borehole, Allendale, Northumberland; Tyne Bottom Limestone, Carraw, Haydon Bridge, Northumberland; Middle Limestone, Mill Gill, Askrigg, Wensleydale; Middle Limestone, N. of Roman Road, N.W. side of Semerwater, Wensleydale.

Description: As for L. decipiens decipiens except for the growth form of the corallum which is predominantly in a horizontal direction instead of vertical. The coralla are therefore very flat as in Orionastraea and have a considerable horizontal extent compared to their height. The proximal surface is covered by an external holothecae showing the concentric pattern of growth bands on the underside of the corallum.

Discussion: This is a late stage growth habit of L. decipiens and Orionastraea may evolve from this type of corallum.

Stratigraphical Range: Tyne Bottom Limestone and Single Post Limestone.

Lithostrotion vorticale (Parkinson)

(Plates 10 - 13.)

1699 *Lithostrotion sive Basaltes minimus striatus et stellatus* Lhwyd, 'Lithophylacii Britanici Ichnographia', p.122, pl.XXIII.
1720 *Corallium arachnion, astroites arachnoides, s. telis quasi araneis obtextus, pentagonus, astroites vorticalis* Volkmann, Silesiae Subterraneae, Cap.IV, § 47, p.120, tab.XVIII, fig.5.
1757 *Marmoroides columnaris stellatus, lithostrotion dictus* Da Costa, 'A Natural History of Fossils', vol.1, p.246.
1760 *Lithostrotion sive Basaltes minimus striatus et stellatus* Lhwyd, 'Editio altera' (of above text), p.125, pl.XXIII.
1808 *Madrepora vorticalis* Parkinson, 'Organic Remains of a Former World', Vol.II, 'The Zoophytes', p.45, pl.V, figs 3 and 6.
1822 *Astraea basaltiformis* Conybeare and Phillips, 'Outlines of the Geol. of England and Wales', p.359.
1828 *Lithostrotion striatum* Fleming, 'A History of British Animals', p.508.
1830 *Columnaria striata* (Fleming), De Blainville, Dict. Sci. Nat., vol.LX, p.316.
1830 *Lithostrotion striatum* Fleming, Woodward, 'A Synoptic Table of Brit. Org. Remains', p.5.
1836 *Cyathophyllum basaltiforme* (Conybeare and Phillips), Phillips, 'Geology of Yorkshire', Vol.II, p.203, pl.II, figs 21 and 22.
1836 *Columnaria striata* (Fleming), Milne-Edwards, Ann. de la 2de edit. de Lamarck, vol.II, p.343.
1843 *Astraea irregularis* Defrance, Portlock, 'Geol. Report on Londonderry', p.333, pl.XXIII, fig.3a. (Not *A. irregularis* Defrance). Not *A. irregularis* var. *minor* Portlock 1843, p.333.
1843 *Astraea hexagona* var. *minor*, Portlock, *Ibid.*, p.332, pl.XXIII, fig.2. (Not *A. hexagona* Portlock, 1843, p.332).
1844 *Lithostrotion striatum* Fleming, McCoy, 'Syn. Carb. Foss. of Ireland', p.188.
1846 *Lithostrotion microphyllum* Keyserling, Reise in Petschora, p.156, pl.1, fig.2.
1848 *Astraea portlocki* Bronn, Index. Palaeont., p.128, (= *A. irregularis* Portlocki).
1849 *Nemaphyllum minus* McCoy, Ann. Mag. Nat. Hist., ser.2, vol.III, p.17.
1849 *Stylaxis flemingi* McCoy, *Ibid.*, ser.2, vol.III, p.121.
1850 *Lithostrotion basaltiforme* (Conybeare and Phillips), D'Orbigny, Prodr. de Pal., vol.I, p.159.
1850 *Lithostrotion microphyllum* Keyserling, D'Orbigny, *Ibid.*, vol.I, p.159.
1850 *Lithostrotion striatum* Fleming, Mantell, 'Pictoral Atlas of Fossil Remains', p.93, pl.XXXVII, figs 3 and 6.
1851 *Stylaxis flemingi* McCoy, Milne-Edwards and Haime, 'Pol. Foss. der Terr. Pal.', p.494.
1851 *Lithostrotion basaltiforme* (Conybeare and Phillips), Milne-Edwards and Haime, *Ibid.*, p.441.
1851 *Lithostrotion aranea* (McCoy), Milne-Edwards and Haime, *Ibid.*, p.443, (Not *N. aranea* McCoy).
1851 *Stylaxis flemingi* McCoy, 'Brit. Pal. Fossils', p.160, pl.IIIA, fig.3.
1851 *Nematophyllum minus* McCoy, *Ibid.*, p.99. (Not pl.IIIB, fig.3).
1851 *Stylastraea basaltiformis* (Conybeare and Phillips)+ McCoy, *Ibid.*, p.107.

1852 *Lithostrotion flemingi* (McCoy), Milne-Edwards and Haime, 'Mon. of Brit. Foss. Corals', p.203.

1852 *Lithostrotion basaltiforme* (Conybeare and Phillips), Milne-Edwards and Haime, *Ibid.*, p.190, pl.XXXVIII, figs 3, 3a, 3b.

1852 *Lithostrotion aranea* (McCoy), Milne-Edwards and Haime, *Ibid.*, p.193, pl.XXXIX, figs 1, 1a. (Not *N. aranea* McCoy).

1876 *Lithostrotion basaltiforme* (Conybeare and Phillips), Thomson and Nicholson, Ann. Mag. Nat. Hist., ser.4, vol.XVII, pl.XIV, fig.1.

1883 *Lithostrotion basaltiforme* (Conybeare and Phillips), Thomson, Proc. R. Phil. Soc. Glasg., vol.XIV, p.399, pl.VIII, fig.6.

1883 *Lithostrotion clavatica* Thomson, *Ibid.*, vol.XIV, p.401.

1883 *Lithostrotion cyathophyllia* Thomson, *Ibid.*, vol.XIV, p.399.

1883 *Lithostrotion flemingi* (McCoy), Thomson, *Ibid.*, vol.XIV, p.401.

1887b *Lithostrotion basaltiforme* (Conybeare and Phillips), Thomson, Trans. Edinb. Geol. Soc., vol.V, pt.III, p.382, pl.XI, fig.1.

1887b *Lithostrotion clavaticum* Thomson, *Ibid.*, vol.V, pt.III, p.385, pl.XI, fig.6.

1887b *Lithostrotion striatum* Fleming, Thomson, *Ibid.*, vol.V, pt.III, p.387, pl.XII, fig.1.

1887b *Lithostrotion flemingi* (McCoy), Thomson, *Ibid.*, vol.V, pt.III, p.389, pl.XII, fig.7.

1887b *Lithostrotion cyathophyllodia* Thomson, *Ibid.*, vol.V, pt.III, p.389, pl.XII, fig.6.

1887b *Lithostrotion dicki* Thomson, *Ibid.*, vol.V, pt.III, p.383, pl.XI, fig.2.

1887b?*Lithostrotion aranea* (McCoy), Thomson, *Ibid.*, vol.V, pt.III, p.386, pl.XI, fig.7. (Not *N. aranea* McCoy).

1887b?*Lithostrotion elegans* Thomson, *Ibid.*, vol.V, pt.III, p.388, pl.XII, fig.4.

1887b *Lithostrotion obovotum* Thomson, *Ibid.*, vol.V, pt.III, p.390, pl.XII, fig.8.

1887b *Lithostrotion ensifer* Edwards and Haime, Thomson, *Ibid.*, vol.V, pt.III, p.387, pl.XI, fig.8. (Not *L. ensifer* Edwards and Haime).

1903 *Lithostrotion basaltiforme* var. *bristoliense* Vaughan, Proc. Bristol Nat. Soc., vol.X, p.106.

1940 *Lithostrotion clavaticum* Thomson, Hill, 'Mon. Carb. Rug. Corals of Scotland', Pal. Soc., p.176, pl.IX, figs 15-21, pl.X, fig.1.

Diagnosis: Cerioid *Lithostrotion* with 20-24 septa, a columella often dilated and a tabularium with a mean diameter of 4.25 mm.

Type Material: Lhwyd's specimen is lost. Parkinson's and Conybeare and Phillips species which were based on Lhwyd's coral probably never had any type material. Hill (1940, p.160) thus interpreted the species on Fleming's specimen of *L. striatum* in the Royal Scottish Museum (Specimen no. RSM.1870.14.370) which was also based on Lhwyd's coral. This specimen was chosen by Kato (1971, p.2) as the lectotype of *L. striatum* and thus it could be considered as the type of *L. vorticale*. However, even though he chose it as lectotype, this specimen had been lost between 1940 and 1971 and so the lectotype had to be interpreted on Thomson's figure of this specimen (Thomson 1887, pl.XII, fig.1). It seems in the author's opinion that this is an unsatisfactory situation, especially as L. striatum is the genotype of Lithostrotion (although it should be known as L. vorticale) as it means that this important genus must be interpreted on a rather poor figure drawn nearly a century ago.

Two alternatives are open to rectify this situation. First, many other subsequent cerioid species have been described which are now considered synonymous with L. vorticale. Of these junior synonyms type material is available for L. portlocki, L. minus and L. flemingi and thus one could choose the type specimen of one of these synonyms as a new type for L. vorticale. L. flemingi would perhaps be the most suitable as McCoy based it on L. striatum of Fleming and so we can be sure that it is synonymous with L. vorticale of Lhwyd.

Secondly we could choose a neotype for Lhwyd's coral (and Parkinson's, Fleming's and Conybeare and Phillips). Lhwyd's coral was from Wales but from his text it is impossible to say where in Wales. However, Parkinson quotes Woodward as saying that, "the Lithostrotion is found on the rocky cliffs about two miles from Tenby towards Milford in Pembrokeshire". Hill (1940, p.166) suggests that this is probably Giltar Point, Tenby in the S2 Zone and adds, "should one need to chose a neotype for Lhwyd's coral we could be justified in taking one from Giltar Point".

I have visited Giltar Point and also the S2 exposure of Lydford Point, two miles W.S.W. along the coast, but found no cerioid Lithostrotion species at these localities; only rare colonies of L. martini.

Unless any future collector can find a cerioid specimen in this area it seems best to interpret the species L. vorticale (and hence the genus Lithostrotion) on the holotype of L. flemingi.

The holotype of L. flemingi is Sedgwick Museum, Cambridge specimen No.A2051a-e (+ slides f-k). Syntype of L. flemingi is SMA2050a, b

(+ slides c and d).

Holotype of *L. minus* is SMA2401a, b, e-h (+ slides c, d, i).

Holotype of *L. portlocki* is I.G.S. Leeds Specimen No.36898 (+ slides PF685-6).

Hill chose a neotype for *L. clavaticum* as specimen No.KM.T1017/D1.K45 in the Thomson Collection, Kelvingrove Museum, Glasgow.

Material: S2 Limestone, Ore Hill Quarry, Nateby, Cumbria; S2 Limestone, Ashfell Edge, Kirkby-Stephen, Cumbria; Beehive Limestone, Potts Beck, Orton, Cumbria; Great Scar Limestone, Hartley Quarry, Kirkby-Stephen, Cumbria; Great Scar Limestone, Aysgarth lower falls, Aysgarth, Wensleydale; Bankhouses Limestone, Tipalt Burn, Northumberland; '*Nematophyllum minus*' Beds, Brampton, Northumberland; Clattering Band, Bewcastle, Cumbria; Great Scar Limestone (S2), Horton-in-Ribblesdale; Great Scar Limestone (S2), Crummuckdale, Austwick, Yorkshire.

Description: External Characters; The corallum is massive and cerioid and can be very tall. Never depressed as in the *Orionastraea* state. The specimen from Brampton shows its distal surface to consist of deep polygonal calices with a prominent columella and a sharp dividing wall. Specimens from Ribblesdale show the sides of the polygonal columns to be ornamented with both longitudinal interseptal ridges and transverse growth bands.

Internal Characters; Major and minor septa are easily distinguishable, the major septa all extending well into the tabularium mostly about half way to the columella. Some septa, usually the cardinal and counter-cardinal septa, and maybe some other primary septa, extend all the way to the columella, but no where near so many septa reach the columella as in *L. decipiens* and *L. maccoyanum*. On the other hand, minor septa only just reach the inner row of dissepiments extending only a very short distance into the tabularium. Septa are usually quite thin but if anything are more dilated in the dissepimentarium being thinner at their axial ends. The maximum number of septa in a colony is normally between 20 and 24 but one specimen from Aysgarth has only 19 septa.

A columella is usually present but rare diphymorphs do occur. The columella may be thick and dilated as in the specimen from Brampton or quite a thin plate as in the Austwick colony. The axial end of the counter septum from which the columella was derived can usually be detected as a dark line running through the middle of the columella, with the dilated zone forming a lighter area on either side. The columella often has radiating bars running at right angles to its length which are presumably the vestigial ends of the other major septa which were joined to the columella at an earlier stage of its ontogeny.

The tabularium of this species is quite constant, normally between 3.5 mm. and 5.5 mm., with a mean of 4.25 mm., although it may be higher in occasional corallites. The dissepimentarium and hence the diameter however are much more variable. For example the specimen from Ribblesdale has a dissepimentarium only 0.8 mm. wide with just 2 - 3 rows of dissepiments and its diameter is just 5.5 mm., while a specimen from Tipalt Burn has a dissepimentarium 2.5 mm. wide with up to eight rows of dissepiments and a diameter of 9.0 mm.

Dissepiments are thus variable in number depending on the width of the dissepimentarium, but are always concave towards the centre. The inner row may be slightly dilated and are generally more vertically displaced than the outer series.

Corallites are polygonal being generally from 4 - 8 sided bounded by a double walled epithecae. This epithecae may be quite straight or as in a specimen from Brampton in a zig-zag fashion with pronounced inter-septal ridges, the septa of one corallite being in direct opposition to an inter-septal loculus of the adjacent corallite.

The tabulae are incomplete and of the α-type (p. 15). They are horizontal in the axial region and slope peripherally to rest on the tabulae beneath. A second series is then developed running to the dissepimentarium.

Discussion: Owing to the fact that Volkman, Da Costa, Fleming, Conybeare and Phillips and Parkinson all stated in their descriptions that their species was based on Lhwyd's coral it is obvious that all these species are synonymous. Moreover, this species should now be known as *L. vorticale* (Parkinson) as this was the first published name. Similarly McCoy based *S. flemingi* on *L. striatum* of Fleming and so this is also synonymous with *L. vorticale*.

Nematophyllum minus only differs from *L. vorticale* on the supposed inseparability of the corallites of *Nematophyllum*. This has been shown (p.67) to be not a worthy generic character and so *Nematophyllum* is shown to be synonymous with *Lithostrotion* (p.117). Thus *N. minus* is synonyous with *L. vorticale*.

L. portlocki (= *Astraea irregularis* Portlock, not Defrance) only differs from *Astraea hexagona* var. *minor* Portlock by the greater irregularity of the number of sides to the corallites. This is not a worthy specific character and so these two species are synonymous. Portlock states the species to have 40 septa and so they are most probably *L. vorticale*.

Vaughan considered *L. bristolense* distinct from *L. basaltiforme* (= *L. vorticale*) on its lower septal counts, but it seems that the coral that Vaughan was calling *L. basaltiforme* was in fact *L. aranea*, and so *L. bristolense* with 20-23 septa is again synonymous with *L. vorticale*.

Similarly Thomsons *L. clavaticum* has 20-24 septa and does not seem to differ significantly from *L. vorticale*.

This species can be distinguished from *L. decipiens* and *L. maccoyanum* by having 20-24 septa and from *L. aranea* which has 26 or more septa.

Statistical Results:

R. = (19)20-24

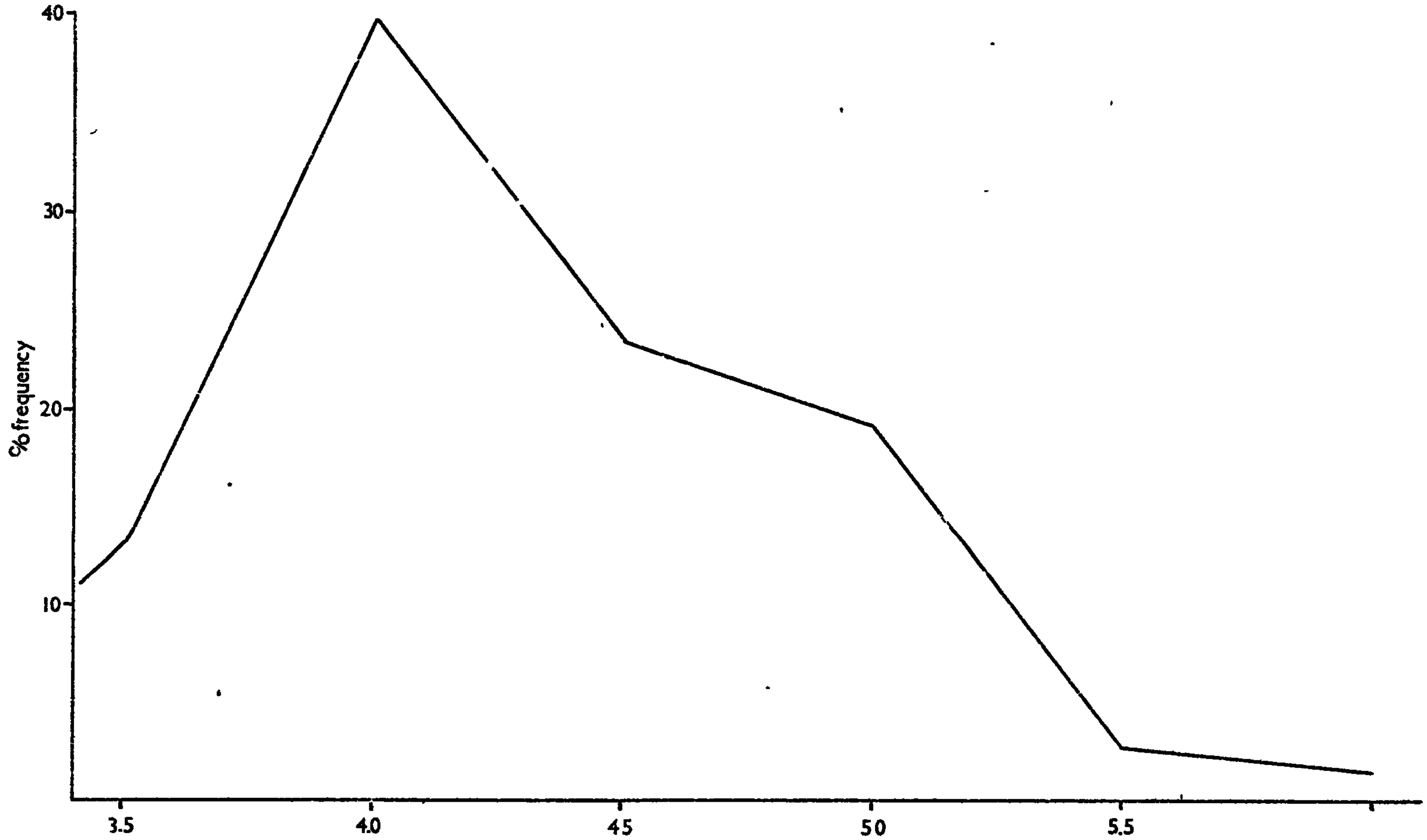
MD. = 8.27 mm.
S.D. = 1.21 mm.
max.D. = 13.2 mm.
min.D. = 5.6 mm.

MT. = 4.25 mm.
S.D. = 0.806 mm.
max.T. = 7.0 mm.
min.T. = 3.2 mm.

Stratigraphical Range: Base of S2 to base of D2 (Smiddy Limestone).

<u>FIGURE 38</u>

Plot of tabularium diameter against percentage frequency in *L.vorticale*. Intervals in mm's.



Tabularium

fig 38

Lithostrotion aranea (McCoy)
(Plates 14 - 18.)

1843 *Astraea hexagona* Portlock, 'Rep. on the Geol. of Londonderry', p.332, pl.XXIII, fig.1. (Not *C. hexagona* Goldfuss).
1843 *Astraea basaltiformis* Portlock, *Ibid.*, p.333. (Not *C. basaltiformis* Conybeare and Phillips).
1844 *Astraea aranea* McCoy, Syn, Carb. Foss. of Ireland, p.187, pl.XXVII, fig.6.
1849 *Nemaphyllum aranea* McCoy, Ann. Mag. Nat. Hist., ser.2, vol.III, p.135.
1849 *Nemaphyllum arachnoideum* McCoy, *Ibid.*, ser.2, vol.III, p.16.
1849 *Nemaphyllum septosum* McCoy, *Ibid.*, ser.2, Vol.III, p.19.
1849 *Stylaxis major* McCoy, *Ibid.*, ser.2, vol.III, p.120.
1850 *Lasmocyathus aranea* (McCoy), D'Orbigny, Prod. de Pal., vol.I, p.160.
1851 *Stylaxis arachnoidea* (McCoy), Milne-Edwards and Haime, 'Pol. Foss. des Terr. Pal.', p.454.
1851 *Lithostrotion septosum* (McCoy), Milne-Edwards and Haime, *Ibid.*, p.444.
1851 *Stylaxis major* McCoy, Milne-Edwards and Haime, *Ibid.*, p.454.
1851 *Nematophyllum arachnoideum* McCoy, 'Brit. Pal. Foss.', p.97, pl.IIIA, fig.6.
1851 *Stylaxis major* McCoy, *Ibid.*, p.101, pl.IIIA, fig.4.
1852 *Lithostrotion arachnoideum* (McCoy), Milne-Edwards and Haime, 'Mon. Brit. Foss. Corals', p.202.
1852 *Lithostrotion septosum* (McCoy), Milne-Edwards and Haime, *Ibid.*, p.196.
1852 *Lithostrotion major* (McCoy), Milne-Edwards and Haime, *Ibid.*, p.201.
1883 *Lithostrotion septosum* (McCoy), Thomson, Proc. Phil. Soc. Glasg. vol.XIV, p.400.
1930 *Lithostrotion arachnoideum* (McCoy), Hudson, Proc. Leeds Phil. Soc., vol.II, pt.II, p.97, pl.I, figs 5a, 5b.
1930 *Lithostrotion arachnoideum* var. *ischnon* Hudson, *Ibid.*, vol.II, pt.II, p.97, pl.I, fig.4.
But not:
1851 *Lithostrotion aranea* (McCoy), Milne-Edwards and Haime, 'Pol. Foss. des Terr. Pal.', p.443, which is *L. verticale*.
1852 *Lithostrotion aranea* (McCoy), Milne-Edwards and Haime, 'Mon. Brit. Foss. Corals', p.193, pl.XXXIX, figs 1, 1a, which is *L. verticale*.

Diagnosis: Large diameter cerioid *Lithostrotion* with 26-32 septa and a columella which may be dilated, thin or absent. Tabularium with a mean diameter of 6.0 mm.; dissepimentarium variable in width, but often very wide, so that corallite diameter may be up to 15 mm.

Type Material: ?Holotype of *L. aranea* is specimen nos 50-1926 and 51-1926, National Museum of Ireland, Dublin.

Holotype of L. arachnoideum is specimen no. A2400a, b, e (+ slides c, d, f, g, h, i) in Sedgwick Museum, Cambridge.

Holotype of L. major is specimen no. A2397a, c-h (+ slides b, j-k, l) in Sedgwick Museum, Cambridge.

Syntype of L. septosum is specimen no. A2907-10 in Sedgwick Museum, Cambridge.

Holotypes of L. arachnoideum var. ischnon are the specimens figured by Garwood and Goodyear, Q.J.G.S., vol.LXXX, pl.XVIII, figs 4a, 4b.

Material: Peghorn or Smiddy Limestone, Birkett Hill, Nateby, Cumbria; Great Scar Limestone (S2), Scalber Quarry, Scalber, Settle, Yorkshire; Porcellanous Limestone, Ingleton, Yorkshire; Great Scar Limestone (S2), Donks Gill, Horton-in-Ribblesdale; Timpony Limestone, Dry Gill House, Stump Cross, Pately Bridge, Yorkshire.

Description: External Characters; The corallum is massive and cerioid with corallites forming polygonal columns showing longitudinal striae and transverse growth bands. Neither the proximal or distal surfaces have been seen.

Internal Characters; Some of the major septa, usually the cardinal and counter cardinal septa, may extend to the columella, but most of them reach only about half way into the tabularium. Minor septa on the other hand only reach to the inner-most row of dissepiments only just penetrating the tabularium. All septa are usually quite thin but they may be dilated at the inner ring of dissepiments. They are thus thinner in the tabularium and in the peripheral regions of the corallites. The maximum number of septa in a colony varies from 25 to 31 but is more often from 26 - 28.

A columella is usually present. This may be thick and dilated as in the holotype of L. aranea or a thin plate-like structure as in the colony from Scalber Quarry. Diphymorphs do occur and are more common in those colonies with a weaker columella.

The tabularium of this species is quite constant, varying in adult corallites from 5.0 - 7.2 mm., with a mean of 6.0 mm., but the width of the dissepimentarium is much more variable so that the diameter of this species is also widely different in different colonies of the same species. The two end members of this wide variation in diameter are represented by the type specimens of *L. major* on the one hand and *L. aranea* on the other, which is presumably why McCoy distinguished different species. For example a corallite in the thin section cut from the type of *L. major* (A2397j-k) has a tabularium of 5.8 mm. and a dissepimentarium of only 1.75 mm. and hence a diameter of 9.3 mm., whereas a corallite from the type of *L. aranea* (50-1926) has a tabularium of 5.4 mm. but a dissepimentarium of 4.2 mm. and hence a diameter of 13.8 mm. Every intermediate diameter can be found and the tabularium and septal counts are always constant. Thus while there is a great variation in diameter, this variation is considered to be completely continuous and only one species is represented.

Dissepiments vary in number from 3 - 4 rows up to ten or more. They are always concave and the inner rows are usually dilated. In those specimens with a very large dissepimentarium (i.e. *L. aranea* S.S. and *L. arachnoideum*) the outer rows are often more obliquely inclined than the inner rows.

Corallites are polygonal and from 4 - 8 sided, bounded by a double walled epithecae.

The tabulae are incomplete and of the α type. The inner series is horizontal in the axial region and slopes peripherally to rest on the tabulae beneath. An outer series slopes downwards to the dissepimentarium.

Discussion: Four different McCoy species have been included in the synonymy of *L. aranea* and it is thus pertinent to explain here why this has been done. First, the types of *N. aranea* and *N. arachnoideum* are almost identical and it is difficult to discover why McCoy separated them in the first place. The type of L. aranea (slide 50-1926) contains very large corallites up to 12 or 15 mm. in diameter. However by far the majority of the corallite is composed of a wide dissepimentarium with up to ten rows of dissepiments. The tabularium is only 5.5 - 6.0 mm. wide supporting 26 septa.

The holotype of L. arachnoideum (slide SMA2400c) has a very different preservation but again its corallites are large (almost 15 mm.). Again the dissepimentarium is very wide having 8 - 10 rows of dissepiments and the tabularium is only 8 mm. wide. (In fact the tabularium of the holotype is the largest ever seen; in topotype material the tabularium is usually only 6.0 mm. wide, but complete gradation from 6 - 8 mm. occurs). This specimen also has 26 - 27 septa. These species only differ in the method of preservation and are quite clearly synonymous.

The synonymy of S. major and N. septosum is less obvious. Stylaxis has been shown to be synonymous with Lithostrotion (p.118). The holotype of S. major (slide SMA2397j, k) contains one corallite, only 9.5 mm. in diameter and with only four rows of dissepiments, but again its tabularium is 6 mm. wide and there are 32 septa. Every number of septa between 26 and 32 has been found both low and high counts occurring in both large and small corallites. S. major differs therefore from N. aranea by being much smaller in diameter and the two species do at first sight appear to be quite different. However both the small S. major and the larger N. aranea have similar septal counts and tabularium diameters; the only difference is thus the width of the dissepimentarium and moreover every intermediate dissepimentarium between S. major and N. aranea has been found, and thus the variation between these two forms is continuous and they represent end members of the same variable species.

The syntype of L. septosum (slide SMA2908b) shows one corallite of 10 mm. diameter, with a tabularium of 6 mm. and 26 septa. Its only difference to L. major is that the septa do not reach quite so far to the centre of the corallite, but this is not regarded as being a suffiently important character to warrant its separation from L. major and so it is also synonymous to L. aranea.

Portlock in 1843 described Astraea hexagona which has 60 septa (in total) and so this is also probably L. aranea.

The first published of these names was N. aranea as Astraea aranea in 1844 by McCoy and this name therefore has priority and so the species must be known by this name. This may cause some confusion as unfortunately Edwards and Haime (1851, 1852) in describing what they considered to be L. aranea were in fact describing the smaller species L. vorticale. Most authors have followed Edwards and Haime thus applying the name L. aranea to the smaller species and so most references in the literature to L. aranea in fact refer to L. vorticale. However, we must interpret L. aranea on its type specimen in the National Museum of Ireland and not on the description by Edwards and Haime. We have no alternative but to apply the law of priority and use L. aranea as the first published name for the larger species in place of the more widely used and better understood name of L. arachnoideum which was used by Edwards and Haime, but was not published until 1849.

The use of L. aranea is doubly unfortunate as the very large type of corallites that occur in the type specimen of L. aranea are considered by the author to be an 'abnormal' state of development as these very large corallites are only found in favourable areas for coral growth, close to the reefs. The smaller 'L. major' type of corallite is more common and represents a more 'normal' condition of the species. This means that the holotype is not a 'normal' example of the species as is insisted by the nomenclatorial rules. However, nothing can be done to rectify this situation other than notification of the problem.

It should be emphasised that this species cannot be distinguished from other cerioid species by its diameter (fig. 40). Smaller examples of L. aranea (i.e. those described by McCoy as L. major and distinguished from his L. aranea by this smaller size) may be smaller than large examples of L. vorticale, only septal counts are exclusively different. This species can be distinguished from all other cerioid species by its high number of septa.

Statistical Results:

R. = (25) 26 - 32

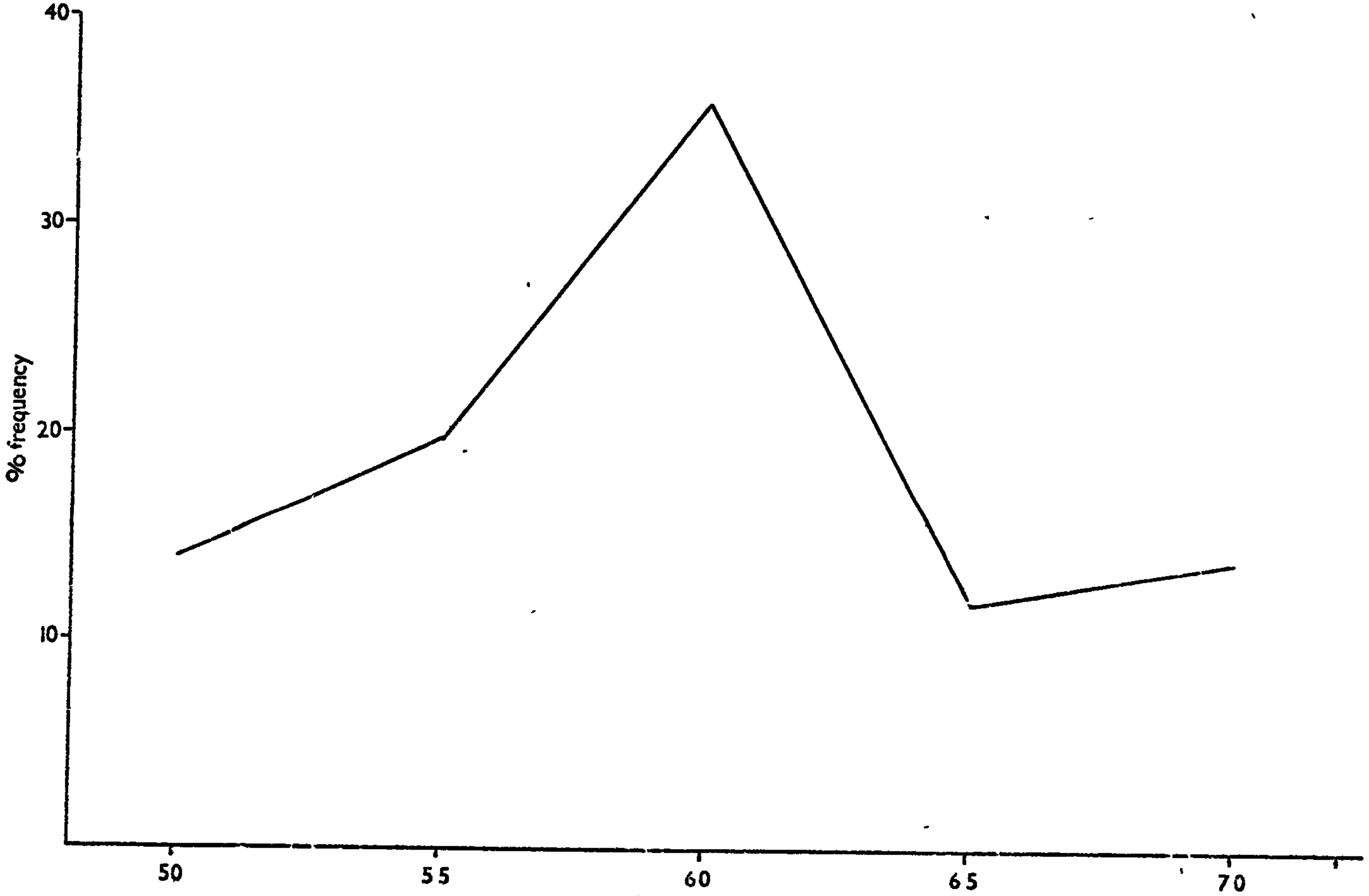
MD. = 13.96 mm.
S.D. = 2.38 mm.
max.D. = 20.4 mm.
min. D.= 9.8 mm.

MT. = 6.01 mm.
S.D. = 0.69 mm.
max.T. = 7.2 mm.
min.T. = 4.9 mm.

Stratigraphical Range: Base of S2 to base of D2 (Smiddy Limestone).

FIGURE 39

Plot of tabularium diameter against percentage frequency in L.aranea. Intervals in mm's.



Tabularium
fig 39

FIGURE 40

Diagrammatic illustration of the continuous variation in diameter between the four cerioid species.

1a. Small example of L.maccoyanum with narrow dissepimentarium.

1b. Large example of L.maccoyanum with wide dissepimentarium.

2a. Small example of L.decipiens (same size as '1b').
This type was distinguished as Stylaxis irregularis by McCoy and L.derbiense by Edwards and Haime.

2b. Normal example of L.decipiens.

2c. Large example of L.decipiens. (same size as 3a).

3a. Small example of L.vorticale.

3b. Large example of L.vorticale. (same size as 4a).

4a. Small example of L.aranea. This type was distinguished as L.major by McCoy.

4b. Large example of L.aranea.

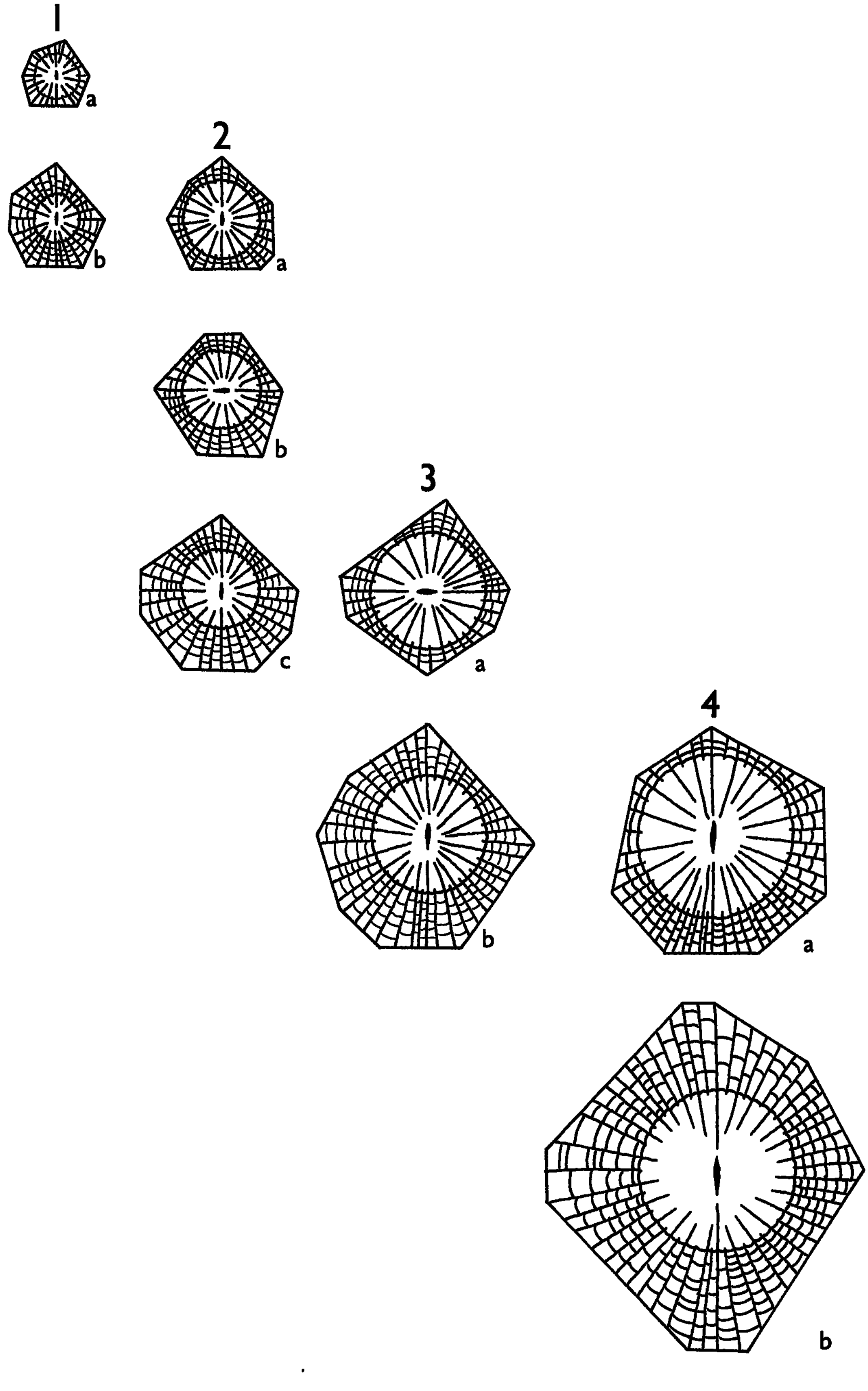


fig 40

Note on the Cerioid species of *Lithostrotion*

Many names have been proposed in the past for the cerioid *Lithostrotion* species, most species being erected on characters not now regarded as specifically important. Some of these names have lapsed while others, rightly or wrongly, have become common place. Much of the muddle has resulted from species being published on the basis of diameter of the corallite. It has been observed that this is a poor character to use as it is dependent on the width of the dissepimentarium, a character which can vary greatly in one species. Moreover, a more favourable and less variable character is the diameter of the tabularium, and using this character only four well defined and separate types of cerioid species can be recognised. Allied to these four sizes of tabularium are septal counts which again fall into four groups and correspond exactly to those groups determined by the tabularium. The four valid cerioid species are *L. maccoyanum*, *L. decipiens*, *L. vorticale* and *L. aranea*.

Thus we are led to the unfortunate conclusion that several of the better known names for the cerioid species of *Lithostrotion* must be allowed to lapse, while other less well known names must be revived. The invalid, but well known names seem to have stuck as later authors have applied these different names to specimens from certain regions of the country, usually the regions from which the species was first described. Thus any cerioid *Lithostrotion* with 20 - 24 septa found in Scotland has been called *L. clavaticum* after Thomson, while the same form from Bristol has been repeatedly called *L. bristoliense* after Vaughan, etc.

On the other hand the valid, but little known names of *L. vorticale*, *L. decipiens* and *L. aranea* were allowed to lapse due to errors of identification by Edwards and Haime whose work most later authors have followed. For example Edwards and Haime, in their revision of *L. striatum*, were aware that Parkinson had described the species, but in their work (1851, p.441; 1852, p.190) referred only to Parkinson's figure where he merely labelled it as '*Lithostrotion*'. They did not refer to his text where he gave it the name of *M. vorticalis* and were thus unaware of this name. Thus, thinking they were exercising the Rules, they called the species by the next published name of *L. basaltiforme* by Conybeare and Phillips, and it is thus this name, not *L. vorticale*, that has been used by later authors.

In the case of *L. aranea* Edwards and Haime were under the misapprehension that this species was a small form with only 24 septa and they therefore considered it to be synonymous with *L. vorticale*. Thus they called the larger species with 27 septa by the next published name of *L. arachnoideum* which has been used by later authors. However examination of the type of *L. aranea* shows it to be synonymous with *L. arachnoideum* and *L. aranea* being the first published name has precedence.

Finally with *L. decipiens* Edwards and Haime were again under a misapprehension that this species was synonymous with *L. portlocki*, and they therefore used the name of *L. portlocki* for this species as it was the first published name. However examination of the type of *L. portlocki* shows it to be a larger form than *L. decipiens* and the name should therefore not be used for this species.

It is hoped that by applying the Rules of Nemenclature strictly now, the species of *Lithostrotion* will be better defined and thus will lead to less misunderstanding in the future.

Lithostrotion junceum junceum (Fleming)

(Plate 19.)

1793 *Junci lapidei* Ure, 'Carb. Rutherglen Lanarkshire', p.327, pl.xix, fig.12.

1828 *Caryophyllia juncea* Fleming, 'Hist. Brit. Anim.', p.508.

1830 *Caryophyllia juncea* Fleming, Woodward, Syn. Table of Brit. Org. Rem., p.6.

1834 *Lithodendron junceum* (Fleming), Keferstein, Nat. der Erdkorp., vol.ii, p.785.

1836 *Lithodendron sexdecimale* Phillips, 'Geol. of Yorks.', p.202, pl.ii, figs 11-13.

1842 *Caryophyllia sexdecimalis* (Phillips), De Koninck, Foss. des Terr. Carb. de Belg., p.17, pl.D, fig.4.

1843 *Lithodendron* (*Calamophyllia*) *coarctatum* Portlock, 'Geol. Rep. Lond. Tyrone', p.335, pl.xxii, fig.5.

1843 *Cladocora sexdecimalis* (Phillips), Morris, Cat. of Brit. Foss., p.33.

1844 *Lithodendron sexdecimale* Phillips, McCoy, Syn. Carb. Foss. of Ireland, p.188.

1844 *Lithodendron coarctatum* Portlock, McCoy, *Ibid.*, p.189.

1845 *Cladocora sexdecimalis* (Phillips), Geinitz, Grund. der Vert., p.570.

1850 *Diphyphyllum sexdecimale* (Phillips), D'Orbigny, Prod. de Palaeont., vol.1, p.159.

1851 *Siphonodendron sexdecimale* (Phillips), McCoy, 'Brit. Pal. Foss.', p.109.

1851 *Lithostrotion junceum* (Fleming), Milne-Edwards and Haime, Pol. Foss. des Terr. Palaeoz., p.435.

1852 *Lithostrotion junceum* (Fleming), Milne-Edwards and Haime, Mon. of Brit. Foss. Corals, p.196, pl.xl, fig.1.

1876 *Lithostrotion junceum* (Fleming), Thomson and Nicholson, Ann. Mag. Nat. Hist., ser.4, vol.xvii, No.4, p.   , pl.xv, figs 4-4b.

1883 *Lithostrotion junceum* (Fleming), Thomson, Proc. R. Phil. Soc. Glasg., vol.xiv, p.403, pl.viii, figs 4, 4a.

1887b *Lithostrotion junceum* (Fleming), Thomson, Trans. Edinb. Geol. Soc., vol.v, p.393, pl.xiii, figs 1, 1b.

1887b *Lithostrotion junceum* var. *intermedium* Thomson, *Ibid.*, vol.v, p.394, pl.xiii, fig.2.

1887b *Lithostrotion simplex* Thomson, *Ibid.*, vol.v, p.395, pl.xiii, figs 3, 3a.

1920 *Lithostrotion junceum* (Fleming), Smith, J. Proc. R. Soc. N.S.W., p159.

1940 *Lithostrotion junceum* (Fleming), Hill, 'Mon. Carb. Rug. Scotland' Pal. Soc., p.171, pl.ix, figs 3-8.

1971 *Kwangsiphyllum junceum* (Fleming), Kato, 'Trans. Proc. Palaeont. Soc. Japan, N.S., No.81, p.7.

Diagnosis: Columellate fasciculate *Lithostrotion* with no dissepiments, slender corallites with a mean diameter of 2.3 mm., only 14 - 20 major septa and minor septa rudimentary or absent.

Type Material: Hill (1940) stated that both Fleming's and Ure's specimens were lost. However Kato (1971) found Ure's specimen of *Junci lapidei* in the Hunterian Museum, Glasgow and chose it as lectotype of the species. This specimen consisted of three boxes containing fragmented corallites of *L. junceum* and other species of *Lithostrotion*. I have now sorted the corallites, removing all pieces that are not *L. junceum* and have had the boxes registered with the Hunterian Museum. The box bearing the registration number HMC 7630a is here chosen as lectotype of the species. Two sections, one transverse and one longitudinal have been cut from a corallite from this box and are numbered HMC 7630b and HMC 7630c.

The type of *L. sexdecimale* Phillips is lost.

The type of *L. coarctatum* Portlock is I.G.S. Leeds specimen No.38539 and 38539a (and slides PF. 1915-6). Portlock Collection.

Material: Melmerby Scar Limestone, Dolfkirk Crag, Murton, Appleby, Cumbria; Melmerby Scar Limestone, Middletongue Crag, Murton, Appleby; Great Scar Limestone, Hartley Quarry, Kirkby Stephen, Cumbria; Great Scar Limestone, High Out Wood, Kirkby Stephen; Great Scar Limestone, Lead Mine Tips, Ladthwaite Bottom, Birkett, Kirkby Stephen; Robinson Limestone, Birkett Hill, Nateby, Kirkby Stephen; Peghorn Limestone, Low Whiterigg, Clouds, Kirkby Stephen; Smiddy Limestone, Fell End, Clouds, Kirkby Stephen; Lower Little Limestone, Cloud Gill, Kirkby Stephen; Jew Limestone, Cloud Gill, Kirkby Stephen; Great Scar Limestone, Brough, Cumbria; Great Scar Limestone, Aysgarth lower falls, Aysgarth, Wensleydale; Hawes Limestone, Hawes/Hardraw road, Wensleydale; Hardraw Scar Limestone, Hawbank, Woodhall, Wensleydale; Simonstone Limestone, Hawbank, Woodhall; Hardraw Scar Limestone, Mill Gill, Askrigg, Wensleydale; Simonstone Limestone, Mill Gill, Askrigg; Middle Limestone, Mill Gill, Askrigg; Middle Limestone, Sar Gill Grange, Wensleydale; Peghorn Limestone, Knock Swindale Beck, Moor House Reserve, Upper Teesdale; Lower Little Limestone, Knock Swindale Beck, Moor House Reserve; Lower Little

Limestone, Rowantree Sike, Moor House Reserve; Jew Limestone, Swindale Beck, Moor House Reserve; Jew Limestone, Rowantree Sike, Moor House Reserve; Bankhouses Limestone, Tipalt Burn, Northumberland; Tyne Bottom Limestone, Tipalt Burn, Greenhead, Northumberland; Tyne Bottom Limestone, N.W. Carrow Farm, Newbrough, Northumberland; Cockle Shell Limestone, High Old Shield, Roman Wall District, Northumberland; Five Yard Limestone, Moss Kennels Quarry, Housesteads, Northumberland; Shale above Five Yard Limestone, Rookhope Borehole, Weardale; Coldstones Limestone, Coldstone Quarry, Pateley Bridge, Yorkshire.

Description: External Characters; The corallum is fasciculate and usually phaceloid, corallites growing parallel and close together. The epithecae may be smooth or show transverse growth markings or be longitudinally striated.

Internal Characters; The mean adult diameter of this species is 2.3 mm. and this is the smallest columellate fasciculate species known in the genus *Lithostrotion*. The mean diameter for different coralla varies from 1.8 mm. to 3.3 mm., but it is usually between 2.0 and 3.0 mm. Dissepiments are completely absent and so the diameter also corresponds to the tabularium.

In some coralla the septa are divided into two orders, major and minor, and the minor septa can be quite strong. In other coralla minor septa are completely absent. However a majority of the colonies contain some corallites with minor septa and other corallites without such structures. The major septa are of variable length even in one corallum. They may all extend to the axis or they may extend only $\frac{1}{2}$ or 2/3 the radius of the corallite. In these cases the axial ends of the major septa usually abut onto the downturned edge of a tabulae. Minor septa when developed are very short, only 1/5 the radius of the corallite. Major septa vary in number from 14 - 20.

A columella is usually present, elongated in the cardinal plane, but diphymorphs may occur. The columella is often quite strong, being dilated, and sometimes bears transverse bars which may join with the ends of the major septa.

The tabulae are usually entire and tent-shaped. They rise steeply to meet the columella, are sub-horizontal in the axial region of the corallite and fall sharply at the periphery where they abut on to the epithecae. Occasionally they are not entire, but rest on the tabulae beneath.

Lithostrotion junceum communicatum subsp. nov.
(Plate 19, fig. 7.)

Diagnosis: Lithostrotion junceum with transverse cylindrical connecting processes between adjacent corallites of the corallum.

Type Material: Holotype is specimen No. P.6529 in the Palaeontological Collection, Dept. of Geological Sciences, University of Durham. From the Scar Limestone, Middletongue Beck, Great Dun Fell, Cumbria.

Material: Scar Limestone, Middletongue Beck, Great Dun Fell, Cumbria; Scar Limestone, Mattergill Sike, Moor House Reserve, Upper Teesdale.

Description: As for L. junceum junceum except that the corallites are temporarily connected to one another by hollow transverse connecting processes.

Discussion of L. j. junceum and L. j. communicatum: Although Ure's name predates Flemings the term 'Junci' in Ure's name is in effect the trivial name of his binomial combination and so Fleming's name is acceptable.

All the characters of L. junceum are very variable. Hill (1940, p.173) states that the variables are, "the form of the corallum (irregularity and regularity of growth), size of corallite (2.5 - 3.8 mm. in diameter), ornament of epithecae (presence or absence of longitudinal striation), presence or absence of rudimentary minor septa, and the degree of development of the diphyphylloid trend ...". Many previous workers have split L. junceum into various sub-species based on these variables. Thus Thomson split the species on the basis of degree of development of the diphyphylloid trend and Birkhill (1963, unpublished thesis) split the species on the presence or absence of minor septa and other characters. These sub-divisions do not seem to have been generally followed and there are two reasons for this. First the variation between all these characters is continuous and no satisfactory dividing line can be drawn, and secondly as Hill points out, "none of these variables has any recognisable stratigraphical significance". Thus they are not recognised in this thesis.

It seems that the only variable with which a firm dividing line can be drawn is the presence or absence of the transverse connecting processes. This also seems to be a very important character as its presence indicates a much higher level of colonial integration (p.67). Thirdly the coralla possessing such structures may be stratigraphically useful as they appear to be restricted to the Scar Limestone, although more collecting is needed to verify this. Thus those coralla possessing transverse connecting processes are here recognised as a separate sub-species from the main L. junceum population.

Note on 'Lithostrotion junceum bigenerum' Birkhill M.S.

In addition to the fasciculate species described here one further species has been described by Birkhill (1963, unpublished thesis) as Lithostrotion junceum bigenerum. This sub-species is intermediate in diameter between L. pauciradiale and L. junceum and it has 14 septa (as in L. junceum) and a single row of dissepiments (as in L. pauciradiale) although these are inconsistant. The species is unpublished and therefore unavailable. More material is needed before it can be published, but it probably represents an intermediate species between L. pauciradiale and L. junceum (so that L. pauciradiale evolves to 'L. bigenerum' and 'L. bigenerum' evolves to L. junceum, rather than L. pauciradiale evolving directly to L. junceum). Moreover it is of similar dimensions to L. maccoyanum and may be the fasciculate ancestor of that cerioid species (see p. 26), both species possessing 14 septa.

If L. variabile, L. irregulare and L. pauciradiale do represent a continuous interbreeding series, and thus are only morpho-species, then 'L. bigenerum' probably is a smaller end member of this series rather than a subspecies of L. junceum which should have no dissepiments.

Lithostrotion pauciradiale (McCoy)

(Plate 20.)

1844 *Lithodendron pauciradialis* McCoy, Syn. Carb. Foss. Ireland, p.189, pl.XVIII, fig.7.
1849 *Siphonodendron pauciradiale* (McCoy), Ann. Mag. Nat. Hist., ser.2, vol.III, p.135.
1850 *Diphyphyllum pauciradiale* (McCoy), D'Orbigny, Prod. de Palaeont., vol.1, p.159.
1851 *Siphonodendron aggregatum* McCoy, 'Brit. Pal. Foss.', p.108, (*nom. nov.* for *S. pauciradiale*).
1851 *Lithostrotion pauciradiale* (McCoy), Milne-Edwards and Haime, 'Pal. Foss. des Terr. Palaeoz.', p.436.
1883 *Lithostrotion sp.* Thompson, Proc. Phil. Soc. Glasgow, vol.XIV, p.403.
1920 *Lithostrotion irregulare* (Phillips), Smith, J. Proc. Roy. Soc. New South Wales, vol.liv, p.59 (Non *L. irregulare* Phillips).
1935 *Lithostrotion carpathicum* Heritsch, Vestn. geol. Ust. csl., vol.X, p.142.
1937 *Lithostrotion irregulare* var. *asiatica* Yabe and Hayasaka, Yu, Acad. Sinica, Mem. Nat. Res. Inst. Geol., vol.XVI, pl.IX, figs 4a-b.
1940 *Lithostrotion pauciradiale* (McCoy), Hill, *partim*, 'Mon. Carb. Rug. Corals Scotland', p.169, pl.IX, figs 1, 2 (Non *L. irregulare* Phillips).

Diagnosis: Columellate fasciculate *Lithostrotion* with one row of dissepiments, corallites 3.0 - 3.5 mm. (4.0 mm.) in diameter with 17 - 20 septa and a tabularium 2.5 mm. wide.

Type Material: Lectotype is specimen No.53-1926 in the Griffith Collection in the National Museum of Ireland, Dublin. From lower limestone of Magheramore, Tobercurry, Co. Sligo.

Material: Hardraw Scar Limestone, West House, Hawes, Wensleydale; Hardraw Scar Limestone, Semer Water, Wensleydale; Hardraw Scar Limestone, Mill Gill, Askrigg, Wensleydale; Tyne Bottom Limestone, Dogen Hill, Moor House Reserve, Upper Teesdale; Jew Limestone, Tepper Moor Burn, Newbrough, Northumberland; Fell Top Limestone, (= Harlow Hill Limestone), Harlow Hill, Northumberland.

Description: Internal Characters; The mean adult diameter of this species is only 3.3 mm., but the range of adult diameter may be up to 4.0 mm. although it is only the occasional corallite that reaches this larger size. The maximum number of septa counted in a colony varies from 18 - 20 of both orders, there never being over 20 septa. Some of the major septa are long extending to the columella, this is usually true of the cardinal and counter septa and often some of the other primary septa. Other major septa are shorter either extending only ½ way to the axis or abutting onto the adjacent major septa. Minor septa are short only just penetrating the tabularium. Both orders of septa may be slightly dilated in the dissepimentarium although this is not marked.

A columella is usually present although diphymorphs do occur. This columella may be very thickened as in the colony from Dogen Hill when it also has radiating bars corresponding to the ends of major septa, or it may just consist of a thin plate as in the lectotype. Usually the columella seems to be more dilated when a lot of the major septa are connected to it.

There is never more than one complete row of dissepiments although two or three rows may be developed in parts of a corallite or in the occasional interseptal loculus. Those colonies that are partly cerioid in habit show this addition of dissepiments in the parts of the corallite that are connected to their adjacent corallite. The single row of dissepiments is usually dilated to some extent and forms quite a regular inner circle, being concave inwards. The dissepimentarium is usually only 0.5 mm. wide and so the tabularium is only slightly smaller than the total diameter. The mean tabularium of this species is thus 2.6 mm. although it may occasionally rise to 3.2 mm.

This species having a constant number of dissepiments and hence a constant dissepimentarium has also quite a constant diameter unlike those larger species with a more variable dissepimentarium.

The corallites are bounded by a variable ~~epitheca,~~ which may be smooth or longitudinally striated with septal grooves and ridges which in transverse section has a wavy appearance.

The tabulae are quite simple and they are often entire. They are normally horizontal in the axial region and slope peripherally to the dissepiments or rest on the tabulae beneath.

Discussion: See p.161.

Statistical Results:

R - 18 - 20

MD. = 3.34 mm.
S.D. = 0.506 mm.
max.D. = 4.2 mm.
min.D. = 2.1 mm.

MT. = 2.652 mm.
S.D. = 0.367 mm.
max.T. = 3.2 mm.
min.T. = 1.9 mm.

Stratigraphical Range: Base of D1 to Tyne Bottom Limestone. Reappears in the Botany Limestone after being absent in the intervening strata.

FIGURE 41

Plot of tabularium diameter against percentage frequency in *L.pauciradiale*. Intervals in mm's.

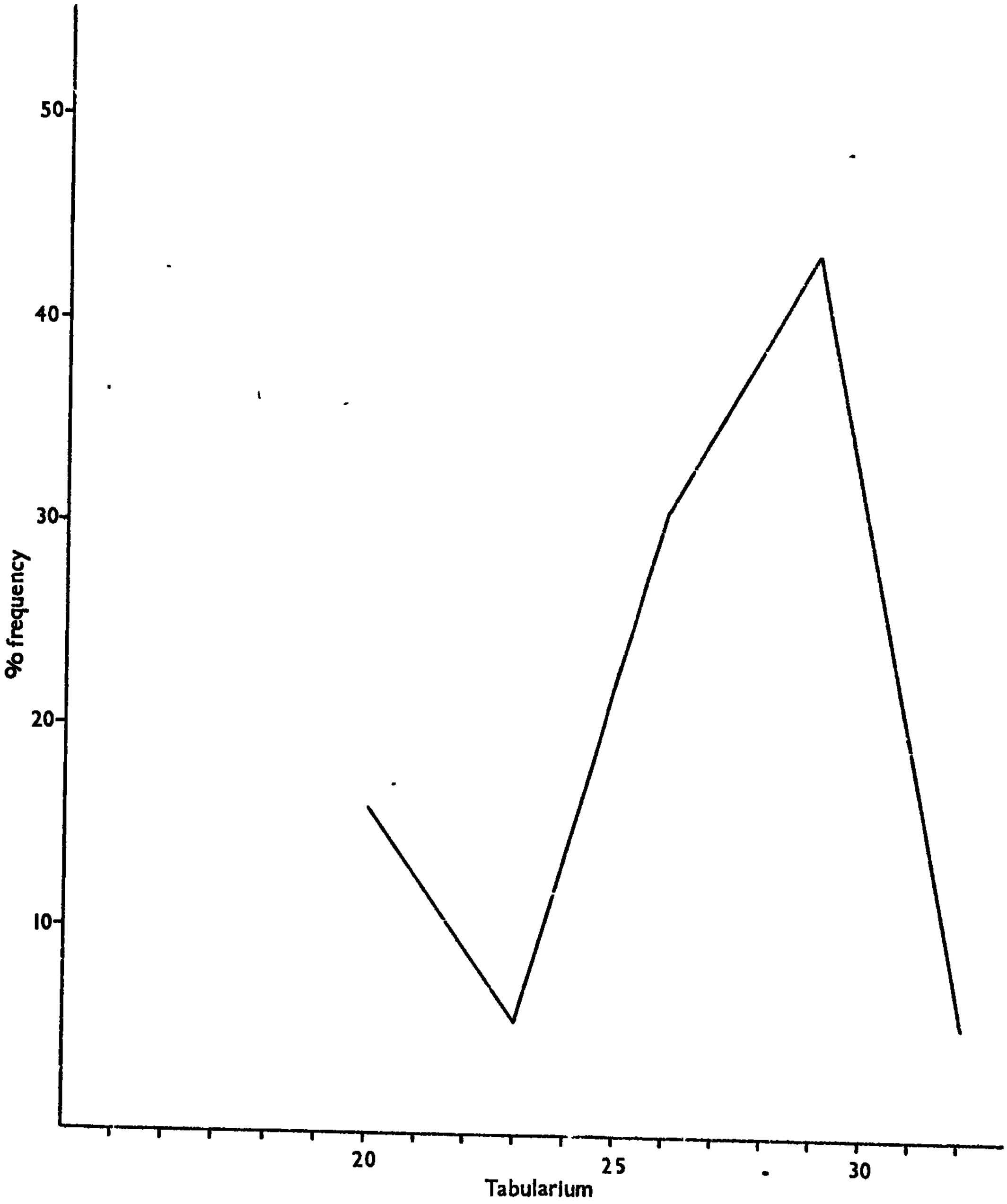


fig 41

FIGURE 42

Plot of corallite diameter against percentage frequency in L.pauciradiale. Intervals in mm's.

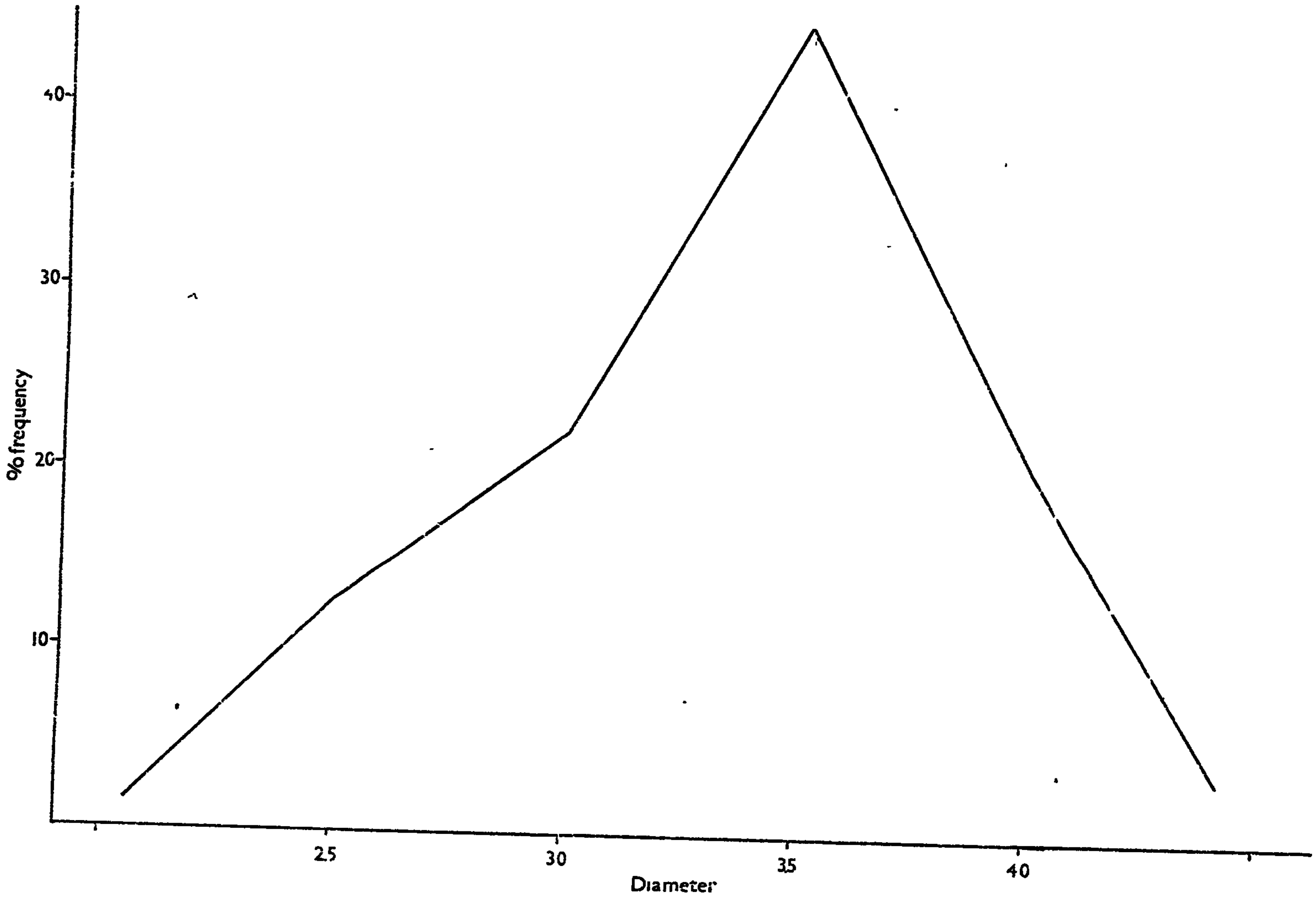


fig 42

Lithostrotion irregulare (Phillips)

(Plate 21 and 22.)

1686 'Screw Stone' Plot, 'Nat. Hist. of Staffordshire', p.195, pl.XII, fig.5.

1830 *Caryophyllia fasciculata* Fleming, De Blainville, Dict. Sc. Nat., vol.ix, p.311 (Non *C. fasciculata* Fleming).

1830 *Caryophyllia fasciculata* Fleming, Woodward, Syn. Tab. Brit. Org. Rem., p.6 (Non *C. fasciculata* Fleming).

1836 *Lithodendron irregulare* Phillips, 'Geol. of Yorkshire', vol.II, p.202, pl.II, figs 14, 15.

1843 *Lithodendron irregulare* (Phillips), Castelnau, Essai Syst. Sil. de l'Am. sept., p.49, pl.23, fig.1.

1843 *Cladocora irregularis* (Phillips), Morris, Cat. of Brit. Foss., p.33.

1843 *Lithodendron irregulare* Phillips, Portlock, 'Rep. on Londonderry', p.336.

1850 *Diphyphyllum irregulare* (Phillips), D'Orbigny, Prod. de Palaeont., vol.1, p.159.

1851 *Siphonodendron fasciculatum* (Fleming), McCoy, 'Brit. Pal. Foss.', p.108 (Non *C. fasciculata* Fleming).

1851 *Lithostrotion irregulare* (Phillips), Edwards and Haime, 'Pol. Foss. des Terr. Pal.', p.436.

1852 *Lithostrotion irregulare* (Phillips), Edwards and Haime, *partim*, 'Mon. Brit. Foss. Corals', p.198, pl.XI, figs 1a-e (Non *L. pauciradiale* McCoy).

1876 *Lithostrotion irregulare* (Phillips), Thompson, Ann. Mag. Nat. Hist., ser.4, vol.XVII, p.304, pl.XV, fig.3.

1883 *Lithostrotion irregulare* (Phillips), Thompson, Proc. Phil. Soc. Glasgow, vol.XIV, p.404.

1887b *Lithostrotion irregulare* (Phillips), Thompson, Trans. Edin. Geol. Soc., vol.V, p.393, pl.XIII, fig.4.

1920 *Lithostrotion irregulare* large variety Smith, J. Proc. Roy. Soc. N.S.W., vol.liv, p.61 (Non *L. irregulare* Smith, p.59).

1937 *Lithostrotion irregulare* (Phillips), Yu, Acad. Sinica, Mem. Nat. Res. Inst. Geol., vol.XVI, p.38, pl.VIII, figs 5, 6, pl.IX, figs 1-3.

1940 *Lithostrotion pauciradiale* (McCoy), Hill, *partim*, 'Mon. Carb. Rug. Corals Scotland', Pal. Soc., p.169 (Not pl.IX, figs 1, 2. See discussion).

Diagnosis: Columellate fasciculate *Lithostrotion* with one row of dissepiments, corallites normally 4.5 - 6.0 mm. in diameter, 21 - 26 septa, and a tabularium normally 4 - 5 mm. wide.

Type Material: Phillips specimens are lost. He gives his type localities as 'Ash Fell' (in Cumbria) and the rather vague locality of 'Northumberland'.

Ash Fell must be ignored as a type locality as this outcrop is in the S Zone and the species does not evolve until the D Zone (Phillips specimen from this locality was a stunted corallite of L. martini (see p.187).

If a neotype is required it can therefore be taken from any locality in Northumberland.

Material: Potts Beck Limestone, Potts Beck, Orton, Cumbria; Moulds Meaburn Limestone, Orton, Cumbria; Great Scar Limestone, Brough, Cumbria; Great Scar Limestone, Birkett Hill, Nateby, Kirkby Stephen; Peghorn Limestone, Birkett Hill, Nateby, Kirkby Stephen; Robinson Limestone, Clouds Gill, Kirkby Stephen; Peghorn Limestone, Low Whiterigg, Clouds, Kirkby Stephen; Great Scar Limestone, Aysgarth lower falls, Aysgarth, Wensleydale; Hardraw Scar Limestone, Friar's Intake, Swaledale; Simonstone Limestone, Cow Pasture Wood, Whernside, Kettlewell, Wharfedale; Bankhouses Limestone, Low Tipalt, Greenhead, Northumberland; Bankhouses Limestone, Dovey Scar, Greenhead, Northumberland; Bankhouses Limestone, Bonnyrigg Quarry, Housesteads, Northumberland; Peghorn Limestone, Knock Ore Gill, Moor House Reserve, Upper Teesdale; Lower Little Limestone, Swindale Beck, Moor House Reserve; Jew Limestone, Rowantree Sike, Moor House Reserve.

Description: Internal Characters; The mean adult diameter of this species is 4.9 mm., but the mean diameter of different coralla can range from 4.0 mm. up to 6.0 mm. The very smallest members of this species are quite rare, but it will be seen that they do grade into L. pauciradiale. However, if the two species cannot be distinguished on diameter they can be separated on septal number whether this is an arbitrary or a natural division. The maximum number of septa in any colony of L. irregulare is always above 20 and ranges from 21 - 24 and occasionally to 26. The attitude of the septa in this species is similar to L. pauciradiale, usually the cardinal and counter septa extend to the columella while the others usually only extend half way to the axis or abut on to the neighbouring major septa. Minor septa just penetrate the tabularium. Both orders of septa are slightly dilated in the dissepimentarium.

The columella shows the same variation as does L. pauciradiale and diphymorphs may occur, but are rare.

Only one series of dissepiments is developed around the entire margin of the corallites but two or more series may be developed in parts of corallites especially when the colony is partly cerioid. These dissepiments are sometimes dilated and when this dilation is marked it fuses with the dilation of the septa in the dissepimentarium. The dissepiments are quite vertically displaced and form a regular inner ring being concave inwards. The dissepimentarium is narrow and the tabularium therefore comprises the greater portion of the corallite. The mean tabularium of the entire species is thus 4.2 mm., although in different coralla this figure ranges from 3.5 mm. to 5.5 mm.

The tabulae change as the species evolves. Initially the tabulae are similar to the ancestral species, L. martini and L. variabile, i.e. they are tent-shaped, rising at the axis, then horizontal outside of this and sloping peripherally to rest on the tabulae beneath. As the tabulae are incomplete a second outer series is developed, which are more horizontal. The tabulae are of the α type (p. 15), when the points of contact of the tabulae onto the tabulae beneath are not vertically aligned. As the species evolves those points of contact gradually become more aligned until a pseudo-aulos (p. 13) is formed, when the tabulae become of the β type. The inner tabulae are then very arched distally and the outer series more horizontal.

Discussion: See p.161.

Statistical Results:

R. = 21 - 26

M.D. = 4.918 mm.
S.D. = 0.786 mm.
max.D. = 8.0 mm.
min.D. = 3.1 mm.

M.T. = 4.211 mm.
S.D. = 0.512 mm.
max.T. = 6.1 mm.
min.T. = 2.4 mm.

Stratigraphical Range: Top of S2 or base of D1 to the Tyne Bottom Limestone.

FIGURE 43

Plot of tabularium diameter against percentage frequency in L.*irregulare*. Intervals in mm's.

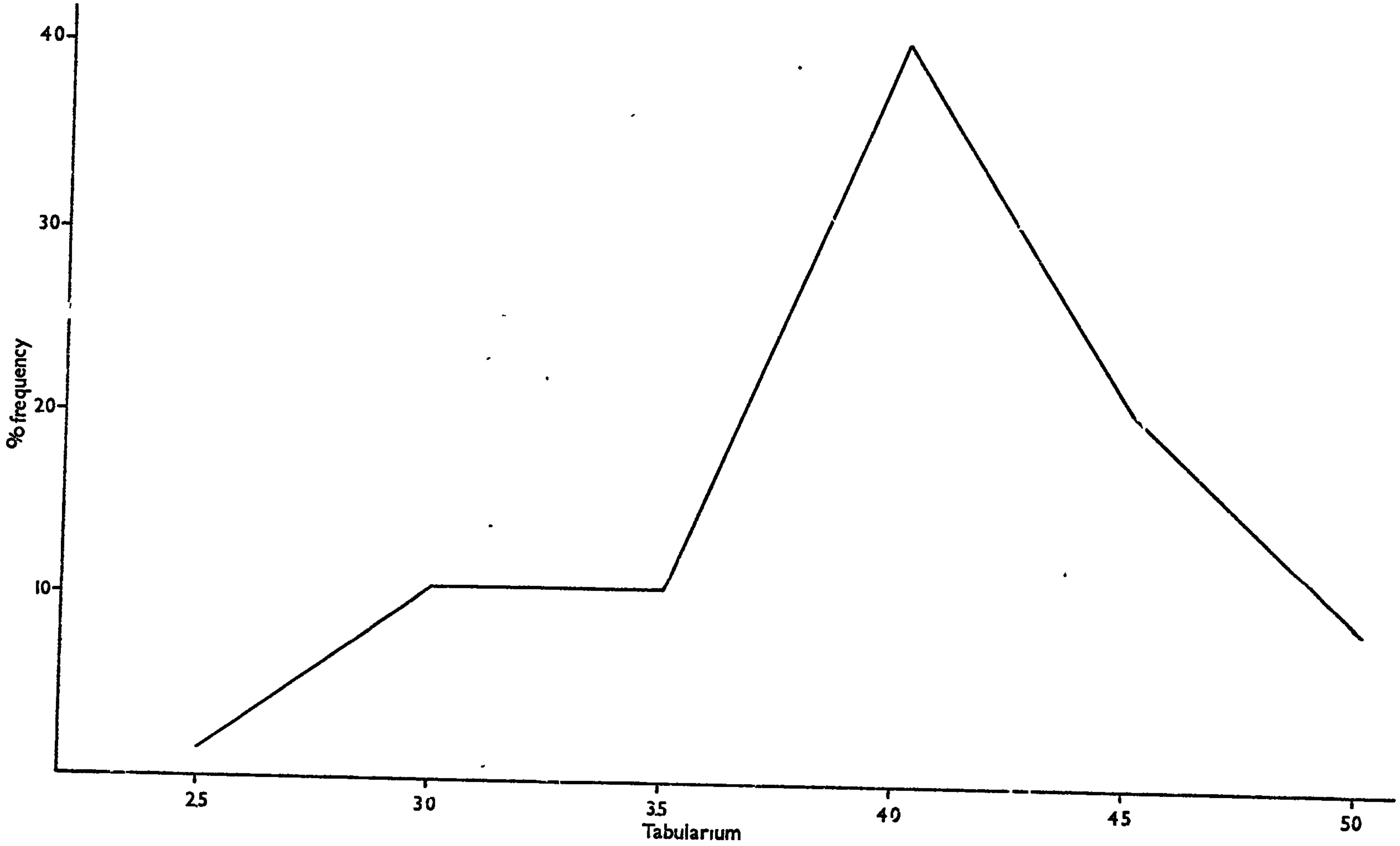


fig 43

FIGURE 44

Plot of corallite diameter against percentage frequency in *L. irregulare*. Intervals in mm's.

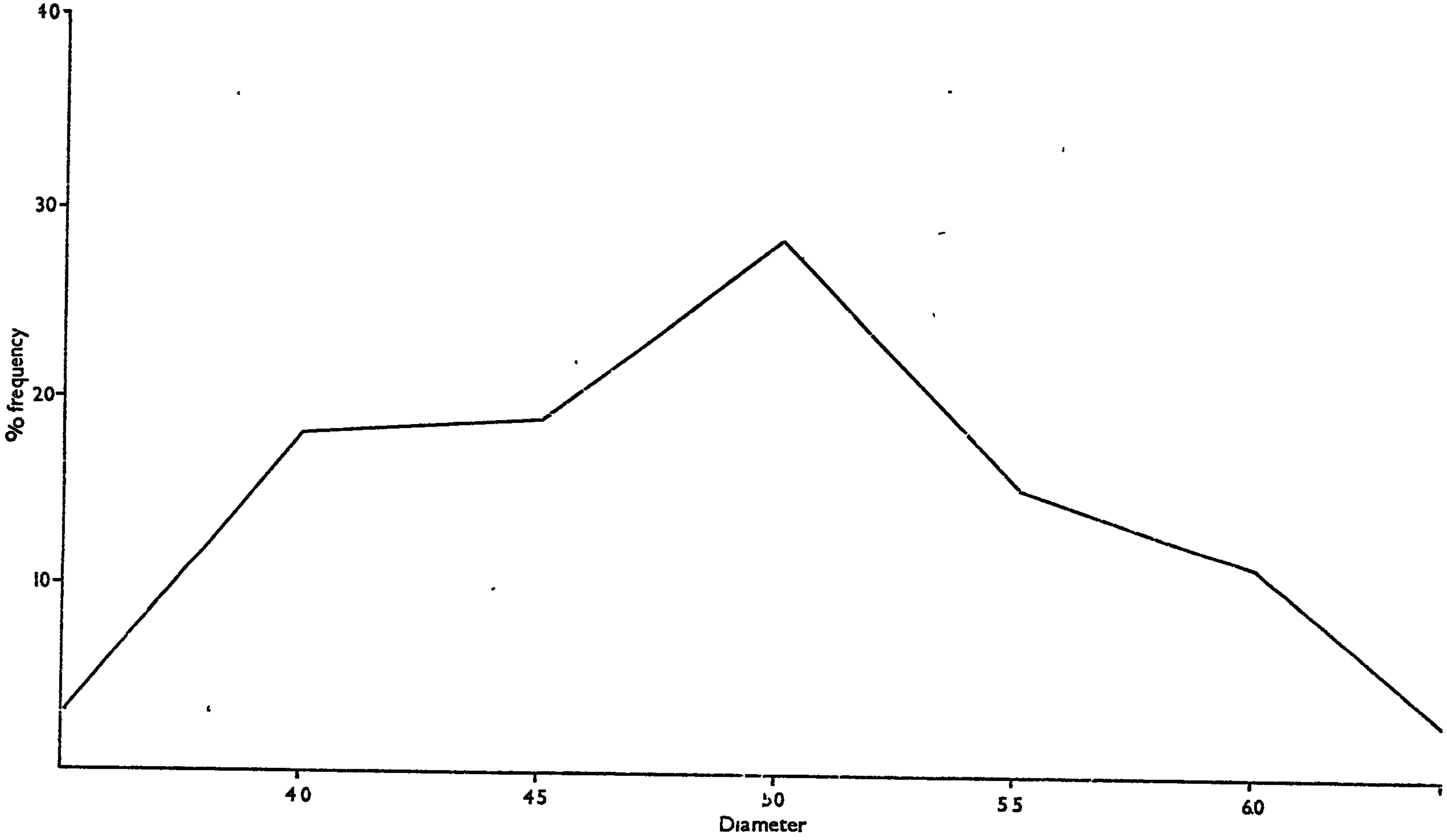


fig 44

Discussion on *L. pauciradiale* and *L. irregulare*

In the years prior to 1845 before Lonsdale's publication of the genus *Diphyphyllum*, for the non-columellate species of *Lithostrotion*, no attention was paid to the presence or absence of the columella. Thus any fasciculate *Lithostrotion* species with a dissepimentarium was called *L. fasciculata* whether it was columellate or, as is the type of that species, a non-columellate form. Thus *L. fasciculata* prior to 1845 included *L. fasciculata* *S.S.* (a diphyphylloid species with axial budding, p.196) plus the columellate species under discussion here.

Now, Phillips split from the columellate members of *L. fasciculata* a species he described as *L. irregulare* (1836, p.202, pl.II, figs 14 and 15). Certain problems have arisen over this species in the years since Phillips original description mainly because he gave the diameter of the species as 1/3 inch (= 8 mm.) with 18 - 20 septa but corallites with this large diameter are never found with this low number of septa. This fact led Hill (1940, p.170-171) to the conclusion that it would be unlikely that any topotype would ever be found which would adequately agree with Phillips diagnosis and thus she suggested the species should be allowed to lapse. This conclusion she backed up with the evidence that her visit to the type locality, Ash Fell Edge in Cumbria produced only one species, of 8mm. diameter, that of *L. martini*, and none with the low septal counts of Phillips.

Phillips illustrated two figures of *L. irregulare*, first an external view of a corallite (*loc. cit.*, fig.14) which we can assume is natural size (as all the other external views on the plate are natural size) and this corallite is 5 mm. in diameter. Thus it seems that Phillips erred in stating 8 mm. for the diameter of the corallite. Secondly he figured an enlarged transverse section of a second corallite, the amount of magnification is unknown, but it has 19 septa (loc. cit., fig.15).

I have carried out extensive research in the new road cuttings at Ash Fell Edge which provide excellent exposure and Hill is quite correct in stating that the only species of fasciculate Lithostrotion that occurs at this locality is L. martini, but in the shale bands of the S1 Ash Fell Sandstone many of the colonies of L. martini have the majority of their corallites stunted (by the adverse environment of the shale) such that they never reach adult dimensions. Most of these stunted corallites are 5 mm. in diameter, the same as Phillips fig.14, and have 20 - 24 septa, and a few have only 18 - 19 septa, the same as Phillips fig.15 and these are 3 mm. in diameter. Thus Phillips was probably illustrating two different types of corallites by his figures and these corallites that he described as L. irregulare from Ash Fell Edge are merely stunted corallites of L. martini.

However in the higher D1 (?S2) Subzone a true species, separate from L. martini, does appear with 20 - 24 septa which is 5 mm. in diameter and is identical to Phillips fig.14 and to the larger stunted corallites of L. martini. Also in 1844 McCoy described a similar columellate species of Lithostrotion to this but the type of this species, L. pauciradiale, is only 3.5 mm. in diameter and has only 18 - 20 septa i.e. identical to Phillips fig.15 and to the smaller stunted corallites of L. martini at Ash Fell. Now, while there may well be a continuous series between these large and small forms, it does appear that the two end members are more widespread than the intermediate forms and also that the two end members are so different as to warrant their recognition either as species or sub-species.

L. pauciradiale is available for the smaller species (3 mm., 18 - 20 septa) which is identical to Phillips fig.15, and L. irregulare can be revived to refer to the larger species (5 mm., 20 - 24 septa).

Now, if Ash Fell were the only type locality for *L. irregulare*, or if type material existed from this locality for *L. irregulare*, we would have no alternative but to concede regretfully that *L. irregulare* was synonymous with *L. martini* and choose a new name for the identical D1 true species (5 mm., 20 - 24 septa). It is fortunate therefore that Phillips' types are lost and also that he stated 'Northumberland' as an alternative type locality and while this is rather vague, and far from ideal for a type locality, at least we are left with an outlet to retain the species *L. irregulare* as a neotype for fig.14 (but not for fig.15) can be chosen from the D1 beds of Northumberland. Such a neotype would be identical to the Ash Fell forms, but would be a true species and not a stunted corallite of *L. martini*. The fact that the stunted corallites of '*L. irregulare*' from Ash Fell are found in colonies together with true *L. martini* corallites of 8 mm. diameter could explain where Phillips' measurement of 1/3 inch came from. Hill was of the impression that he took his measurement from an Ash Fell form and his structure from 'Northumberland' but she was not aware of the presence of the stunted corallites at Ash Fell. (Yu (1937) also visited Ash Fell and claimed to have found corallites agreeing with Phillips' description and thus he also recognised Phillips' species as valid, but while his corallites were indeed 8 mm. in diameter and had the low number of 20 - 24 septa, these corallites had three rows of dissepiments and are the species described here as *L. variabile*, identical to *L. irregulare* in every respect except for the wider dissepimentarium and diameter.)

Choosing of such a neotype would be quite justified as in the years immediately succeeding Phillips many other authors used this name of *L. irregulare* and these authors, for example Edwards and Haime (1851), applied Phillips' name to corallites 5 mm. in diameter and having 24 septa. We can therefore interpret the species to some extent on their definitions. It is interesting to note in this respect that Edwards and Haime also stated that the young corallites of *L. irregulare* only had 18 septa (i.e. the same as Phillips fig.15).

Now, in 1851 Edwards and Haime recognised the two species L. pauciradiale and L. irregulare as distinct, but in 1852 changed their mind and considered them synonymous, presumably as they thought that all intermediates could be found or because they had not seen the small size of McCoy's type. Their listing of these two species as synonymous has led to problems. Later authors have followed Edwards and Haime in considering the names synonymous and these authors have sometimes used one name and sometimes another to describe these two forms and many records in the literature of one species may refer in fact to the other. Moreover at the same time as considering these species synonymous and, therefore, using only one of the two available names, these same authors have often realised that two types could be recognised and have thus used new names to describe these two types. First Thomson in 1887 described L. irregulare correctly as the larger form with 22 septa and described separately as Lithostrotion sp. a smaller coral 1½ times as big as L. junceum but with one row of dissepiments. This is L. pauciradiale but Thomson was not using McCoy's name. Secondly Smith (1920, p.59) defined L. irregulare as having a tabularium 2.5 mm. wide (this is really L. pauciradiale) but he admitted the existence of 'L. irregulare larger variety' which is L. irregulare S.S. Thirdly Heritsch said that the small, one dissepiment species of 3.5 mm. diameter differed from L. irregulare on size factors and he called these small types L. carpathicum. This is synonymous with L. pauciradiale but he gave it a new name as he was following McCoy's original description of L. pauciradiale when he wrongly considered it to have only 10 septa. Fourthly Yabe and Hayasaka (1915) and Yu (1937) correctly identified L. irregulare as 5 mm. and 20 - 24 septa and separated L. irregulare var. asiatica as being 3.5 mm. with 18 - 20 septa. Again this is L. pauciradiale. Finally Hill (1940) as already mentioned allowed L. irregulare to lapse and used L. pauciradiale for all the forms with one row of dissepiments large and small. However she seemed to be unaware of the wide variation that such types exhibit, thus stating that in diameter they ranged from 4.0 - 5.5 mm. while in reality they range from 3.5 mm. - 6.5 mm., a range which gives more justification for splitting the two end members than she realised.

It should perhaps be pointed out that McCoy's name of L. pauciradiale (paucity of septa) was given at a time when he wrongly considered these corals to have only 10 septa. On realising his mistake he changed this now misleading name to L. aggregatum, but by the Rules of Nomenclature we are bound to use his first name however inapplicable.

In summary therefore, L. irregulare is a true and valid species, but does not appear until D1; those identical forms in S1 being L. martini homeomorphs, but his second type locality of 'Northumberland' means that we can retain this species.

Phillips was unfortunate in choosing a homeomorph for his type, but in this complex situation we are fortunate that his type has been lost.

Lithostrotion variabile *sp. nov.*

(Plates 23 - 25.)

1937 *Lithostrotion irregulare* (Phillips), Yu, Acad. Sinica, Mem. National Research Inst. Geology, No.16, p.38, pl.viii, figs 5-6, pl.ix, figs 1-3 (non *L. irregulare* Phillips).

Diagnosis: Columellate fasciculate *Lithostrotion* with 2 - 3 rows of dissepiments, corallites 5.0 - 7.0 mm. in diameter, 20 - 24 (26) septa, and a tabularium 4 - 5 mm. wide.

Type Material: Holotype is specimen No.188b (including this sections) in the author's collection, Dept. of Geological Sciences, University of Durham. From Hardraw Scar Limestone, West side of Semerwater, Wensleydale.

Material: Ash Fell Sandstone, Ash Fell Edge, Ravenstonedale, Cumbria; S2 Limestone, Ash Fell Edge, Ravenstonedale; Great Scar Limestone (D1), Hartley Quarry, Kirkby Stephen; Potts Beck Limestone (D1), Potts Beck, Orton, Cumbria; Hardraw Scar Limestone, Mill Gill, Askrigg, Wensleydale; Hardraw Scar Limestone, Semerwater, Wensleydale; Hardraw Scar Limestone, Friar's Intake, Swaledale; Simonstone Limestone, Cow Pasture Wood, Whernside Pasture, Kettlewell, Wharfedale; Bankhouses Limestone, Low Tipalt, Greenhead, Northumberland; Great Scar Limestone (?S2), Scalber, Settle, Yorkshire.

Description: External Characters; The corallum is fasciculate, either dendroid or phaceloid. As with *L. martini* many coralla are partly cerioid. Neither the calices nor ~~a~~ well preserved epitheca~~e~~ have been seen. Internal Characters; The mean adult diameter of this species is 5.6 mm.

and the maximum number of septa in a colony varies from 20 - 24 and may rarely be 25 or even 26.

The septa, the columella, the dissepiments and the tabulae are exactly the same as in *L. martini* (see that species) and the epitheca shows the same features.

The tabularium is of constant dimensions and the mean adult diameter of the tabularium is 4.6 mm.

Discussion: This species is exactly intermediate between *L. martini* and *L. irregulare* and has been confused with both species. *L. martini* has 28 septa and 2 - 3 rows of dissepiments, *L. variabile* has 20 - 24 (26) septa and 2 - 3 rows of dissepiments and *L. irregulare* has 20 - 24 (26) septa and only one row of dissepiments. Thus *L. variabile* has the septa of *L. irregulare* and the dissepimentarium of *L. martini*. It will be seen that in some rare cases the septal counts of this species do overlap with those of *L. martini*. However the two species can still be distinguished by the smaller tabularium of *L. variabile*.

Although there may be continuous variation from *L. martini* to *L. variabile* they are recognised as distinct species on a stratigraphic basis, *L. variabile* not appearing until the very top of the S1 sub-zone.

See also discussion on the fasciculate columellate species on p.

Statistical Results:

R. = 22 - 26

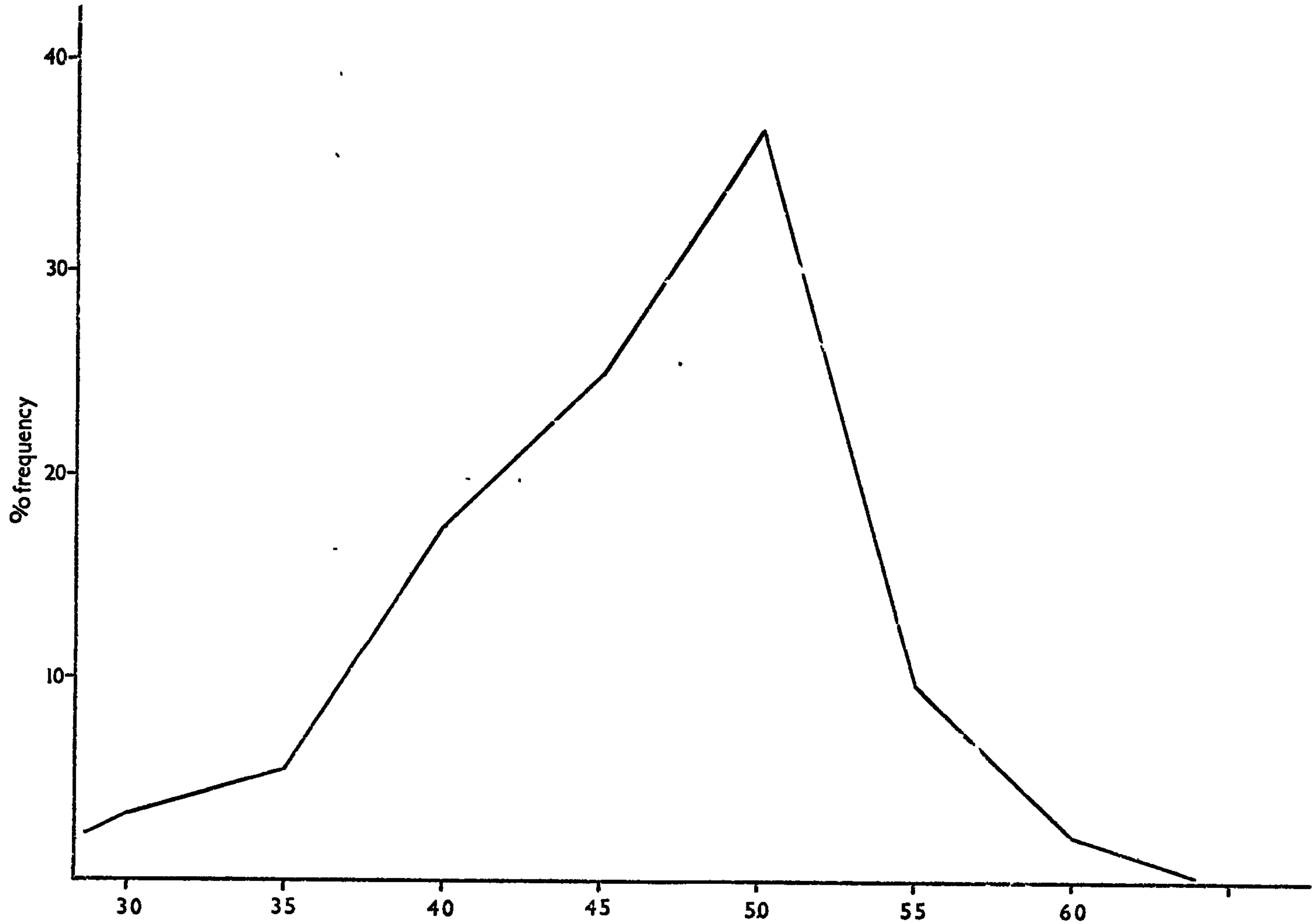
M.D. = 5.694 mm.
S.D. = 0.728 mm.
max.D. = 7.0 mm.
min.D. = 4.0 mm.

M.T. = 4.62 mm.
S.D. = 0.616 mm.
max. T. = 6.0 mm.
min.T. = 3.0 mm.

Stratigraphical Range: Top of S1 or base of S2 to Tyne Bottom Limestone.

FIGURE 45

Plot of tabularium diameter against percentage frequency in *L. variabile*. Intervals in mm's.



Tabularium

fig 45

FIGURE 46

Plot of corallite diameter against percentage frequency in L.variabile. Intervals in mm's.

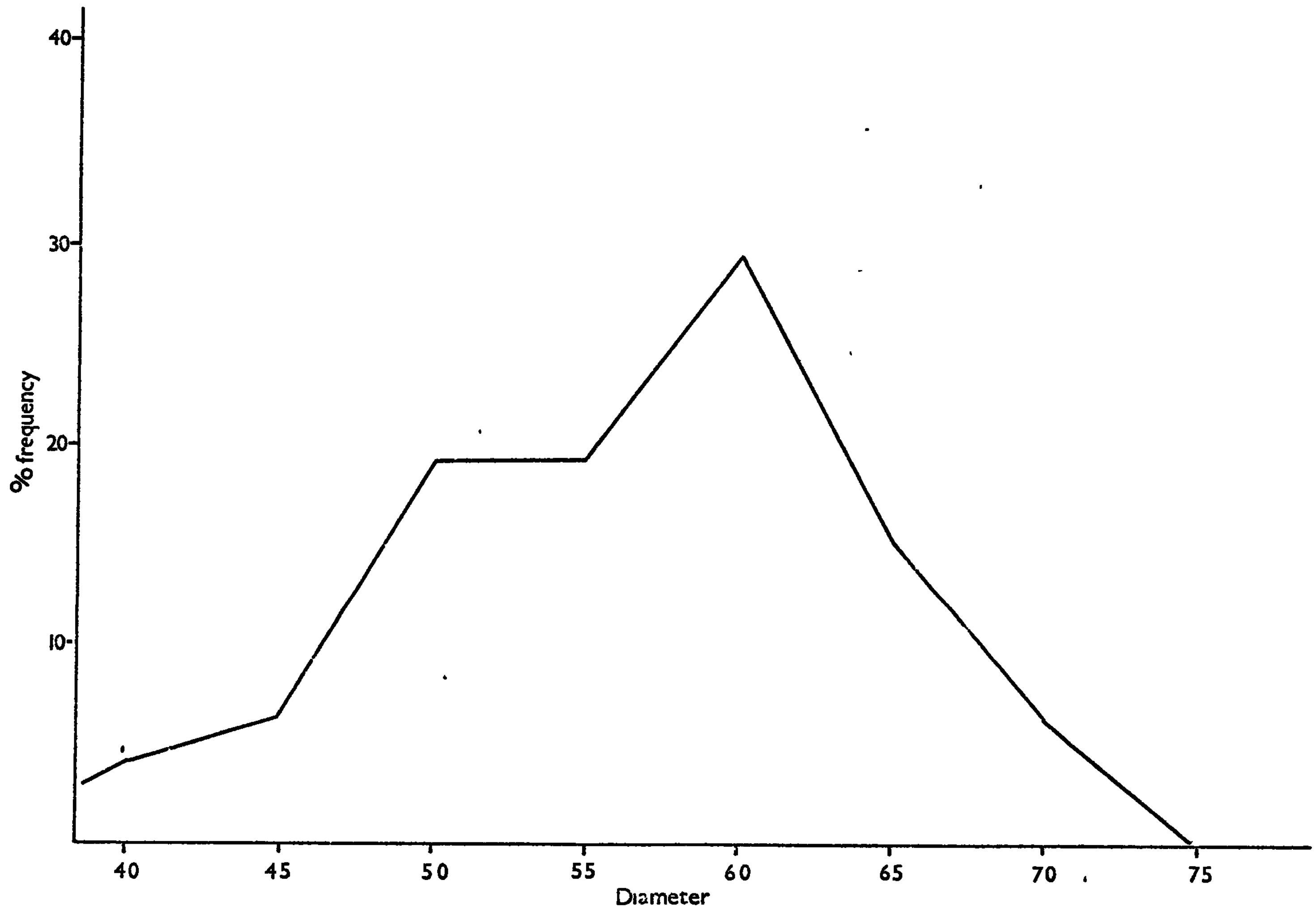


fig 46

Lithostrotion martini martini Milne-Edwards and Haime
(Plates 27 and 28.)

1809 *Erismatolithus* (*Madreporae cespitosae*) Martin, 'Petrif. Derb.', pl.XVII.

1836 *Lithodendron fasciculatum* (Fleming), Phillips, 'Geol. of Yorkshire', vol.II, p.202, pl.II, figs 16, 17.

1842 *Caryophyllia fasciculata* (Fleming), De Koninck, 'Anim. Foss. des Terr. Carb. de Belg.', p.17, pl.D, fig.5, pl.G, fig.9. (Non Lamarck).

1844 *Lithodendron caespitosum* McCoy, Syn. Carb. Foss. of Ireland, p.188. (Non Goldfuss).

1845 *Lithodendron fasciculatum* (Fleming), Lonsdale, in: Murch., Vern., et Keys., 'Russ. and Urals', Vol.I, p.600.

1846 *Cladocora fasciculata* (Fleming), Geinitz, Grundr. der Verst., p.570.

1850 *Diphyphyllum fasciculatum* (Fleming), D'Orbigny, Prod. de Palaeon., vol.I, p.159.

1851 *Lithostrotion martini* Milne-Edwards and Haime, 'Pol. Foss. des Terr. Palaeoz.', p.436.

1851 *Lithostrotion phillipsi* Milne-Edwards and Haime, *Ibid.*, p.439.

1852 *Lithostrotion martini* Milne-Edwards and Haime, 'Mon. Brit. Foss. Corals', p.197, pl.XL, figs 2a-g.

1852 *Lithostrotion phillipsi* Milne-Edwards and Haime, *Ibid.*, p.201, pl.XXXIX, fig.3.

1876 *Lithostrotion phillipsi* Milne-Edwards and Haime, Thompson and Nicholson, Ann. Mag. Nat. Hist., ser.4, vol.XVII, No.1, p.304, pl.XV, figs 1, 1a.

1883 *Lithostrotion phillipsi* Milne-Edwards and Haime, Thompson, Proc. Phil. Soc. Glasg., vol.XIV, p.404, pl.VIII, fig.5.

1887b *Lithostrotion fasciculatum* (Fleming), Thompson, Trans. Edin. Geol. Soc., vol.V, p.392, pl.XIII, fig.6.

1887b *Lithostrotion phillipsi* Edwards and Haime, Thompson, *Ibid.*, vol.V, p.391, pl.XII, figs 5, 5a.

1903 *Lithostrotion martini* Milne-Edwards and Haime, Vaughan, Proc. Bristol. Nat. Soc., vol.X, p.106.

1920 *Lithostrotion martini* Milne-Edwards and Haime, Smith, J. Proc. Roy. Soc. N.S.W., vol.LIV, p.59.

1940 *Lithostrotion scoticum* Hill, 'Mon. Carb. Rug. Corals Scotland', Pal. Soc., p.173, pl.IX, figs 9, 10.

1940 *Diphyphyllum smithi* Hill, *Ibid.*, p.181.

But not:

1876 *Lithostrotion martini* Thompson, Ann. Mag. Nat. Hist., ser.4, vol.XVII, p.304, pl.XV, fig.2 which is *L. sociale*.

1883 *Lithostrotion martini* Thompson, Proc. Phil. Soc. Glasg., vol.XIV, p.404, which is *L. sociale*.

1887 *Lithostrotion martini* Thompson, Trans. Edin. Geol. Soc., vol.V, p.391, pl.XIII, fig.5, which is *L. sociale*.

Note: All references to *L. fasciculatum* are non *L. fasciculatum* Fleming.

Diagnosis: Columellate fasciculate Lithostrotion with 2 - 4 rows of dissepiments, corallites 7.0 - 8.0 mm. in diameter, 26 - 28 septa, and a tabularium 6.0 mm. wide. Columella elongate and normally dilated, but may be narrow or absent.

Type Material: No type material exists in the Edwards and Haime collections in the Museum National D'Histoire Naturelle and the L'Ecole de Mines, Paris, except for one unfigured specimen labelled 'L. martini' from the type locality at Corwen, North Wales. However this has recently been sectioned by Dr. P. Semenoff-Tian-Chansky and Nudds who agree that the specimen has degenerate minor septa and a complex axial structure and is probably Corwenia. As this specimen is only a topotype it has no nomenclatorial significance and so a neotype can be chosen.

Edwards and Haime state their type localities as Corwen, Oswestry and Rugley. The outcrop at Corwen is an outlier of D2 limestones and my visit to the only quarry in this outlier produced no specimens of L. martini, only cerioid Lithostrotion. It may be that the only specimen of 'L. martini' found by Edwards and Haime from Corwen was the specimen of Corwenia in the Museum at Paris mentioned above. If a neotype is to be chosen then Oswestry seems to be the most likely area.

The holotype of L. phillipsi is specimen No.Z 95a in the Museum National D'Histoire Naturelle, Paris which is Edwards and Haimes figured specimen (1852, pl.XXXIX, fig.3).

The holotype of L. scoticum is specimen No.KM.T2008 in the Kelvingrove Museum, Glasgow.

Material: C2 Limestone, Bleaflatt Lane, Ravenstonedale, Cumbria; C2 Limestone, Bowber Head Farm, Ravenstonedale; C2 Limestone, Ashfield Farm, Ravenstonedale; Ash Fell Sandstone, Ash Fell Edge, Ravenstonedale; S2 Limestone, Ash Fell Edge, Ravenstonedale; S2 Limestone, Mire Close Bridge, Ravenstonedale; S2 Limestone, Lanehead Quarry, Ravenstonedale; Great Scar Limestone (D1), Wisebar Plantation, Ravenstonedale; Potts Beck

Limestone (D1), Potts Beck, Orton, Cumbria; Beehive Band (base of D1), Beehive Quarry, Ravenstonedale; S2 Limestone, Ore Hill Quarry, Nateby, Kirkby Stephen, Cumbria; Great Scar Limestone (D1), Ladthwaite Bottom, Nateby, Cumbria; Gayle Limestone, Mill Gill, Askrigg, Wensleydale; Hardraw Scar Limestone, Skell Gill, Grange, Askrigg; Great Scar Limestone (?S2), Scaleber, Settle, Yorkshire.

Description: External Characters; The corallum is fasciculate, usually dendroid or dendroid/phaceloid. Many coralla which are partly cerioid show adjacent corallites growing in periodic coalescence in which case a continuous epitheca surrounds the two corallites although they are still separated by a dividing wall. The epitheca often shows well developed growth banding of diurnal and monthly duration. The calice is conical and deep with a prominent columella.

Internal Characters; The mean adult diameter of this species is 7.8 mm. and the maximum number of septa in a colony varies from 26 - 28 of both orders (usually 27). The major septa are of variable length. Usually one or both of the axial septa extend to the columella and in some coralla a majority of the other major septa also are continuous to the axis. However, in most coralla the major septa extend only 2/3 the radius of the corallite. In these cases the minor septa are about ½ the length of the major septa just penetrating the tabularium. Both major and minor septa are more dilated in the dissepimentarium than in the tabularium. In rarer examples a third (tertiary) order of septa is also developed, but these are little more than projections from the epithecae. In one coralla the minor septa are degenerate or absent and the major septa may become lonsdaleoid.

The species is characterised by a columella elongated in the cardinal plane and this may be quite a variable structure. It may be strongly dilated in which case it often has transverse projections at right angles to the cardinal plane, or it may just be a thin plate. Diphymorphic colonies are common (see Discussion) in which case the septa may be shorter; only half the radius of the corallite.

Dissepiments vary from 2 - 4 rows and are generally regular and concentric. The inner row is usually dilated (although not always) and the dilation fuses with the dilation of the septa in the dissepimentarium. All dissepiments are quite vertically displaced. The width of the dissepimentarium is variable depending on the number of dissepiments present.

The tabularium is a more constant feature in this species and the mean adult diameter of the tabularium is 5.7 mm.

The epitheca is often dilated and on its external surface may show septal grooves and interseptal ridges. In many coralla that are becoming cerioid the epithecae of adjacent corallites may temporarily coalesce. However, such a fused epithecae is always a double walled structure; the adjacent corallites never share a common epitheca.

The tabulae are tent-shaped, rising at the axis to meet the columella. They are horizontal in the tabularium and then bend steeply downwards in the dissepimentarium where they meet the dissepiments. Some tabulae are entire, but more usually when the tabulae bend down in the dissepimentarium they come to rest on the tabulae beneath in which case a second series of tabulae is developed peripheral to the tabularium. Tabulae are of the α type.

In the diphymorphic corallites the tabulae are identical except that they are horizontal across the whole of the tabularium, failing to rise at the axis.

Discussion: This species can be distinguished from *L. junceum*, *L. pauciradiale* and *L. irregulare* by having more than one series of dissepiments and by its larger size. It can usually be distinguished from *L. variabile* by the greater number of septa (27 or 28) but both species can have 26 septa in which case *L. martini* has a larger tabularium. It can be distinguished from *L. sociale* and *L. scalberense* which always have more than 28 septa. *L. martini praenuntius* has more dissepiments and closer spaced tabulae, and *L. m. simplex* has only one row of dissepiments.

Hill (1940) described *L. scoticum* as having 26 - 28 septa and one row of dissepiments and so it would appear more similar to *L. m. simplex*, but most of the corallites of the holotype of *L. scoticum* seem to have two rows of dissepiments and so in reality it is more similar to *L. m. martini* although close to *L. m. simplex*.

Smith (1928) figured *Diphyphyllum* α which he said was probably *D. lateseptatum*. However Hill (1940) said this was not *D. lateseptatum* as it had α instead of the β tabulae of *D. lateseptatum*. Thus she gave it the new name of *D. smithi*. There does not seem to be any type material for this species and the only material I have collected with tabulae in the condition shown by Smiths figure have lateral budding and not the calicular budding characteristic of the true diphyphylloid species of *Lithostrotion*. Therefore it seems to be a diphymorphic colony of *L. martini* and so is considered synonymous with this species.

Edwards and Haime (1851, p.439; 1852, p.201) described *L. phillipsi* as having 30 septa, but the holotype in the Museum National, Paris has only 28 septa and thus seems to be *L. martini*. *L. phillipsi* differs only in its partly cerioid habit and this is not regarded as being of specific importance.

Statistical Results:

R. = 26 - 28

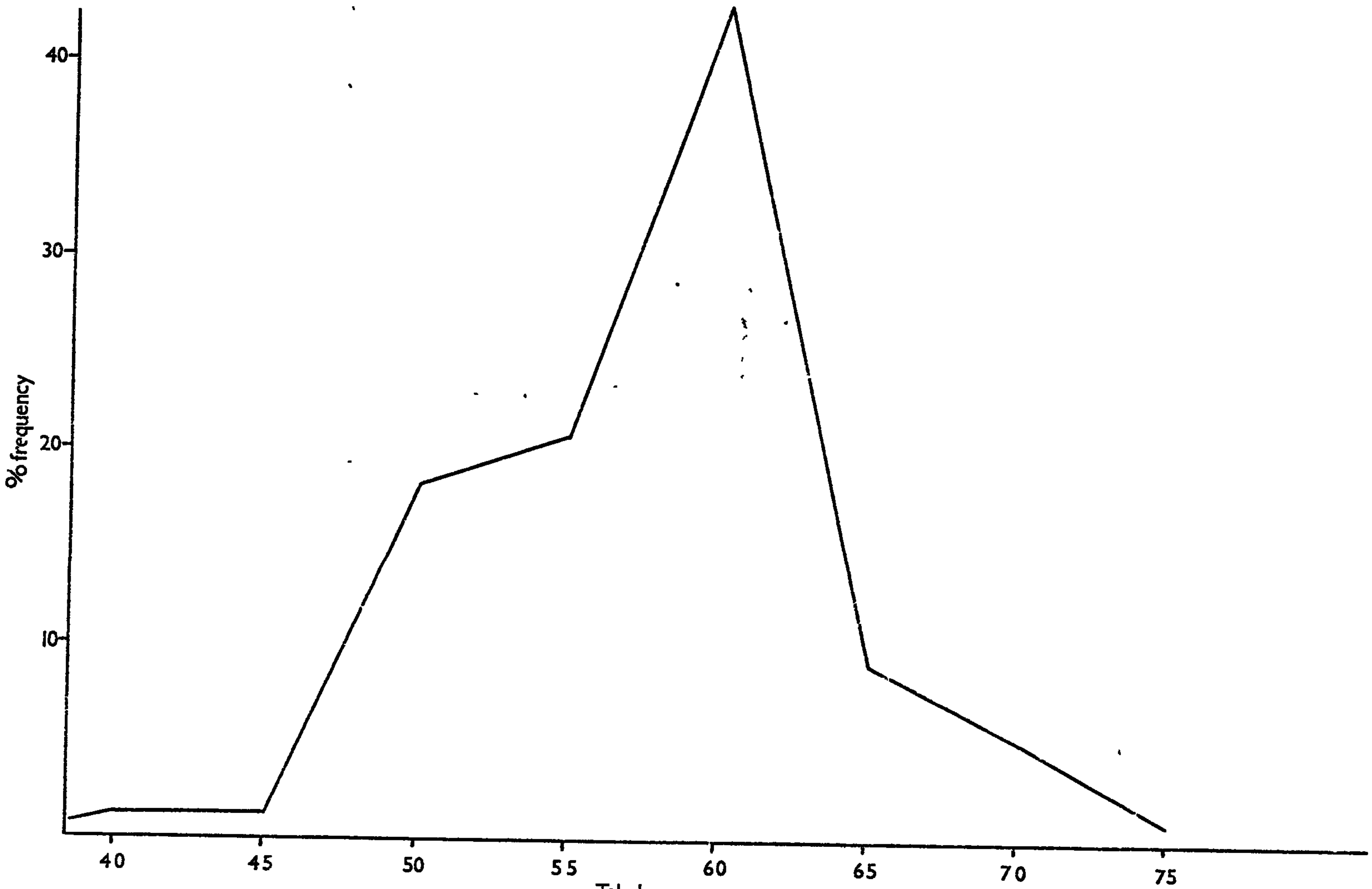
M.D. = 7.8 mm.
S.D. = 0.745 mm.
max.D. = 10.0 mm.
min.D. = 5.0 mm.

M.T. = 5.796 mm.
S.D. = 0.632 mm.
max.T. = 7.3 mm.
min.T. = 4.0 mm.

Stratigraphical Range: C2 (*Lithostrotion* Limestone) to Jew Limestone.

FIGURE 47

Plot of tabularium diameter against percentage frequency in *L. martini*. Intervals in mm's.



Tabularium
fig 47

FIGURE 48

Plot of corallite diameter against percentage frequency in *L.martini*. Intervals in mm's.

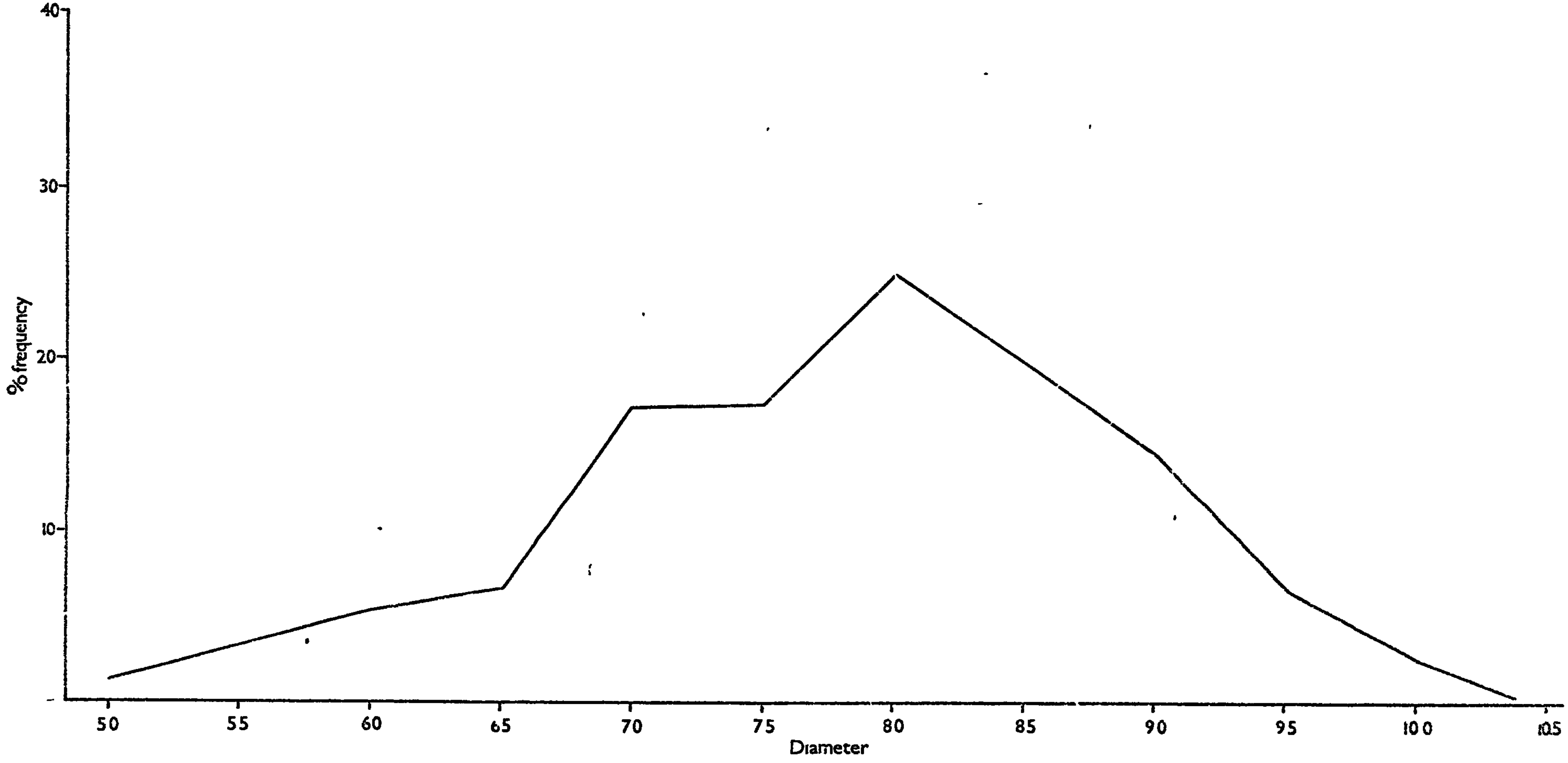

40
30
20
10
% frequency
50
55
60
65
70
75
80
85
90
95
100
105
Diameter

fig48

Lithostrotion martini praenuntium subsp. nov.

(Plate 26.)

Diagnosis: *Lithostrotion martini* but with up to six rows of dissepiments and very closely spaced tabulae.

Type Material: Holotype is specimen No. 10a (including thin sections) in the author's collection, Dept. of Geological Sciences, University of Durham. From *Thysanophyllum* Limestone, Pothole 200 yards W. of Back Dub, Ravenstonedale Moor, Cumbria.

Material: *Thysanophyllum* Limestone, Old Quarry, $\frac{1}{2}$ mile W.N.W. of Pinfold Bridge, Kirkby Stephen, Cumbria; *Thysanophyllum* Limestone, 200 yds. W. of Back Dub, Ravenstonedale Moor, Kirkby Stephen.

Description: External Characters; As for *L. m. martini* except that the colony is more dendroid and the corallites are more conical in shape taking longer to reach maturity. Growth lines on the epithecae are very closely spaced.

Internal Characters; As for *L. m. martini* except that in mature individuals there can be up to six rows of dissepiments. Tabulae very closely spaced (20 per cm.) and are tent-shaped rising sharply at the axis to meet the columella. These two facts have the result that any transverse section across a corallite cuts both a high number of dissepiments and tabulae and has the appearance of a closely spun web.

Stratigraphical Range: C2 (*Thysanophyllum* Limestone).

Lithostrotion martini simplex subsp. nov.

Diagnosis: *Lithostrotion martini* but with only one row of dissepiments.

Type Material: Holotype is specimen No. 18b (including thin sections) in the author's collection, Dept. of Geological Sciences, University of Durham. From S2 Limestone, Smardale Quarry, Kirkby Stephen, Cumbria.

Material: Only the type locality is known.

Description: As for *L. m. martini* except for the single row of dissepiments.

Stratigraphical Range: S2.

Lithostrotion sociale (Phillips)
(Plates 29 and 30.)

1836 *Lithodendron sociale* Phillips, 'Geol. of Yorkshire', vol.II, p.203, pl.II, fig.19.
1836 *Lithodendron longiconicum* Phillips, *Ibid.*, vol.II, p.203, pl.II, fig.18.
1843 *Lithodendron sociale* Phillips, Portlock, 'Geol. Rep. on Londonderry', p.335.
1843 *Lithodendron longiconicum* Phillips, Portlock, *Ibid.*, p.336.
1844 *Lithodendron sociale* Phillips, McCoy, Syn. Carb. Foss. of Ireland, p.188.
1850 *Diphyphyllum sociale* (Phillips), D'Orbigny, Prod. de Palaeont., vol.I, p.159.
1850 *Diphyphyllum longiconicum* (Phillips), D'Orbigny, *Ibid.*, vol.I, p.159.
1851 *Lithostrotion affine* (Fleming), Milne-Edwards and Haime, Pol. Foss. des Terr. Pal., p.437. (Not *C. affinis* Fleming).
1852 *Lithostrotion affine* (Fleming), Milne-Edwards and Haime, 'Mon. Brit. Foss. Corals', p.200, pl.XXXIX, figs 2, 2a, 2b. (Not *C. affinis* Fleming).
1876 *Lithostrotion martini* Milne-Edwards and Haime, Thompson and Nicholson, Ann. Mag. Nat. Hist., ser.4, vol.XVII, p.304, pl.XV, fig.2. (Not *L. martini* Edwards and Haime).
1887b *Lithostrotion martini* Milne-Edwards and Haime, Thompson, Trans. Edin. Geol. Soc., vol.V, p.391, pl.XIII, fig.5. (Not *L. martini* Edwards and Haime).

But not:
1930 *Lithostrotion sociale* (Phillips), Hudson, Proc. Leeds Phil. Soc., vol.II, pt.2, p.98, pl.I, fig.1, which is *L. scalberense*.

Diagnosis: Columellate fasciculate and partly cerioid *Lithostrotion* with 2 - 4 rows of dissepiments, corallites 9 - 10 mm. in diameter, 29 - 33 septa and a mean tabularium diameter of 7.2 mm. Increase is lateral.

Type Material: All of Phillips material of both *L. sociale* and *L. longiconicum* is lost. Hudson chose a neotype for *L. sociale* but this neotype is different to Phillips description of *L. sociale* (see discussion) and is here rejected.

Phillips gave his type locality for *L. sociale* as Settle (Yorkshire) and so, if necessary, a neotype can be chosen from the Great Scar Limestone of this area.

Material: Great Scar Limestone (D1), High Out Wood, Kirkby Stephen, Cumbria; Great Scar Limestone (D1), Hartley Quarry, Kirkby Stephen; Great Scar Limestone (D1), Top of Hartley Quarry, Kirkby Stephen; Great Scar Limestone (D1), Foggy Gill Farm, Kirkby Stephen; Potts Beck Limestones Potts Beck, Orton, Cumbria; Bankhouses Limestone, Low Tipalt Quarry, Greenhead, Northumberland.

Description: External Characters; Corallites cylindrical and tall and often partly cerioid. Epithecae often transversely wrinkled. Specimen from Potts Beck shows calices 5 - 6 mm. deep with a prominant columella. Internal Characters; Major septa variable in length. Usually the cardinal and counter-cardinal septa extend to the columella and other major septa may also do so, but more often the major septa end just before the centre. Minor septa much shorter, usually only just reaching into the tabularium. Both orders of septa are usually dilated in the dissepimentarium, but are thinner at their axial ends. The maximum number of septa in a colony varies from 29 - 33.

A columella is usually present although diphymorphs may occur. The columella may be quite thick with radiating bars or very thin. It is always elongated in the cardinal plane and often continuous to the cardinal septum.

There are usually 2 - 3 rows of dissepiments and the innermost row may be dilated. The dissepiments are concave inwards and concentrically arranged, usually quite vertical. The width of the dissepimentarium is variable depending on the number of dissepiments.

The innermost row of dissepiments defines a tabularium with a mean diameter of 7.28 mm. and an adult range of 5.6 mm. - 9.4 mm. Diameter is more variable due to the variable dissepimentarium and is thus a poorer specific character. It ranges from 7.6 - 12.5 mm. inadult corallites, with a mean of 9.6 mm. Corallites are bounded by an epitheca which is usually quite thick.

The tabulae are of the α type, but are more variable. They rise at the axis to meet the columella, are horizontal peripheral to this, and slope peripherally to the dissepimentarium. Sometimes they are entire, more usually they are incomplete and a second series is developed extending to the dissepiments. Sometimes, however, the second series are small and blister-like, and do not reach the edge. In this case a third or even fourth series may develop.

Discussion: Edwards and Haime considered L. sociale and L. longiconicum to be synonymous with L. affine Fleming. They are certainly very similar, but Kato (1971) has recently rediscovered Fleming's type of L. affine and shows it to have axial budding, whereas L. sociale and L. longiconicum have lateral budding and so L. affine is a separate species.

Phillips described both L. sociale and L. longiconicum as having 32 major septa. The present author has shown that two fasciculate species of Lithostrotion with lateral budding can be distinguished both having 32 septa, one being about 9 mm. in diameter (similar to L. affine) while the other is about 15 mm. in diameter. However it is doubtful whether Phillips was using his two names to refer to these two species as he gives his diameter for both L. sociale and L. longiconicum as $\frac{1}{2}$ inch. Thus it appears that his two species were similar in size and supposedly distinguishable on some other character (probably the partly cerioid habit of L. sociale shown in his original figure and to which the name refers) which is not now regarded as being specifically important. Moreover we cannot be sure whether he was describing the large or small forms as his measurement of $\frac{1}{2}$ inch could equally well apply to the largest corallites of the smaller species and to the smallest corallites of the larger species. It is difficult to tell from his figures which type he was referring to and all his type specimens are lost, but it is probable that he was using both names to refer to the smaller species as he was more likely to give a maximum measurement rather than a minimum measurement and also his figure, which it seems is natural size, is more similar to the smaller species. Thus initially the two species were probably synonymous. However, Hudson has chosen a neotype for *L. sociale* (1930, p.98, pl.i, fig.1) and this neotype is of the larger species. It seems best therefore to reject Hudson's neotype of *L. sociale* and to choose a new one so that *L. longiconicum* again becomes synonymous with *L. sociale*. This action also necessitates finding a new name for Hudsons larger species represented by his 'neotype' (see p.180).

Edwards and Haime described *L. phillipsi* as having 30 septa and being partly cerioid. As Phillips did in fact distinguish *L. sociale* on this partly cerioid character it seems that Edwards and Haime may have been referring to Phillips' species, but decided to rename it after the original author. The fact that the type of *L. phillipsi* is about ½ inch in diameter backs up the rejection of Hudson's neotype for *L. sociale*. (In fact the holotype of *L. phillipsi* has only 28 septa and is therefore a partly cerioid *L. martini*. Edwards and Haime erred in considering this species to have 30 septa as they took their counts from the poorly preserved calicular surface).

By rejecting Hudson's neotype, and reverting to the more standard definition of this species, means that most references to *L. sociale* in the literature do in fact refer to this species as most authors have followed Phillips and not Hudson.

This species can be distinguished from *L. martini*, *L. variabile*, *L. irregulare* and *L. pauciradiale* by its larger diameter and by having over 29 septa. It can be distinguished from *L. scaleberense* which also has over 29 septa as this latter species has a much larger tabularium and overall diameter.

Statistical Results:

R. = 29 - 33

M.D. = 9.66 mm.
S.D. = 1.26 mm.
max.D. = 12.5 mm.
min.D. = 7.6 mm.

M.T. = 7.28 mm.
S.D. = 1.01 mm.
max.T. = 9.4 mm.
min.T. = 5.6 mm.

Stratigraphical Range: Base of D1 to base of D2 (Smiddy Limestone).

FIGURE 49

Plot of tabularium diameter against percentage frequency in *L. sociale*. Intervals in mm's.

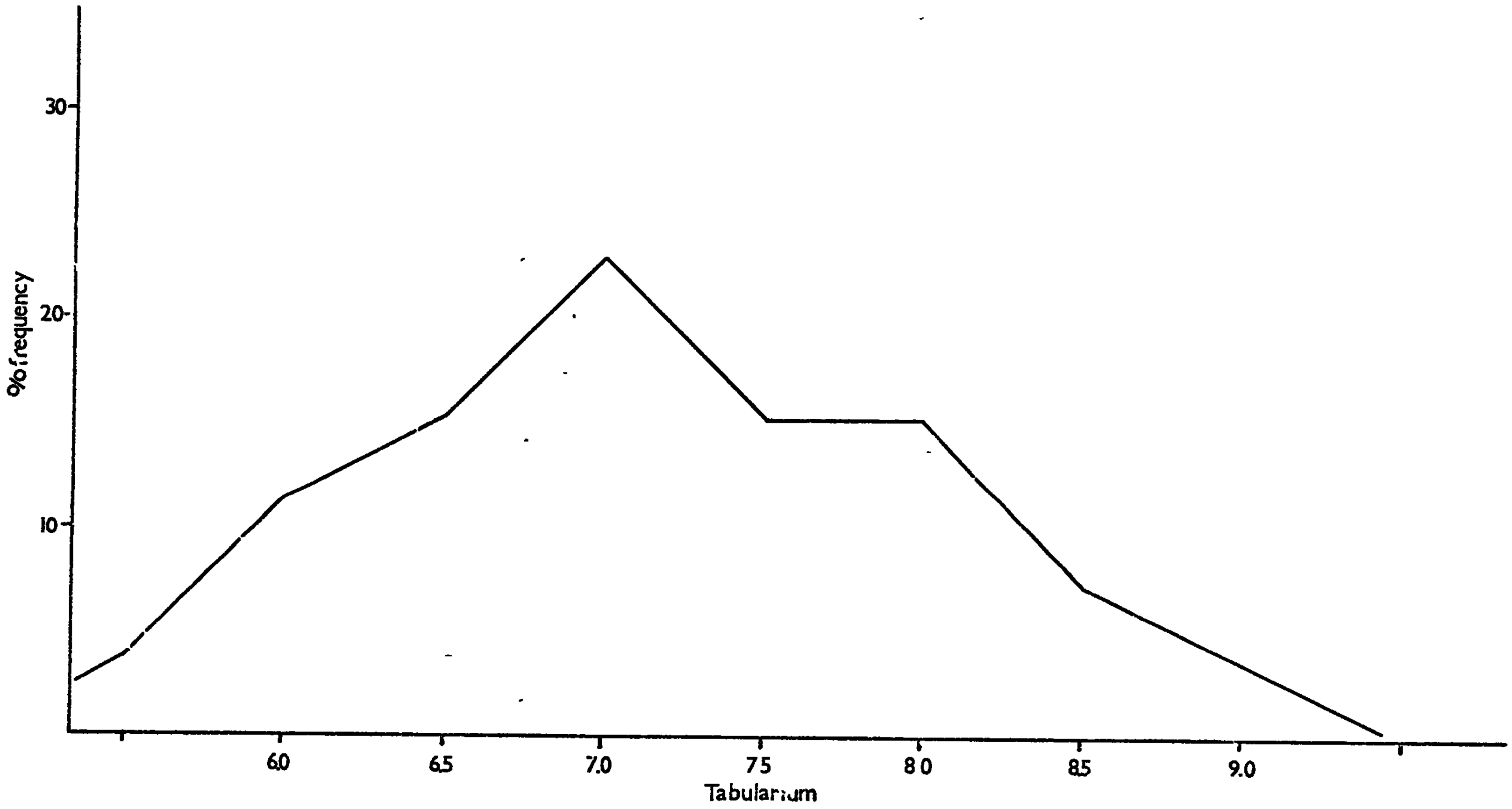


fig 49

FIGURE 50

Plot of corallite diameter against percentage frequency in L.sociale. Intervals in mm's.

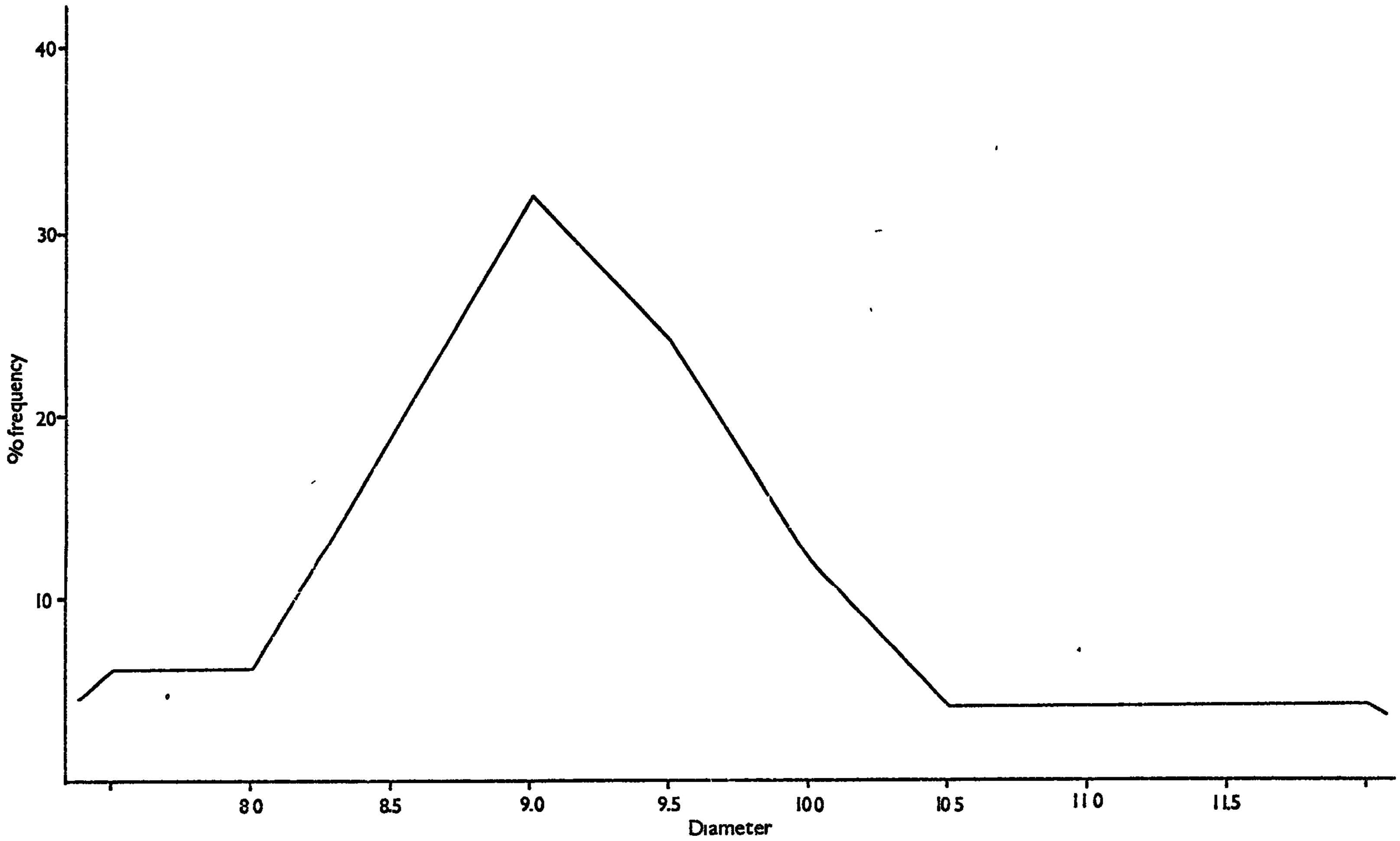


fig 5G

Lithostrotion scaleberense sp. nov.
(Plate 31.)

1930 *Lithostrotion sociale* (Phillips), Hudson, Proc. Leeds Phil. Soc., vol.II, pt.2, p.98, pl.I, fig.1. (Not *L. sociale* Phillips).

Diagnosis: Columellate fasciculate *Lithostrotion* with 2 - 4 rows of dissepiments, corallites 15 mm. in diameter, 32 - 39 septa and a mean tabularium of 11.8 mm. Increase is lateral.

Type Material: Holotype is the rejected neotype of *L. sociale* chosen by Hudson. Specimen in R.G.S. Hudson~~s~~ Collection. Figured Hudson, 1930, pl.I, fig.1. From Scaleber Quarry, near Settle, Yorkshire.

Material: Only the type locality is known.

Description: External Characters; Corallum fasciculate, corallites cylindrical but often partly cerioid in habit. Hudson (1930, p.98) describes the epithecae as being longitudinally striated and transversely undulated. Calices have not been seen.
Internal Characters; The maximum number of septa in a colony varies from 32 - 39 with a mean of 34.5 and this is rather more than the smaller *L. sociale*. The major septa rarely meet the axis except for the cardinal and counter-cardinal septa which may do. Most major septa however only extend about ½ way into the tabularium. Minor septa are much shorter only just penetrating the tabularium. A third order of very small septa may be present as small projections from the epithecae into the dissepimentarium. There is some dilation of both orders of septa this being greater in the dissepimentarium. A columella is sometimes present isolated

in the centre of the corallite but this is never particularly strong and diphymorphs are common.

Dissepiments are variable in number from 2 - 5 rows and the inner row is often somewhat dilated. All dissepiments are concave and concentric.

The tabularium is exceedingly large varying from 10.4 - 13.4 mm. in adult corallites. This is by far the largest tabularium of any species of the Lithostrotiontidae.

Diameter is more variable due to the variable dissepimentarium and ranges from 13.2 - 17.2 mm.

The tabulae are tent-shaped, rising at the axis. Peripheral to the axis they are more horizontal and then they bend down towards the dissepiments. They may be entire or divided into two series when they are of the α type.

Discussion: This species can be distiaguished from all other fasciculate Lithostrotion species by its immense tabularium diameter. See discussion of L. sociale for reasons behind the proposal of this new species.

Statistical Results:

R. = 34 - 39.

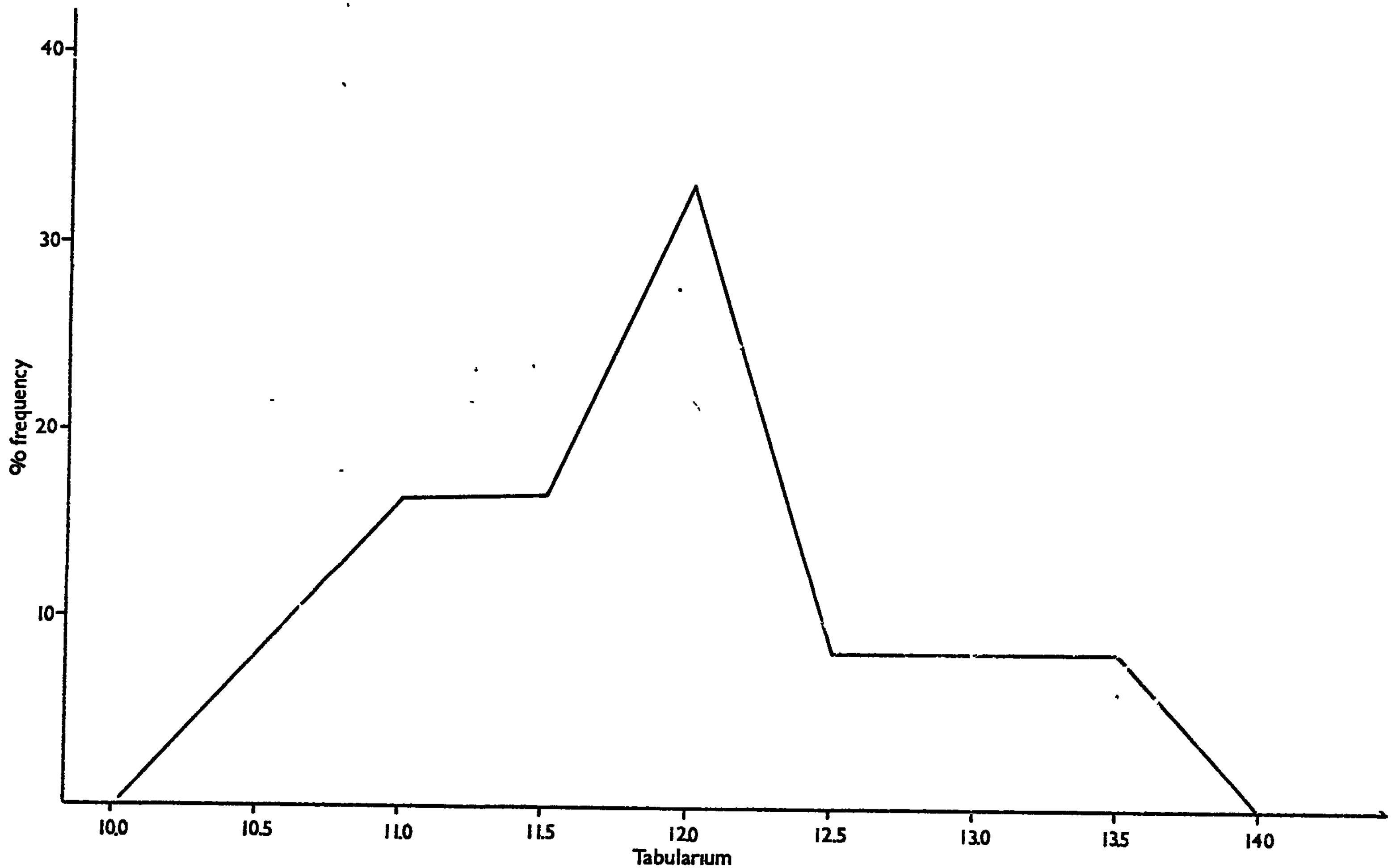
M.D. = 15.24 mm.
S.D. = 1.466 mm.
max.D. = 17.2 mm.
min.D. = 13.2 mm.

M.T. = 11.83 mm.
S.D. = 0.866 mm.
max.T. = 13.4 mm.
min.T. = 10.4 mm.

Stratigraphical Range: S2.

FIGURE 51

Plot of tabularium diameter against percentage frequency in L.scaleberense. Intervals in mm's.



Tabularium

fig 51

Lithostrotion affine (Fleming)
(Plate 32.)

1809 Erismatolithus madreporites (affinis) Martin, 'Petrif. Derb.', pl.xxxi.
1828 Caryophyllia affinis Fleming, 'History of Brit. Animals', p.509.
1830 Caryophyllia affinis Fleming, De Blainville, Dict. Sci. Nat., vol.lx, p.311.
1830 Caryophyllia affinis Fleming, Woodward, Syn. Table of Brit. Org. Rem., p.6.
1834 Lithodendron affine (Fleming), Kerferstein, Nat. der Erdk., vol.II, p.785.
1844 Lithodendron affine (Fleming), McCoy, Syn. Carb. Foss of Ireland, p.189.
1876 Koninckophyllum proliferum Thomson and Nicholson, Ann. Mag. Nat. Hist., ser.4, vol.XVII, No.1, pl.XII, fig.1.
1940 Lithostrotion proliferum (Thomson and Nicholson), Hill, 'Mon. Carb. Rug. Corals of Scotland', Pal. Soc., p.174, pl.IX, figs 11-14.
1971 Siphonodendron affine (Fleming), Kato, Trans. Proc. Palaeont. Soc. Japan, N.S., No.81, p.5, pl.1, figs 1-4.
1972 Lithostrotion affine (Fleming), Mitchell, partim, Bull. Geol. Survey of Great Britain, No.42, p.105-6. (Not L. sociale (Phillips)).
But not:
1851 Lithostrotion affine (Fleming), Milne-Edwards and Haime, 'Pol. Foss. des Terr. Pal.', p.437, which is L. sociale.
1852 Lithostrotion affine (Fleming), Milne-Edwards and Haime, 'Mon. Brit. Foss. Corals', Pal. Soc., p.200, pl.XXXIX, figs 2, 2a, 2b, which is L. sociale.

Diagnosis: Columellate fasciculate Lithostrotion developing both lateral and peripheral increase, 32-39 septa, 2-4 rows of dissepiments and 10 mm. in diameter.

Type Material: Lectotype chosen by Kato (1971) as RSM.1870.14.381. From West Lothian, Scotland. In Royal Scottish Museum, Edinburgh.

Description: External Characters; The corallum is compound, fasciculate and phaceloid. Kato (1971) describes the lectotype as having cylindrical corallites which are subparallel and often in contact.

Internal Characters; The septa are of two orders; major septa extend half way to the axis of the corallite, while the minor septa are very short often ending in the dissepimentarium without reaching the tabularium. Both orders of septa are usually quite thin. The septa usually number from 30-34 of both orders although there can be as many as 40.

A columella is usually present at the axis of the corallites and this is usually thin and lath shaped. However diphymorph corallites are very common in this species.

Dissepiments are numerous; there are usually 3-4 rows. The outer dissepiments near the periphery are regular and concentric, but axial to this, in the inner dissepimentarium, where the minor septa are absent, the dissepiments are more irregular and often pseudoherringbone in pattern. The inner series is rarely dilated as in the other species of Lithostrotion, and so the boundary between the dissepimentarium and the tabularium is not well defined. This tabularium has a diameter of about 7 - 8 mm. in adult corallites, while the diameter of the corallite is from 10 - 12 mm. The corallites are bounded by a thin epitheca.

Tabulae are often complete, but a second series may develop. When a columella is present the tabulae rise at the axis to meet the columella.

The characteristic feature of the species is that increase may be either lateral or calicular in which case it is peripheral.

Discussion: Martin was the original author of the species, but his species were officially rejected from nomenclatorial pupposes by the International Commission of Zoological Nomenclature in 1948 as he did not employ binomial nomenclature. Thus the species is attributed to Fleming who was the first to legally describe it in 1828. Many authors including Edwards and Haime ignored the peripheral increase that this species shows and hence considered this species synonymous with L. sociale (Phillips) with which it is similar except for the method of increase. Thus many records in the literature of L. affine refer to L. sociale. In fact the peripheral nature of the increase in L. affine was unknown until 1971 when Kato re-examined Fleming's types. Thus L. proliferum of Hill

(1940), which she distinguished by its peripheral increase, is synonymous with *L. affine*.

This species can be distinguished from all other species of columellate *Lithostrotion* by its peripheral increase, and from the diphyphylloid species of *Lithostrotion* by its columella. It is therefore the only species in the genus which has both a columella and calicular increase. This seems at first sight to conflict with the argument on p.58 which suggests that calicular increase cannot develop in corallites possessing a columella. However, the species does also show lateral increase and if fresh material could be collected it would be interesting to discover if it is the columellate corallites that are budding laterally and if it is the diphymorph corallites that are budding calicularly. Diphymorphs are, after all, more common in this species than in any other species of *Lithostrotion*.

This species is similar to *L. lateseptatum* and morphologically it seems exactly intermediate between *L. martini* and *L. lateseptatum* with the columella breaking down and calicular increase developing. The calicular increase is peripheral in both *L. lateseptatum* and *L. affine*. (The higher septal counts in *L. affine* and *L. lateseptatum* as compared to *L. martini* are a result of the peripheral increase, see p. 98). However *L. affine* does not occur at the correct stratigraphical horizon for this evolutionary link to be possible; it first appears after *L. lateseptatum*, so unless examples of the species can be found lower in the Visean, it must be regarded as the development of peripheral increase in the *L. martini* lineage for the second time.

However, it should be pointed out that certain features of the species do throw some doubt on its affinities with the *Lithostrotiontidae*. First, is the occurrence of both lateral and peripheral increase in a columellate fasciculate species. Secondly, the lack of dilation of the inner dissepiments, and the inability of the minor septa to reach the tabularium are uncharacteristic of the *Lithostrotiontidae*. Finally, its high statigraphic occurrence makes it difficult to fit into the phylogeny of the group.

L. proliferum, a junior synonym of *L. affine*, was first described by Thomson and Nicholson (1876) as a species of *Koninckophyllum*. It may be that *L. affine* is, after all, related to that genus; more work is needed to solve this problem.

Stratigraphical Range: Undetermined.

Note on the columellate fasciculate species

The descriptions of the columellate fasciculate Lithostrotion species refer to the mature adult corallites in the coralla of these species. Certain of these species (L. martini, L. variabile, L. irregulare and L. pauciradiale), however, show peculiarities in that some coralla of these species may possess a few corallites with a morphology different to that described for the species. This is a result of the phenomena of stunting that appeara to be very common in these four species. Certain corallites in the coralla of these species fail to reach the adult dimensions of the species and remain throughout their length in a suspended immature state. This stunting takes place at various stages in the ontogeny of the corallites so that a number of different 'types' of corallite may exist in one corallum.

Now as the species L. martini, L. variabile, L. irregulare, L. pauciradiale and L. junceum evolve from eabh other respectively by the process of neoteny, the morphology of the mature corallites of L. variabile, L. irregulare, L. pauciradiale and L. junceum represents successively earlier stages in the ontogeny of L. martini. Likewise, the morphology of L. irregulare, L. pauciradiale and L. junceum represents successively earlier stages in the ontogeny of L. variabile, etc.

Thus the immature stunted corallites of L. martini will appear identical to the mature corallites of L. variabile, L. irregulare, L. pauciradiale and L. junceum respectively.

In addition some corallites occur being the same size as L. junceum, but retaining the dissepiments. I have only been seen such corallites as stunted individuals in the larger species, and hever as a true species on their own, but these may be identical to L. junceum bigenerum (p.153) the smallest fasciculate species as yet described.

The stunted corallites occurring in these fasciculate species can thus be divided into a number of different 'types':

(a) variabile type corallites (20 - 24 septa, 2 - 3 dissepiments)

(b) irregulare type corallites (20 - 24 septa, 1 dissepiment)

(c) pauciradiale type corallites (17 - 20 septa, 1 dissepiment)

(d) bigenerum type corallites (14 - 17 septa, 1 dissepiment)

(e) junceum type corallites (14 - 18 septa, no dissepiments)

Coralla of L. martini have been collected high in the S1 Subzone containing types 'a', 'b' and 'c' (plus normal mature L. martini corallites). Coralla of L. variabile have been collected in D1 and D2 containing types 'b', 'c', 'd' and 'e'. (The name of this species is derived from this phenomena). Coralla of L. irregulare have been collected containing types 'c', 'd' and 'e', and coralla of L. pauciradiale have been collected in D2 containing types 'd' and 'e'. This seems to be a common occurrence in the fasciculate columellate lineage and the stunting in the larger species always occurs just before the smaller species appears (i.e. stunting in L. martini producing corallites of variabile type occurs at the top of S1 and L. variabile evolves as a true species also at the top of S1 or at the base of S2). This type of phenomena where the environment produces phenotypes identical to later genotypes occurs in other lineages in the Lithostrotiontidae, i.e. non-columellate, diphymorphic corallites appear in columellate Lithostrotion species, and the discussion on p.45 considers whether these phenotypes can have any bearing on the evolution of the later species.

Such a phenomena can be very confusing and it is thus not advisable to identify a species on the evidence of a single corallite. For example L. pauciradiale does not evolve until D1 and yet pauciradiale type corallites can occur as low as S1 (in the Ash Fell Sandstone). A number of corallites are needed for an accurate identification and the species must be identified according to the most mature corallite present in the corallum.

It was this phenomena that confused Phillips in 1836 when he chose as a type specimen of L. irregulare an irregulare type corallite of L. martini from the Ash Fell Sandstone (p.162).

Lithostrotion lateseptatum (McCoy)

(Plates 43 - 45.)

1845 *Diphyphyllum concinnum* Lonsdale, in Murch., Vern., Keys, 'Russ and the Ural Mountains', vol.1, p.624, pl.A, fig.4.

1849 *Diphyphyllum lateseptatum* McCoy, Ann. Mag. Nat. Hist., ser.2, vol.III, p.8.

1850 *Diphyphyllum concinnum* Lonsdale, D'Orbigny, Prod. de Palaeont., p.159.

1851 *Diphyphyllum lateseptatum* McCoy, 'Brit. Palaeoz. Foss.', p.88, pl.IIIc, fig.10.

1851 *Lithostrotion* (?) *concinnum* (Lonsdale), Milne-Edwards and Haime, 'Pol. Foss. des Terr. Pal.', p.446.

1852 *Lithostrotion* (?) *concinnum* (Lonsdale), Milne-Edwards and Haime, 'Mon. Brit. Foss. Corals', Pal. Soc., p.195.

1883 *Diphyphyllum concinnum* Lonsdale, Thomson, Proc. Phil. Soc. Glasg., vol.XIV, p.384, pl.VIII, fig.2.

1883 *Diphyphyllum approximatum* Thomson, *Ibid*., vol.XIV, p.385, pl.VIII, fig.1.

1887a *Diphyphyllum concinnum* Lonsdale, Thomson, Q.J.G.S., vol.43, p.35, pl.IV, fig.1.

1887a *Diphyphyllum lateseptatum* McCoy, Thomson, *Ibid*., vol.43, p.37, pl.V, fig.6.

1887a *Diphyphyllum lateseptatum* var. *giganteum* Thomson, *Ibid*., vol.43, p.37, pl.V, figs 7, 8.

1887a *Diphyphyllum lateseptatum* var. *interruptum* Thomson, *Ibid*., vol.43, p.37, pl.V, fig.9.

1928 *Diphyphyllum lateseptatum* McCoy, Smith, Ann. Mag. Nat. Hist., ser.10, vol.1, pl114, *partim*; i.e. *non Diphyphyllum* .

1930 *Lithostrotion* sp. {*Diphyphyllum concinnum*}(Lonsdale) , Smith and Lang, *Ibid*., ser.10, vol.V, p.180.

1930 *Lithostrotion* sp. {*Diphyphyllum lateseptatum*}(McCoy) , Smith and Lang, *Ibid*., ser.10, vol.V, p.181, pl.VII, figs 1-4.

1940 *Diphyphyllum lateseptatum* McCoy, Hill, 'Mon. Carb. Rug. Corals Scotland', p.184, pl.X, figs 14, 15.

1940 *Diphyphyllum ingens* Hill, *Ibid*., p.186, pl.XI, figs 2, 3.

Diagnosis: Non-columellate fasciculate *Lithostrotion*; mature corallites with 26 - 28 septa, super-mature corallites with 29 - 34 septa, dissepiments in 2 - 3 rows. Strong dilation of the inner dissepiments and of the septa in the tabularium. Tabulae in two series of the β type with a pseudo-aulos.

Type Material: Holotype is Sedgwick Museum specimen no. SM.A2409.

Material: Ashfell Sandstone, Smardale, Kirkby Stephen, Cumbria; Peghorn Limestone, Fell End, Clouds, Kirkby Stephen; Peghorn Limestone, Low Whiterigg, Clouds, Kirkby Stephen; Peghorn/Smiddy Limestone, Birkett Hill, Nateby, Cumbria; Gayle Limestone, Mill Gill, Askrigg, Wensleydale; Hardraw Scar Limestone, West House, Wensleydale; Simonstone Limestone, Whernside Pasture, Kettlewell, Wharfedale; Middle Limestone, Dry Park Gill, Whernside, Kettlewell; Great Limestone, Weardale.

Description: Internal Characters; The different corallites of any one colony of this species are very variable in diameter (and hence in all other characters) due to the prevalence of axial increase. This means that the majority of corallites seen in any one transverse section may be immature as no sooner does a corallite reach maturity than it divides again into two, three or four new corallites.

The diameter of a mature corallite varies in different coralla from 8 mm. to 12 mm., but just before budding there is a sudden increase to a super mature diameter of 9 - 14 mm. The small buds are approximately 5 - 6 mm. in diameter. (The total mean diameter of this species is 8.7 mm., this figure including both mature and immature corallites).

In this species the mature number of septa varies from 26 to 28 and the super mature number of septa varies from 29 to 34. The maximum number of septa in any colony of this species thus varies from 28 to 34. Immature buds just after splitting from the parent may have only 20 septa. The major septa are usually quite short in this species as the species has evolved along the diphyphylloid trend by losing its columella and by the septa becoming amplexoid. They usually only extend from the epithecae less than half the radius of the corallite coming to an abrupt end in the outer regions of the tabularium when they abut on to the downturned edges of the inner series of tabulae. The axial ends of the major septa are thus connected in transverse section by these tabulae and a pseudo-aulos is formed. As the major septa are short the pseudo-aulos is quite wide in proportion to the diameter of the corallite. In a corallite 9 mm. in diameter the pseudo-aulos is 4.5 mm. wide. However in some colonies the tabulae fail to develop the superimposed downturned edges and so the septa do not abut against them but extend almost to the centre of the corallite. The minor septa are only half the length of the major septa extending just into the tabularium. Both orders of septa are somewhat dilated and unlike other fasciculate Lithostrotion species this dilation of the septa is in the tabularium as opposed to the dissepimentarium. Septa are often quite thin in the dissepimentarium. Also the inner series of dissepiments are dilated, this zone of dilation merging with the thickening of the septa. The dilation of the septa in the tabularium is a characteristic feature of this species.

Dissepiments are in two or three series and are concave inwards and concentrically arranged. The inner series defines a tabularium with a mean diameter of 6.9 mm. although this is also variable depending on the state of maturity. In a super mature corallite it can be up to 10 mm. while in an immature corallite just after splitting it is only 5 mm. The size of the tabularium in mature corallites is approximately the same as the mean.

The tabulae are of the β type (p. 15) and a pseudo-aulos is therefore formed. The inner tabulae are horizontal in the axial region, but slope almost vertically peripheral to the axis where they rest on the tabulae below. The vertical sides of the downturned tabulae form the tube of the pseudo-aulos. The outer series are sub-horizontal.

In early members of this species the points of contact of the downturned edges onto the tabulae below are not particularly well aligned vertically and so the pseudo-aulos is poorly developed.

Discussion: D. lateseptatum was first described by McCoy in 1851. He differentiated it from the earlier described species D. concinnum Lonsdale (1845) only on the greater proportional width of its tabularium.

This is now not considered an important specific character and so the two are probably synonymous, and the species should really be known as *L. concinnum*. However the type specimen of *D. concinnum* is lost and so it is impossible to be absolutely sure of the synonymy and so it is best to allow *D. concinnum* to lapse as a *nom dubium*. *D. lateseptatum* is, after all, by far the most widely used and better known name

Moreover, although *D. concinnum* was originally the genotype of *Diphyphyllum*, when the type was lost Smith and Lang (1930, p.180) re-based *Diphyphyllum* on *D. lateseptatum*.

Thomson (1887) described *D. lateseptatum* var. *giganteum* and *D. lateseptatum* var. *interruptum*. However his conception of spedific characters was rather narrow and these varieties are not here recognised as being significantly different from the type.

Similarly *D. ingens* Hill (1940) may just be a large variety of *L. lateseptatum*.

This species is the largest of all the diphyphylloid species. It is most similar to *L. furcatum* and there are certain problems in distinguishing these spedies (p. 96). While the mature number of septa in *L. furcatum* and *L. lateseptatum* are sufficiently separated, they are still close enough for a supermature quadripartite corallite of *L. furcatum* to have more septa than a bipartite corallite of *L. lateseptatum*. However, using the means of the septa it is easier to distinguish the species. In *L. lateseptatum* the majority of corallites will have a high number of septa (26 - 34) as both mature and supermature corallites have this number of septa, whereas in *L. furcatum* only a minority of corallites will have the high number of septa as it will only be the few supermature corallites that support this number of septa, the mature corallites having only the low ancestral number of septa (22 - 24).

Statistical Results:

R. = 28 - 34.

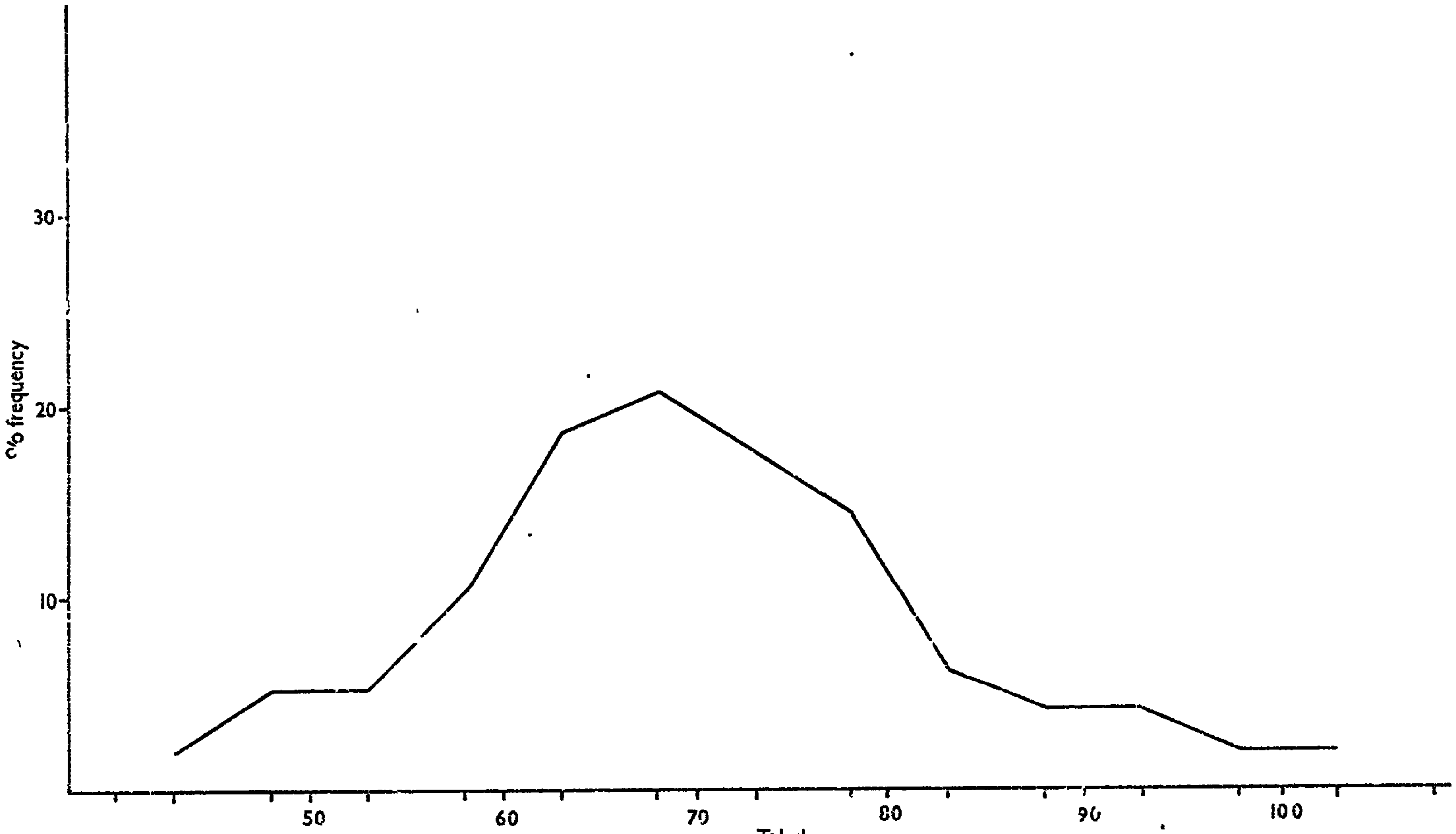
M.D. = 8.76 mm.
S.D. = 2.65 mm.
max.D. = 13.6 mm.
min.D. = 6.0 mm.

M.T. = 6.92 mm.
S.D. = 1.36 mm.
max.T. = 10.3 mm.
min.T. = 4.0 mm.

Stratigraphical Range: Top of S1 to base of Namurian (Great Limestone).

FIGURE 52

Plot of tabularium diameter against percentage frequency in *L.lateseptatum*. Intervals in mm's.



Tabularium

fig 52

Lithostrotion furcatum (Hill)

(Plates 39 - 42.)

1887a *Diphyphyllum concinnum* var. *furcatum* Thomson, Q.J.G.S., vol.43, p.36, pl.IV, fig.2.

1940 *Diphyphyllum furcatum* Thomson (sic), Hill, 'Mon. Carb. Rug. Corals Scotland', p.185, pl.X, fig.16, pl.XI, fig.1.

Diagnosis: Non-columellate fasciculate *Lithostrotion*; mature corallites with 22 - 25 septa, super mature corallites with 26 - 30 septa, dissepiments irregular in 2 - 3 rows. Dilation of septa and dissepiments is poorly developed. Tabulae in two series of the β type, but they are often irregular and a pseudo-aulos is rarely formed.

Type Material: Lectotype is specimen KMT2002 in Kelvingrove Museum, Glasgow. Includes transverse and longitudinal thin sections.

Material: Great Scar Limestone, Aysgarth lower falls, Wensleydale; Gayle Limestone, Mill Gill, Askrigg, Wensleydale; Hardraw Scar Limestone, Semerwater, Wensleydale; Middle Limestone, N. of Roman Road, Semerwater; Middle Limestone, Arn Gill, Askrigg; Middle Limestone, West Burton, Wensleydale; Middle Limestone, Scar Gill, Grange, Wensleydale; Middle Limestone, Quarry E. of Sargill gate, Askrigg; Middle Limestone, Mill Gill, Askrigg; Undersett Limestone, Blue Scar, Woodhall, Wensleydale; Middle Limestone, Birks Gill, Swaledale; Simonstone Limestone, Whernside Pasture, Kettlewell, Wharfedale; Middle Limestone, Middlesmoor Pasture, Kettlewell.

Description: Internal Characters; Although this species, like *L. lateseptatum*, shows axial increase there is not such a great variation in diameter in any one colony as the young buds tend to reach maturity fairly quickly. The corallites are somewhat smaller in diameter than *L. lateseptatum*, the diameter of a mature corallite varying from 6.5 to 7.5 mm. but immediately prior to budding corallites may increase to a super mature diameter of 8 - 8.5 mm. The mean diameter of the species is 6.5 mm., this figure including both mature and immature corallites.

The number of septa is also somewhat lower than in *L. lateseptatum*. The mature number of septa for this species is only 22 to 25. However, a minority of super mature corallites in any colony will have from 26 to 30 septa. The major septa are quite short only extending a half to a third the radius of the corallite. Unlike the other three non-columellate species however they do not come to an abrupt end abutting on to the downturned edges of the tabulae. The inner series of super-imposed domed tabulae is not so well developed and does not form a continuous pseudo-aulos with any degree of consistency. Only a weak structure is formed and the septa usually pass through it. Minor septa are about half the length of the major septa, just penetrating the tabularium. As with *L. lateseptatum* the major septa are somewhat dilated in the tabularium and the inner row of dissepiments may also dilate and fuse with the dilation of the septa, but this feature is rarely well developed and so strong as in *L. lateseptatum*. Moreover, dissepiments are never so regularly organised in this species as in the latter, the inner row not forming so perfect a circle as in *L. lateseptatum*, and the outer rows often being unequally developed in different parts of the corallite.

Dissepiments are in 2 - 3 series but the younger individuals may have only a single row and hence appear identical to *L. fasciculatum*. The inner row of dissepiments defines a tabularium with a mean diameter of 5.3 mm.

The tabulae are the same as in *L. lateseptatum*, but the pseudo-aulos is rarely formed.

Discussion: This species was first described by Thomson in 1887 as a variety of *D. concinnum* (= *L. lateseptatum*) but was not raised to specific level until 1940 by Hill. Hill cites Thomson as the author of the species, but according to the Rules of Nomenclature (Secretary's report, Paris Meeting, 1948) any infra-subspecific name (e.g. a variety) that is elevated to subspecific or specific rank by a subsequent reviser shall be attributed to the author by whom it was so elevated. Thus, Hill should be recognised as the author of this species.

This species can be distinguished from *L. fasciculatum* by having over one row of dissepiments. It is more similar to *L. lateseptatum*. See discussion of that species for distinguishing characteristics. In addition to the differences discussed in that section, the poorly developed pseudo-aulos and the irregular dissepiments give this species a much less organised and symmetrical appearance than *L. lateseptatum*.

Statistical Results:

R. = 26 - 30.

M.D. = 6.53 mm.
S.D. = 0.77 mm.
max.D. = 8.0 mm.
min.D. = 4.5 mm.

M.T. = 5.36 mm.
S.D. = 0.62 mm.
max.T. = 6.0 mm.
min.T. = 4.0 mm.

Stratigraphical Range: Base of D1 to top of Viséan.

FIGURE 53

Plot of tabularium diameter against percentage frequency in L.*furcatum*. Intervals in mm's.

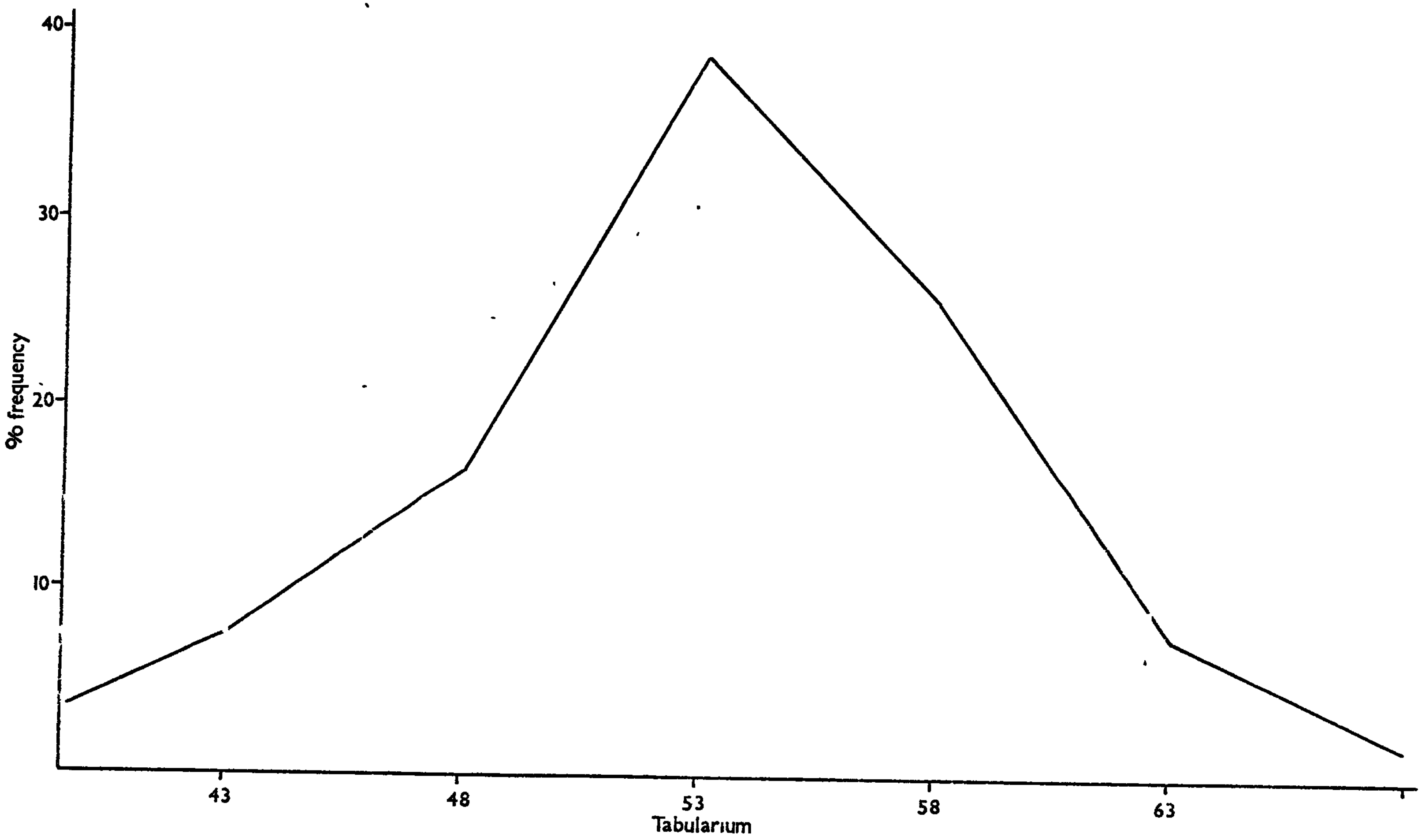


fig 53

FIGURE 54

Plot of corallite diameter against percentage frequency in L.furcatum. Intervals in mm's.

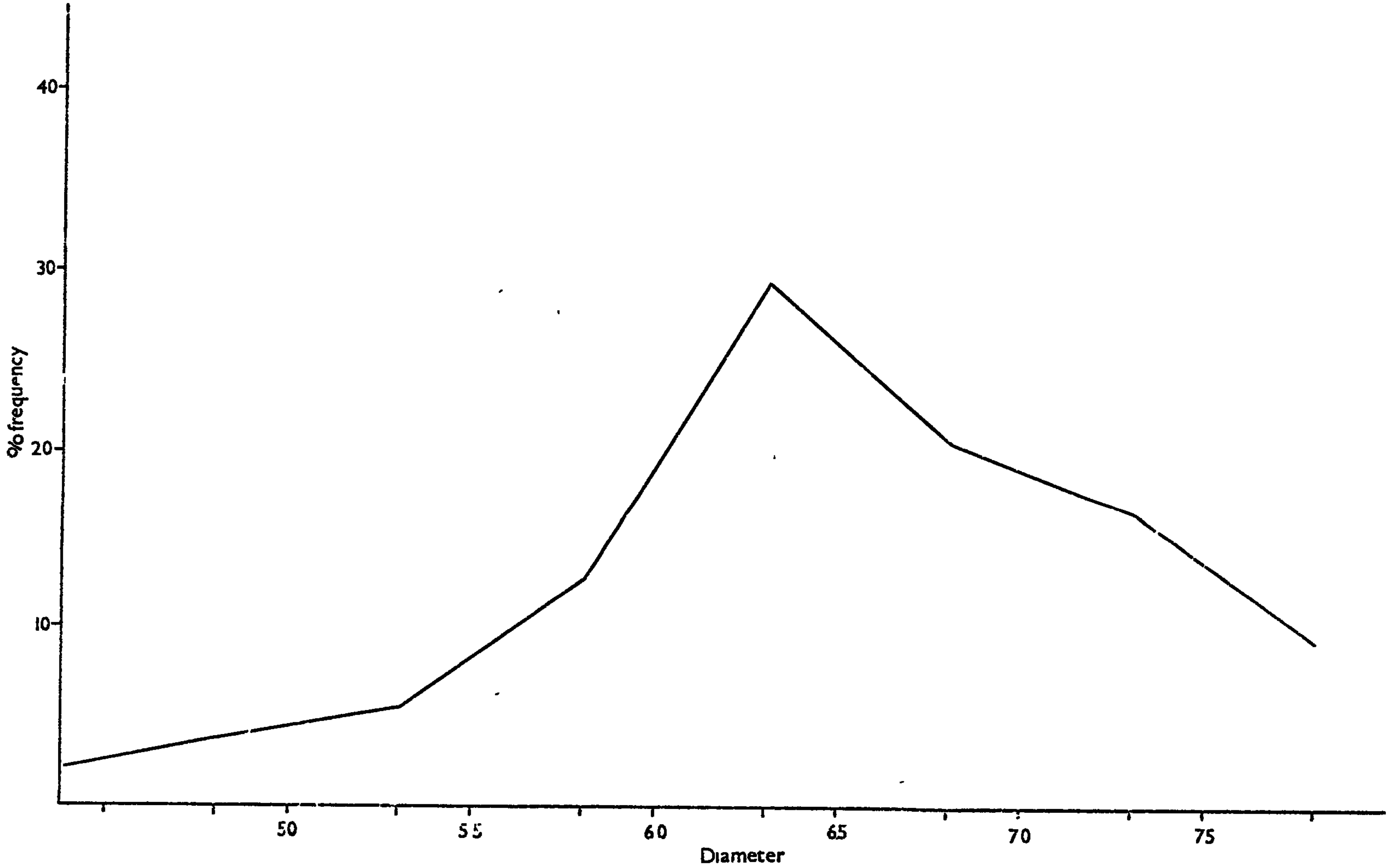


fig 54

Lithostrotion fasciculatum (Fleming)

(Plates 36 - 38.)

1828 *Caryophyllea fasciculata* Fleming, 'Hist. of Brit. Animals', p.509. (Non Lamarck homonym).
1843 *Lithodendron fasciculatum* (Fleming), Portlock, 'Geol. Rep. on Londonderry', p.335.
1876 *Lithostrotion irregulare* (Phillips), Thomson and Nicholson, Ann. Mag. Nat. Hist., ser.4, vol.XVII, pl.XV, fig.3. (Non *L. irregulare* Phillips).
1883 *Diphyphyllum interruptum* Thomson, Proc. Phil. Soc. Glasgow, vol.XIV, p.384, pl.VIII, fig.3. (Non *D. lateseptatum* var. *interruptum* Thomson 1887).
1883 *Diphyphyllum fasciculatum* (Fleming), Thomson, *Ibid*., vol.XIV, p.384.
1887a *Diphyphyllum Blackwoodi* var. *approximatum* Thomson, Q.J.G.S., vol.43, p.36, pl.IV, fig.4. (Non *D. approximatum* Thomson 1883).
1887a *Diphyphyllum Blackwoodi* Thomson, *Ibid*., vol.43, p.36, pl.IV, fig.3.
1887a *Diphyphyllum cylindricum* Thomson, *Ibid*., vol.43, p.36, pl.IV, figs 5,5a.
1887a *Diphyphyllum gracile* McCoy, Thomson, *Ibid*., vol.43, p.37, pl.V, fig.10. (Non *D. gracile* McCoy).
1930 *Lithostrotion* sp.{*Diphyphyllum fasciculatum*}(Fleming), Smith and Lang, Ann. Mag. Nat. Hist., ser.10, vol.V, p.183, pl.VII, figs 7, 8.
1940 *Diphyphyllum fasciculatum* (Fleming), Hill, 'Mon. Carb. Rug. Corals of Scotland' Pal. Soc., p.182, pl.X, figs 9-11, and ?12, 13.

But not:

1816 *Caryophyllia fasciculata* Lamarck, p.226, which is a recent coral.
1830 *Caryophyllia fasciculata*, De Blainville, p.311, which is *L. irregulare*.
1830 *Caryophyllia fasciculata*, Woodward, p.6 which is *L. irregulare*.
1836 *Lithodendron fasciculatum*, Phillips, p.202, pl.II, figs 16, 17, which is *L. martini* or *L. variabile*.
1842 *Caryophyllia fasciculata*, De Koninck, p.17, pl.D, figs 5a-c, pl.G, figs 9a-b, which is *L. martini*.
1845 *Lithodendron fasciculatum*, Lonsdale, which is *L. martini*.
1846 *Lithodendron fasciculatum*, Keyserling, p.170, pl.III, figs 2, 2a, 2b, which is *L. sociale*?
1846 *Cladocora fasciculata*, Geinitz, p.570, which is *L. martini*.
1850 *Diphyphyllum fasciculatum*, D'Orbigny, p.159, which is *L. martini*.
1851 *Siphonodendron fasciculatum*, McCoy, p.108, which is *L. irregulare*.
1887 *Lithostrotion fasciculatum*, Thomson, which is *L. martini*.

Diagnosis: Non-columellate *Lithostrotion*; mature corallites with 21 - 24 septa, super mature corallites with 25 - 28 septa and a single row of dissepiments.

Type Material: Lectotype chosen by Smith and Lang 1930 (p.184) as R.S.M. 1870. 14. 374. In Royal Scottish Museum, Edinburgh. From Skate Craig, Dunbar. Syntype is R.S.M. 1870. 14. 377.

Material: Simonstone Limestone, Whernside Pasture, Kettlewell, Wharfedale; Middle Limestone, Long Acres Quarry, Middleton Tyas, Yorkshire; Undersett Limestone, Blue Scar, Woodhall, Wensleydale; Undersett Limestone, Thackthwaite beck, Woodhall; Great Limestone, Harehope Quarry, Frosterley, Weardale; Great Limestone, Bollihope Burn, Frosterley; Great Limestone, Langdon Beck, Teesdale; Great Limestone, Sandales, Cockermouth.

Description: Internal Characters; As with L. lateseptatum the corallites in any colony show considerable variation in diameter due to the existence of axial increase in this species. The corallites are similar to those of L. furcatum but differ in having only one row of dissepiments. Hence they are slightly smaller in total diameter as the dissepimentarium is narrower. The mean diameter of this species is 4.8 mm. although this figure includes all corallites both mature and immature. The diameter of a mature corallite varies from 5 mm. to 6 mm. while the super mature diameter may rise to 6.5 mm. The diameter of new buds is only 3 mm.

The number of septa is similarly variable. The mature number of septa for this species is similar to L. furcatum varying from 21 - 25, and the super mature number just before splitting can be anything up to 29. The maximum number of septa in a colony, therefore varies from 21 - 29. Immature buds just after splitting from their parent have only about 15 septa. The major septa are usually quite short only extending half way to the centre of the corallite coming to an abrupt end in the tabularium as in L. lateseptatum when they abut on to the downturned edges of the inner series of tabulae. Thus as with L. lateseptatum a pseudo-aulos is formed in some corallites, the diameter of this being more than half the diameter of the corallite. Thus in a corallite 5 mm. in diameter, the pseudo-aulos will be approximately 3 mm. in diameter. The greater proportional width of the pseudo-aulos to the diameter in this species compared to L. lateseptatum (when it is only half the diameter) can be explained by the narrower dissepimentarium in this species. The ratio of the pseudo-aulos to the tabularium is approximately constant in all the diphyphylloid species. However the state of development of this structure is very variable from corallite to corallite.

The minor septa only just penetrate the tabularium and hence as the dissepimentarium is so narrow they are very short indeed, and in some of the smaller corallites, in their early stages of development, they are entirely absent.

The mature corallites of this species are identical in every respect to the small buds of the larger L. lateseptatum and thus L. fasciculatum also shows the dilation of the septa in the tabularium which is so characteristic of that species. Again the single row of dissepiments is also dilated and fuses with the thickening of the septa. Although there is only one complete row of dissepiments two rows may be sporadically developed in parts of some corallites.

The tabularium of the mature corallites is from 4 - 5 mm. In the majority of corallites there is no columella of any kind, but in a few individuals a weak axial structure can be observed in transverse section. However, this is never a persistent structure and in longitudinal section can be seen to consist merely of a series of spines on successive tabulae.

The tabulae are β tabulae as in L. lateseptatum, and the pseudo-aulos is usually well developed.

Discussion: When the name was first proposed by Fleming no attention was paid to the presence or absence of a columella and thus many references prior to 1845 (when Lonsdale first published Diphyphyllum) may refer to a columellate species of similar dimensions, either

L. pauciradiale, L. irregulare or L. martini.

This species is similar in number of septa to L. furcatum but can be distinguished by its single row of dissepiments. L. gracile also has one row of dissepiments but this species is smaller with correspondingly fewer septa, L. fasciculatum having from 21 - 29. However, septal number does not differ exclusively from L. gracile as this species can also have up to 24 septa (although only rarely). The difference between the two is however that in L. fasciculatum a majority of the corallites will have over 20 septa as both mature and super mature corallites support such numbers, whereas in L. gracile only the few super mature corallites will have over 20 septa, the majority (i.e. the mature corallites) having under 20 septa. This species therefore bears the same relationship to L. gracile as does L. lateseptatum to L. furcatum.

Statistical Results:

R. = 22 - 29

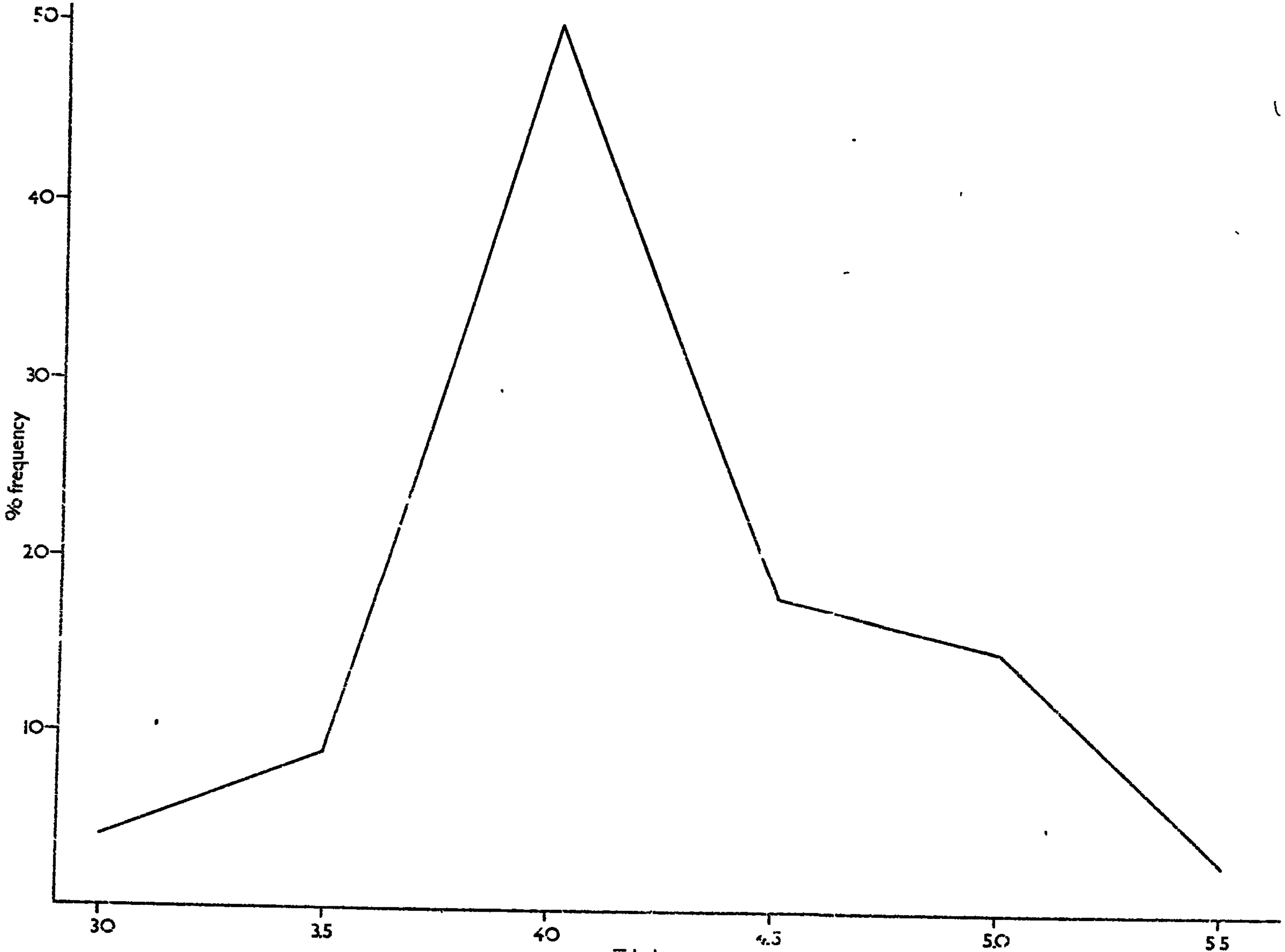
M.D. = 4.80 mm.
S.D. = 0.6 mm.
max.D. = 6.0 mm.
min.D. = 3.5 mm.

M.T. = 4.25 mm.
S.D. = 0.6 mm.
max.T. = 5.5 mm.
min.T. = 3.0 mm.

Stratigraphical Range: Tyne Bottom Limestone to base of Namurian (Great Limestone).

FIGURE 55

Plot of tabularium diameter against percentage frequency in L.fasciculatum. Intervals in mm's.



Tabularium
fig 55

FIGURE 56

Plot of corallite diameter against percentage frequency in *L. fasciculatum*. Intervals in mm's.

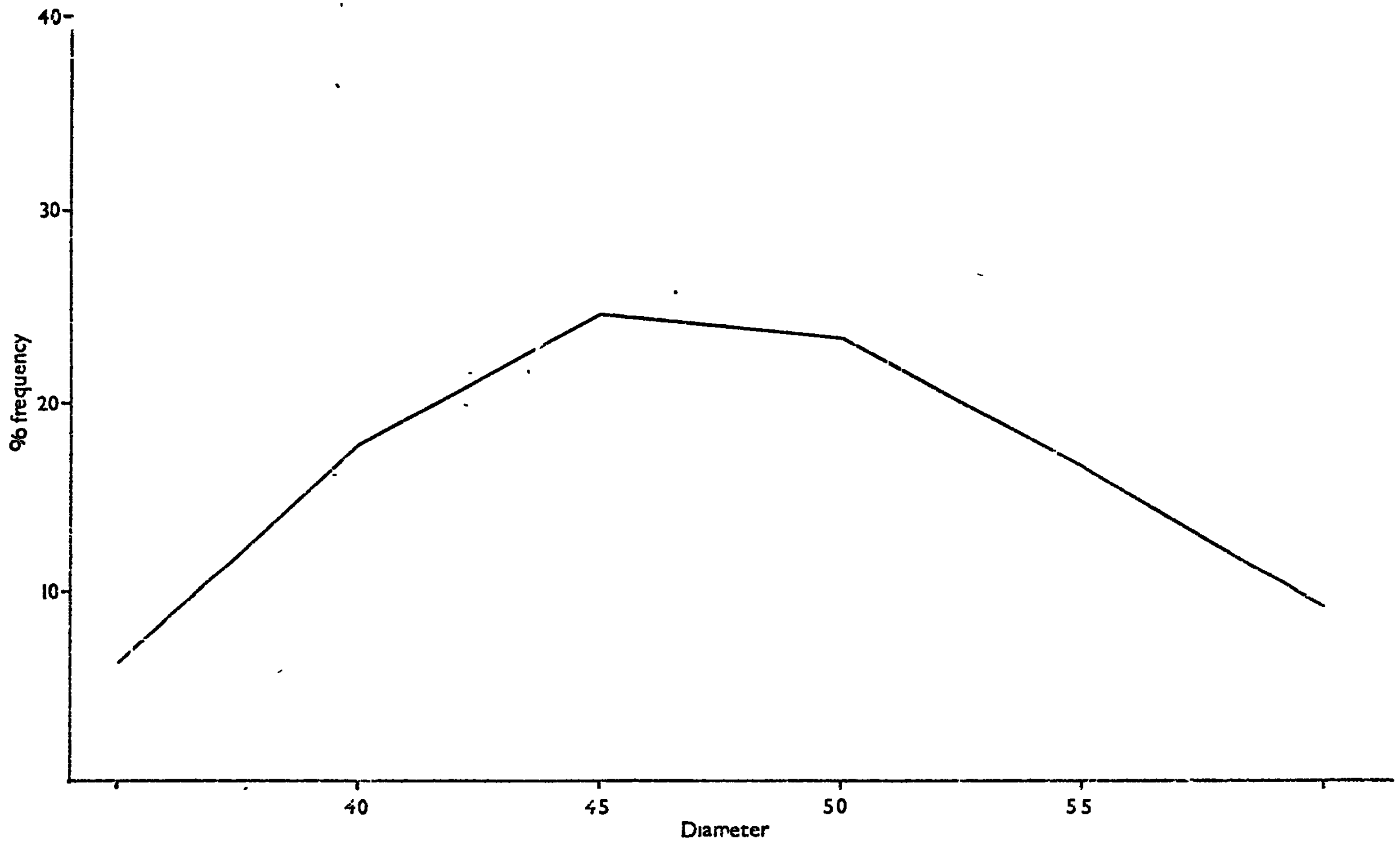


fig 56

Lithostrotion gracile (McCoy)

(Plates 33 - 35.)

1851a Diphyphyllum gracile McCoy, Ann. Mag. Nat. Hist., ser.2, vol.VII, p.168.
1851b Diphyphyllum gracile McCoy, 'Brit. Palaeoz. Foss.', p.88, text-figs d, e, f.
1930 Lithostrotion sp. {Diphyphyllum gracile}(McCoy), Smith and Lang, Ann. Mag. Nat. Hist., ser.10, vol.V, p.182, pl.VII, figs 5, 6.
But Not:
1887a Diphyphyllum gracile McCoy, Thomson, Q.J.G.S., vol.43, p.37, pl.V, fig.10, which is L. fasciculatum.

Diagnosis: Non-columellate Lithostrotion; mature corallites with 16 - 20 septa, super mature corallites with 21 - 22 septa (and occasionally 24). One row of dissepiments only.

Type Material: Holotype is Sedgwick Museum specimen No. A.2418 (includes A.2418b, c) thin sections). McCoys specimen is from the 'Impure limestone Lowick, Northumberland'. (= ?Dryburn = Great Limestone).

Material: Simonstone Limestone, Haw Bank, Woodhall, Askrigg, Wensleydale; Middle Limestone, West Burton, Wensleydale; Middle Limestone, Sargill, Grange, Wensleydale; Middle Limestone, Sar Gill, Grange; Undersett Limestone, Low Clint, Hardraw, Wensleydale; Main Limestone, High Clint, Hardraw; Main Limestone, Swinehaw bottom, Woodhall, Askrigg; Middle Limestone, Birks Gill, Swaledale; Middle Limestone, Dry Park Gill, Coverdale; Great Limestone, Harehope Quarry, Frosterley, Weardale; Great Limestone, Rookhope, Weardale; Middle Limestone, Long Acres Quarry, Middleton Tyas, Yorkshire; Lower Limestone group, Fife; 'Carboniferous', Cambois, Northumberland.

Description: Internal Characters; Again the corallites of any colony show considerable variation in diameter due to the existence of axial increase in this species. The corallites are smaller than those of L. fasciculatum but the mature corallites of this species are almost identical to the small buds of L. fasciculatum. The total mean diameter of this species is 3.2 mm., this figure including all corallites mature or immature. Moreover this species shows considerable variation from colony to colony, the total mean for different colonies ranging from 2.5 to 3.9 mm. The diameter of a mature corallite is usually from 3.5 to 4.5 mm., but they may be as low as 3.2 mm. or as high as 5.0 mm. in the super mature corallites. The young buds just after splitting from their parents range from 1 mm. to 2 mm.

The number of septa is similarly variable. The mature number of septa ranges from 16 to 20, while the super mature number of septa is 21 or 22 (and occasionally 24). Thus the majority of corallites in a colony will have under 20 septa with only a few super mature corallites supporting over 20 septa.

The major septa are short, only extending one-third or one-half the distance to the centre of the corallite, again coming to an abrupt end in the tabularium where they abut on to the pseudo-aulos. This pseudo-aulos is over half the diameter of the corallite. However, this structure is only formed perfectly in a few corallites, more usually some of the septa penetrate the tabularium to a certain degree. In some colonies the inner tabulae do not have well formed downturned edges and the septa can then extend close to the centre. The minor septa only just penetrate the tabularium and hence are very short. In the smaller corallites of this species some or maybe all of the minor septa may fail to develop, but some minor septa are usually present somewhere in every colony.

This species has one complete row of dissepiments but two rows can be developed in parts of the corallites. As with the minor septa, these dissepiments may be completely absent in some of the smaller corallites.

This species can show the same dilation of the dissepiments and the septa, as do the other diphyphylloid species, but it is rarely well developed. Also in those corallites in which the dissepiments have failed to develop the septa are dilated along their whole length.

The tabularium is approximately 3 mm. to 3.5 mm. in diameter although in the larger colonies it can be 4 mm.

There is never a continuous columella present but in a few corallites a discontinuous axial structure can be observed as small spines rising from the tabulae.

The tabulae are β tabulae as in L. lateseptatum, but the pseudo-aulos is not usually well developed.

Statistical Results:

R. = 18 - 24

M.D. = 3.67 mm.
S.D. = 0.54 mm.
max.D. = 5.0 mm.
min.D. = 2.5 mm.

M.T. = 3.01 mm.
S.D. = 0.46 mm.
max.T. = 4.0 mm.
min.T. = 2.0 mm.

Stratigraphical Range: Tyne Bottom Limestone to base of Namurian (Great Limestone).

FIGURE 57

Plot of tabularium diameter against percentage frequency in *L.gracile*. Intervals in mm's.

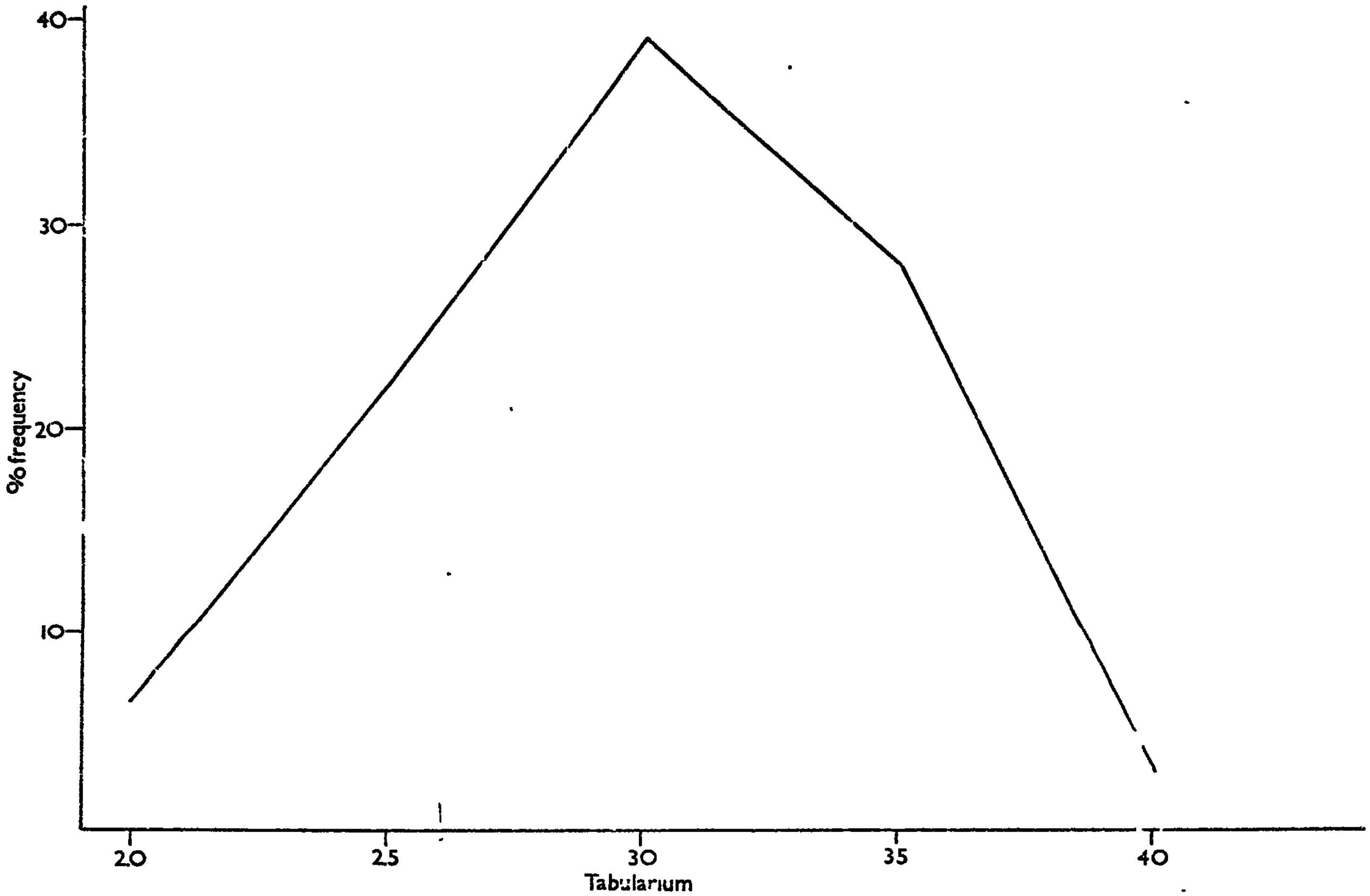


fig 57

FIGURE 58

Plot of corallite diameter against percentage frequency in *L.gracile*. Intervals in mm's.

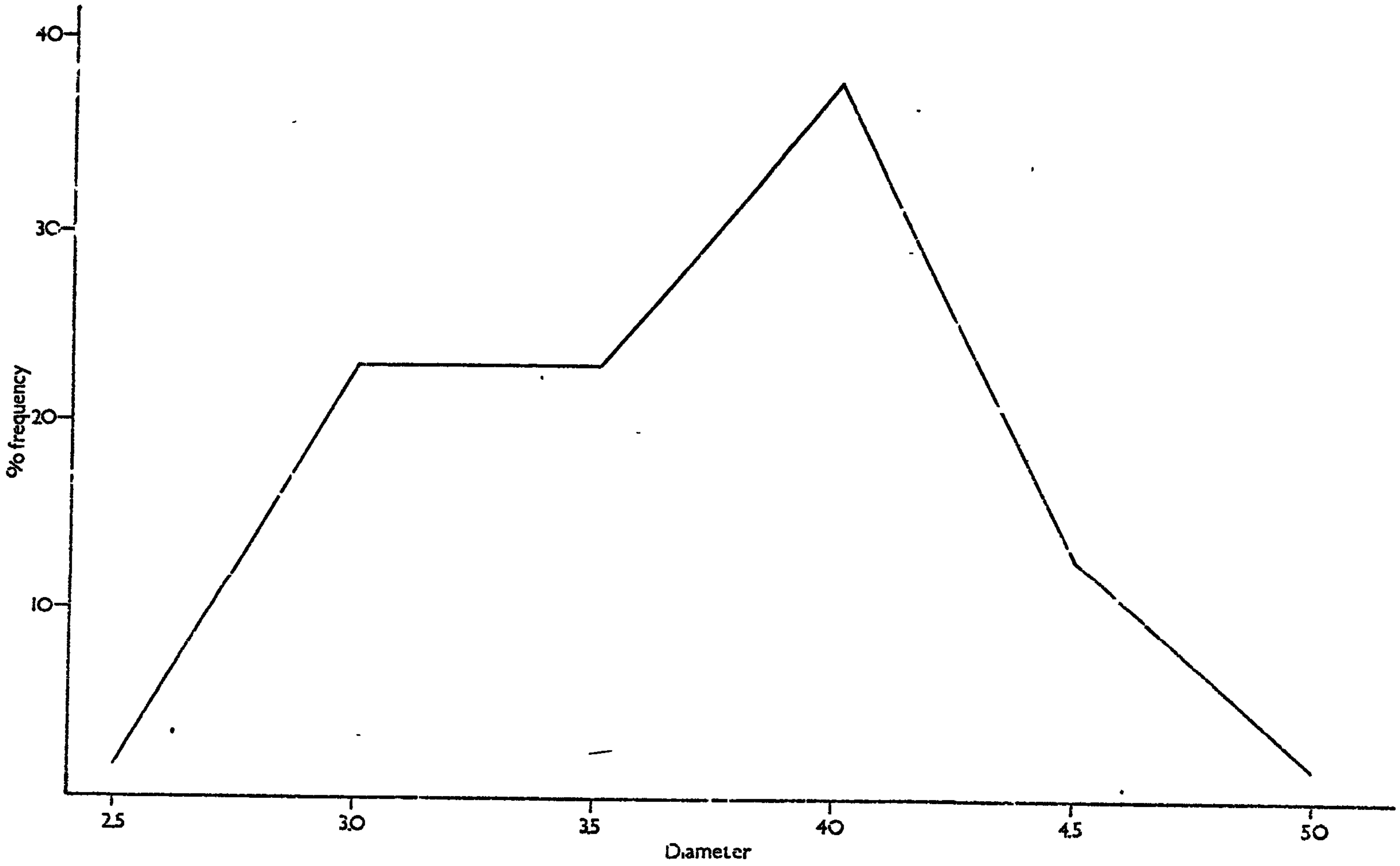


fig 58

Lithostrotion edmondsi (Smith)

(Plates 46 - 47.)

1928 Nemistium edmondsi Smith, Ann. Mag. Nat. Hist., ser.10, vol.I, p.116.

Diagnosis: Corallum compound and fasciculate. Corallites 5 - 6 mm. in diameter with 20 - 24 (25) septa, no columella, but an irregular axial structure consisting of an impersistent median plate with lamellae and taballae.

Type Material: Holotype is British Museum specimen no. R25488 (and section R25489 cut from it). From 'D2 Zone', Eskett Quarry, near Frizington, West Cumbria.

Material: Jew Limestone, Force Burn, Moor House Reserve, Alston; Jew Limestone, Upper Tees Section, Moor House Reserve; Jew Limestone, Moulds Meaburn, Cumbria.

Description: External Characters; In growth habit and gemmation L. edmondsi is almost identical to L. fasciculatum. Calices have not been seen.

Internal Characters; Major septa variable in length; some extend into the centre and become a part of the axial structure, others reach only about half way towards the centre. Minor septa only just penetrate the tabularium and as there is only a small dissepimentarium they are thus very short indeed. Both orders of septa are usually dilated andmay be quite considerably so. The specimen from Moor House Reserve, Alston, has very thick septa. Dilation is usually in the dissepimentarium.

There is never a true columella formed but instead a loose and irregular axial structure which is a diggnostic character of the species. This consists of a thin, irregular and inpersistent medial plate which may be continuous but usually arises from successive tabulae and does not reach the tabulae above. Radiating from this plate are a few lamellae and these may be connected by steeply inclined concentrically arranged tabellae. None of these elements are particularly persistent and while the axial structure is sometimes continuous it is just as often absent altogether in some corallites. More usually the vertical elements arise from the distal surfaces of the tabulae without reaching the tabulae above. The structure is thus very variable even within one corallite.

The tabularium of this species is similar to L. irregulare and L. fasciculatum, that is from 3.5 - 5 mm. and septal numbers are also similar, the maximum number of septa in a colony varying from 20 - 24 (25).

The tabulae are divided into two series as in the diphyphylloid species of Lithostrotion, an inner and an outer series. The inner series are strongly arched and are superimposed on one another so that their sides form a vertical tube running down the length of the corallite. The outer tabulae connect this tube to the dissepimentarium and are usually inclined downwards. The tube formed by the inner tabulae is a pseudo-aulos and the major septa abut against it rarely penetrating it. Thus in those corallites with a strong pseudo-aulos few septa actually reach the axial structure.

The dissepimentarium is very narrow. Usually there is only one row of dissepiments although there may be two or three rows formed in parts of a corallite. All dissepiments are concave and the inner row is usually very thickly dilated as are the major septa passing through this dissepiment. In some colonies (i.e. the holotype) the dissepiments may fail to develop at all in some corallites or in parts of corallites.

Corallites are from 5 - 6 mm. in diameter and are defined by an epitheca~~e~~ which is usually slightly dilated.

As in all the non-columellate species budding is parricidal and usually peripheral.

Discussion: The reasons behind the rejection of the genus Nemistium are given on p. 27.

In his description of the species Smith (1928, p.116) states that in the larger examples of this species the corallites may be 9 mm. in diameter and have up to 30 septa. In this respect he quoted two coralla, first a specimen from Ward Hall East Quarry, Aspatria, Cumbria, which he figured (loc. cit., p.118, pl.V, fig.1) and secondly a specimen from Brynhyfryd Quarry, Kidwelly, Wales (loc. cit., p.118). However, the figured colony never has more than 25 septa and is not as large in diameter as it appears from Smiths drawing. The largest corallite is only 7 mm. in diameter as opposed to the 10 mm. suggested by Smiths stated magnification of X2 for the drawing. Secondly the specimen from Wales, which does have 30 septa, is not this species, but is a large non-columellate species, possibly L. furcatum.

L. edmondsi is identical in all respects except for the axial structure to L. fasciculatum and L. irregulare.

Stratigraphical Range: Jew Limestone.

Note on the Genus *Orionastraea*

It has generally been considered by later workers that Hudson, in his revision of the genus *Orionastraea* (1929), may have rather oversplit the *Orionastraea* population describing too many species and varieties. The problem has been that every intermediate form between Hudson's 'species' has been observed and thus led to confusion over correct identification. It is therefore pertinent to explain at this point a few facts concerning such intermediate forms. If the fossil record were perfectly preserved one would expect, as one traced the evolution of a species with time, that every intermediate between that species and a later chronospecies would be found. Divisions between such artificially designated chronospecies are always arbitrary and so some sort of convenient division would have to be drawn between the two chronospecies so that they could be separated and therefore identified. It is quite acceptable to do this as the two delineated chronospecies occupy two distinct horizons, the later evolving species occurring at a higher horizon than its ancestor and thus can be separated exclusively by time if not by morphology. Howevef, one may also find such intermediate fomms between two other 'species' occurring at one geological horizon. In this case the intermediates do not represent an evolving lineage from one species to another. They merely represent a continuous variation at one point in time, i.e. a continuous gene pool, and thus the two 'species' are in fact only end members of a continuous population. Thus in this case the two species can only be regarded as subspecies as they do not occupy exclusively distinct horizons but occur together in one bed.

In the revision of Hudson's species it may be advantageous to view his 'species' in the light of these facts.

Genus *Orionastraea* Smith, 1916

1828 *Tubipora*, Fleming, *partim*, p.529 (Not *Tubipora* L.)
1830 *Tubipora*, Woodward, *partim*, p.5 (Not *Tubipora* L.)
1841 *Astraea*, Phillips, *partim*, p.12 (Not *Astraea* Lam.)
1849 *Sarcinula*, McCoy, p.124 (Not *Sarcinula* Lam.)
1850 *Phillipsastraea*, D'Orbigny, *partim*, p.107 (Not *Phillipsastraea* *S.S.* D'Orb.)
1851 *Sarcinula*, McCoy, p.110 (Not *Sarcinula* Lam.)
1851 *Lithostrotion*, Milne-Edwards and Haime, *partim*, p.432 (Not *Lithostrotion* Fleming)
1851 *Phillipsastraea*, Milne-Edwards and Haime, p.447 (Not *Phillipsastraea* *S.S.* D'Orbigny)
1852 *Lithostrotion*, Milne-Edwards and Haime, *partim*, p.190 (Not *Lithostrotion* Fleming)
1852 *Phillipsastraea*, Milne-Edwards and Haime, p.203 (Not *Phillipsastraea* *S.S.* D'Orbigny)
1889 *Phillipsastraea*, Schafer, *partim*, p.401 (Not *Phillipsastraea* *S.S.* D'Orbigny)
1903 *Lithostrotion*, Vaughan, *partim*, p.106 (Not *Lithostrotion* Fleming)
1905 *Lithostrotion*, Vaughan, *partim*, p.199 (Not *Lithostrotion* Fleming)
1916 *Orionastraea*, Smith, p.294
1925 *Orionastraea*, Hudson, p.185
1926 *Orionastraea*, Hudson, p.145
1929 *Orionastraea*, Hudson, *partim*, p.441
1934 *Orionastraea*, Hill, p.90
1940 *Orionastraea*, Hill, p.187
1950 *Orionastraea*, Wang, *partim*, p.222
1952 *Orionastraea*, Lecompte, p.473
1956 *Orionastraea*, Hill, p.283
1964 *Orionastraea*, Yoh and Wu, p.102
1967 *Orionastraea*, Ivanovsky, p.33

But Not:
1924 *Orionastraea*, Garwood and Goodyear, p.219
1958 *Orionastraea*, Dobrolyubova, p.291
1970 *Orionastraea*, Kato and Mitchell, p.49

Diagnosis: Rugose corals resembling cerioid *Lithostrotion*, but having little or no epithecae in an astraeoid, thamnastraeoid, aphroid or indivisoid colony. Septa of adjacent corallites may be confluent, non-confluent, may retreat peripherally, or may be absent altogether. Tabularium diameter is from 2 - 3 mm. and there are between 20 and 36 septa.

Genotype: *Orionastraea phillipsi* (McCoy, 1849, p.125).

Discussion: Smith proposed *Orionastraea* in 1916 to include three species as follows: (1) *Orionastraea phillipsi* = *Sarcinula phillipsi* McCoy, 1849 = ? *Erismatolithus tubiporites* (*radiatus*) Martin, 1809

(2) *Orionastraea placenta* = *Sarcinula placenta* McCoy, 1849

(3) *Orionastraea ensifer* = *Lithostrotion ensifer* Edwards and Haime, 1851. Smith chose *O. phillipsi* as genotype.

The genus here excludes *O. ensifer* var. *matura* Hudson, (1929, p.445) and *O. magna* Kato and Mitchell (1970, p.49), which are assigned to the new genus *Hudsonia* (see p.235).

Stratigraphical Range: The genus appears at the top of D1 and persists to the middle of D2. (The highest specimen of *Orionastraea* so far recorded is from the Single Post Limestone. This marks the top of the *Orionastraea* Zone as designated by Hudson (1929, p.440)).

Orionastraea ensifer (Edwards and Haime)
(Plate 48, fig. 1.)

1851 Lithostrotion ensifer Milne-Edwards and Haime, 'Polypiers Fossiles des Terrains Paleozoiques', p.442.
1852 Lithostrotion ensifer Milne-Edwards and Haime, 'Monograph of the British Fossil Corals' Pal. Soc., p.193, pl.XXXVIII, figs 2 and 2a.
1889 Phillipsastraea radiata (Martin), partim Schafer, Geol. Mag., dec. 3, vol.vi, p.401-407, pl.XII, figs 2, 5 and ?6.
1903 Lithostrotion ensifer Milne-Edwards and Haime, Vaughan, Proc. Bristol Nat. Soc., n.s. vol.X, p.109.
1905 Lithostrotion ensifer Milne-Edwards and Haime, Vaughan, Q.J.G.S., vol.lxi, p.199.
1916 Orionastraea ensifer (Milne-Edwards and Haime), Smith, Ibid., vol.lxxii, p.301, pl.xxiv, figs 3, 4, 5.
1929 Orionastraea ensifer (Milne-Edwards and Haime), Hudson, Proc. Leeds Phil. Soc., vol.1, pt.IX, p.445.

But Not:
1887b Lithostrotion ensifer Milne-Edwards and Haime, Thomson, Trans. Edinb. Geol. Soc., vol.V, pt.III, p.387, pl.XI, fig.8.
1924 Orionastraea ensifer (Milne-Edwards and Haime), Garwood and Goodyear, Q.J.G.S., vol.lxxx, p.231, which is H. matura.
1929 Orionastraea ensifer var. matura Hudson, Proc. Leeds Phil. Soc., vol.1, pt.IX, p.445, pl.4 which is H. matura.

Diagnosis: Cerioid/astraeoid Orionastraea with very thin epithecae or discontinuous beaded epithecae, a stout 'lithostrotion' type of columella and 36 continuous septa often non-confluent.

Type Material: Edwards and Haime specimens from Bristol were preserved in the British Museum, but they are now lost. Thus a neotype was chosen by Smith (1917) as British Museum specimen R.17084 (in the S.G.Perceval Collection).

Description: External Characters, the corallum is depressed in the typical Orionastraea state and is cerioid/astraeoid. The distal surface shows shallow calices bounded by a beaded discontinuous epithecal wall. A columella is often present in these calices.

Internal Characters, The internal features of this species are for the most part identical to those of its ancestor, L. decipiens (see description of that species). The only significant point of difference is the fact that the epithecal wall dividing the corallites is thin and in places is incomplete. However, where this wall is present it has been observed that it is always a double walled structure, divisible into two halves, with a dark line running down the centre.

One significant point of difference between this species and later species of Orionastraea is that the minor septa are very short, rarely extending into the tabularium. This gives the impression that there is a paucity of septa in this species, but in fact there are from 14 - 18 septa of both orders (i.e. from 28 - 36 in total). The tabularium is roughly 3 mm. in diameter, as in L. decipiens.

Stratigraphical Range: Top of D1 to Jew Limestone.

Orionastraea phillipsi (McCoy)

(Plate 48, fig. 2. and Plate 49, fig. 1.)

?1809 *Erismatolithus tubiporites* (*radiatus*) Martin, 'Petrificata Derbiensia', pl.XVIII, figs 2 and 3. (This is *O. phillipsi*, *O. tuberosa* or *O. placenta*)
?1828 *Tubipora radiata* Fleming, 'A History of British Animals', p.529. (*O. phillipsi*, *O. tuberosa* or *O. placenta*)
?1830 *Tubipora radiata* Fleming, Woodward, 'A Synoptical Table of British Organic Remains', p.5. (*O. phillipsi*, *O. tuberosa* or *O. placenta*)
1841 'Specimen from the Mountain Limestone much allied to *Astraea hennahi* Lonsdale', Phillips, 'Palaeozoic Fossils etc.', p.12, pl.vii, fig.15D.
1849 *Sarcinula phillipsi* McCoy, Ann. and Mag. Nat. Hist., ser.2, vol.III, p.125.
1850 *Phillipsastraea hennahi* Lonsdale, *partim* D'Orbigny, 'Prodrome de Palaeontologie', vol.1, p.107.
1851 *Phillipsastraea radiata* (Fleming), *partim* Milne-Edwards and Haime, 'Pol. Foss. des Terr. Pal.', p.448.
1851 *Sarcinula phillipsi* McCoy, 'British Palaeozoic Fossils', p.110.
1852 *Phillipsastraea radiata* (Fleming), *partim* Milne-Edwards and Haime, 'Mon. of the Brit. Foss. Corals', Pal. Soc., p.203, pl.XXXVII, figs 2 and 2a.
1883 *Phillipsastraea radiata* (Fleming), Thomson, Proc. Phil. Soc. Glasgow, vol.XIV, p.394, pl.iv, figs 1, 1a, 1b and 2.
1916 *Orionastraea phillipsi* (McCoy), *partim* Smith, Q.J.G.S., vol.72, p.298, pl.XXIII, figs 1, 2 and 3. (Not figs 4 and 5 which are *O. tuberosa*). Pl.XXIV, figs 1 and 2.
1929 *Orionastraea phillipsi* (McCoy), Hudson, Proc. Leeds Phil. Soc., vol.1, pt.IX, p.444, pl.iv, fig.1.
1940 *Orionastraea phillipsi* (McCoy), Hill, 'Monograph of the Carboniferous Rugose Corals of Scotland', p.189, pl.XI, figs 4 and 5.
Note: *Phillipsastraea radiata* (Fleming) includes in all cases quoted *Sarcinnla phillipsi* and *Sarcinula placenta*.

Diagnosis: Plocoid *Orionastraea* with no epithecae, a swollen 'Lithostrotion' type columella and 36 continuous septa either confluent in thamnastraeoid colonies or non-confluent in astraeoid colonies.

Type Material: Lectotype chosen by Smith (1917) from McCoy's two syntypes as specimen A2188 in the Sedgwick Museum Cambridge (fig'd Smith 1917, Q.J.G.S., lxii, p.299, pl.23, fig.1). Specimen from Corwen, Merionethshire, N. Wales. Lectotype includes transverse section (cut from the specimen) with the same registration number, fig'd Smith 1917, Q.J.G.S., lxii, p.299, pl.23, fig. 2 and 5.

McCoy's second syntype is specimen A2189 in the Sedgwick Museum, Cambridge.

Material: Clints Quarry, Cleator, Cumbria. Pot Holes Limestone (D2).

Description: External Characters, The corallum is plocoid, either astraeoid or thamnastraeoid and is depressed in the typical Orionastraea state with a flat distal surface. The calices are often bounded by a sharply elevated border and are at variable distances apart. A columella is present and is often prominent in these calices. A holotheca covers the lower surface of the corallum with distinct growth banding. Internal Characters, The septa are divisible into two orders, major and minor, the major septa extending just into the tabularium whereas the minor septa and in the dissepimentarium. All of the septa are continuous to the septa of adjacent corallites and some of the septa are confluent, but this is not always the case. No distinction should be drawn between coralla with confluent and non-confluent septa, as both cases can be found in the same corallum. The septa are often dilated where they meet the innermost series of dissepiments. The maximum number of septa in a colony is always more than 30 and may be as high as 36.

Dissepiments are numerous filling the intervening space between the corallite centres. The innermost two or three series are always dilated and are concave towards the centre. The outer series are fine and may be concave or slightly convex towards the centre.

The characteristic feature of this species is its columella. This is dilated, usually continuous with the counter septum and often connected to many of the other major septa by radiating bars.

The tabularium varies from 2 - 3 mm. in diameter but is usually 2.5 mm. The distance between calices varies from 3.6 mm. to 7.8 mm., but is usually from 4.5 mm. to 6 mm.

Discussion: McCoy's name is used in preference to Fleming's as it is impossible to tell whether or not Martin's original figured specimen, upon which Fleming's species is based, has a columella or how many septa it supports. Edwards and Haime considered that is was columellate and hence called this species *Phillipsastraea radiata* but *P. radiata* might equally well be synonymous with *O. tuberosa* or *O. placenta*.

O. phillipsi can be distinguished from *O. ensifer* by its complete lack of epithecal wall, and from all other species of *Orionastraea* by the presence of a columella.

Stratigraphical Range: Base of D2 to Jew Limestone.

Orionastraea tuberosa (McCoy)

(Plate 49, fig. 2 and Plate 50, figs. 1 and 3.)

?1809 Erismatolithus tubiporites (radiatus) Martin, 'Petrificata Derbiensia', pl.XVIII, figs 2 and 3. (O. phillipsi, O. tuberosa or O. placenta)
?1828 Tubipora radiata Fleming, "A History of British Animals', p.529. (O. phillipsi, O. tuberosa or O. placenta)
?1830 Tubipora radiata Fleming, Woodward, 'A Synoptical Table of Brit. Org. Rems.', p.5. (O. phillipsi, O. tuberosa or O. placenta)
1849 Sarcinula tuberosa McCoy, Ann. Mag. Nat. Hist., ser.2, vol.III, p.124
1849 Sarcinula placenta McCoy, partim, Ibid., ser.2, vol.III, p.124. (i.e. those with '30 curved radii').
1851 Phillipsastraea tuberosa (McCoy), Milne-Edwards and Haime, 'Pol. Foss. des Terr. Pal.', p.449.
1851 Sarcinula tuberosa McCoy, 'British Palaeozoic Fossils', p.110, pl.IIIB, figs 8 and 8a.
1852 Phillipsastraea tuberosa (McCoy), Milne-Edwards and Haime, 'Mon. of the Brit. Foss. Corals' Pal. Soc., p.204.
1916 Orionastraea phillipsi (McCoy), partim Smith, Q.J.G.S., vol.72, p.298, pl.XXIII, figs 4 and 5. (Not figs 1, 2 and 3 which are O. phillipsi)
1916 Orionastraea placenta (McCoy), partim Smith, Ibid., vol.72, pl.XXIII, figs 8 and 9. (Not figs 6 and 7 which are O. placenta)
1929 Orionastraea tuberosa (McCoy), Hudson, Proc. Leeds Phil. Soc., vol.1, pt.IX, p.447, pl.iv, fig.3.
1929 Orionastraea edmondsi var. laciniosa Hudson, Proc. Leeds Phil. Soc., vol.1, pt.IX, p.447, pl.iv, fig.2.

Diagnosis: Plocoid Orionastraea with no epithecae, no columella, but only a prolongation of the thin counter septum which crosses the axial region. 30 - 34 continuous septa, either confluent in thamnastraeoid colonies or non-confluent in astraeoid colonies.

Type Material: Holotype specimen A2187 in the Sedgwick Museum, Cambridge (fig'd Smith 1917, Q.J.G.S., lxxii, pl.23, fig.4). Holotype includes transverse section with the same registration number (fig'd Hudson 1929, Proc. Leeds Phil. Soc., p.447, pl.4, fig.3). Specimen from 'Carb. Limestone, Derbyshire'.

Holotype of O. edmondsi var. laciniosa is specimen 27865 (and slides

PF2703-6) in I.G.S. Museum, Leeds.

Description: External Characters, The corallum is plocoid, either astraeoid or thamnastraeoid and is typically depressed with a holotheca covering its lower surface. The distal surface is usually flat although the holotype displays an exaggerated mammillate surface. The calices show no prominent columella.

Internal Characters, It is often difficult to distinguish between the major and minor septa as both are of similar lengths, both reaching just into the tabularium. They are often slightly dilated on their inner (axial) edges. The septa are continuous to the septa of adjacent corallites and may or may not be confluent. Maximum number of septa in a colony is always at least 30 and may be as high as 36.

As with *O. phillipsi* the innermost series of dissepiments are dilated and concave inwards whereas the outer series of dissepiments may be convex.

In fact this species is identical in all respects to *O. phillipsi* except that it lacks the diagnostic swollen columella. While most of the centres of corallites of *O. tuberosa* are empty, some do show a continuation of the counter septum into the axial region. This has been mistaken for a columella, but it is never dilated as is the columella of *O. phillipsi*.

Tabularium diameter is from 2.5 - 3 mm. and distances between corallites (counted in the holotype only) is from 8 - 10 mm.

Discussion: This species can be distinguished from *O. ensifer* by its lack of epithecal wall, from *O. phillipsi* from the lack of columella, from *O. edmondsi* by its continuous septa, and from all other species of *Orionastraea* by the septal counts of over 30.

Smith considered that the character on which this species was distinguished (i.e. its mammilated calicular surface) was not of specific importance and he considered this species synonymous with *O. phillipsi* as he thought that *O. tuberosa* had a columella. The present author agrees with Smith that *O. tuberosa* cannot be distinguished on the basis of its calicular surface, but close examination of the type of this species shows that it has no true columella, only an extension of one of the septa into the axial region. This projection is never dilated as is the true columella of *O. phillipsi*, but is of the type of structure seen in many other species of non-columellate *Orionastraea* species. Thus the present author thinks it better to merge *O. tuberosa* with *O. placenta*, at least on the basis of the columella.

However, there is an unfortunate problem concerning *O. placenta*. I am convinced that on publishing this name McCoy intended it to include all of the non-columellate species of *Orionastraea* with continuous septa. However, I have observed that this group of corals can be divided into two types, as all those occurring above the base of the Tyne Bottom Limestone have under 30 septa while the majority of those below this boundary have over 30 septa, only a minority having under 30 septa. McCoy was collecting his specimens in rocks older than this boundary and therefore the majority of those that he collected and called *S.* (=*O*) *placenta* would have over 30 septa. Many later authors have followed this and also applied this name to those corals with over 30 septa, and indeed McCoy in his original description of the species (1849, p.124-5) said that there were "about 30 curved radii". However, in choosing his type specimen he was unfortunate in choosing one which was not the 'norm' in these older rocks, i.e. one of the small minority having only 25 septa. He clearly realised this and in his work of 1851 when he revised the species he gave an almost identical description of it but amended the figure '30' to '25' and figured this type specimen (pl.3B, fig.9). According to the Rules of Nomenclature we must interpret the species on the holotype, now in the Sedgwick Museum, Cambridge, and not on his original description. Therefore we must use the name *O. placenta* to include those forms with under 30 septa, even though McCoy probably originally intended the name to refer mostly to those with over 30 septa. We must also look for a new name for the larger forms. We have already stated that *O. tuberosa* is identical to *O. placenta* on the basis of its lack of its columella but the type of this species does have over 30 septa and therefore we can revive the name *O. tuberosa* to apply to the non-columellate species with over 30 continuous septa. It is interesting to note in this respect that Smith in a note upon the holotype of *O. placenta* (1916, p.301) did observe, "that the thecae are somewhat smaller than in the average examples, and the number of septa correspondingly less - about 25".

Hudson (1929) also thought that this species had a columella, but he still distinguished it from *O. phillipsi* as the type of *O. tuberosa* has non-confluent septa, whereas *O. phillipsi* has confluent septa. However, this is not thought to be an important specific character in this case as all intermediate conditions between confluent and non-confluent septa can be found in both the columellate *O. phillipsi* and the non-columellate *O. tuberosa*. While the astraeoid colony is probably more primitive, the thamnastaeoid colony must have developed very quickly in this group as both types of colony are found even at the first appearance of the species, and both persist throughout the range of the species. (In other species the confluence of the septa may be a useful specific character if the different colony types occur at exclusively different horizons.)

Hudson (*loc. cit.*) also described *O. edmondsi* var. *laciniosa* which has 30 septa, the same as *O. edmondsi*, but different in having continuous septa, whereas *O. edmondsi* is aphroid. Hudson was of the opinion that this variety differed from *O. tuberosa* as he thought that *O. tuberosa* had a columella, whereas *O. e. laciniosa* had not. However, as *O.* tuberosa also is non-columellate, the only difference between these two taxa is the supposed non-confluence of the septa in *O. tuberosa*. This we have already stated is not important in this species and so

O. e. laciniosa is synonymous with *O. tuberosa*.

Although *O. tuberosa* is distinguished from *O. placenta* on the number of septa, when the species first appear there is continuous variation between them from 20 - 36 septa. There is no discontinuity in this variation and therefore the two species were still capable of interbreeding. Thus they are not true biological species. However, as stated previously, above the base of the Tyne Bottom Limestone no forms are found with over 30 septa, only the smaller types occur here. Thus there is a vertical discontinuity between the two groups and they can thus be regarded as chrono-species.

Stratigraphical Range: Undetermined.

Orionastraea placenta placenta (McCoy)

(Plates 51 - 54.)

?1809 Erismatolithus tubiporites (radiatus) Martin, 'Petrificata Derbiensia', pl.XVIII, figs 2 and 3. (O. phillipsi, O. tuberosa or O. placenta)
?1828 Tubipora radiata Fleming, 'A History of British Animals', p.529. (O. phillipsi, O. tuberosa or O. placenta)
?1830 Tubipora radiata Fleming, Woodward, 'A Synoptical Table of Brit. Org. Rems.', p.5. (O. phillipsi, O. tuberosa or O. placenta)
1849 Sarcinula placenta McCoy, partim, Ann. Mag. Nat. Hist., ser.2, vol.III, p.124. (i.e. Not those with, "30 curved radii")
1851 Sarcinula placenta McCoy, 'Brit. Pal. Fossils', p.110, pl.IIIB, figs 9, 9a and 9b.
1851 Phillipsastraea radiata (Fleming), partim, Edwards and Haime, 'Pol. Foss. des Terr. Pal.', p.448.
1852 Phillipsastraea radiata (Fleming), partim, Edwards and Haime, 'Mon. Brit. Foss. Corals', Pal. Soc., p.203, pl.XXXVII, figs 2 and 2a.
1916 Orionastraea placenta (McCoy), partim, Smith, Q.J.G.S., vol.72, p.300, pl.XXIII, figs 6 and 7. (Not figs 8 and 9 which are O. tuberosa)
1929 Orionastraea prerete Hudson, Proc. Leeds Phil. Soc., vol.1, pt.1X, p.448, pl.1, figs 1, 1a and 1b.

Note: Phillipsastraea radiata (Fleming) includes in all cases quoted O. phillipsi and O. placenta.

Diagnosis: Plocoid Orionastraea with no epithecae, no columella, 20 - 29 continuous septa either completely confluent or never confluent. Concave outer dissepiments.

Type Material: Holotype is specimen A2370 in the Sedgwick Museum, Cambridge (fig'd Smith 1916, Q.J.G.S., 72, pl.XXIII, figs 6 and 7). Holotype includes thin sections cut from this specimen A2370 a-c. Specimen from 'Carb. Limestone, Derbyshire'. Holotype of O. prerete is British Museum specimen R.26483-5 (includes sections R26486-90).

Material: Base of Middle Limestone, Sargill Gate, Askrigg, Wensleydale; Base of Middle Limestone, near 'The Mount', Wensley, Wensleydale; Middle Limestone, Dry Park Gill, Whernside, Kettlewell, Wharfedale; Tyne Bottom Limestone, Green Holes, Moor House Reserve, Upper Teesdale;

Single Post Limestone, Burnhope, Weardale; Upper Monsal Dale beds, Intake Dale, Derbyshire.

Description: External Characters, Smith (1917) described the holotype of O. placenta as being, 'part of a depressed corallum measuring some 6 cms. by 4 cms. and is about 2 cm. thick. Both the upper and lower surfaces are remarkably flat'. The calices are preserved and are quite deep but show no columella. They are from 4 - 5 mm. apart. The corallum is plocoid, either astraeoid or thamnastraeoid.

Internal Characters; Major and minor septa often distinguishable, the minor septa just penetrating the tabularium whereas the major septa often extend right to the centre to join with a prolongation of the counter septum. Septa are usually dilated at their axial edge and thin in the periphery. Septa are always continuous and may be completely confluent or completely non-confluent. The maximum number of septa in a colony varies from 20 - 29, there are never 30.

The inner few rows of dissepiments are concave inwards and slightly dilated. Outer dissepiments are concave in O. p. placenta S.S. but every intermediate between this state and the convex outer dissepiments of O. p. garwoodi can occur.

There is never a columella although the counter septum may extend into the tabularium which is about 2 mm. in diameter.

Discussion: Fleming's Tubipora radiata based on Martin's specimen may have been this species, but McCoy's name is used in preference as it is impossible to decide from Martin's figure whether or not it possessed a columella.

O. p. placenta is distinguished from O. ensifer by its lack of epithecae, from O. phillipsi by its lack of columella, from O. tuberosa on the lower number of septa and corresponding smaller tabularium, and from all other species of Orionastraea by its continuous septa.

See p.216 for notes on the restricted use of this species.

Hudson (1929) distinguished O. prerete from O. placenta on the basis of it having non-confluent septa, but as all intermediate types can be found, and as the two end members of such a continuous variation series does not occur at two distinct horizons, it is thought best that O. prerete be merged with O. placenta (see argument on p.217).

Stratigraphical Range: Jew Limestone to Single Post Limestone.

Orionastraea placenta garwoodi Hudson

(Plates 55 and 56.)

1929 Orionastraea garwoodi Hudson, Proc. Leeds Phil. Soc., vol.1, pt.IX, p.449, pl.II, figs 1, 1a, 1b and 2.

But Not:
1929 Orionastraea garwoodi var. sera Hudson, Proc. Leeds Phil. Soc., vol.1, pt.1X, p.450, pl.II, fig.3.

Diagnosis: Plocoid Orionastraea with no epithecae, no columella, 20 - 29 continuous septa either confluent or non-confluent with convex outer dissepiments.

Type Material: Holotype is British Museum specimen R.26497 and sections R.26498-502 cut from it (R.26502 fig'd Hudson 1929, Proc. Leeds Phil. Soc., vol.1, pt.IX, pl.II, fig.1a, R.26498 fig'd Hudson, Ibid, pl.II, fig.1b). From Sargill, Low Abbotside, Wensleydale. Base of Middle Limestone. Paratypes are BMR.26503 and sections cut from it, R.26504-6, and also A.2196 in Sedgwick Museum, Cambridge, and specimen number 48575 and slides PF.2714-18 cut from it in the I.G.S. Museum, Leeds.

Material: Simonstone Limestone, Arn Gill, Askrigg, Wensleydale; Base of Middle Limestone, Sargill Gate, Askrigg; Middle Limestone, Mill Gill, Askrigg; Tyne Bottom Limestone, Moor House Reserve, Upper Teesdale.

Description: As for O. p. placenta only differing in that the outer series of dissepiments are strongly convex.

Discussion: Hudson (1929) described this as a separate species as O. garwoodi, distinguished by the fact that the outer series of dissepiments were strongly convex. The present author has found that it is true that a number of specimens from the Yoredale beds of Northern England are in this condition, but here a problem exists in that absolutely every intermediate condition is found between the concave inwards dissepiments of *O. placenta* and the convex dissepiments of *O. garwoodi*. As has been explained (p.206) this might be expected as evolution occurred gradually and the species could be accepted if it were the case that those forms with convex dissepiments were found at a distinct horizon above those with concave dissepiments, i.e. if the two forms occupied two distinct horizons. Unfortunately, however, this does not seem to be the case, instead every type of dissepiment condition appears to occur throughout the stratigraphic range of the species. Moreover, if the species were to be accepted, an arbitrary dividing line would have to be drawn between the two species and this would be difficult to exercise considering the character in question, that of curvature of dissepiment plates. Indeed one of Hudson's varieties *O. garwoodi* var *pristina* is nothing more than one of those intermediate stages between *O. placenta* and *O. garwoodi* and Hudson actually states (p.451) that this variety is "a less advanced form of *O. garwoodi*". Thus the species and this variety is best allowed to lapse, but the name is retained as subspecies of *O. placenta*, i.e. *O. placenta garwoodi*, which should be referred to only those forms representing the most advanced end member of the continuous series.

Stratigraphical Range: Jew Limestone to Single Post Limestone.

Orionastraea sera sp. nov.

(Plates 57 and 58.)

1929 Orionastraea garwoodi var. sera Hudson, Proc. Leeds Phil. Soc., vol.1, pt.IX, p.450, pl.II, fig.4.

Diagnosis: Plocoid Orionastraea with no epithecae and no columella, 24 - 28 continuous and sometimes confluent septa with an outer series of dissepiments that are extremely convex, some of them running parallel to and lining the septa.

Type Material: Holotype is British Museum specimen R.26507 and sections R.26508-11 cut from it. From Broughton Craggs Quarries, N.W. of Papcastle Railway Station, Great Broughton, Cumberland. ? "junceum" bed Fourth Limestone, (Slide R.26510 fig'd Hudson 1929, Proc. Leeds. Phil. Soc., vol.1, pt.IX, pl.II, fig.3). Paratypes include specimen number 48576 and Z17362 in the I.G.S. Museum Leeds. Locality and horizon as for holotype.

Material: Base of Middle Limestone, Crag Sike, Swaledale.

Description: External Characters; The corallum is plocoid, either astraeoid or thamnastraeoid and is typically depressed. The specimen from Crag Sike is only 2 cm. tall. Calicular surface and holothecae not seen.

Internal Characters; Major and minor septa of similar length both just penetrating the tabularium. All septa are quite thick, dilated more at the axial ends and thinner at the peripheral ends. Septa are always continuous and may be confluent. Number of septa varies from 24 in the holotype, to 28 in the specimen from Crag Sike. The inner two or three rows of dissepiments are concave and very slightly dilated. The distinguishing feature of this species is the outer series of dissepiments which are always very convex, some of them breaking at the angle of the convexity and turning to run parallel to the septa, lining the calicular edges of the septa.

Their is never a columella although a thin prolongation of the counter septum may extend into the tabularium.

The tabularium is approximately 2 mm. in diameter and individual corallites are usually roughly 8 mm. apart.

Discussion: The continuous series from concave to convex dissepiments, as seen in O. p. placenta and O. p. garwoodi, is continued to a further stage in O. sera, more developed than O. p. garwoodi, when the dissepiments break at the convex angle and turn to run parallel to the septa, lining their sides. This form was described by Hudson (1929) as O. garwoodi var. sera. However, when Hudson first described this taxa as a variety only the holotype and paratypes were known. It has since been recorded from a second locality in Swaledale. Both of these occurrences are at similar stratigraphic levels, the holotype coming from the "junceum" beds (Fourth Limestone) of Cumbria and the Swaledale specimen from the Middle Limestone. Therefore the present author considers that as it occupies a horizon distinctly higher than the early members of the O. placenta population it can be regarded at least as a chrono-species distinct from O. placenta. This situation is satisfactory for two reasons. First, as it occurs at one limited horizon it will be a useful zonal species, and secondly, the distinguishing character is such that a least an arbitrary line can be drawn between O. p. garwoodi and O. sera.

O. p. garwoodi is thus the subspecific stage intermediate between O. p. placenta and O. sera. The obvious discontinuity between O. p. garwoodi and O. sera marks the speciation, at least morphologically, of O. sera from the subspecific stage of O. p. garwoodi.

This species can be distinguished from all other Orionastraea species by the dissepiments lining the septal walls.

This species cannot unfortunately be attributed to Hudson, who first described the form as a variety, because the Rules of Nomenclature (Secretary's report, Paris Meeting, 1948) state that, "a name originally published as the name of an infra-subspecific form, if elevated to ... specific rank by a subsequent reviser ... shall be attributed to the author by whom it was so elevated".

Although Hudson was probably using his varieties in the sense that we now use sub-species (i.e. for a population) we must treat all varieties by their present day definition (Linsley, 1944) which is as an infra-subspecific taxa referable only to individual Mendelian variations. (This argument also applies to Hudsonia matura (p.237).)

Stratigraphical Range: Single Post Limestone.

Orionastraea rete Hudson

(Plates 59 - 61.)

1924 Orionastraea phillipsi (McCoy), Garwood and Goodyear, partim, Q.J.G.S., vol.lxxx, p.206.

1929 Orionastraea rete Hudson, Proc. Leeds Phil. Soc., vol.1, pt.IX, p.448, pl.1, figs 2, 2a and 2b.

Diagnosis: Aphroid Orionastraea with no epithecae or columella, having 22 - 28 discontinuous septa.

Type Material: Holotype is British Museum specimen R.26492 and sections R.26493-6 cut from it. (Section R.26494 fig'd. Hudson, 1929, pl.1, fig.2a, R.26495 fig'd Hudson, 1929, pl.1, fig.2b). From the base of the Middle Limestone, Whernside Pasture, Great Whernside, Kettlewell, Wharfedale. Paratypes include specimen number A2201 Sedgwick Museum, Cambridge and specimen number 48573 (and slide PF2702 cut from it) in the I.G.S. Museum, Leeds.

Material: Middle Limestone, West Burton, Wensleydale; Middle Limestone, 'The Mount', Wensleydale; Middle Limestone, Morpeth Scar, Penhill, Wensleydale; Middle Limestone, Whernside Pasture, Kettlewell, Wharfedale; Middle Limestone, Nidd Valley, near Lofthouse, Yorkshire; Middle Limestone, Masham, Yorkshire.

Description: External Characters; Corallum tabular; the specimen from West Burton is only 6 cm. tall while the horizontal spread of the colony is 46 cm. The upper surface has only been seen in the West Burton specimen and is peculiar, the areas immediately surrounding the calices standing up as bosses with the calice itself forming a depression in the boss. The corallum is plocoid and aphroid, the septa not continuing to the septa of the adjacent corallite, instead there is an area of dissepimentary tissue separating the corallites. It is the areas without any septa that form the hollows between calicular bosses seen on the upper surface.

Internal Characters; O. rete is identical in all respects to O. placenta except for the aphroid nature of the corallum. It is often difficult to distinguish between major and minor septa although the minor septa usually end in the dissepimentarium, while the major septa just penetrate the tabularium. Major septa never extend far into the centres which are usually empty. All septa are very slightly dilated at their axial edges. At their peripheral ends the septa die out in the dissepimentarium, the colony being aphroid. The actual length of the septa is very variable, they may be very short, almost vestigial, while on the other hand they may extend almost to adjacent corallites. The maximum number of septa in a colony varies from 22 - 28. Dissepiments are also very variable, the inner two or three rows being small and concave while the outer series cam be divided into two types. First, are the outer dissepiments secreted between the septa which may also be concave or strongly convex; the latter are found in those members of O. rete that have evolved from the O. placenta garwoodi end of the gene pool. Secondly are the outer dissepiments peripheral to the septa which fill the intervening spaces between adjacent corallites and these are much larger, more globose and very irregular. The diameter of the tabularium is approximately 1.5 mm. - 2.0 mm. and corallites are spaced from 5.00 mm. - 6.00 mm. apart. There is never a columella.

Discussion: It should perhaps be explained at this point that every intermediate condition between astraeoid and aphroid coralla occurs between O. tuberosa and O. edmondsi and between O. placenta and O. rete. Using the same argument as for O. placenta and O. garwoodi one might consider that these aphroid colonies were only sub-species of O. tuberosa and O. placenta. However the situation with these two aphroid species is rather different. Here the aphroid colonies occur at a distinctly higher horizon than do their astraeoid ancestors and the intermediate colonies occur in the intervening beds. Thus in these cases the intermediate colonies represent the evolutionary lineage between two chronospecies one astraeoid and the other aphroid, and so the chronospecies can be accepted. As intermediate colonies do occur, however, some arbitrary line must be drawn to divide the two chronospecies and this must be here defined.

Several alternatives present themselves, first we could say that only those specimens showing a completely astraeoid/thamnastraeoid corallum should be known as O. placenta, while specimens showing any signs of an aphroid condition, however slight, should be known as O. rete. By this definition it will be seen that some members of O. rete may now be almost completely astraeoid/thamnastraeoid. Secondly, we could say that only those specimens with a complete aphroid colony, with no continuous septa, be known as O. rete, while specimens with any continuous septa, however few, be known as O. placenta. By this definition it would be possible for O. placenta to occur in an advanced aphroid state.

Neither of these situations seem completely satisfactory as it is difficult to draw such a rigid dividing line when the distinguishing character is continuously variable. It may be more realistic and more practicable in such a case if the distinction between the two species was more subjective. That is to say that a corallum which is dominantly aphroid shall be referred to O. edmondsi or O. rete, whereas a corallum dominantly astraeoid/thamnastraeoid shall be referred to O. tuberosa or O. placenta.

Hudson (1929) considered O. rete to have evolved from O. prerete, but O. prerete is here considered synonymous with O. placenta and so the present author considers O. rete to have evolved from O. placenta (including O. p. garwoodi). This situation would seem to be supported by the fact some specimens of *O. rete* do show convex dissepiments which would be difficult to reconcile if, as Hudson suggested *O. garwoodi* and *O. prerete* represent separate gene pools. In the revision suggested here Hudson's *O. garwoodi* and *O. prerete* are end members of the continuous gene pool of *O. placenta* and we would expect characters of both types to appear in their successor *O. rete*.

O. rete can be distinguished from *O. edmondsi* by the latter having over 30 septa, and from all other species of *Orionastraea* by its aphroid corallum.

Stratigraphical Range: Single Post Limestone.

Orionastraea edmondsi Hudson

(Plate 50, fig. 2.)

1929 Orionastraea edmondsi Hudson, Proc. Leeds Phil. Soc., vol.1, pt.IX, p.446, pl.III, figs 1a, 1b, 2, 3a, 3b.

But Not:
1929 Orionastraea edmondsi var. laciniosa Hudson, Proc. Leeds Phil. Soc., vol.1, pt.IX, p.447, pl.iv, fig.2, which is O. tuberosa.

Diagnosis: Aphroid Orionastraea with no epithecae or columella, having 30-34 discontinuous septa.

Type Material: Holotype is British Museum specimen R.26466-9 and sections R.26470-82 cut from it. From the top of the Potholes Limestone, Clints Quarry, S.E. of Bigrigg, Cumbria. Paratype is specimen 48803 I.G.S. Museum, Leeds. (Locality and horizon same as for holotype).

Description: External Characters; The corallum is tabular with a holothecae covering the proximal surface. The distal surface has shallow calices and dissepimental tissue between adjacent corallites, the corallum being aphroid.

Internal Characters; O. edmondsi is identical to O. tuberosa except for the aphroid nature of the corallum. Major septa and minor septa are of similar length, both only just penetrating the tabularium, although the major septa are very slightly longer. The centre is therefore usually empty although one major septa (usually the cardinal septum) may cross the axial region. All the septa are dilated at their axial ends and thinner at their peripheral ends. In the dissepimentarium the septa die out before reaching adjacent corallites so that the space between adjacent corallites is filled with dissepiments only and the corallum is aphroid.

The maximum number of septa in a colony may be as high as 34 and is never less than 30. Dissepiments are variable, the inner two or three rows being small, concave towards the centre, vertically displaced and often dilated. The outer dissepiments are in two series as in O. rete; those between the peripheral ends of the septa also being small and concave (or slightly convex), while those peripheral to the septa, and lying inbetween adjacent corallites, are much larger, randomly orientated and less vertical in disposition.

The tabularium diameter is just under 3 mm. and corallites are usually about 9 mm. apart.

Discussion: As with O. rete and O. placenta every intermediate condition can be found between the aphroid O. edmondsi and the thamnastraeoid/astraeoid O. tuberosa. See discussion of O. rete for remarks on this feature.

O. edmondsi can be distinguished from O. rete by having over 30 septa, and from all other species of Orionastraea by being aphroid.

Stratigraphical Range: Jew Limestone.

Orionastraea indivisa Hudson
(Plate 62.)

1925 Orionastraea sp. n., Hudson, Geol. Mag., vol.lxii, p.185.
1926 Orionastraea indivisa Hudson, Ann. Mag. Nat. Hist., ser.9, vol.XVIII, p.145 and 146, text-fig.1, pl.VIII, figs 1, 1a, 1b, 1c, 2, 2a, 2b, 3.
1929 Orionastraea indivisa Hudson, Proc. Leeds Phil. Soc., vol.1, pt.IX, p.446.

Diagnosis: Indivisoid Orionastraea with no epithecae, no columella and no septa.

Type Material: Holotype is British Museum specimen R.25235 and sections R.25236-8 cut from it. (R.25236 fig'd. Hudson 1926, pl.VIII, fig.1a, R.25237 fig'd Hudson, 1926, pl.VIII, fig.1b, R.25238 fig'd Hudson 1926, pl.VIII, fig.1c). From Simonstone Limestone, Birks Gill, High Whitaside, Swaledale, Yorkshire.

Material: Toft Gate Limestone, Toft Gate Quarry, Pately Bridge, Yorkshire; Simonstone Limestone, Malham, Yorkshire; Tyne Bottom Limestone, Knock Ore Gill, Great Dunn Fell, Moor House Reserve, Upper Teesdale.

Description: External Characters; The corallum is depressed and may be only a few mm.'s thick as in the Toft Gate specimen or more upright attaining up to 5 cm. in height. None of the specimens collected by the author had the calicular surface preserved but Hudson (1926) described this distal surface being, "smooth and flat with the calices showing as small depressions". A holothecae covers the proximal surface. The corallum is plocoid and has no septa; this condition has been termed 'indivisoid' in this thesis (p. 17).

Internal Characters; The individual corallites are composed of an inner series of two to three rows of small dissepiments only, which may be concave or convex towards the axial region. These dissepiments surround a tabularium which is empty except for the tabulae. The tabularium is very small, usually only 1.5 mm. in diameter. Adjacent corallites are separated by an outer series of dissepiments which are larger and more globose and irregular. There is no columella and no septa.

Discussion: This species is developed from an aphroid species of Orionastraea by a further reduction in the septa. The small size of the tabularium would suggest that it is more akin to O. rete than O. edmondsi but the statigraphic evidence does not back this. O. indivisa occurs in the Simonstone Limestone whereas O. rete does not appear until the Middle Limestone, above the Simonstone Limestone. O. edmondsi on the other hand occurs in the Hardraw Scar Limestone which is immediately below the Simonstone Limestone, and therefore it would appear that O. indivisa has evolved from O. edmondsi with a reduction in the tabularium as well as the septa.

It would seem that O. indivisa is a useful zonal indicator having so far only been recorded in the Simonstone Limestone and its equivalents. (i.e. the Toft Gate Limestone and the Tyne Bottom Limestone). O. indivisa can be distinguished from all other species of Orionastraea by its lack of septa.

Stratigraphical Range: Tyne Bottom Limestone.

Genus *Hudsonia nov.*

1924 *Orionastraea*, Garwood and Goodyear, *partim*, p.231.
1929 *Orionastraea*, Hudson, *partim*, p.445.
1958 *Orionastraea*, Dobrolyubova, p.201.
1970 *Orionastraea*, Kato and Mitchell, p.47.

Diagnosis: Rugose corals resembling *Orionastraea* in having little or no epithecae and a plocoid colony, but corallites are large having a tabularium diameter from 4 - 5 mm. and from 34 - 46 septa.

Genotype: *Orionastraea magna* (Kato and Mitchell, 1970, p.49) here chosen.

Discussion: The genus is proposed to contain two species as follows:

(1) *Orionastraea ensifer* var. *matura* Hudson, 1929.

(2) *Orionastraea magna* Kato and Mitchell, 1970.

Hudson considered that his variety 'matura' was an exceptionally large form of *Orionastraea ensifer*. However, I consider that the large size and the high number of septa in *O. e. matura* are indicative of its having evolved from a larger diameter cerioid species of *Lithostrotion* than did the *Orionastraea* species (p. 30). The *Orionastraea* species seem to have evolved from the cerioid *L. decipiens*, whereas *O. e. matura* is more akin to the larger cerioid *L. vorticale*. *O. e. matura* is therefore an intermediate condition between a second species of *Lithostrotion* and the plocoid state. Thus *O. e. matura* is here removed from the genus *Orionastraea* as it is a member of a different line of descent from *Lithostrotion* than is *Orionastraea*.

Kato and Mitchell described *Orionastraea magna* as a separate species on account of its size. I agree that it should indeed be recognised as a distinct species, but also consider that the close resemblance in size between O. e. matura and O. magna suggests that O. magna has also evolved from L. vorticale through O. e. matura and thus that it should also be referred to Hudsonia.

Stratigraphical Range: The genus occurs low in the D1 Zone and in the 'Orionastraea' band of D2 at Settle (which is equivalent to the Hardraw Scar Limestone). It has not, as yet, been recorded from the intervening strata.

Hudsonia matura *sp. nov.*

(Plate 63, fig. 1.)

1929 *Orionastraea ensifer* var. *matura* Hudson, Proc. Leeds Phil. Soc., vol.1, pt.IX, p.445, pl.4, fig.4.

But Not:
1851 *Lithostrotion ensifer* Milne-Edwards and Haime, 'Pol. Foss. des Terr. Pal.', p.442.

Diagnosis: Cerioid/astraeoid *Hudsonia* with very thin epithecae or discontinuous beaded epithecae, a stout 'Lithostrotion' type of columella, 46 continuous septa often non-confluent and a tabularium diameter of 4 - 5 mm.

Type Material: Holotype is stated by Hudson (1929, p.445) to be specimen no.622 in the Garwood Collection, University College, London. From a boulder in the Bowland Shale, Black Gill Beck, Scaleber, Settle, Yorkshire. I have been unable to trace this specimen in the University College collection and it seems that it may have been destroyed during the war when the College Museum was bombed. After the war the residue of the Garwood Collection in University College was removed to the British Museum and to the Institute of Geological Sciences, but I have not found the specimen in these collections either.

Hudson collected specimens himself from the flanks of High Hill, Settle, Yorkshire (Hudson, loc. cit., p.445), but he gives no registration number for these specimens and they are not in the Hudson Collection at the University of Leeds.

Thus until further specimens can be collected, the species must be interpreted on Hudson's figure of the holotype (Hudson, *loc.* *cit.*, pl.4, fig.4).

Description: External Characters; Owing to the fact that no specimens are traceable at present the external characters cannot be described and the internal features can only be described from Hudson's figure of the holotype.

Internal Characters; The internal features of this species are generally identical to those of its ancestors, *L. vorticale* (see description of that species). The only significant point of difference is that in this species the epithecae is very thin and often discontinuous and so the corallum is intermediate between cerioid and plocoid. Where the epithecae is discontinuous the septa of adjacent corallites may be confluent, but usually they are not and so the corallum is usually cerioid/astraeoid.

The number of septa ranges from 40 - 46 (total) and the tabularia are from 4 - 5 mm. in diameter.

Discussion: This species can be distinguished from *L. vorticale* by its discontinuous epithecal wall, and from *H. magna* which has no epithecae or columella. It differs from *O. ensifer* by its larger tabularium and greater number of septa (46 as compared to 36). See also discussion of the genus *Hudsonia* (p.235) and discussion of *H. magna* (p.240).

This species cannot unfortunately be attributed to Hudson who first described it as a variety of *O. ensifer*. A summary of the nomenclatorial rules relating to such variety names is given in the discussion of *O. sera* on p.226 of this thesis.

Stratigraphical Range: Low D1.

Hudsonia magna (Kato and Mitchell)

(Plate 63, fig. 2 and Plate 64.)

1924 Orionastraea phillipsi (McCoy), 'exceptionally large variety', Garwood and Goodyear, Q.J.G.S., vol.80, p.219, 227 and 232 (in text only).
1958 Orionastraea phillipsi (McCoy), Dobrolyvbova, Trudy vses. nauchno-issled. Inst. miner. Syr'ya, vol.103, p.201, pl134, fig.2 and pl.35.
1970 Orionastraea magna Kato and Mitchell, Palaeontology, vol.13, pt.1, p.49, pl.13, figs 1-5.

Diagnosis: Hudsonia with no epithecae or columella, 30 - 38 continuous septa, either confluent (astraeoid) or thamnastraeoid and a tabularium 4 - 5 mm. wide.

Type Material: Holotype is G.S.M. 65802 in the I.G.S. Museum, Leeds. From D2 Zone, low escarpment 1/3 mile N.E. of Brunton House, 1/3 mile S. of Feizor, near Settle, Yorkshire. Includes slides PL309, PL310, PL312, PL313 fig'd Kato and Mitchell, 1970, pl.13, figs 2-5.
Paratypes include G.S.M. 65800-1 and 65803 in I.G.S. Museum, Leeds (includes slide PF3387 cut from 65803, fig'd Kato and Mitchell, 1970, pl.13, fig.1). Horizon and locality as for holotype. Also G.S.M. 66699, 66700, 66703-6, from Low South Bank, S. side of Stockdale Beck, opposite Stockdale Farm, 2 miles E. of Settle, and finally SME 13857 in the Sedgwick Museum, Cambridge, from right bank of Cow Gill, 1/4 mile N. of New Houses, 2/3 mile S.W. of Bordley, near Settle, Yorkshire.

Material: S.E. of Ranes Lane, Feizor, Settle, Yorkshire.

Description: External Characters; The corallum is plocoid, there being no epithecae, and is usually astraeoid/thamnastraeoid and sometimes slightly aphroid. The coralla are tabular, but often quite large. Kato and Mitchell (1970, p.49) describe the largest fragments seen by them as 129 mm. x 91 mm. in area, and 44 mm. thick. The proximal surface is covered by a holothecae showing fine growth banding.

Internal Characters; The septa are divisible into two orders; the minor septa only just reaching the tabularium, whereas the major septa extend into it and may reach the centre which is otherwise empty; there is never a columella. All septa are thin and never dilated. Usually the septa are continuous to the adjacent corallite, but occasionally this may not be so in which case the intervening space between adjacent corallites is filled by large dissepiments and the corallum is partly aphroid. When the septa are continuous they are usually also confluent, but again they may not be and the corallum can be astraeoid or partly astraeoid. In some coralla the minor septa are weak and may die out in the dissepimentarium. The maximum number of septa in a colony ranges from 34 - 38 (total). The tabularia are from 4 - 5 mm. in diameter and often poorly defined.

Dissepiments are variable; the inner 2- 3 rows, defining the tabularium, are small, vertical and concave inwards, but irregular and never dilated. Outer dissepiments are larger, more obliquely inclined and often quite random in orientation. Because the septa are always thin, and sometimes even break down the periphery of the corallite is dominated by these large dissepiments. This is made even more apparent by the wide spacing of the corallites, which are often as much as 20 mm. apart, such that the greater portion of the coralla is composed of dissepiments.

Discussion: The large size of the tabularia distinguishes this species from any species of <u>Orionastraea</u>. It is distinguished from <u>H. matura</u> by its complete lack of epithecal wall. The similar tabularium diameter of <u>H. matura</u> and <u>H. magna</u> suggests that they are related, but <u>H. magna</u> has fewer septa (only 38 as compared to 43 in H. matura) and so there has been a reduction in septal number in the evolution of this lineage. This is not surprising considering the fact that all the septa of H. matura are thin and often impersistant.

The specimens of H. magna all come from the Orionastraea band of the Settle district, which Hicks (1959, p.33-7) regards as equivalent to the Hardraw Scar Limestone of Wensleydale. It will be seen that there is quite a stratigraphical gap between the occurrence of this species and H. matura at the top of D1. If H. magna does belong to the same lineage as H. matura then evolution of H. magna from H. matura is clearly not direct. This stratigraphic evidence is backed up by the fact that these two species are not directly related to each other morphologically as one would expect to find a columellate form with no epithecae occurring between these two species and also one would expect the direct plocoid descendant of H. matura to be less aphroid than is H. magna. Such forms may be found in the intervening strata.

Stratigraphical Range: Jew Limestone.

SYSTEMATICS OF THE AULATE GENERA EXCLUDED FROM THE LITHOSTROTIONTIDAE

Taxonomic History

The genus Aulina was first published by Smith (1916, p.290) when it included only one species, the genotype, Aulina rotiformis. Prior to this the species had been confused with Orionastraea, a genus also first published in the same paper. Thus Aulina had previously been called Phillipsastraea radiata by Smith (1910, p.629) and Garwood (1912, p.542). The species is plocoid and possesses a well developed aulos, the characteristic feature of the genus. In the original description of this genus Smith considered it to have evolved from Phillipsastraea.

The next review of this genus was again by Smith when he emended the original diagnosis of Aulina to include fasciculate forms and described one such species, Aulina furcata (1925, p.490), a species having small corallites and only 18 septa. With this new knowledge Smith also changed his views on the phylogeny of the genus, now considering A. rotiformis to have evolved through A. furcata from the Lithostrotiontidae. Hill, however, contested this view when she described A. simplex (1934, p.92), a simple coral from Australia, thus considering that the English compound species had developed from this simple aulate form rather than from Lithostrotion. Hill added further to the genus when she published another new species, A. senex (1940, p.193), again plocoid, but much larger than A. rotiformis. Hill (loc. cit., p.190) also placed Campophyllum carinatum, originally described by Carruthers (1909, p.150), in the genus Aulina, this being a further simple coral species, but much larger than A. simplex.

Smith and Yu (1943) made a complete revision of the genus describing several new species from Britain and China. First they rejected Hill's A. simplex from the genus, considering it to be a caninoid species which had followed an aulate trend. Secondly they rejected the other simple species, A. carinatum. This they supposed was related to some other simple coral, probably Koninckophyllum. Having done this they reverted to Smith's original theory of the descent of *Aulina*, that it had evolved from *Lithostrotion* and not from a simple ancestor. However, they modified this theory, no longer believing the massive forms to have evolved from the fasciculate forms, but instead that *Aulina* had evolved from *Lithostrotion* polyphyletically. Thus they stated (*loc. cit.*, p.38), "it is clear that all the species of the former have not arisen from the same species of the latter". Finally they described in this paper a second fasciculate aulate species to which they gave the name *A. horsfieldi* (*loc. cit.*, p.49), this differing from *A. furcata* by its much larger size.

The final British species was added to the genus by Clarke (1966, p.222) who described a third fasciculate species from Ireland, *A. hibernica*, intermediate in size between *A. horsfieldi* and *A. furcata*.

As already stated Smith and Yu (1943, p.38) did suggest that the *Aulina* species had developed polyphyletically from different species of the *Lithostrotiontidae*, but to what extent they were aware that this polyphyleticism has occurred is not clear. It seems that they considered that the massive forms had all arisen from *L. maccoyanum*, while the fasciculate forms arose from *Diphyphyllum*. However, although they were aware that the genus was polyphyletic, they made no attempt to correct this anomally.

Minato and Rowett (1967) arrived at a similar conclusion and took steps to correct this situation by restricting the genus *Aulina* to include only the massive species. Their reasons for this action were that the development of an aulos in different species does not necessarily imply that those species are related, the same structure being developed in unrelated stocks. They also divided the remaining massive species of *Aulina* into two subgenera, *Aulina* (*Aulina*), for the astraeoid/thamnastraeois species, and *Aulina* (*Pseudoaulina*) for the aphroid species.

Minato and Rowett suggested, as had Sando (1963, p.1076) that the fasciculate forms might be assigned to a new genus. However, they neglected to erect such a new genus.

Family Uncertain

Genus Aulina Smith

1910 Phillipsastraea, Smith, p.629. (Not Phillipsastraea S.S. D'Orbigny)
1912 Phillipsastraea, Garwood, p.542. (Not Phillipsastraea S.S. D'Orbigny)
1916a Aulina, Smith, p.2.
1916b Aulina, Smith, p.290.
1925 Aulina, Smith, partim, p.486.
1933 Aulina, Yu, p.80.
1937 Aulina, Yu, p.54.
1940 Aulina, Hill, partim, p.193.
1943 Aulina, Smith and Yu, partim, p.43.
1944 Aulina, Yabe and Minato, p.148.
1958 Aulina, Dobrolyubova, p.208.
1960 Aulina, Vassiljuk, partim, p.98.
1962 Aulina, Lu and Zhao, p.177.
1962 Aulina, Yu, Lin and Fan, p.19.
1963 Aulina, Sando, p.1077.
1964 Aulina, Vassiljuk, p.92.
1964 Aulina, Wu, p.32.
1966 Aulina, Dobrolyubova, p.163.
1967 Aulina, Minato and Rowett, p.383.
But Not:
1934 Aulina, Hill, p.93.
1961 Aulina, Fontaine, p.119.
1966 Aulina, Clarke, p.221.

Diagnosis: Massive, thamnastraeoid or aphroid rugose corals with major septa that normally coalesce at their axial ends to form a tube, or aulos, running the length of the corallite. Major septa usually carinate.

Genotype: Aulina rotiformis by designation (Smith, 1916, p.290).

Discussion: Smith proposed Aulina in 1916 to include Phillipsastraea radiata Smith, 1910, p.629, non P. radiata (Martin), and he named this Aulina rotiformis.

The genus here includes only those species previously assigned to Aulina that have a massive corallum. The fasciculate species previously included in this genus are assigned to the new genus Fascicaulina (see p.257). This division was originally suggested by Minato amd Rowett (1967) the reason being that the development of an aulos does not necessarily indicate phylogeneric relationships (see p. 33) and that several diverse stocks may possess a similar structure. Minato and Rowett (loc. cit.) also divided the remaining massive species of Aulina into two subgenera, Aulina (Aulina), for the astraeoid/thamnastraeoid species, and Aulina (Pseudoaulina), for the aphroid species. This appears to me to conflict with their original argument, as the development of an aphroid habit is no more indicative of phylogenic relationships than is the development of an aulos; the aphroid habit also occurs in many widely diverse stocks. Moreover, some species (e.g. Aulina rotiformis) may be either aphroid or thamnastraeoid and it would be misleading if the two types of corallum in one species were placed in different subgenera. These subgenera should therefore be allowed to lapse as they are polyphylletically derived.

Stratigraphical Range: In Britain the genus is restricted to the Namurian (E2) Harlow Hill Limestone and its equivalents, the Botany Limestone, the Newton Limestone and the Upper Limestone Series of Scotland.

Aulina senex Hill
(Plate 65.)

1937 Aulina sp. Yu, Acord. sinica, Mem. Nat. Research Inst. Geol., vol.XVI, p.54, 55.
1940 Aulina senex Hill, 'Men. Carb. Rug. Corals Scotland', p.193, pl.XI, figs 9, 10.
1943 Aulina senex Hill, Smith and Yü, Q.J.G.S., vol.99, p.47, pl.IX, figs 6-10.

Diagnosis: Aphroid Aulina with large corallites, 20 carinate septa of both orders and a pseudo aulos developed.

Type Material: Holotype is Royal Scottish Museum specimen R.S.M.1911.62.2120 (including thin sections). In Neilson Collection. From Superior beds Upper Limestone Series, Old Quarry, Glencart, near Dalry, Scotland. (Fig'd Hill, 1940, pl.XI, figs 9, 10).

Material: Quarry E. of road, 440 yds. N.W. of Church, Newton, Northumberland. (From Newton Limestone = Harlow Hill Limestone = Botany Limestone).

Description: Internal Characters; Major and minor septa easily distinguishable, the major septa extending about half the distance from the inner row of dissepiments to the centre, while the minor septa only just reach the inner row of dissepiments. The septa are dilated in the tabularium and thin in the periphery as they die out. In the tabularium the septa end abruptly, without reaching the centre, when they abut onto the downturned edges of the tabulae. These downturned tabulae produce a pseudo-aulos of the type seen in the diphyphylloid Lithostrotion species, but the septa themselves never turn through 90° to join with the adjacent septa and so never contribute to the pseudo-aulos. A true aulos is not, therefore, produced in this particular species and this is supported by the fact that some of the major septa do penetrate the pseudo-aulos of the tabulae. Thus this species represents an early stage in the development of the aulos when that structure is traced through the phylogeny of the group.

The septa are strongly carinate especially in the dissepimentarium and number 20 of both orders.

The tabularium varies from 4 mm. - 6 mm. in diameter and the pseudo-aulos from 2mm. - 3 mm. in diameter, this structure thus being wide in proportion to the tabularium (p. 33). The centre is always empty there never being a columella. The distance between corallites is usually at least 10 mm., but the septa are only 3 - 4 mm. long. The corallum is therefore aphroid with areas between corallites filled with an outer series of large globose dissepiments. The aphroid condition is not so well developed as in A. botanica as the septa of A. senex are generally longer. The inner series of dissepiments between the septa of a corallite are more regular, concave and slightly dilated. They number 2 - 3 rows.

The tabulae of the pseudo-aulos are flat axially but downturned at their edges, resting on the tabulae below. The outer tabulae are small inclined plates horizontal or sub-horizontal.

Discussion: This species can be distinguished from A. rotiformis and A. botanica by its larger diameter of the tabularium and by the high number of septa.

In some colonies a few corallites in this otherwise aphroid colony may become laterally free and cylindrical with their distal parts then being bordered by an epitheca (Smith and Yu, 1943, pl.IX, fig.7). When this happens these corallites look very similar to A. vesiculata (Dobrolyubova 1966, p.163, pl.XXXIII, fig.1) a fasciculate aulate coral with lonsdalaeoid dissepiments. It may be therefore that A. senex is developed from A. vesiculata by the latter species becoming massive. It may not pass through a cerioid stage, instead the wall could disappear as soon as the corallites come into contact. If this is true it will be noted that an aphroid colony can be produced in two entirely different ways. First, as in O. tuberosa to O. edmondsi the aphroid condition is produced by the septa of an astraeoid corallum (O. tuberosa) retreating peripherally. But in the case of A. vesiculata to A. senex the retreat of the septa has taken place at an earlier stage in the group's phylogeny, in the fasciculate A. vesciculata, and this retreat produced the lonsdalaeoid dissepiments. Thus the aphroid condition is here produced by a lonsdalaeoid fasciculate corallum becoming massive and losing its wall and thus as soon as the epithecae disappears the corallum is immediately aphroid, there being no astraeoid stage. An aphroid colony is after all nothing more than a plocoid colony with lonsdalaeoid septa, the method of producing an aphroid colony therefore depends on at what atage in the phylogeny of the group the septa become lonsdalaeoid. This also determines whether or not an astraeoid stage is present. If A. senex is developed from A. vesiculata one should not expect to find an intermediate astraeoid stage.

Stratigraphical Range: Botany Limestone.

Aulina botanica sp. nov.

(Plates 66 and 67.)

1916 ?*Aulina rotiformis*, large mammiferous form, Smith, Q.J.G.S., vol.72, p.290.

Diagnosis: Strongly aphroid *Aulina* with corallites intermediate in size between *A. senex* and *A. rotiformis*, having 16 carinate septa of both orders and an incomplete aulos.

Type Material: Holotype is specimen JN 61b (and sections 61bi, ii and iii cut from it). In the authors collection, University of Durham. From Botany Limestone, How Gill, Botany, Hunderthwaite Moor, near Botany farm, 2½ miles W.S.W. of Romaldkirk, Teesdale.

Material: Only the type locality is known.

Description: External Characters: Corallum typically depressed and flat, horizontal extent being far greater than the vertical extent. The holotype is only 1.7 cm. in height and before sectioning the corallum had a horizontal area of 9 x 18 cm. Neither the calices nor the proximal surfaces have been seen but the weathered distal surface of the holotype shows the corallum to be completely aphroid with the corallites some 8 - 12 mm. apart. The wide areas between adjacent corallites are filled with very large globose dissepiments. There is no epithecae present, but we must assume that a holothecae exists.

Internal Characters; The major and minor septa are easily distinguishable the major septa extending about half the distance from the inner row of dissepiments to the centre, whereas the minor septa only just reach the inner row of dissepiments. All septa are dilated, perhaps more so in the tabularium becoming gradually thinner in the dissepimentarium as the septa die out peripherally. In the tabularium some of the major septa turn through 90° to join up to the adjacent major septa. When this feature is seen persistently in a corallite a true aulos is produced, but in this species the joining of adjacent septa is not a regular feature and therefore in most corallites the aulos is only partly produced and may be absent altogether. Never is there as perfect an aulos as in A. rotiformis, but it is usually better than the same structure in A. senex. This species represents an early stage in the phylogeny of the lineage as regards the development of an aulos. Even when a corallite of this species shows development of a complete aulos the aulos produced can be seen to differ from the aulos of later species in the lineage in that it is a more primitive kind of structure. The difference is that in this species the 'bend' of the septa at their axial ends is convex inwards so that the aulos is irregular in plan (fig.21b). In later species of the lineage (A. rotiformis) the aulos has evolved to a more advanced shape giving a stronger kind of tube, the 'bend' of the septa being now concave so that the aulos is circular in cross section (fig.21c).

Axially to the aulos the centre is empty; there is never a columella.

Major septa in the holotype number 16 with an equal number of minor septa. Some of the major and minor septa are feebly carinate although carinae are not so well developed as in A. senex or A. rotiformis.

The tabularium varies from 2.5 mm. - 3.5 mm. and the aulos from 1 mm. - 2 mm. The distance between centres is usually approximately 10 mm. and yet the major septa are only 1 - 2 mm. long. The corallum is therefore strikingly aphroid with large areas between the corallites. These are filled with extremely large, obliquely set, irregular dissepiments which are peripheral to the septa. The inner series of dissepiments that occur between the septa of a corallite are much smaller, more vertical, regularly concave in attitude and may be slightly dilated, numbering 1 - 2 rows only.

The tabulae are divisible into two series an inner and an outer series. The inner series are strongly arched and are superimposed on one another so that their sides form a vertical column running down the length of the corallite. This column corresponds to the position of the septal aulos, but it is the tabulae that are playing the greater part in building this aulos with the septa only occasionally adding to it. The outer series of tabulae are more horizontal and connect the aulos to the dissepimentarium. In transverse section the outer dissepiments can be seen to be almost horizontal whereas the inner 1 or 2 series are vertical.

Discussion: This species can be distinguished from A. senex and A. rotiformis by septal counts and diameter; A. senex being larger with 20 major septa, A. rotiformis being smaller with only 11 major septa and A. botanica being intermediate with 16 major septa.

A. botanica appears to be most similar to the Chinese species A. manchuriensis which is slightly larger with 18 - 20 septa.

Stratigraphical Range: Botany Limestone.

Aulina rotiformis rotiformis Smith
(Plates 68 and 69.)

1910 *Phillipsastraea radiata* (Fleming), Smith, Trans. Nat. Hist. Soc. Northumberland, vol.III, pt.3, p.629, 630.
1912 *Phillipsastraea radiata* (Fleming), Garwood, Q.J.G.S., vol.lxviii, p.542, 543.
1916 *Aulina rotiformis* Smith, Abs. Proc. Geol. Soc., No.995, p.2, 3.
1916 *Aulina rotiformis* Smith, Q.J.G.S., vol.72, p.290, text-figs 3, 4 on p.291, 292, pl.XXII, figs 6-11.
1924 *Aulina rotiformis* Smith, Garwood and Goodyear, *Ibid*., vol.80, p.252.
1925 *Aulina rotiformis* Smith, Ann. Mag. Nat. Hist., ser.9, vol.XVI, p.487, pl.XXIV, figs 1, 2.
1933 *Aulina rotiformis* Smith, Yu, Palaeont. Sinica, ser.B, vol.XII, p.80, pl.XIII, figs 1a-d.
1933 *Aulina carinata* Yu, *Ibid*., ser.B, vol.XII, p.81, pl.XIV, figs 4a-c.
1933 *Aulina carinata* var. *chui* Yu, *Ibid*., ser.B, vol.XII, p.82, pl.XIII, figs 2a, 2b.
1940 *Aulina rotiformis* Smith, Hill, 'Mon. Carb. Rug. Corals Scotland', p.191, pl.XI, figs 6, 7.
1943 *Aulina rotiformis* Smith, Smith and Yu, Q.J.G.S., vol.99, p.43, pl.VIII, figs 9-11, pl.IX, figs 1-4.
1958 *Aulina rotiformis* Smith, Dobrolyubova, Acad. Sci. SSSR, Rep. of Palaeont. Inst., vol.70, p.208, pl.34, figs 3a-b.
1958 *Aulina rotiformis* Smith, Dobrolyubova, Translation of above text by E. Lees, National Lending Library for Sci. and Technology, p.422, pl.XXXIV, figs 3a-b.
1960 *Aulina rotiformis* Smith, Vassiljuk, Acad. Sci. Ukraine, SSR., Ukrainian SSR., Inst. Geol. series on Stratigraphy and Palaeontology, Bull.13, p.98, pl.23, figs 1-1c.
1962 *Aulina rotiformis* Smith, Lo and Zhao, Geol. of the Chilien-shan Mountain Range, vol.4, pt.3, p.177, pl.24.
1962 *Aulina rotiformis* Smith, Yu, Lin and Fan, Sci. articles for the Commemoration of the 10th Anniversary of the Changchun Geol. College, p.19, pl.4, figs 2a-b, figs 5a-b, pl.25, figs 2a-b.
1964 ?*Aulina rotiformis* Smith, Vassiljuk, Acad. Sci. Ukraine, SSR, Ukrainian SSR, series on Stratigraphy and Palaeontology, p.92, pl.7, fig.8.
1967 *Aulina rotiformis* Smith, Minato and Rowett, J. Fac. Sci. Hokkaido Univ., ser.IV, Geology and Mineralogy, vol.XIII, No.4, p.389, pl.47, figs 1-9, pl.48, figs 1-2.

Diagnosis: Thamnastraeoid or astraeoid *Aulina* with small corallites having 11 carinate septa of both orders and a complete aulos.

Type Material: Holotype cut in two halves; British Museum specimen R17497 and Sedgwick Museum specimen A1801 and A1802 (including thin sections). From Harlow Hill Limestone, Harlow Hill, Northumberland.

Material: Harlow Hill Limestone, Harlow Hill, Northumberland; Botany Limestone, Botany, Hunderthwaite Moor, Romaldkirk, Teesdale.

Description: External Characters; The corallum is characteristically depressed, horizontal extent being far greater than vertical height. The colony from Harlow Hill is only 2.2 cm. tall but 12 cm. x 8 cm. in surface area. The distal surface is either horizontal or slightly convex and is usually hummocky, the calicular depressions being raised above the general level of the corallum surface. The septa of adjacent corallites can be seen to be continuous and so the corallum is thamnastraeoid or astraeoid. The proximal surface is either flat or obtusely conical and is covered by a wrinkled holothecae.

Internal Characters; The major and minor septa are easily distinguishable, the major septa extending well into the tabularium whereas the minor septa only just penetrate the tabularium. All septa are dilated at the point where they cross the inner row of dissepiments. They thin slightly towards the axis and even more so in the outer dissepimentarium when they become confluent with the septa of the neighbouring corallite. In the tabularium the major septa bend through 90° to join up with the neighbouring septa and so produce a septal tube or aulos running down the length of the corallum. This aulos is always very well developed in this species with all the septa of almost every corallite contributing to the tube. Only rarely does a corallite fail to produce this structure. This species therefore represents a late stage in the phylogeny of the lineage as regards the development of the aulos. The 'bend' of the septa at their axial ends is concave inwards so that the aulos is circular in cross section (compare with A. botanica on p.249). The centre is empty except for the aulos, never is there a columella.

Septa usually number 11 of both orders but 12 have occasionally been seen. These septa are usually carinate but the development of the varinae is variable.

The tabularium varies in diameter from 1.5 mm. to 2 mm. and the aulos from 0.5 mm. to 0.8 mm., the aulos therefore occupying 1/3 of the tabularium. Corallites are closely spaced being only about 2 - 4 mm. apart and the septa of adjacent corallites are continuous and may be confluent.

The inner series of dissepiments which is usually restricted to a single row is regularly arranged in a concave fashion. They may be slightly dilated and are quite vertical. The outer series between the peripheral ends of the long septa however are more irregular in arrangement and are obliquely set, sometimes almost horizontal.

The tabulae of this species differs from those of *A. senex* and *A. botanica* due to the fact that the aulos is much better developed. Whereas in the previous two species it is the downturned edges of the inner tabulae that were mostly producing the 'tube', in *A. rotiformis* the tube is produced entirely be the bending septa. Hence in *A. rotiformis* the inner tabulae no longer need to be downturned at their edges. Thus the inner tabulae are simply horizontal, with the septal aulos dividing the two series.

Stratigraphical Range: Botany Limestone.

Aulina rotiformis aphroidia subsp. nov.

(Plate 70.)

1943 Aulina rotiformis Smith, Smith and Yu, partim, Q.J.G.S., vol.99, p.43. (Aphroid corallum only, not the more typical astraeoid corallum).

Diagnosis: A. rotiformis with an aphroid corallum.

Type Material: Holotype is specimen No. JN.61a (and sections 61ai, ii and iii cut from it). In the authors collection, University of Durham. From Botany Limestone, How Gill, Botany, Hunderthwaite Moor, near Botany Farm, Romaldkirk, Teesdale.

Description: The morphology is identical to A. rotiformis rotiformis except that the corallum is aphroid; adjacent corallites being separated by large globose dissepiments.

Discussion: It has long been recognised that A. rotiformis can occur with either an astraeoid/thamnastraeoid corallum or with an aphroid corallum, but these two different forms have never been separated. In other lineages it is usually the case that such different coralla are assigned to separate species, one being more specialised than the other (for example Orionastraea tuberosa and O. edmondsi). In the case of A. rotiformis the aphroid coralla have not been described here as a separate species as both aphroid and thamnastraeoid coralla occur at the same stratigraphical horizon, and, as intermediate conditions do also occur, the two different types of colony probably represent only end members of a continuously variable population. Thus they have been described as subspecies. If it were the case that the two types of colony occurred at distinctly separate horizons then the intermediate colonies could be considered as the evolutionary stages between two chronospecies (as with O. tuberosa and O. edmondsi), but this does not seem to be the case, at least in Britain. When the complete stratigraphical ranges of these two forms are known from Asia, where the species is much more common, it may then be seen that the aphroid corallum does occur at a higher horizon than the thamnastraeoid corallum, in which case *A. r. aphroidia* could be raised to specific level.

Stratigraphical Range: Botany Limestone.

Family Uncertain

Genus Fascicaulina nov.

1869 Diphyphyllum, Kunth, p.200. (Not Diphyphyllum Lonsdale).
1925 Aulina, Smith, partim, p.486. (Not Aulina S.S. Smith).
1930 Diphyphyllum, Delepine, partim, p.35. (Not Diphyphyllum Lonsdale).
1940 Aulina, Hill, partim, p.193. (Not Aulina S.S. Smith).
1943 Aulina, Smith and Yu, partim, p.43. (Not Aulina S.S. Smith).
1961 Aulina, Fontaine, p.119. (Not Aulina S.S. Smith).
1966 Aulina, Clarke, p.221. (Not Aulina S.S. Smith).

Diagnosis: Fasciculate rugose corals with major septa that tend to coalesce at their axial ends to form a tube or aulos running the length of the corallite. Major septa normally carinate.

Genotype: Aulina furcata (Smith, 1925, p.490) here chosen.

Discussion: This genus is proposed to include the fasciculate species previously assigned to the genus Aulina. The British species are as follows: (1) Fascicaulina furcata = Aulina furcata Smith, 1925, p.490; (2) F. horsfieldi = A. horsfieldi Smith and Yu, 1943, p.49; (3) F. hibernica = A. hibernica Clarke, 1966, p.222.

Fascicaulina is separated from the genus Aulina as it is thought that these species are derived from ancestors unrelated to Aulina (see p.32).

Fascicaulina horsfieldi (Smith and Yu)
(Plates 71 - 73.)

1930 Diphyphyllum concinnum Lonsdale, Delepine, Mem. Soc. Linn. Normandie, N.S.(2), p.35 in partim, pl.III, figs 11a-c.
1933 Diphyphylloid lithostrotionids, George, Q.J.G.S., vol.lxxxix, p.241, in partim.
1943 Aulina horsfieldi Smith and Yu, Ibid., vol.99, p.49, pl.X, figs 3-6.
1963 Aulina horsfieldi Smith and Yu, Clarke, Sci. Procs. Roy. Dublin Soc., ser.A, vol.2, No.14, p.222.
1967 Aulina horsfieldi Smith and Yu, Minato and Rowett, J. Fac. Sci. Hokkaido Univ., ser.iv, Geology and Mineralogy, vol.XIII, No.4, p.385.

Diagnosis: Corallum fasciculate; corallites large with an adult diameter of 9 - 14 mm., 28 - 32 carinate septa of each order, three or more series of dissepiments and a variable aulos.

Type Material: Holotype is British Museum specimen R 34238 from C1 Zone, Bell Busk, West Yorkshire. (Sedgwick Museum specimen no.E.10.304 is part of the same corallum).

Description: External Characters; Complete colonies have not been collected by the author but Smith describes them as being large and squat with sub-parallel, well separated tall, cylindrical corallites. Calices have not been seen.

Internal Characters; The relative proportions of lateral and calicular increase within a colony varies from corallum to corallum. In some, for example the paratype BMR34240 from Bell Busk, lateral increase is predominant and in such colonies there is little variation in corallite size as a corallite, once mature, stays in that state and remains of adult dimensions. However in others, for example BMR 30975 from Glamorgan, calicular (peripheral) increase is more common and in these types of colony there is a great variation in corallite size as a corallite no sooner reaches its mature dimensions than it divides again into two or three smaller immature buds. Thus in the latter case there is a greater number of immature corallites in the colony and the mean size is somewhat smaller than in the former case.

The maximum adult diameter varies in different colonies from 7.5 mm. in the Linney Head specimen, which is unusually small, to 12 mm. in the Bell Busk specimen, and may occasionally rise to 14 mm. The diameter of the young calicular buds is about 3. 5 mm.

The septa are of two orders, the major septa extending 4/5 the distance between the epithecae and the centre where they then bend through 90° to join up with the adjacent major septa producing a septal tube or aulos. This feature is not particularly consist~~a~~ent in this species and while some corallites may show a perfectly developed aulos, others may have only a partly developed aulos or no aulos at all. The development of the aulos also varies from colony to colony. In the specimen from Glamorgan it is well developed in most corallites, while in the Linney Head colony it is hardly developed at all.

Thus the development of the aulos can be seen to gradually improve within this species. In the colonies from Linney Head and Bell Busk when the septa bend at their axial ends the bend is convex inwards producing an irregular shaped aulos (as in <u>Aulina</u> <u>botanica</u>). The Glamorgan Colony, however, shows a more developed aulos, the 'bend' of the septa being concave inwards producing a stronger circular aulos (as in <u>A.</u> <u>rotiformis</u>).

In an adult corallite the aulos is about 2 mm. in diameter. The centre of the aulos is always empty there never being any columella. This species also shows a peculiar feature in that many of the minor septa also bend through 90° and join on to the adjacent major septa. This obviously however does not produce a continuous structure.

There are usually at least three rows of dissepiments and these define a tabularium from 4 - 6 mm. in diameter, in adult corallites and the minor septa only just penetrate this tabularium. Major and minor septa may be dilated in the dissepimentarium but unlike Lithostrotion the inner row of dissepiments is rarely dilated. Also the dissepiments are much less regularly arranged than in Lithostrotion and the tabularium is much less well defined.

The maximum number of septa in a colony varies from 28 - 32. The septa are always carinate but the degree of carination is variable from strong to hardly detectable.

The tabulae are divisible into two series, an outer and an inner series, both of which are horizontal and are separated by the septal aulos.

Fascicaulina hibernica (Clarke)

(Plate 74.)

1963 *Aulina furcata* Smith, Shephard-Thorn, Proc. R.I.A., B, p.286-7. (non *A. furcata* Smith).
1966 *Aulina hibernica* Clarke, Sci. Proc. of the Royal Dublin Society, ser.A, vol.2, No.14, p.222, pl.20, figs 1a, 1b, 2a, 2b.

Diagnosis: Corallum fasciculate; corallites intermediate in diameter between *A. horsfieldi* and *A. furcata* with an adult diameter of 5.5 mm. - 7 mm., 24 - 27 carinate septa of both orders, 2 - 3 rows of dissepiments, and a variable aulos.

Type Material: Holotype is Trinity College, Dublin, specimen no. T.C.D.2645 from beds of basal D1 age, Brownstowns House, Co. Meath, Ireland (includes thin sections T.C.D.2645h and T.C.D.26451).
Geological Survey Museum, London, thin sections PF2687 and PF2688 were cut from the same corallum.

Description: External Characters; The corallum forms low bush-like colonies and Clarke reports them to be about 1' in diameter. The corallites are tall and flexuous. Calices have not been seen.
Internal Characters; There is a great variation in corallite diameter due to the prevalence of calicular increase, the corallites just reaching maximum mature diameter when they immediately divide into 2, 3 or 4 smaller buds. The diameter of mature corallites just before splitting is approximately 7 mm. and the diameter of young buds immediately after splitting is approximately 3 mm.

The septa are of two orders with the major septa extending 5/7 of the distance between the epithecae and the centre, where they then bend through 90° and join up with the adjacent major septa. This feature is not particularly consistent in this species and while in some corallites a well developed aulos may be formed, in others only half of the aulos may be developed or it may be absent altogether. Again, as will *A. horsfieldi* the state of development of the aulos is variable within this species, it may be primitive with a convex bend to the axial ends of the septa, or advanced with a concave bend.

In a mature corallite 7 mm. in diameter the aulos is thus only 2 mm. in diameter, in a corallite 5 mm. in diameter it is 1.5 mm., and in a young bud 3.5 mm. in diameter it is only 0.75 mm. in diameter. The centre of the aulos is empty, there is never a columella.

There are usually two or three series of dissepiments which define a tabularium 4 - 4.5 mm. in diameter in adult corallites and the minor septa only just penetrate this tabularium. Major and minor septa may be slightly dilated in the dissepimentarium but unlike *Lithostrotion* the inner ring of dissepiments is not dilated. Also the inner row of dissepiments is not so regularly arranged nor so concentric as in the species of the *Lithostrotiontidae*.

The maximum number of septa in a colony varies from 24 - 27. In a colony with 27 septa in an adult corallite there are only 16 septa in a young bud when it first becomes free from its parent corallite. The septa are carinate but carinae are by no means seen in every corallite. They may be rare but are always present in some corallites and can be quite strongly developed.

Fascicaulina furcata (Smith)

(Plate 75.)

1869 Diphyphyllum irregulare Kunth, Zeitschr. Deutsch. Geol. Gesellsch; vol.XXI, p.200, pl.II, figs 5a, 5b.

1925 Aulina furcata Smith, Ann. Mag. Nat. Hist., ser.9, vol.XVI, p.490, pl.XXIV, figs 3-7.

1940 Aulina furcata Smith, Hill, 'Mon. Carb. Rug. Corals of Scotland', Pal. Soc., p.192, pl.XI, fig.8.

1943 Aulina furcata Smith, Smith and Yu, Q.J.G.S., vol.99, p.48, pl.X, figs 1, 2.

1961 Aulina furcata Smith, Fontaine, Archives geologiques du Viet Nam, Numero 5, p.120, pl.10, figs 10, pl.14, fig.2, pl.18, fig.1, pl.19, fig.6.

1963 Aulina furcata Smith, Clarke, Sci. Proc. Roy. Dublin Soc., ser.A, vol.2, No14, p.222.

1967 Aulina furcata Smith, Minato and Rowett, J. Fac. Sci. Hokkaido Univ., ser.IV, Geology and Mineralogy, vol.XIII, p.385.

Diagnosis: Corallum fasciculate; corallites small with an adult diameter of 4 mm., 18 - 22 carinate septa of both orders, a single series of dissepiments and a complete aulos.

Type Material: Holotype is British Museum specimen R 24967. From Siggate, near Castleton, Derbyshire. Paratype is Sedgwick Museum specimen no.A1800.

Description: External Characters; The colony forms large bush-like growths and Smith (1943) reports that these may be of considerable size, the colony from which the type material was collected measured over 1 m. in diameter and ½ m. in height. The corallites are cylindrical, tall and flexuous and the epithecae is transversely wrinkled. Calices have not been seen but Smith (1925) says, "as far as one can judge ... they consist of a narrow steep-sided depression with a flat bottom and surrounding this is a raised platform. The depression is not formed by the thecae but by the tube which undoubtedly stood out prominently above the platform".

Internal Characters; There is a great variation in corallite diameter due to the prevalence of peripheral increase, the corallites just reaching maximum diameter when they divide again into two, three or four buds. Diameter of mature corallites just before splitting is approximately 4 mm. and diameter of young buds immediately after splitting is approximately 2 mm.

The septa are of two orders with the major septa extending 3/4 of the distance between the epithecae and the centre where they then bend through 90° and join up with the adjacent major septa. This feature is seen consistantly in all corallites and so a well developed aulos is formed, but occasionally some major septa do not reach the aulos and so do not contribute to it. This species represents a late stage in the phylogeny of the group as regards development of the aulos. The 'bend' of the septa at their axial ends is always concave inwards so that the aulos is circular in cross section (as in A. rotiformis). In a mature corallite 4 mm. in diameter the aulos is only 1 mm. in diameter and in young bud 2 mm. in diameter the aulos is only 0.5 mm. wide. Septa rarely penetrate the aulos and its centre is empty, there never being a columella.

There is usually only one row of dissepiments but in parts of a corallite there may be two rows developed. The dissepiments define a tabularium 2.5 - 3 mm. in adult corallites and the minor septa only just penetrate this tabularium. Major and minor septa may be slightly dilated in the dissepimentarium, but unlike Lithostrotion the inner row of dissepiments is not dilated. Also while the dissepiments are concave they are never so perfectly and regularly arranged as in the fasciculate species of Lithostrotion.

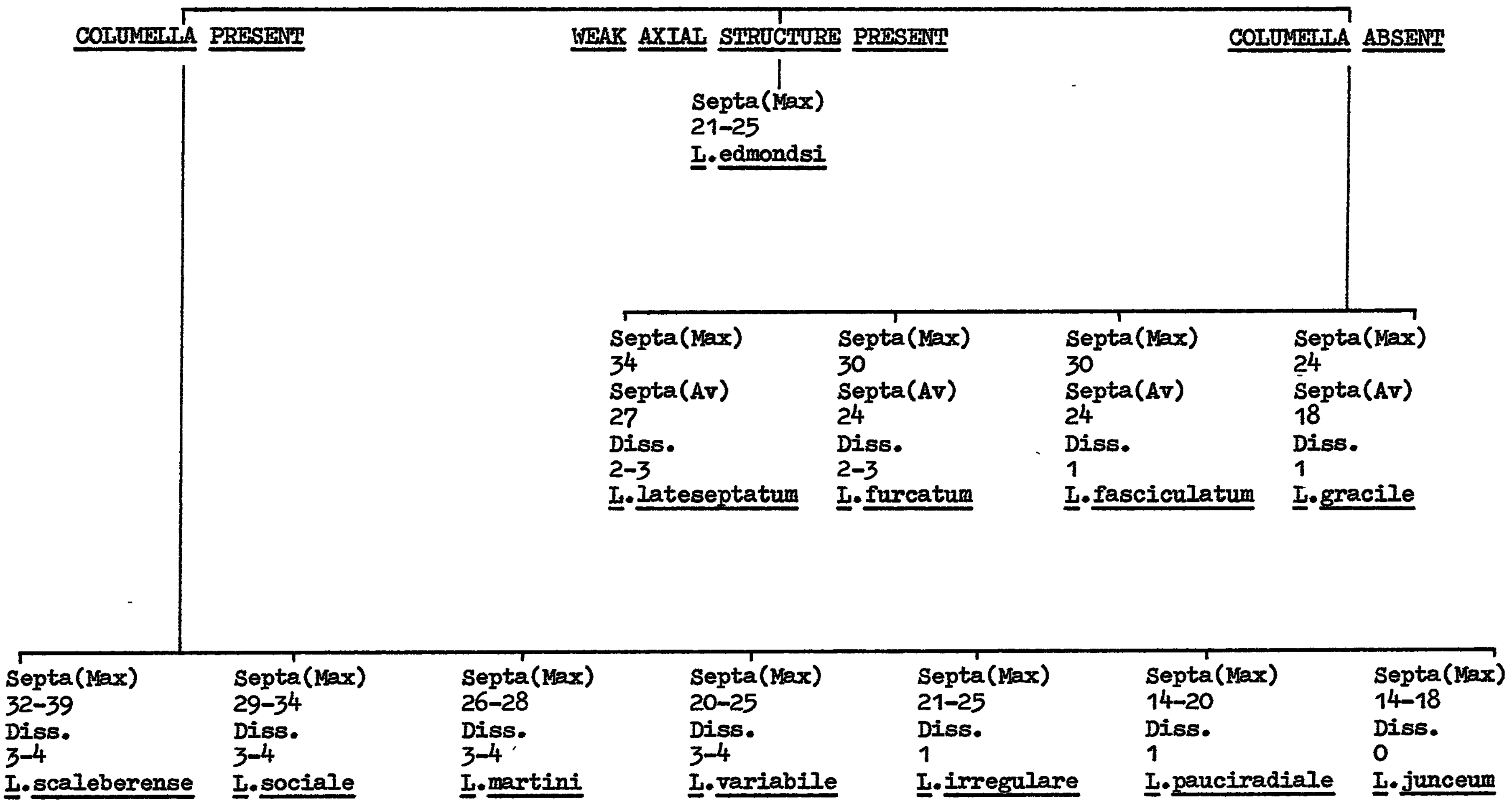
The maximum number of septa in a colony varies from 18 - 22. In a colony with 18 septa in an adult corallite there are only 10 septa in a young bud when it first separates from its parent.

The septa are carinate but carinae are by no means seen in every corallite; they may be very rare, but are always present in some corallites, though they are often only feebly developed.

The tabulae are as in *F. horsfieldi*.

APPENDIX

FASCICULATE COLONIES



N.B.

Diss. = Dissepiments

Tab. = Tabularium

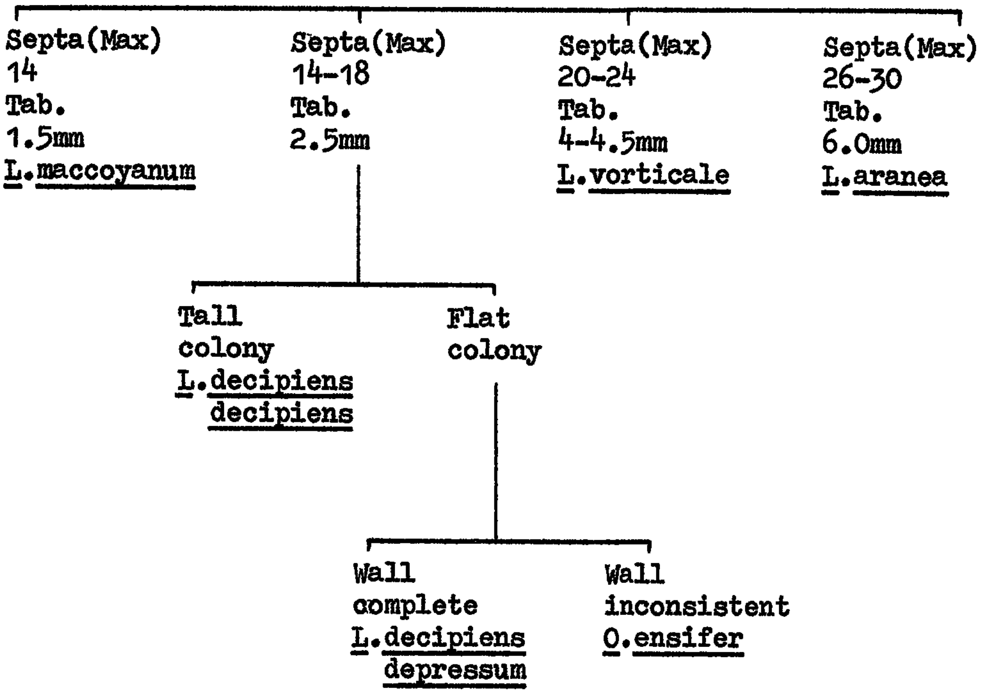
Max. = Maximum

Av. = Average

L. = *Lithostrotion*

O. = *Orionastraea*

CERIOID COLONIES



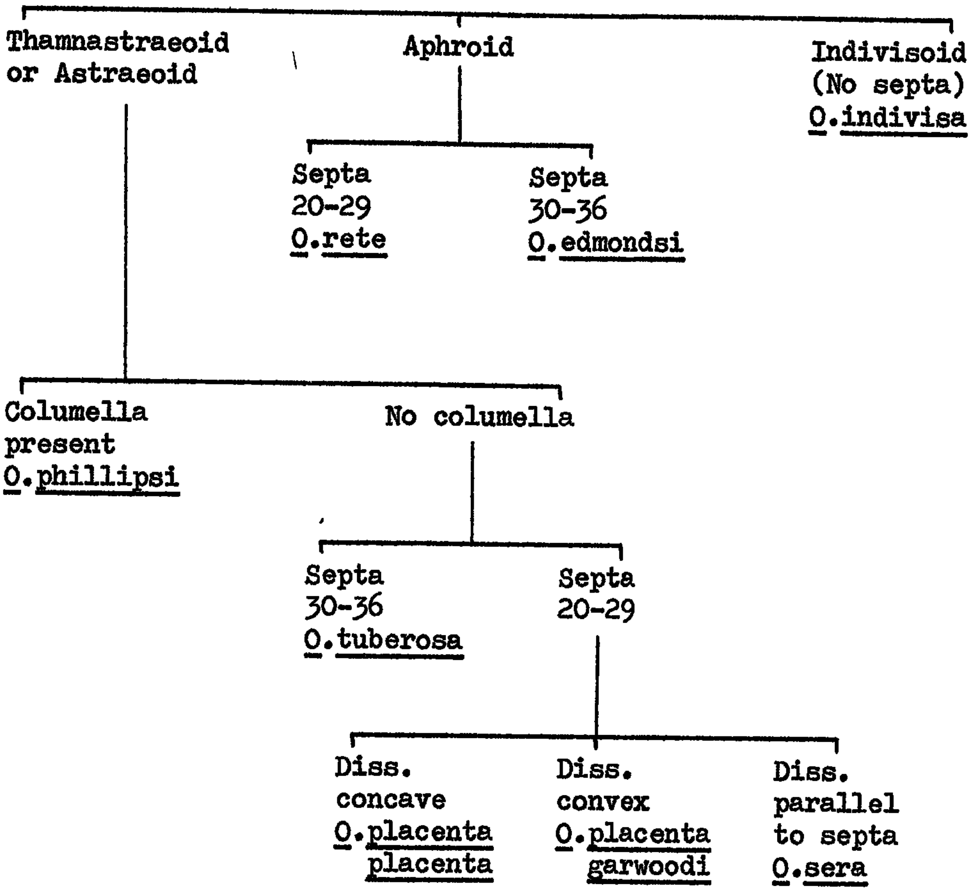
N.B.

L.vorticale
=*L.minus*
=*L.basaltiforme*
=*L.flemingi*
=*L.clavaticum*
=*L.portlocki* s.s
=*L.striatum*
=*L.bristoliense*

L.decipiens
=*L.clissioides*
=*L.derbiense*

L.aranea
=*L.major*
=*L.septosum*
=*L.arachnoideum*

PLOCOID COLONIES



N.B.

O.placenta=*O.prerete*

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CARBONIFEROUS CORAL GEOCHRONOMETERS

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Abstract

Preservation of the fine ornament of the epitheca of rugose corals is unusual, but it has been found in 6 genera from the marine limestones and shales of Carboniferous age in northern England. These specimens show the daily growth bands with some indication of monthly banding. No specimens have been found that show the detail of the epitheca over the complete length of the corallite and the best specimens show only a limited number of consecutive monthly bands. The best developed epithecal banding has been found in fasciculate *Lithostrotion*. In *L. martini* M. Edwards and Haime epithecal banding gives an average monthly count of 30·2 days, indicating 391·09 days in the Lower Carboniferous year; this figure compares well with the estimate of 393 days based on geophysical methods (Wells, 1963). Growth rate in this species varies between 3 and 5 mm per month and seems to be controlled partly by environmental factors though there is a general trend for the growth rate to quicken up the stratigraphical column. With the increase in growth rate of *L. martini* up the geological column it has been found that there is a gradual wider spacing of the tabulae. Initial calculations have shown that the number of tabulae formed during a month may be constant for this species at 7–8 tabulae per month. If the constancy of tabulae development could be proved in other species of rugose corals the possibilities of using them as geochronometers would be greatly increased.

Introduction

The time-growth significance of parallel concentric markings on the epitheca of well-preserved corals was first recognized by Whitfield (1898) who suggested that they were annual growth increments brought about by seasonal temperature changes. Fossil corals were used as geochronometers by Wells (1963) to supply an independent check to radiometric age dating and compile an absolute geological time-scale based on fossil data. He recognized epithecal banding of 2 orders, annual banding well separated on the corallum and finely spaced ridges caused by daily growth increments. The annual growth banding is thought to be caused by temperature control of lime deposition by the coral polyp. Where seasonal temperature changes are sufficient lime secretion by the polyp would either be slowed down or cease altogether during the colder part of the year, giving the annual epithecal banding. Wells checked annual and daily banding in living corals in which the annual linear growth-rate was fairly well known and found reasonable confirmation of his deductions. The cause of the daily increment ridges is the variation in the rate of lime intake by the tissue of coral polyps between the light conditions of the day and the darkness of night. Despite the difficulty of finding fossil corals of sufficiently fine preservation to show the daily and annual growth increments Wells (1963) obtained specimens of Middle Devonian corals, including *Heliophyllum halli* M. Edwards and Haime, from which it was possible to count 385 to 410 (average 400) fine daily ridges per annual increment. He postulated therefore that the Middle Devonian year contained roughly 400 days. This figure agrees well with the calculated estimate assuming that the Earth's rotation about its polar axis has been slowing down owing to loss of rotational energy by tidal friction of about 2 sec per 100,000 years, as Wells was able to show.

Further important advance in the understanding of epithecal banding was made by Scrutton (1965), again working on Middle Devonian corals. He was able to recognize daily growth ridges and regular bands of much shorter period than the annual growth increment which he was unable to identify. By counting he found that there was an average of some 30·59 daily ridges to each of the bands; this figure was recalculated in 1970 as 30·66 daily ridges per band. Using Wells' (1963) data Scrutton assumed that there were 399 days in the Middle Devonian year. This means that 13·04 bands of daily ridges (later recalculated to 13·01 bands per year) were produced every year and Scrutton concluded that this suggested a lunar monthly effect on the accretionary growth of the coral skeleton. Studies of modern corals give little support to this, but less lime may be deposited at the full Moon when the corals are preoccupied with breeding and a monthly constriction has been recorded in the epitheca in some cases. Alternatively, a direct tidal influence may play an important role, but in either case it is the synodic month that is presumably being recorded. Scrutton and Hipkin (1973) stress that the supposed lunar monthly banding is not supported by satisfactory observations on living corals and the status of the bands is based on a numerical relationship between them and other accretionary banding of the epitheca.

Further analysis of daily growth increments and monthly banding on Silurian and Devonian corals and brachiopods has been completed by Mazzullo (1971). His figures are in general agreement with those of previous workers except that he uses maximum counts rather than the mean or mode of a group of data and his figures are thus proportionately exaggerated. Growth rhythms in bivalves have also been used as a source of growth increment data and cephalopods and stromatolites have also received some attention. This work is ably summarized by Scrutton and Hipkin (1973) who review the whole field of fossil geochronometers and the application of the results obtained from them.

The recognition of regular epithecal banding in corals corresponding to the synodic month allows important calculations to be made in material which does not show annual banding. Thus, as long as the monthly banding is finely preserved, 2 important measurements can be made. First, the number of days in the month can be counted and by simple multiplication by the number of lunar months in a year the number of days in the year can be calculated: the calculation of the number of synodic months in the year is discussed later in the text.

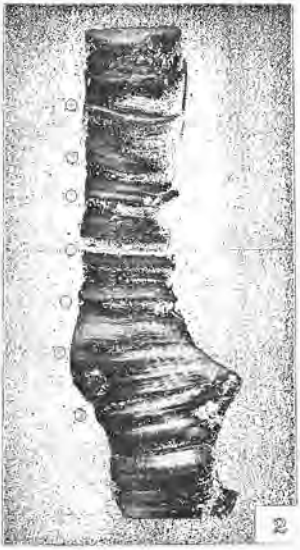
Secondly, the rate of accretionary growth of the epitheca of the corals can be measured per synodic month. Figures derived by this method are only available for the Middle Devonian corals at the present time. To supply an independent check various rugose coral genera from the marine limestones and shales of Lower Carboniferous (Viséan) and Upper Carboniferous (Namurian) age from Northern England have been studied and the results of this work are presented in this paper.

Annual and monthly growth increments

In northern England marine sediments with thick limestones containing rich coral faunas occur in both the Dinantian and the Namurian. An extensive unstable shallow shelf sea covered the region during this period in which bottom conditions were often marked by strong current action. Overturned and displaced coral colonies are common and rolled corals, in which the epitheca is highly abraded, are ubiquitous. Preservation of the fine detail of the epitheca is very rare and is normally associated with corals found in shale and limy shale matrices. In cerioid colonies of *Lithostrotion* and *Lonsdaleia* well-preserved epithecal banding has been found on internal corallites when the partly weathered corallum is split. Thamnastraeoid colonies of *Orionastraea* show fine banding on the holotheca when preservation is in soft calcareous shale. It must be stressed that though well-preserved accretionary growth banding has been found in 6 genera of Carboniferous corals in northern England, preservation of this excellence is rare and the specimens referred to here have been brought together over a period of some 10 years.

Though the corals from northern England show clearly defined daily-growth bands and some indication of monthly banding (Figures 1 and 2), no annual growth increments have been observed. Annual growth increments have been recorded in living corals by Whitfield (1898) and Vaughan (1915) and in Middle Devonian corals by Wells (1963). Seasonal temperature fluctuation is thought to be responsible for the annual banding on the coral epitheca with reduced secretion or non-secretion of lime in the skeleton during the colder winter period. If this mechanism for the production of the annual banding is correct the annual bands would be expected to be strongest away from the equator where the seasonal temperature effects are more marked. Conversely, near the equator, where the seasonal temperature changes are slight, annual banding would be expected to be poorly developed or absent. It is therefore significant that the Viséan and Namurian corals of northern England show no indications of annual banding, particularly as they have been collected within 10° of the position of the Carboniferous equator (Figure 3). In agreement with this hypothesis the Middle Devonian corals which Wells (1963) used to demonstrate annual banding come from seas which must have been almost 40° south of the Devonian equator (Figure 4). The absence of annual banding would seem to indicate coral growth within the broad equatorial belt of the Earth.


1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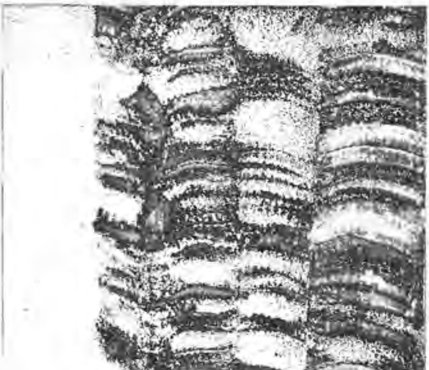
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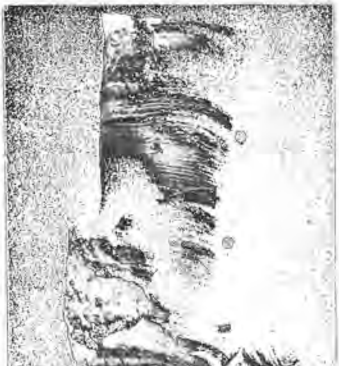
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Epithecal banding, believed to be produced by synodic month periodicity, is clearly developed in a few corals from northern England when preservation is in lime-rich sediment. Unfortunately, well-preserved daily banding in specimens preserved in shale does not show satisfactory monthly banding. Up to 5 monthly bands have been found on a single broken corallite of *Lithostrotion martini* and on specimens of this type accurate counts of the days in a month can be made (Figure 1).

Scrutton (1970) states, from studies of Middle Devonian corals, that there are 13·01 synodic months in the Devonian year. At the present day there are 12·53 months in the year, thus by comparison of these figures it appears that the synodic month is increasing in length with time. Assuming that this rate of increase in the length of the month is constant we can calculate that there must have been 12·95 months in the Lower Carboniferous (Viséan) year. Another assumption which has to be made in using epithecal banding data is that the period of the Earth's rotation about the Sun, giving us the year, has been constant during the Phanerozoic.

Number of days in the Viséan year

Rugose corals from northern England used in the present study show daily growth bands and some indications of monthly banding. In no case has annual banding been observed in these corals. By far the best epithecal banding has been found in fasciculate *Lithostrotion* preserved in shale and shaly limestone. The soft nature of the surrounding sediment does seem to play a part in the preservation of fine detail of the ornament of the epitheca though, as Wells (1963) states, epithecal diurnal growth-lines are commonly abraded or corroded in living corals even before the death of the polyp. Still water conditions and relatively quick burial in a protective medium would help to preserve the fine epithecal detail. Corallites of *Lithostrotion martini* M. Edwards and Haime from the lower Viséan C_2-S_1 zone beds of Ashfell Edge, Westmorland, show distinctive synodic monthly banding with well-preserved diurnal banding. The coralla are crushed in the enclosing calcareous shale matrix and no corallites long enough to contain a year of 13 monthly bands have been collected; yearly increments cannot therefore be recognized. The number of diurnal ridges per monthly band

GURE 1. 1. *Lithostrotion junceum* (Fleming). Jew Limestone, Orton, Westmorland.
$_2$ zone, Viséan. Well-developed daily increments, but no apparent monthly banding.
P3581, × 4
and 4. *Lithostrotion martini* M. Edwards and Haime. Ashfell Sandstone, Ashfell Edge,
estmorland. C_2-S_1 zone, Viséan. 2: well-developed daily and monthly banding.
o. 3Ci, × 2. 4: clear daily ridges run from parent to lateral offset. No. 3Ck, ×3·2.
White dots mark the monthly bands
Lithostrotion minus (McCoy). Great Scar Limestone, Horton-in-Ribblesdale, Yorks.
Daily increments and well-developed monthly banding. P4688, ×2

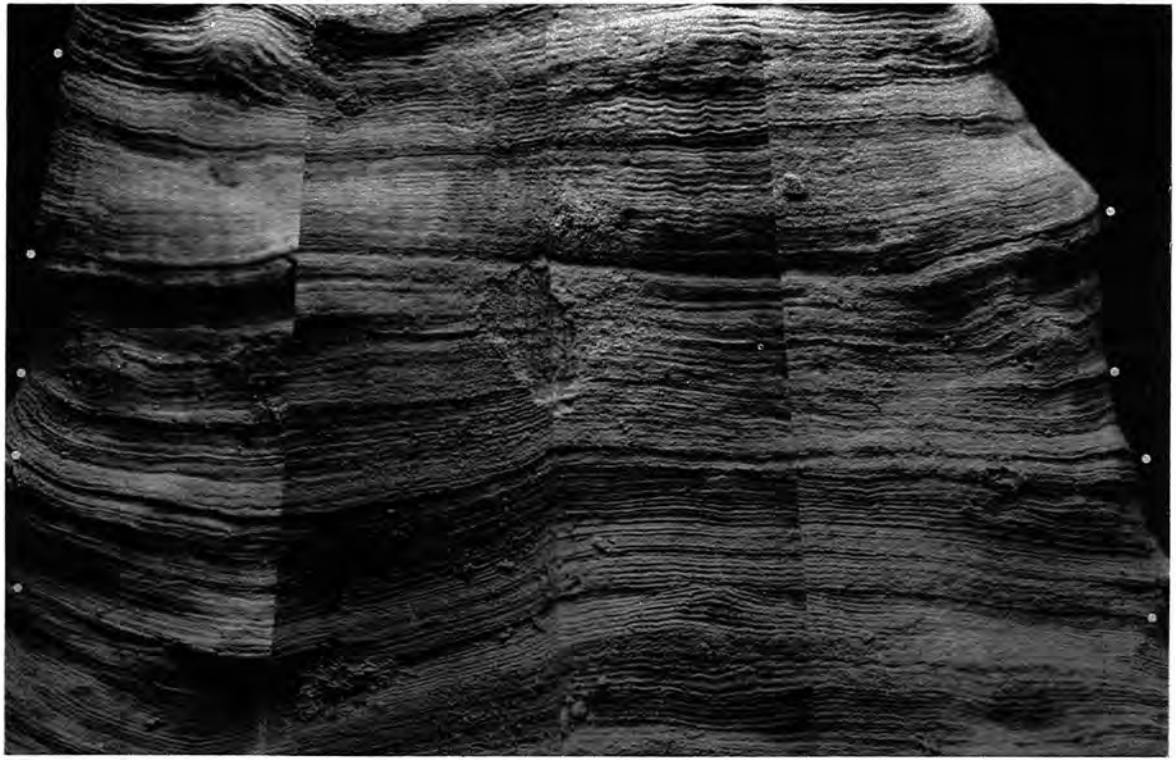

FIGURE 2. *Lithostrotion martini* M. Edwards and Haime. Ashfell Sandstone, Ashfell Edge, Westmorland. C_2–S_1 zone, Viséan. Composite photograph showing the entire epithecal surface of a cylindrical corallite. Four monthly bands are shown with daily increments, marginal dots mark the monthly boundaries. No. 3Ci, × 6·5

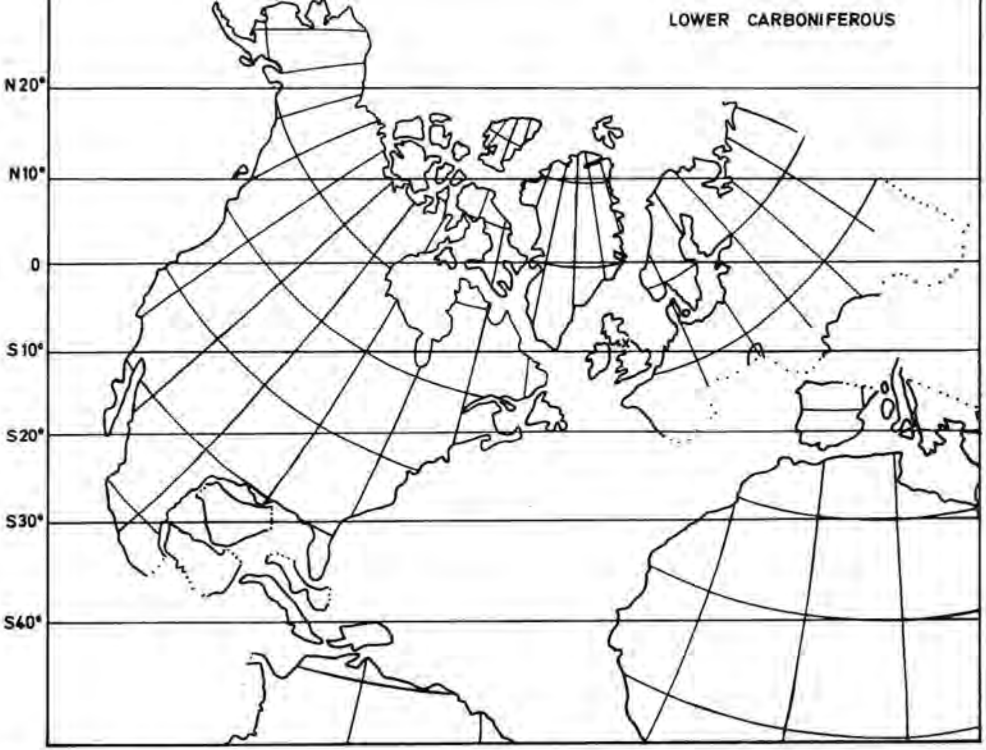

FIGURE 3. Palaeogeographical map of the North American–European region during Lower Carboniferous times. The position of the shelf sea in which the Westmorland *Lithostrotion martini* fauna grew is shown at the point in Britain marked X. After Smith, A. G., Briden, J. C. and Drewry, G. E. (1973) in 'Organisms and Continents through Time', *Spec. Pap. Palaeont.*, **12.** Reproduced by permission of The Palaeontological Association

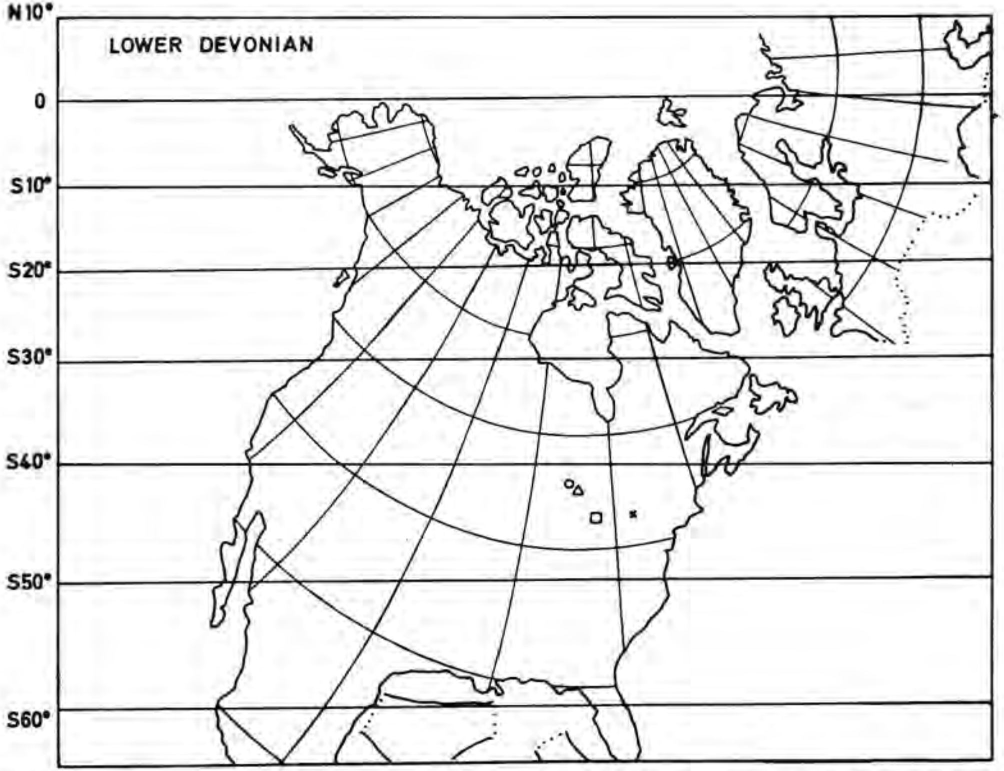

FIGURE 4. Palaeogeographical map of the North American–European region during Lower Devonian times. The position of the shelf seas from which Devonian corals were obtained by Wells and Scrutton is shown by the following symbols: ○, Roger's City, Michigan; △, Alpena City, Michigan; □, London, Ontario; ×, Western New York State. After Smith, A. G., Briden, J. C. and Drewry, G. E. (1973) in 'Organisms and Continents through Time'. *Spec. Pap. Palaeont.*

has been calculated using corallites where the epithecal surface is particularly well preserved and these counts give a mean figure of 30·2 days to the synodic month. This figure has been checked with other corallites from the same horizon in which the epithecal surface is less well preserved and counts for the days in the month agree well. If we calculate that there are 12·95 synodic months in the Viséan year we arrive at a figure of 391·09 days in the Viséan year. The deduced Viséan year can now be compared with the Middle Devonian year of 399 days calculated by Wells and Scrutton and we have clear evidence supplied by coral geochronometer evidence alone that the number of days per year is decreasing and that the Earth's rotation about its polar axis must be slowing down.

Slowing down of the Earth's axial rotation

From the epithecal banding data obtained from corals the rate of slowing down of the rotation of the Earth can be calculated and compared with the rates worked out by the geophysicist. Using work on astronomical observations over the past 200 years, Bott (1971) states that the slowing down of the rotation of the Earth about its axis is attributable to 2 factors. Lunar tidal friction causes a slowing down of about 18·1 sec/My, while tidal interaction between the Sun and the Earth contributes a further slowing down of up to 5 sec/My, a total slowing down of some 23 sec/My. The reliability of these figures over periods of the Earth's history longer than 200 years is doubtful as the factors causing deceleration are variable. They depend largely on frictional forces of ocean tides caused by the distribution of land and sea, the shape and number of large tidal estuaries and the relative development of wide shallow shelf seas.

Now only average values for the rate of deceleration of the Earth's rotation about its axis through geological time can be obtained from the estimate in recent times and also from the evidence provided by epithecal banding of Middle Devonian corals. The new figures provided by the counts of epithecal banding of Viséan corals make possible a comparison of the rate of deceleration between different periods of geological time using the following equation:

$$R = \left(\frac{31471200}{D_t} - \frac{31471200}{D_0}\right)\frac{1}{t} \tag{1}$$

where R = Rate of deceleration
D_t = Days per year of the younger period
D_0 = Days per year in the older period
t = Time in My between D_t and D_0
31471200 = Sec per present day year of 364·25 days.

A calculation of the rate of deceleration of the Earth's rotation can now be made between the present day and the Middle Devonian using Wells' figures. Wells did not calculate the rate of slowing down from his coral data, but he did plot a

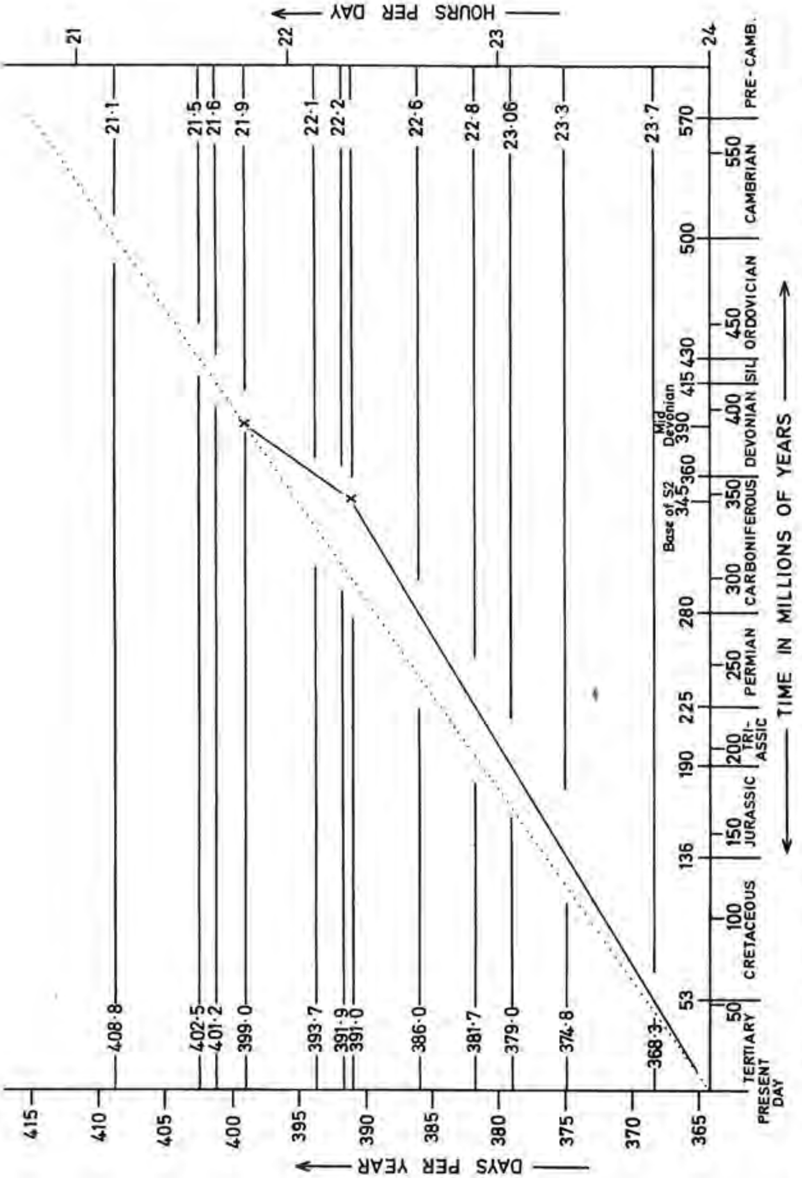

FIGURE 5. Plot of days in the year against geological time showing the changes in the rate of the Earth's axial rotation. The solid line shows changes in the rate of rotation between the Devonian to Carboniferous and Carboniferous to present day. Devonian and Carboniferous counts for days/year based on coral epithecal data. Age date of Carboniferous corals from Fitch *et al.* (1970) and date for Devonian corals from Lambert (1971). The dotted line is the average rotation rate between the present day and the Devonian and projected back to the Cambrian as originally published by Wells (1963)

graph of days in the year against geological time based on his counts for the Middle Devonian year (Wells, 1963, Figure 1). From this graph the rate of deceleration is seen to be 20·8 sec/My. For this graph Wells was using radiometric age data of Kulp (1961) which has since been revised: in particular the base of the Devonian system is now believed to be some 10–20 My older than was previously estimated (Lambert, 1971). This revision has the effect of reducing the rate of deceleration of rotation of the Earth to 19·29 sec/My, i.e. the length of the day increases by 19·29 sec every My.

The overall rate of deceleration of the rotation of the Earth between the present day and the Viséan (Lower Carboniferous) can be calculated using the epithecal counts of *Lithostrotion martini* from Westmorland. This produces a rather slower rate of deceleration of 17·18 sec/My (from equations (1) and (2), where $D_0 = 391{\cdot}09$ and $D_1 = 364{\cdot}25$). A comparison of the Devonian and the Carboniferous rates of deceleration with the present day suggests that the rate was unusually high between the Devonian and the Carboniferous. This deceleration rate comes out at 35·45 sec/My (from equations (1) and (2), where $D_0 = 399$ and $D_1 = 391{\cdot}09$). It has already been noted that the cause of deceleration in the rate of rotation of the Earth is largely brought about by frictional forces of oceanic tides that are increased by shallow shelf seas and wide tidal estuaries. Palaeogeography of later Devonian and Lower Carboniferous times involves the widespread marine transgression of mature coastal plains and lowland basins by a shallow shelf sea (Gignoux, 1955; Johnson, 1967). Clearly the palaeogeographical conditions are right for tidal forces to be abnormally high during this period of time and this is supported by the high deceleration rate for the rotation of the Earth at this time, calculated from the epithecal banding data of fossil corals.

The graph plotted by Wells (1963) of days in the year against geological time produced a straight line that assumes a constant rate of deceleration of the rotation of the Earth during the Phanerozoic. We now know from the comparison of the Devonian and Carboniferous data from fossil corals that this rate is variable. A future aim will be to make further epithecal counts on corals from other geological periods and in this way deduce the pattern of change in the rate of the Earth's rotation through as much of the Phanerozoic as possible. The graph can now be redrawn, modified by using the most recent radiometric age dates for the Phanerozoic and including the Carboniferous epithecal counting data (Figure 5). Calculations of the number of days in the year at unknown points in geological time cannot be made directly from the rate of deceleration of the Earth's rotation owing to the errors involved with variations in the deceleration rate. In the graph (Figure 5) the number of days in the year between two known points has been calculated independently of deceleration rate using the following equation:

$$N_x = \left(\frac{D_0 - D_1}{t_1}\right) t_0 + D_1 \tag{2}$$

where N_x = Number of days at required time x
D_0 = Days per year in older period
D_1 = Days per year in younger period
t_0 = My between required time x and D_1
t_1 = My between D_1 and D_0.

Growth rate in Carboniferous corals

An independent check on the identity and authenticity of the epithecal banding of fossil corals can be made by growth rate comparison with living corals. If the growth rate of fossil corals from the Carboniferous falls within the known range of growth rate of present-day corals we have further evidence that the growth behaviour is similar and that the epithecal banding is directly comparable. According to Wells (1956) growth rate in living scleractinian corals varies in different areas and is greater in places where the average water temperature throughout the year is moderately higher. It also varies according to the structure of the skeleton, being slower in types with dense coralla and faster in types with light porous skeletons. Annual increments in overall height between 5–82 mm are given by Wells (1963) for warm-water reef corals of differing skeletal morphology. Growth rates recorded by Whitfield (1898) and Vaughan (1915) on *Acropora palmata* from the Bahamas was reviewed by Wells (1963) who shows that annual increments of between 40–100 mm per year are reliable estimates. The Bahamas lie at latitude 24° north in warm seas and they are broadly comparable to the conditions during Viséan times in Britain though here the position was only 10° south of the equator. Calculated growth rates from the diurnal and monthly epithecal ridges of 6 genera of Viséan corals give figures which vary from 36–69 mm per year (Table 1). From the table it can be seen that the growth rates of Viséan corals do fall within the known growth rates of present-day corals. Furthermore, those from the Viséan of northern England, living near to the equator (see Figure 4), show faster rates of growth (up to 69 mm per year) than those for the Devonian of New York living 40° south of the equator (20 mm per year).

A factor which has become apparent during the study of *Lithostrotion martini* from Westmorland is that the development of monthly banding on the epitheca may vary widely, particularly in different lithologies of rock matrix. Thus *L. martini* normally has well-developed monthly banding, but specimens collected from shaly beds have no monthly banding developed. If the monthly banding is a lunar breeding periodicity feature expressed on the epitheca of the corals then possibly the muddy environment had an adverse effect on the breeding. A further factor which came out of this study was that the growth rate of *L. martini* quickens up the Viséan stratigraphical column from 3·6 mm per month in the centre of the C_2-S_1 zone to 4·5 mm per month at the top of the zone. This variation is independent of lithology, for at each horizon growth rate is influenced by environmental

TABLE 1. Rates of growth of some Carboniferous rugose corals

	Growth/month in mm									Mean growth/month	Mean growth/year
	1	2	3	4	5	6	7	8	9		
Aulophyllum fungites (Fleming) Horizon uncertain (Viséan)	3·0	3·0	3·87	3·0	3·25					3·22	41·7
Cyathaxonia cornu Michelin Tyne Bottom Lst.	3·9	3·5	3·5	3·6						3·6	46·6
Dibunophyllum bipartitum (McCoy) E_1, Great Lst.	4·5	3·6	4·2							4·1	53·1
Dibunophyllum bipartitum (McCoy) E_2, Botany Lst.	3·0	3·8	3·1	4·0	4·5					3·68	47·7
Lithostrotion minus (McCoy) Great Scar Lst.	4·8	5·0	3·1	3·0	4·0	5·5	6·0	5·5	4·2	4·45	57·7
Lithostrotion martini Edwards and Haime Low C_2-S_1 zone	3·9	4·2	3·0	4·0	4·0	4·0	3·2	3·0	3·3	3·6	46·6
L. martini, Ashfell Sandstone (limestone band)	4·3	5·1	5·4	3·5	4·0	5·0				4·5	58·3
L. martini, Ashfell Sandstone (shaly limestone)	4·4	4·5	4·5	4·5						4·5	58·3
L. martini, Ashfell Sandstone (limey shale)	3·0	2·5	3·0	2·5						2·75	35·6
Lithostrotion junceum (Fleming) Jew Lst.	3·0	3·0	3·0	3·0	3·1	3·6	3·0	3·1	3·0	3·1	40·1
Lonsdaleia floriformis (Martin) Tyne Bottom Lst.	5·0	5·0	7·0	4·0	5·0					5·2	67·3
Orionastraea phillipsi (McCoy) Bankhouses Lst.	6·0	4·4	4·3	6·0	6·0					5·33	69·0

differences. The lithology factor is demonstrated by *L. martini* from limestone and slightly shaly limestone (up to 20% clastic material) with a growth rate of 4·5 per month, whereas in an adjacent limey shale (60% clastics) the growth rate was only 2·75 mm per month; the latter conditions are clearly poor for coral growth.

TABLE 2. Insertion of tabulae in *L. martini* from the Viséan of Westmorland, England

Horizon	Growth/month (mm)	Tabulae/5 mm	Tabulae/month
Ashfell Sandstone (limestone band) top of C_2-S_1 zone	4·55	7·5	6·8
Ashfell Sandstone (shaly limestone band)	4·50	7·5	6·7
Ashfell Sandstone (calcareous shale band)	2·75	13·0	6·5
Thysanophyllum Lst. low C_2-S_1 zone	3·60	10·0	7·2

The variation in the growth rate of *L. martini* seems to be linked to the spacing of the internal horizontal skeletal plates termed tabulae. In the specimens from the C_2-S_1 zone of Westmorland, there is firstly a tendency for the tabulae to become wider spaced, passing up the succession and secondly, closer spacing of tabulae develops in specimens collected from shaly horizons. The growth rate per month has been calculated for four samples from this zone and in each case longitudinal sections have been cut and the number of tabulae per 10 mm counted. From these figures the number of tabulae per month was determined (Table 2). These figures indicate that in *L. martini* there may be a time relationship to the formation of tabulae with 6·5–7·5 tabulae being deposited every lunar month. It is probable that this relationship in *L. martini* is caused by the polyp building up sufficient lime to form a new tabula once every 4·6 days. Further work is required to substantiate the relationship between growth rate and the formation of tabulae, but if a similar constancy of tabula formation could be arrived at in other species and genera a method of estimating growth rate independently of the preservation of the epitheca would be possible. In this case the use of corals as geochronometers might be greatly increased.

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DISCUSSION

PANNELLA: Were your counts carried out by independent observers, as well as by you?

JOHNSON: Only Nudds and I made our counts, but they were independent of each other, and they were consistent.

SCRUTTON: Were they made by continuous consecutive counting or were they counted between what you first determined were individual constrictions (monthly series)?

JOHNSON: We tried to count consecutively if possible, where not possible we did try to distinguish good constrictions and count between them.

EVANS: Why couldn't you just assume the growth lines were tidal lines, then the constrictions would be semi-monthly?

JOHNSON: Our specimens were not from the tidal zone, their morphology indicated they were subtidal. Assuming the rugose corals are somewhat similar to modern scleractionian species, I infer that reproduction in the fossils occurred by lunar periodicity. Thus, to account for the growth periodicity I said it was monthly.

BUDDEMEIER: You must be careful counting tabulae, for my experience shows tabulae pseudo-periodicities which are not time-dependent. Also your tendency to multiply numbers with 2 significant digits, to get numbers with 4 significant digits (as in your 399·0 day Devonian year), lends an aura of spurious precision to the data.

HIPKIN: It seems that the essential difference between the use of corals and molluscs as geochronometers is the matter of the morphology of the unit. Could you give a unique description of the counting unit, that is, could you recognize the monthly unit without first counting the approximate number of growth lines between apparent ridges?

JOHNSON: Our corals displayed periodic constrictions, a constant distance apart with constant growth, and these periodic constrictions were clearly the monthly unit.

O'HORA: What is the range in monthly counts?

JOHNSON: 28–31 increments per month, and there is no trend with age of the animal.