

SKELETAL VARIATION IN COLONIAL RUGOSE CORALS

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by

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Summary

Skeletal variation in a number of colonial Rugose corals from the Carboniferous Limestone of Derbyshire is described. The variation is attributed to the presence of corallites representing different stages of ontogenetic development, to genetic variation and the consequent appearance of phylogenetic trends, and to the effects of external environmental controls. Some types of extreme variation may be caused by pathological factors.

Introduction

A brief glance at any thin section cut from a colony of Rugose corals, (Plate 1, figs. 2, 4; cover of vol. 1, no. 1; vol. 3, no. 2; or vol. 5, no. 1 of the Mercian Geologist) may suggest that in any one colony, there is little variation to be seen between the morphology of one corallite and that of another, but with closer observation, differences become apparent. All the examples quoted above show variations of corallite size, usually indicated by differences of diameter of the corallites and small differences in the arrangement of the skeletal components. These include the epitheca or outer wall, the inner wall, if present, septa, tabulae, dissepiments and axial structures (text-fig. 1).

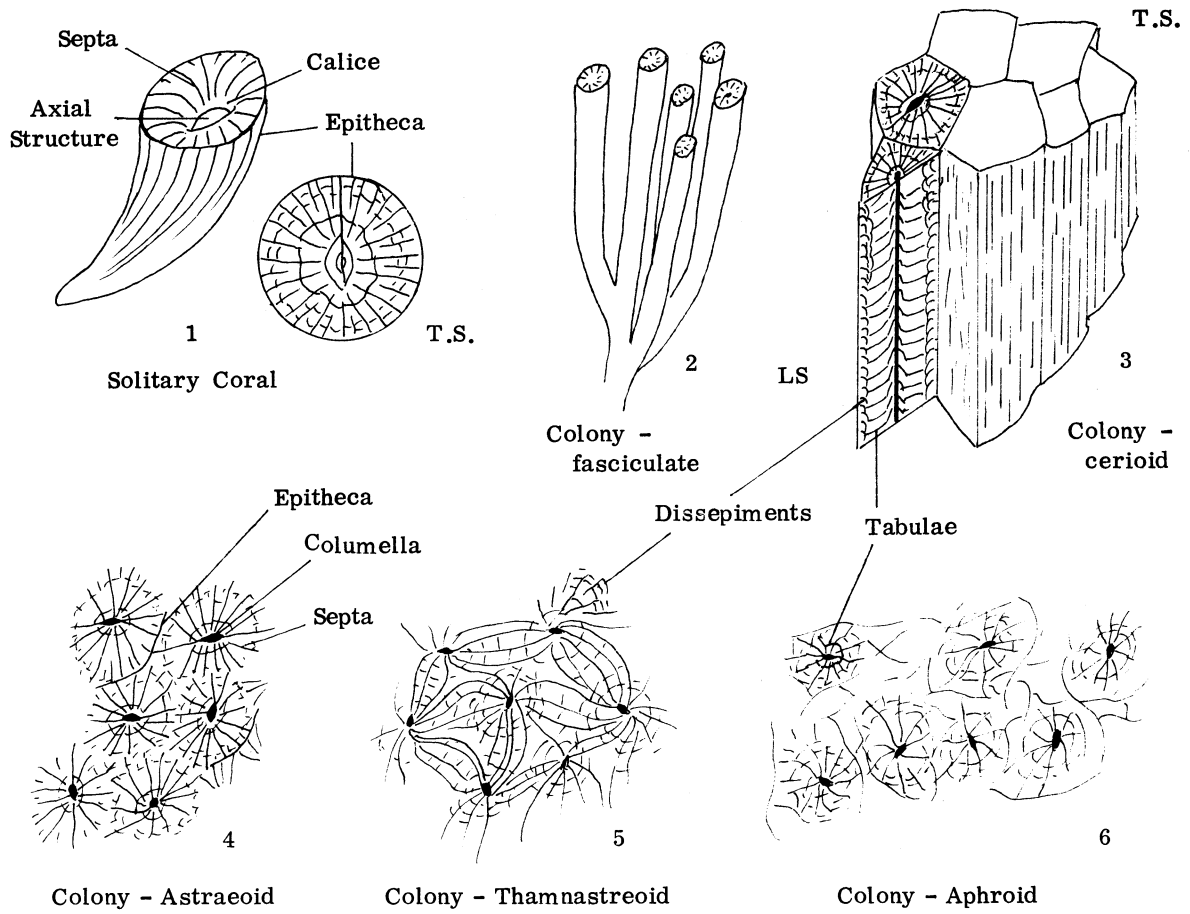
The first variation, that of size, is due to the development of new corallites within the colony. The life-history, or ontogeny, as recorded by the developing skeletal structures, is very rapid, and can only be examined satisfactorily by preparing serial sections cut at 0.5 mm. intervals or less, at the start of development. The second variation, which affects the adult corallites, may be due to evolutionary changes, which Lang (1923) referred to as coral trends and which could be controlled by genetic variation. Similar skeletal variation may be the result of external environmental factors. The morphology of certain rare corallites differs so markedly from that of their neighbours that other reasons must be advanced to account for this extreme variation.

It is proposed in this Presidential Address to illustrate these three types of skeletal variation and to conclude with comments on their taxonomic significance. The text-figs. 4 - 11, which illustrate the variations, are drawn from either thin coral sections or acetate peel sections cut transversely across, or longitudinally through, the coral tubes.

Mercian Geol. Vol. 5, No. 1.
1974, pp. 1-18, 12 text-figs.
Plate 1, Cover.

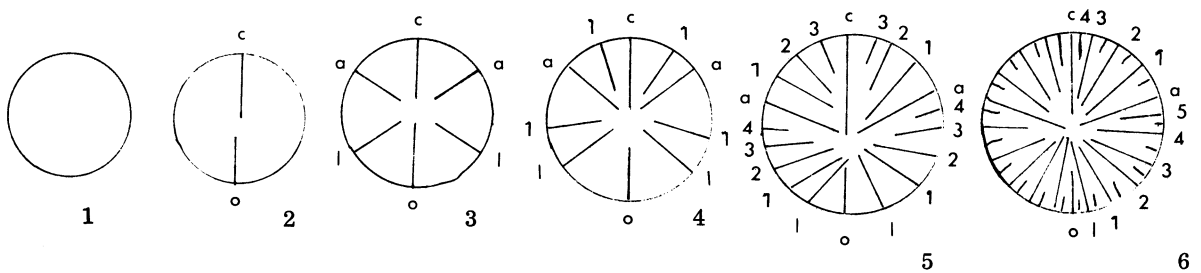
EXPLANATION OF TEXT-FIGURES

- Text-fig. 1 Terminology used in this address to describe the Rugose corals. The progression from fig.1 to fig.6 also illustrates the colonial trend, see text-fig.10. p.13.
- No particular species are illustrated. Figs. 4, 5 and 6 are transverse sections only.
- T.S. = transverse section. L.S. = longitudinal section.
- Text-fig. 2 Insertion of septa in solitary corals illustrating the zaphrentoid, or delayed method of insertion of minor septa. No particular species is shown and all figs. are transverse sections.
- c = cardinal septum o = counter septum = counter lateral septum
a = alar septum m = minor septa
- nos. 1, 2, 3, 4, and 5 are successive major septa.
- Text-fig. 3 Insertion of all skeletal elements, including the simultaneous development of minor septa (cyathaxonid method). No particular species is illustrated and all figs. are transverse sections.
- Letters and numbers as in text-fig. 2.
- Figs. 5 and 6 are numbered on the right-hand side only.
- Text-fig. 4
(p. 5) Ontogeny of *Lithostrotion junceum*. Immature corallites (y) illustrating development from an early stage, (figs. 1, 2) to an early adult stage, about half the adult diameter, (fig. 11). The skeletal details of the parent corallite (P) has not been completely illustrated.
- fig. 1 Initial bulge is illustrated with incomplete epitheca.
- fig. 2 Epitheca is developing from opposite sides and one septum is present.
- fig. 3 Epitheca developing mainly from one side and a single septum is present.
- fig. 4 Incomplete epitheca.
- fig. 5 Epitheca is complete and one septum is present.
- fig. 6 Three septa shown and advanced separation of the young corallite from the parent.
- fig. 7 A rare example of two young corallites developing almost simultaneously from the same parent corallite. A developing epitheca can be seen in one corallite and in the more advanced corallite there are seven septa and tabulae present.
- fig. 8 Seven septa are present.
- fig. 9 In this corallite there are twelve septa, one of which is elongated with two short septa adjacent.
- fig. 10 Separation of the young corallite has now been achieved. There are nine septa present, one elongated and tabulae can be seen.
- fig. 11 In this young adult there are thirteen septa, one long and the columella is formed. Dissepiments are not formed in this species.
- fig. 12 The longitudinal section shows the incomplete epitheca at the point of origin of the young corallite.



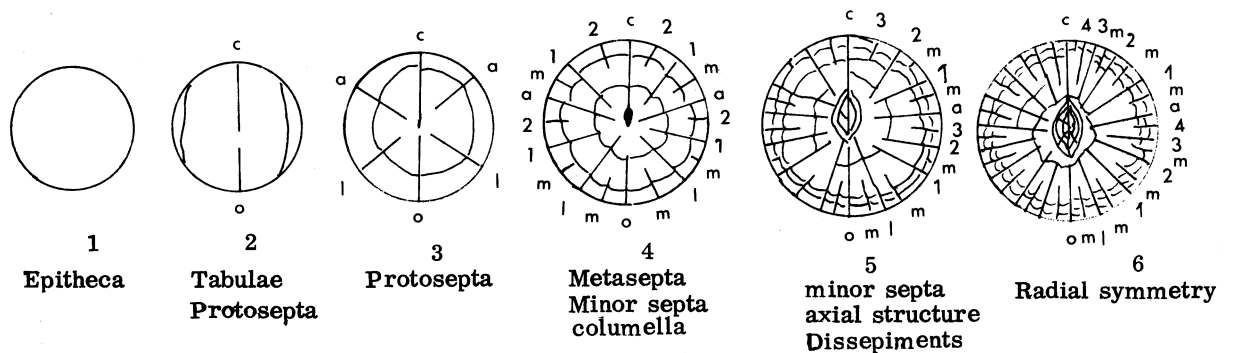
Text-fig. 1

Coral form and main skeletal elements of Rugose Corals.



Text-fig. 2

Transverse section of corallite, showing septal insertion with delayed minor septa.



Text-fig. 3

Transverse section of corallite - development of all skeletal elements, with simultaneous minor septa.

Ontogeny of Colonial Rugose Corals

(Text-fig. 4-9, Plate 1).

Almost all books on palaeontology, including treatises (Hill 1956, Dobrolyubova 1962, 197b) and popular works (Pinna 1972), faithfully reproduce diagrams (text-fig.2) to illustrate the insertion of septa in solitary corals. Little has been added to the pioneer work of Kunth (1869), Carruthers (1906) or Thompson (1883) or the later detailed work in various papers by Lewis, Ryder and Hudson. There was little information available about the development of the other skeletal elements (compare text-fig.3, with text-fig.2) or the growth of corallites in colonies when I commenced work on corals in 1953. Smith (1916, 1917) had described the ontogeny of *Lonsdaleia* and *Aulina*. Dobrolyubova published her work on colonial Rugosa from Russia in 1958 (English transl. 1964) reprinted with some additions in the Russian Handbook on Palaeontology (1962, English transl. 1971); Jull (1965, 1967) has made further contributions on *Lithostrotion* and *Lonsdaleia* from Australian and Canadian Rugosa. It is proposed to illustrate this review of the ontogeny of colonial rugose corals with special reference to the following species from Derbyshire. (Taylor 1957).

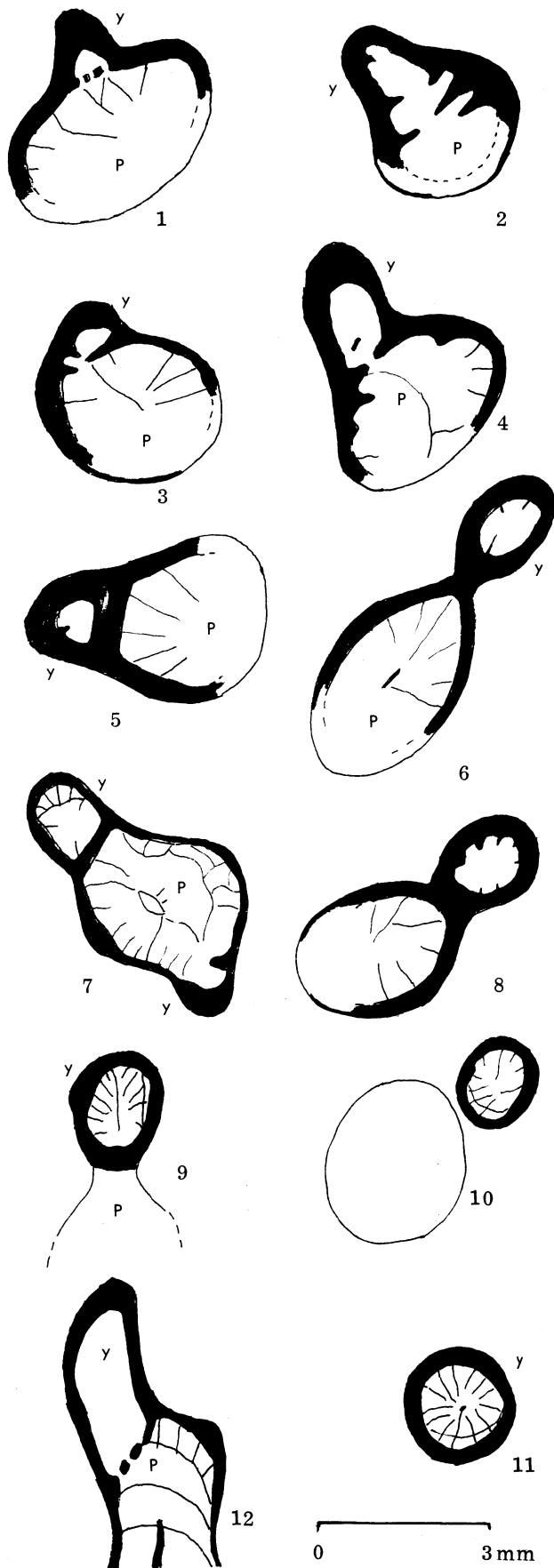
<i>Lithostrotion junceum</i> (Fleming)	}	Branching or fasciculate colonies
<i>Diphyphyllum lateseptatum</i> (McCoy)		
<i>Lonsdaleia duplicata</i> (Martin)		
<i>Lithostrotion decipiens</i> (McCoy)	}	Massive, cerioid colonies
<i>Lonsdaleia floriformis</i> (Martin)		
<i>Thysanophyllum minus</i> (Thomson)		
<i>Palaeosmilia regia</i> (Phillips)	-	Aphroid colony

Initial development of corallites

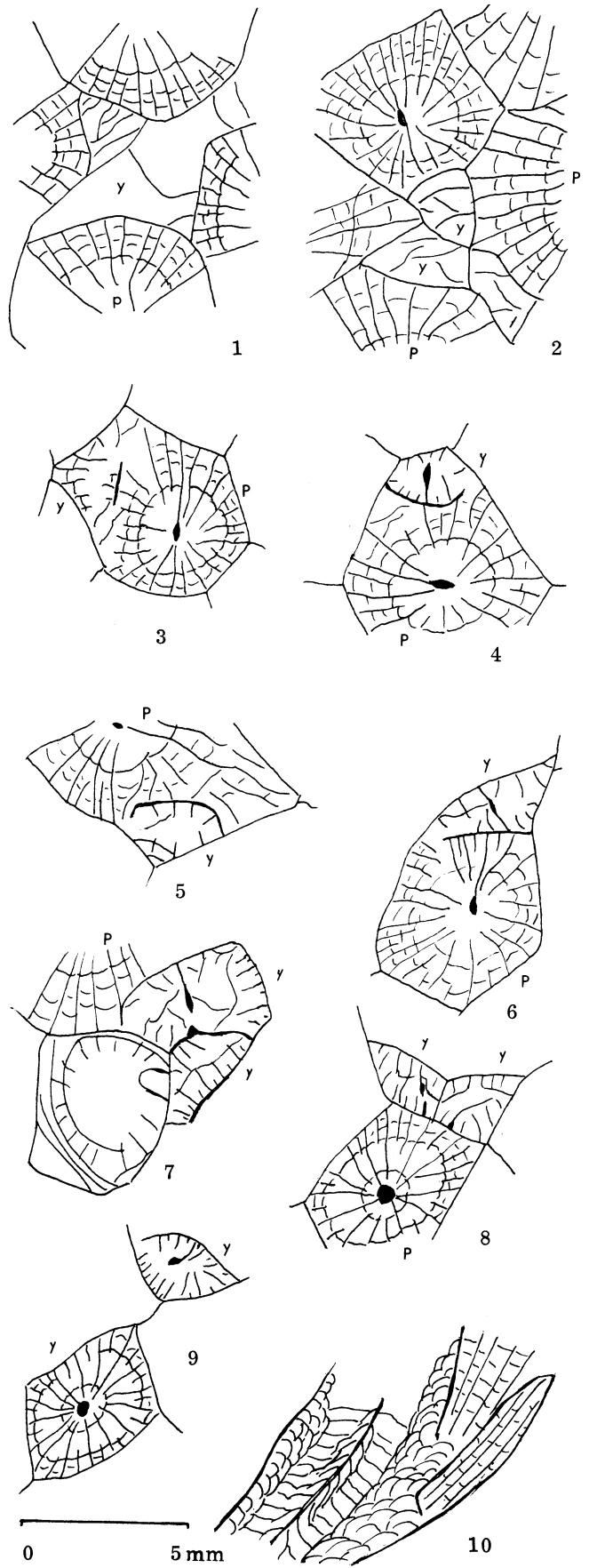
The appearance of some irregularity in skeletal structure usually precedes the development of the skeleton of a new corallite. In *L. junceum* (text-fig.4, figs. 1, 2, 3) and in some colonies of *L. duplicata* (text-fig.5, figs. 1, 2, 3) the corallite epitheca begins to bulge outwards. The regular septal plan of the other corals and most colonies of *L. duplicata* becomes disrupted by the appearance of an open area, devoid of septa or dissepiments, close to the epitheca. The same type of open structure occurs in an angle of the epitheca of the cerioid *L. decipiens* (text-fig.6, fig.1) and within the extracalicular structures of the aphroid *P. regia* (text-fig.9, fig.1). In some specimens of *L. duplicata*, the skeletal thickening of the inner wall extends towards the periphery of the corallite (text-fig.6, figs. 9 and 10) forming the initial platform for the new polyp. One or two skeletal elements, basal tabulae, may cross the newly designated area. As the new polyp begins to secrete its own skeletal structures they replace those of the parent in this area and it can be considered that the soft body of the new polyp has displaced that of the parent.

Tabulae

Although not always the first new element to appear, the tabulae are amongst the first to be secreted in all the colonies, preceding the epitheca and the septa. The initial tabulae are often irregular in shape, making distinction between septa and tabulae difficult in the early stage. Regular shaped tabulae are a feature of *Diphyphyllum* (text-fig.8, fig.2) from an early stage, new tabulae being small replicas of the previous ones. In the other corals the tabulae eventually attain the adult characteristics, gradually increasing in diameter. If two or more series of tabulae are formed, as in *L. decipiens*, *L. decipiens*, or *D. lateseptatum*, the inner set appear before the outer set(s).



Text-fig. 4
 Young corallites of *L. junceum*.
 See p. 2.



Text-fig. 5
 Young corallites of *L. decipiens*.
 See p. 8.

The epitheca

The epitheca of the new corallite is developed in two parts. First of all there is the continuous upward growth of the original epitheca. As there is no break in the growth of the structure close to the developing new polyp, it must continue secreting the epitheca, after it has replaced the parent polyp, in exactly the same position as before. The second stage is for a new epitheca to be secreted around the remaining periphery of the new polyp separating the new polyp completely from the parent. In *L. junceum* the old epitheca bulges outwards (text-fig. 4, figs. 1, 2, 3) whilst the new structure crosses from one side of the bulge to the other, or commences from both sides of the bulge, meeting on the centre (text-fig. 4, fig. 4). Growth is initially fastest on the outside wall and the result is a cup-shaped depression for the new corallite (text-fig. 4, fig. 5). As growth continues at a more uniform rate, a cylinder is formed which gradually becomes separated from the parent corallite (text-fig. 4, figs. 7, 8, 9, 10). This method of increase applies to other fasciculate species including *L. duplicata*. The new wall in the cerioid species may commence from a point along the straight section of the parent epitheca and grow across the angle of the parent corallite to join up with the epitheca on the opposite side, producing a polygonal tube. (text-fig. 5, figs. 3, 4, 5, text-fig. 7, fig. 2.) It is not uncommon for the new epitheca to appear within the parent dissepimentarium and then extend outwards (peripherally) towards the parent epitheca, again enclosing a small polygonal tube. The resulting enclosure is now occupied by the new polyp developing its own skeletal structures. The wall separating the two individuals is maintained by both at an equal rate of growth and contact is maintained throughout the length of the corallite, producing the massive coral structure. The new epitheca commences fractionally after the first tabula has been laid down, so that there is always skeletal continuity between the parent and the new corallite at its apex (text-fig. 5, fig. 10). In *Diphyphyllum* new walls commence from the centre of the old calice and grow outwards towards the old epitheca. If two new polyps are formed, the new wall will bisect the old calice. As many as four (three and the original?) new polyps may appear together, resulting in the simultaneous development of four new tubes (text-fig. 8, fig. 1). An epitheca is not developed in the aphyroid colony of *P. regia*.

The septa

The first septa frequently appear before the epitheca is complete. In *L. junceum* and in some other fasciculate species, the new septa appear first of all on the outside wall, as this structure develops more quickly and is of greater length than the new epitheca. A single long septum has been seen in a corallite, but usually the first group, made up of 5, 6, 7 or 8 septa, appear together. Text-fig. 4 illustrates the development of septa in *L. junceum*. Within 5 mm. of growth, up to two-thirds of the adult number of septa may be present. Initial growth of septa in corallites which eventually attain large diameters may be relatively slow, there being less than half the adult number in *P. regia* at the 10 mm. stage. If the minor septa are strongly developed in the adult, they will alternate with the major septa at an early stage (text-fig. 5, fig. 7), but frequently the appearance of the minor septa is delayed. As the adult number of septa is approached in *L. junceum* or *L. decipiens*, the rate of septal development slows, allowing one to see the appearance of two septa on either side of an elongated septum (text-fig. 4, fig. 4, fig. 9, (text-fig. 5, fig. 9)). Through further successive serial sections the two short septa are seen to develop to normal septum length, with two further small septa taking their place on the cardinal side. In *L. junceum*, where the minor septa develop very late, if at all, one may conclude that the small septa are short major septa and that the cardinal septum lies between them. In *L. duplicata* (Text-fig. 6, fig. 5) and *P. regia* (text-fig. 9, fig. 2) the cardinal septum may be diagnosed when there are about 15 major septa present. The identification of the alar septa is more difficult, but once the cardinal septum has been identified, two other positions of septal insertion can be recognised in the septal plan. (text-fig. 6, fig. 7, text-fig. 9, fig. 2).

The late appearance of minor septa is characteristic of *L. junceum* and *D. lateseptatum*, where the minor septa are seen only in the corallites with the largest diameters. Again, only the normal adult corallites of *L. duplicata* and *Thysanophyllum minus* possess minor septa. The small *L. decipiens* may well develop minor septa before all the major septa are present or the epitheca complete. Minor septa are developed simultaneously with the major septa in

P. regia, which eventually attains the largest diameter and possesses the largest number of septa of any of the colonies studied. This difference in the time of appearance of the minor septa is also a feature of some solitary corals. (Hill, 1938)

Thus the insertion of major septa in colonial corallites follows the same tetrameral pattern that has been described for solitary corals (text-fig. 2) but in the colonial corallites septa are initially developed at a far faster rate.

The inner wall (text-fig. 6)

Of the genera referred to in this address, *Lonsdaleia* and *Diphyphyllum* develop an inner wall. In *Diphyphyllum*, the structure appears with the formation of an inner series of tabulae with vertical edges, separated from the epitheca by an outer series. In longitudinal section, the appearance of the inner tabulae is rectangular or box-like and it is the vertical continuity of the sides of the box which produces the inner wall. The special mode of division of this genus ensures that the inner wall develops within a few mm. of corallite growth. In *Lonsdaleia*, the inner wall develops in a different way. The junction of the tabulae, dissepiments and septa is thickened and as growth continues, the rate of increase of diameter of this thickened area is less than that of the epitheca. Text-fig. 6, fig. 8-12, show the commencement and development of an area of thickening which will result in a new set of corallites. The continued development of these corallites would follow a course similar to that portrayed in figs. 4-7 (text-fig. 6). The space between the epitheca and the inner wall, the dissepimentarium, thus enlarges, as upward growth continues, with the formation of large blister-like dissepiments. In the cerioid species, *L. floriformis*, the diameter of the corallite increases more slowly and the inner wall is really only well developed in the oldest corallites.

The columella (text-figs. 4 & 5).

A columella is developed by *L. junceum* and *L. decipiens* and is one of the last structures to form in the corallite. In colonies where the columella is strongly developed in the adult corallites, the cardinal septum becomes elongated across the centre of the corallite within the first few mm. of growth but may appear later in corallites of other colonies. The cardinal septum may be permanently attached to the columella and at a later stage be joined by the counter septum and some of the other major septa. The typical septal plan of the genus *Lithostrotion* is now evident. At a later stage, and in those colonies with a weakly developed columella, the major septa, including the cardinal septum, become detached leaving the columella as a rod-like axial structure.

If the columella fails to grow for any reason after it has been formed, it is doubtful if a subsequent columella is an extension of the cardinal septum. Colonies with an incipiently developed columella in the corallites show that the structure develops from the centre of the inner set of tabulae and is not in contact with the cardinal septum, which is withdrawn towards the periphery of the corallite. Such structures usually continue through a few tabulae before ending at the under-surface of another. A similar 'columella' may begin at a higher level. There are therefore two possible methods of formation of the columella.

In *Diphyphyllum*, no true columella or axial structures are formed. An incipient columella, formed from the centres of the tabulae, may be present in occasional corallites of a colony. A dividing wall, indicating the early stages of division of the corallites of *Diphyphyllum* may be mistaken for a columella.

The axial complex (text-figs. 6 & 7)

More complicated than the columella, the axial structure is made up of median plate, conical tabellae and the septal lamellae. Of the corals reviewed here, an axial structure is a feature of *L. duplicata*, *L. floriformis* and *Thysanophyllum*. As with the columella, the first element to appear is the elongated cardinal septum (text-fig. 6, fig. 5) and

Explanation of text-figs. continued.

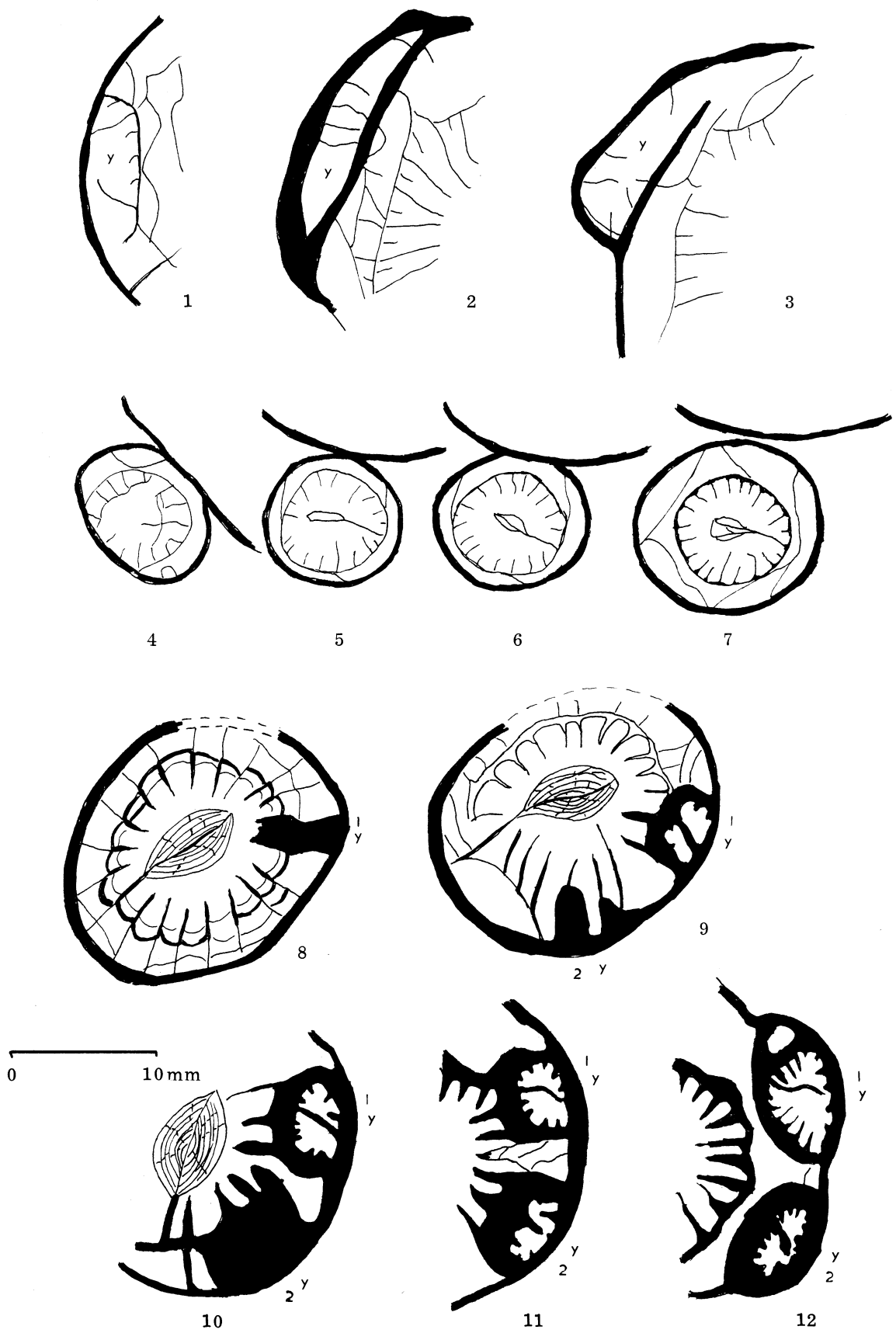
Text-fig. 5 Ontogeny of *Lithostrotion decipiens*. Immature corallites (y) illustrating development from an early stage, (figs. 1, 2,) to an early adult stage, (fig. 9). Parent corallites are marked with the letter, P.

- fig. 1 An open space exists between corallites, one or two basal tabulae are already present.
- fig. 2 A rare example of three young corallites grouped together, with complete epitheca and a few tabulae.
- fig. 3 More usually an incomplete epitheca can be detected and new septa are already present.
- fig. 4 Epitheca is now almost complete, new septa are present including 1 long septum with swollen axial end (columella) and two short adjacent septa.
- fig. 5 The epitheca is incomplete but seven septa and tabulae are present.
- fig. 6 The epitheca is incomplete. 12 - 13 septa are present including joined cardinal and counter septa with columella in the centre.
- fig. 7 Two young corallites are illustrated with complete epitheca. Minor septa are evident in the youngest corallite and a columella is present in the oldest.
- fig. 8 Two young corallites with complete epitheca.
- fig. 9 Two young corallites, the oldest has a dissepimentarium and is about $\frac{3}{4}$ adult size.
- fig. 10 The longitudinal section shows the incomplete epitheca at the point of origin of young corallites.

Text-fig. 6 The ontogeny of *Lonsdaleia duplicata*. Immature corallites (y) illustrating development; extracalicular gemmation figs. 1 - 7. Development within the dissepimentarium to an advanced stage, figs. 8 to 12. Figs. 1 - 7 from the same colony; figs. 8 - 12 from the same corallite.

- fig. 1 Epitheca is incomplete but there are five or six septa present.
- fig. 2 Epitheca is complete and an outward bulge is evident. Approximately 7 septa are present.
- fig. 3 Outward bulge has commenced although the epitheca is incomplete. 6 septa can be seen.
- fig. 4 Isolation is now imminent, 13 septa, one of which is elongated, tabulae and the first dissepiment can be seen.
- fig. 5 The inner wall is now complete separating the tabularium from the dissepimentarium. Tabellae attached to the long septum indicates the start of the axial complex.
- fig. 6 Same corallite as fig. 5, with additional tabellae.
- fig. 7 Same corallite as fig. 5, separation is now complete and a small axial complex has formed. Note the small septa adjacent to the long septum.
- fig. 8 Corallite 1 - A thickened basal tabula is formed between two septa.
- fig. 9 Corallite 1 - Epitheca is complete and the first few septa are present. Corallite 2 - Basal tabula develops as thickening around a group of septa.
- fig. 10 Corallite 1 - There are now 11 septa including a joined cardinal-counter septum.
Corallite 2 - First few septa formed.

/contd. p. 10.



Text-fig. 6
 Young corallites of *Lonsaleia duplicata*

Text-fig. 6 Contd.

fig. 12 Corallite 1 - 16 septa are present including a long septum with short septa adjacent.

Corallite 2 - 15 or 16 septa present.

Further development as figs. 4 to 7.

Text-fig. 7 Ontogeny of *Thysanophyllum minus*.

fig. 1 New epitheca appears.

fig. 2 Epitheca is still incomplete but 12 septa are present.

fig. 3 Epitheca is now complete with 16 septa one of which is elongated with short septa on either side.

fig. 4 Epitheca is complete at an earlier stage than fig. 3. 6 septa are present one of which is long.

fig. 5 Further septa are added and the inner wall develops.

fig. 6 Development of the axial tabellae.

fig. 7 Loss of the axial tabellae.

figs. 4-7 from the same corallite.

Text-fig. 8 Development of new corallites in *Diphyphyllum lateseptatum*.

fig. 1. Group of 3 corallites, showing the epitheca best developed in the centre. Separation of the corallites is imminent.

fig. 2. Longitudinal section to show the origin of the epitheca from the centre of the tabularium.

Text-fig. 9 The ontogeny of *Palaeosmilia regia*.

figs. 1 - 4 are ontogenetic stages of the same corallite.

c = cardinal septum in the cardinal fossula.

a = alar septum in the alar fossula

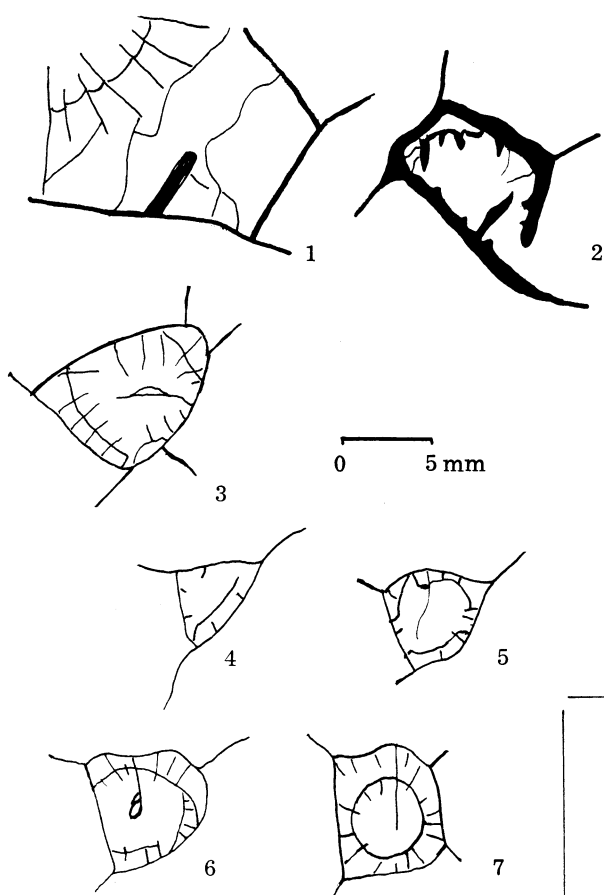
o = counter septum.

Explanation for Plate 1

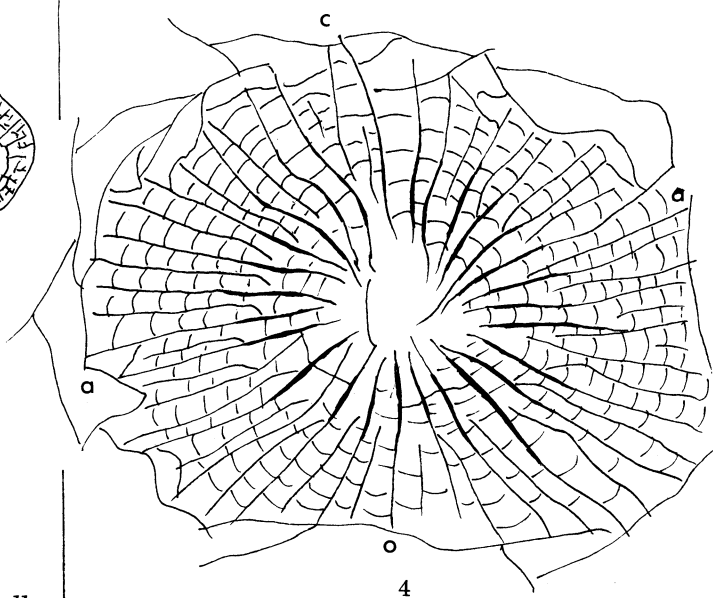
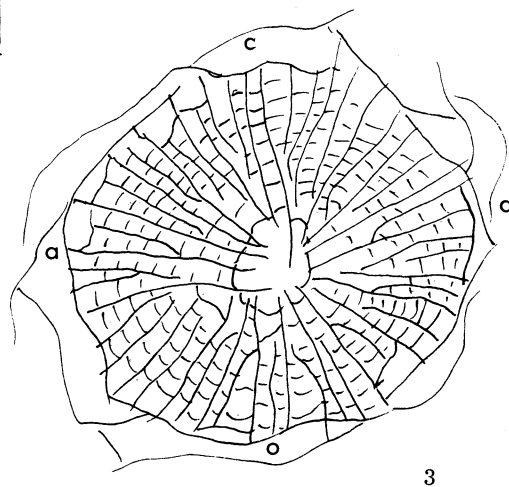
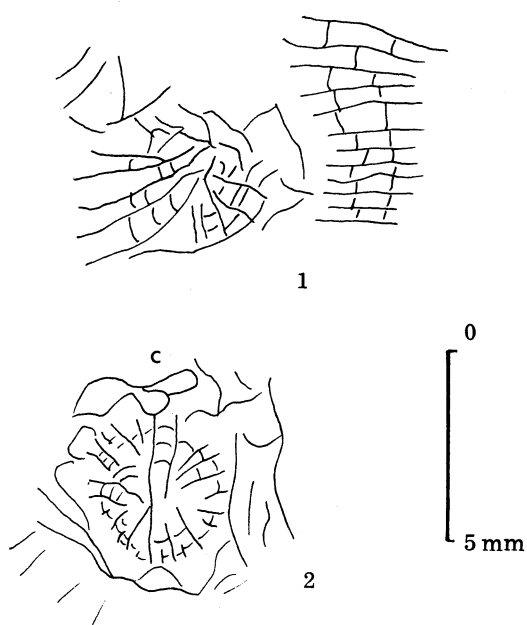
Transverse and longitudinal sections of *Lithostrotion decipiens*. Figs. 1, L.S., fig. 2, T.S., of a variety with conical inner series and wide flat outer series of tabulae.

Fig. 3, L.S., fig. 4, T.S., of a variety with flat, wide inner series and poorly developed outer series of tabulae.

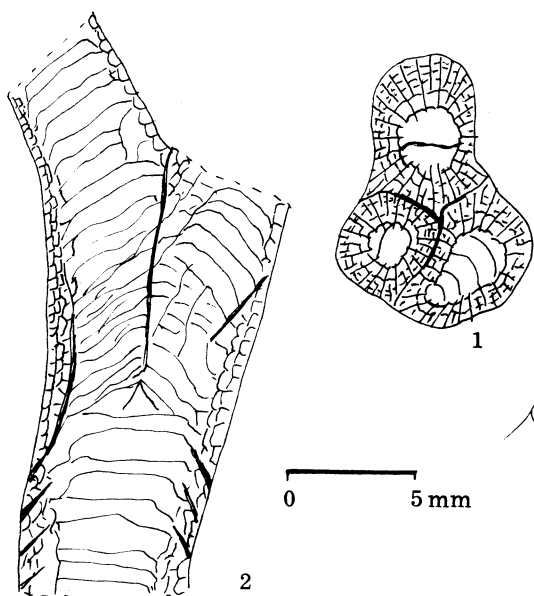
Fig. 2 shows the incipient development of the astreaoid trend. The white patches on the photograph is the mineral ankerite.



Text-fig. 7
Young corallites of *Thysanophyllum minus*



Text-fig. 9
Young corallites of *Palaeosmilia regia*.



Text-fig. 8
Development of the epitheca in *Diphyphyllum lateseptatum*.

not the counter septum, as stated by Smith (1916). A single tabella is often located at the axial end of the long septum. In *L. duplicata*, this stage is reached at about the time the new corallite separates from the parent. In the cerioid species, the same stage is reached after the appearance of the 12th major septum and before the formation of the dissepiments. The median plate eventually becomes separated from the cardinal septum and further tabellae and the septal lamellae are added. The development of the axial structure is very slow in most colonies of *L. duplicata*, despite the increase in diameter, compared with the faster development of the structure in the cerioid species, *L. floriformis*. Specimens of the genus *Thysanophyllum* follow the same type of development as indicated for *L. floriformis*, but before the corallite is halfgrown (as indicated by the diameter) the axial structure becomes less well developed and in the adult it will compare with the early stages of *Lonsdaleia*.

Dissepiments

The last elements to appear in the corallite are usually the dissepiments. Initially one row will be present but others are added as the diameter of the corallite increases. In *L. junceum*, the diameter of the adult corallite is rarely greater than 6mm. and dissepiments are not formed. Specimens of *L. decipiens* display an increase in the number of dissepiments in the angles of the corallites. Corallites of *Lonsdaleia*, develop small elements close to the inner wall and large blister-like structures against the epitheca. The maximum development of dissepiments is seen in *P. regia*, where they comprise the extracalicular tissue of this aphyroid colony. It is in the area of the dissepiments that most new corallites of the colonial *Rugosa* are formed.

Rate of development of new corallites

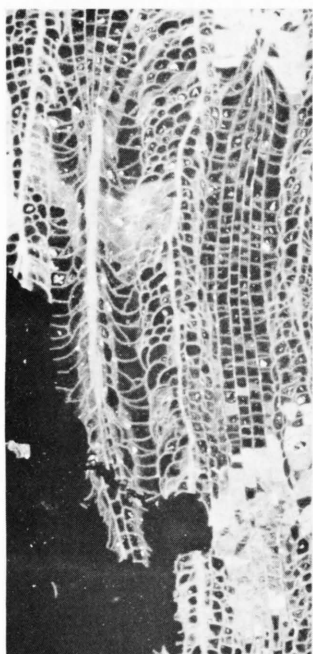
Initial development of the skeletal structures is rapid in all the species studied. This would be followed in some species, for example *L. decipiens* and *L. junceum*, by an almost complete cessation of septal insertion or increase in diameter, growth being restricted to increase in length of the corallite and the addition of new tabulae at regular intervals. The diameter and number of septa in such corallites is relatively constant within the colony. Other species continue to insert new septa into the corallite and increase its diameter as upward growth continues, but the addition of septa and the increase in diameter occurs at a much slower rate than in the initial stage. This is the mode of skeletal development in *L. duplicata* or *P. regia*. Text-fig.11 illustrates these two rates of development. It follows that there will be maximum variation of diameter and number of septa in the corallites of colonies where there is continued slow increase of size.

Certain colonies, for example *L. junceum*, produce new corallites at specific levels within the colony, resulting in the long parallel tubes of a phacelloid colony. New corallites are formed continuously in other species, for example *L. duplicata*, two corallites often being produced simultaneously, resulting in the formation of a dendroid colony.

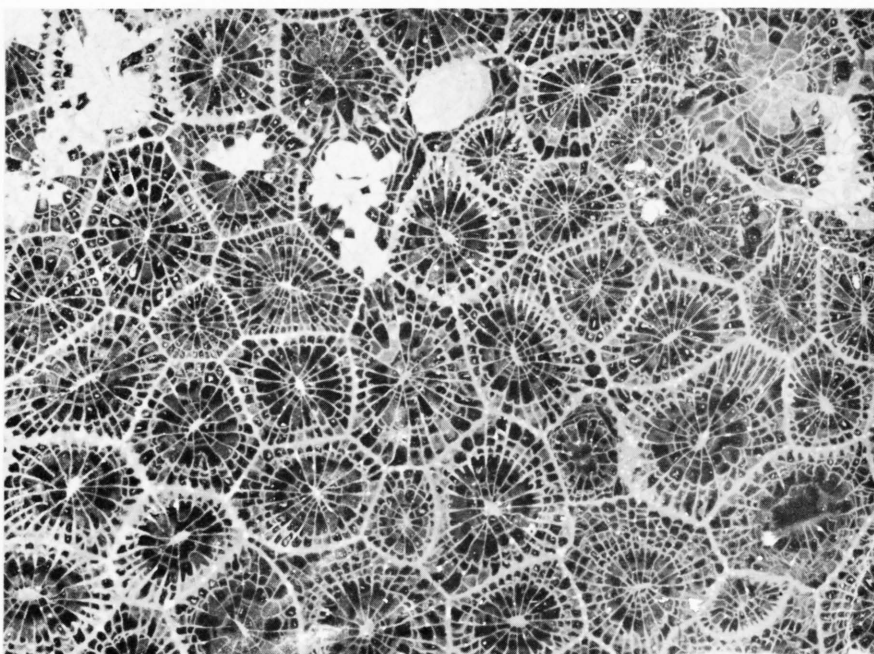
It may be possible to define the attainment of the adult stage by stating the minimum diameter above which the initial period of rapid growth has ceased. The diameters calculated for some of the species referred to in this paper are indicated on text-fig.11.

Variation in the morphology of the adult corallites

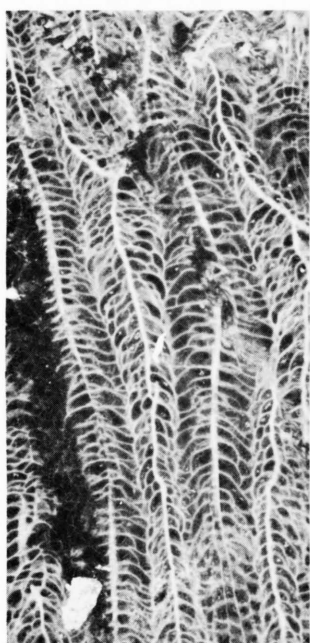
Having determined variation which results from the growth of immature corallites, attention can now be concentrated on variations which occur in the mature corallites of the colony. New polyps are produced by budding, an asexual means of reproduction, which should result in the development of identical adult corallites. In the colonies studied, this was seen to be far from the truth. Lang (1923, 1938) described adult variation as the result of evolutionary trends and those relevant to the colonial species studied are summarised as follows and illustrated in text-fig.10.



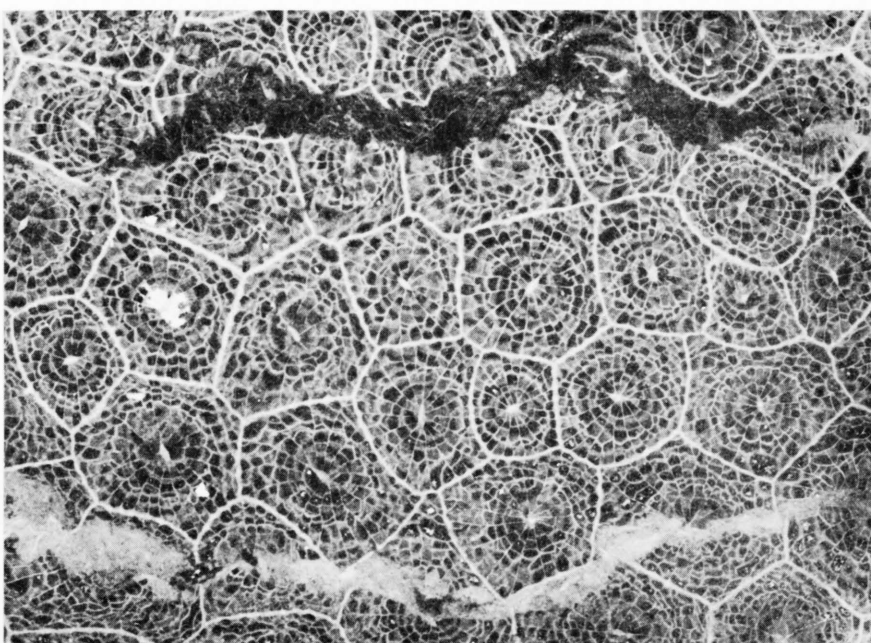
1



2



3



4

Axial length of the septa

In the standard corallite, (text-fig.10, fig.1a, b) the major septa extend from the epitheca to the centre (axis) of the corallite, joining with, or ending adjacent to, the columella or axial structure if present. In many corallites, the major septa fail to reach the centre and the columella or axial structure is isolated in the centre (text-fig.10, fig. 2, 3). This is the amplexoid trend.

Peripheral length of the septa

If the major septa are not in contact with the epitheca, but are separated from it by the presence of large blister-like dissepiments, the corallites are said to be affected by the lonsdaleoid trend (text-fig.10, fig. 5).

The axial structure

Lang considered that the genus *Diphyphyllum* differed from *Lithostrotion* in the absence of an axial structure and any weakening in the development of the columella or axial complex is referred to as the diphyphylloid trend. The columella can vary, from a cylindrical shaped structure extending throughout the corallite to a thin discontinuous plate. If the axial complex is affected by the same trend, the median plate is weakly developed and sinuous when seen in cross-section, becoming indistinguishable from the irregularly shaped tabellae. The tabellae and septal lamellae decrease in number (text-fig.10, figs. 2, 3, 4; 5, 6, 7).

Conversely, the acquisition of an axial structure occurs in a few corallites of *Diphyphyllum*, where the upturned central section of a tabula continue upwards for a few centimetres and in *Thysanophyllum*, where the axial structure persists in mature corallites.

The tabulae

In the genus *Lithostrotion* the presence of a strong columella is usually associated with an inner series of conical tabulae. Those of the outer series are broad flat discs. Corallites with a weak columella usually possess a wide flat inner series and a narrow flat outer series of tabulae, often incompletely developed. (Compare text-fig.10, figs. 1a, 2a, 3a; Plate 1, figs. 1-4).

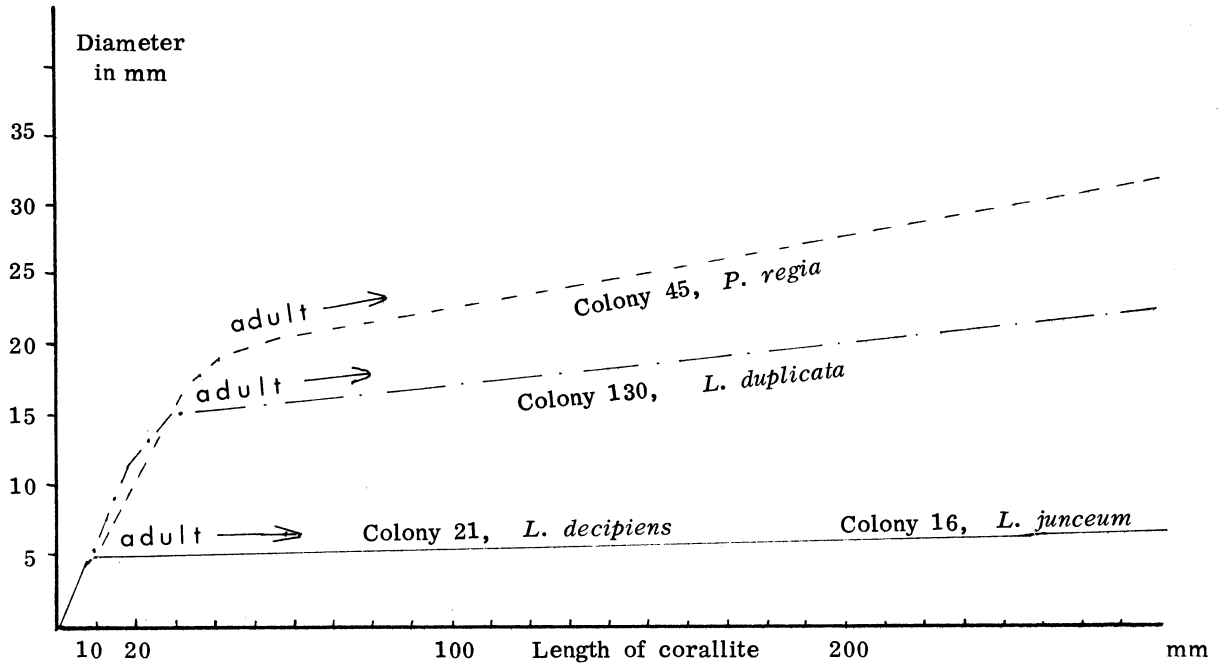
The epitheca

According to Lang, colonies originated by means of a trend which initially produced branching or fasciculate colonies from related solitary species. The next stage (text-fig.1, fig.3) is the production of the massive cerioid colony and then, by disappearance of the epitheca, the more complex astraoid, thamnastreoid and aphroid colonies evolved (text-fig.1, figs. 4, 5, 6). There is some doubt that this series can be demonstrated, but the only variation of the mature corallites which is attributed to this trend is the breakdown of the epitheca in some corallites of *L. decipiens*, and the presence of confluent septa. This change results in the development of the thamnastreoid colony. In most areas of the colony where this variation occurred, there was also deposition of ankerite, but it has not been ascertained which came first, the mineral or the extraordinary skeletal structure.

Certain colonies situated in isolated positions often showed different colonial forms, usually cerioid in the centre and fasciculate at the outer edge.

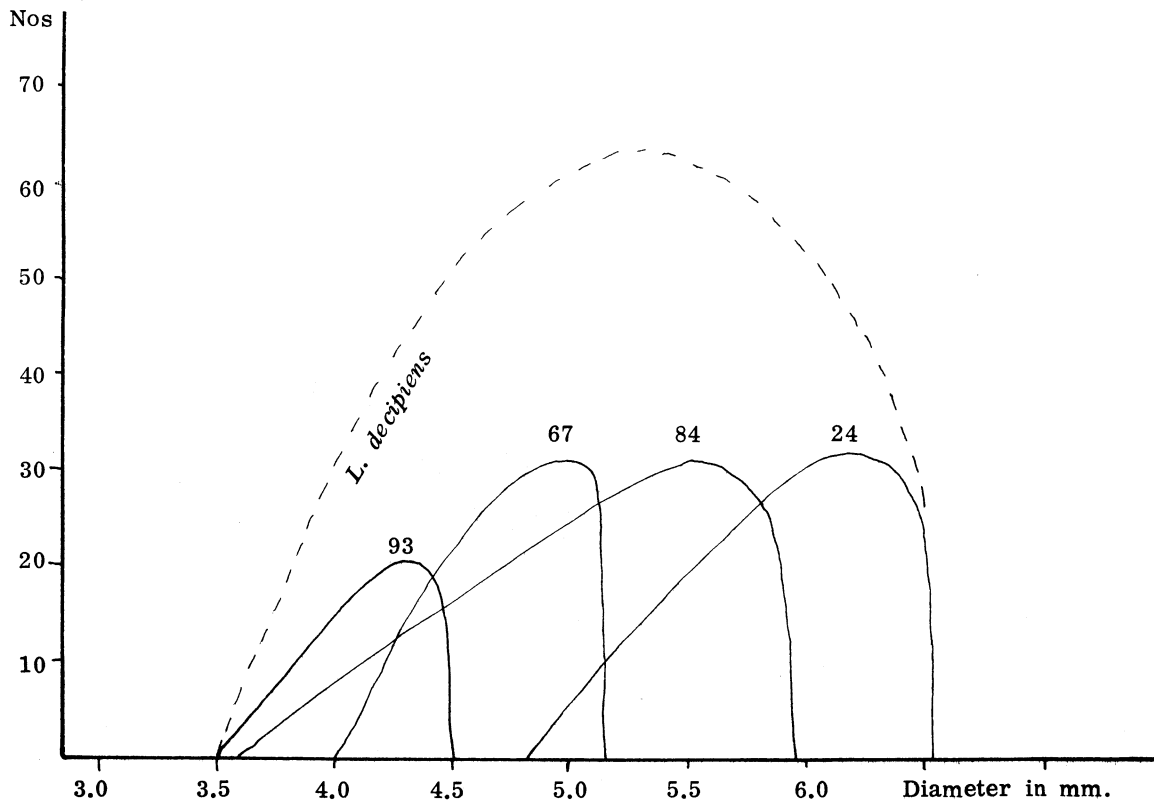
Other possible variations, which might affect colonies but which were not particularly apparent in those studied, would be concerned with the shape of the corallites, the development of fibrous skeletal tissue and the production of more complex microstructures of the skeletal elements (Hill 1956).

The main variations affecting the adult corallites in *Lithostrotion* were those concerned with the septa (amplexoid) the columella and the tabulae (diphyphylloid). The development of



Text-fig. 11

A comparison of increase of corallite diameter and length, showing initial rapid development. Graphs for *L. junceum* and *L. decipiens* are so similar that one line represents both species. Colony numbers refer to specimens in the author's collection.



Text-fig. 12

Frequency distribution curves of diameters of corallites of colonies of *L. decipiens*. Young corallites are excluded. Skew is due to most corallites having maximum diameter (See fig. 11). No single colony has maximum variation indicated by graph for the species as a whole.

lonsdaleoid dissepiments was a minor variation. The main skeletal differences seen in *Lonsdaleia* and *Thysanophyllum* affected the axial structure. The morphology of *Palaeosmilia regia* was remarkably constant.

The effect of the environment

In a previous presidential address, (Taylor 1972), the coral environments of Derbyshire were examined in detail. The main form of coral reef during the Lower Carboniferous Period was considered to be the patch reef. Colonies on the fringe of the patch, or located in an isolated position, are the ones that show the most variation within the colony. Those in the centre of the patch reef, the usual position for colonies of *Palaeosmilia regia*, exhibit the least amount of variation. So far no objective testing of this observation has been attempted and the possible effects of erosion on the edges of the patch reefs prior to fossilisation, removing the more variable colonies, has not been considered.

Extreme skeletal variation

So far, the morphological variation described from a single colony has been shown to be within certain limits and could be considered to be the result of a trend causing increase change away from a norm. In a number of colonies of *L. decipiens*, one or two corallites showed extreme variation (text-fig.10, fig.8). The incipient development of thamnastroid corallites associated with ankerite may be an extreme example of variation. This type of variation is not characteristic of the species and there is no sign of the intermediate type of colonial development, the astreoid colonial form. The development of confluent septa is characteristic of the genus *Orionastraea*.

Elsewhere in the colony can be seen the extreme development of the amplexoid and diphyphylloid trends affecting the septa, columella and tabulae (text-fig.10, fig.8). The result is a corallite composed essentially of an epitheca, dissepiments and flat tabulae. Such corallites are far outside the expected variation of the species, let alone the colony. There is no circumstantial evidence available to blame the environment for this extreme variation. Instead one must consider the possibility of peculiar gene mutation which has emphasised the trend producing the diphyphylloid corallites. It is possible that this extreme variation could be the result of pathological factors affecting the polyp.

Comparison of variation in different colonies of the same species

From the examination of a number of corallites of different colonies of the same species, it can be seen that the morphology of the skeletal elements may be relatively constant in one colony, whilst another may display considerable variation. The point is best illustrated by taking one variable, for example the diameter of the adult corallite and producing a frequency distribution curve. The curves for a number of colonies of *L. decipiens* have been plotted on text-fig.12. A comparison of the curves showing the distribution of the diameter of adult corallites for colonies 67 and 84 illustrates the greater variation of this character in colony 84 compared with 67. Similar graphs have been produced for other variables, including the number of septa and the spacing of the tabulae.

Many colonial Rugose coral species have been named with reference to specimens composed of a small number of corallites. This is particularly true of McCoy's species described from specimens from the Carboniferous Limestone of Derbyshire, Ireland and the north of England. (McCoy, 1849). It is clear from the above discussion that, with only a few corallites on which to base the description, insufficient information may have been available for the complete variation of the species to be appreciated. Many colonies should be studied before the description of a species is attempted.

Summary of Conclusions

Increase in the size of a colony, by the production of new corallites, can take place in more than one way in a species, although one method may be dominant. *L. junceum* demonstrates epithecal budding, the polyp developing a bud outside the ring of tentacles (extratentacular gemmation). *L. duplicata* may produce buds in the same way but more usually the bud or buds develop within the tentacle ring and within the dissepimentarium (intracalicular gemmation). Development in this marginal (peripheral) area is standard for the massive colonies of *L. decipiens*, *Lonsdaleia floriformis* and *Thysanophyllum minus* which rarely produce more than one new individual at a time from a single parent. *Diphyphyllum* is exceptional in that division takes place in the axial position, resulting in the production of multiple corallites. The generic separation of *Diphyphyllum* from *Lithostrotion* would be justified on this evidence alone.

The skeletal tissue of new corallites is not completely separated from that of the parent, there being approximately 1 mm. of common skeletal tissue at the base of the new corallite.

The study of the ontogeny of a number of colonial Rugose coral species indicates that, after initial rapid insertion of septa, the typical tetrameral pattern of septal insertion becomes established and the counter, alar and cardinal septa may be identified. Insertion of minor septa may be delayed until a late stage of the ontogeny, or may occur simultaneously with the major septa.

The orientation and initial development of the columella and the median plate of the axial complex is controlled by the cardinal septum.

The rate of development of the skeletal elements is very variable. In some species, (*Lithostrotion* sp.) the adult characteristics are present after only a few mm. of corallite growth, followed by many cm. of constant adult morphology. In others, (*Lonsdaleia* sp., *Palaeosmilia* sp.), after initial rapid development there is a continued but decelerated increase in the complexity of the skeletal structure, usually associated with an increase in diameter. Such colonies appear to be more varied in their morphology than those where increase in diameter ceases at an early stage.

Variation of adult morphology, although partly attributed to ontogeny of the corallites, may also be accounted for by phylogenetic trends. The relative importance of genetic and environmental factors cannot be ascertained, as both seem to produce a similar morphological result. Variation within the colonies is most marked at the fringes of patch reefs and in single isolated colonies.

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References

- CARRUTHERS, R.G. 1906. The primary septal plan of the Rugosa. *Ann. Mag. nat. Hist.* ser. 7, vol.18, pp. 356-363.

- DOBROLYUBOVA, T.A. 1958. Lower Carboniferous colonies of tetracorals from the Russian Platform. *Akad. Nauk. U.S.S.R., Trud. Pal. Inst.* vol.70, pp.1-224. (In Russian).
1964. English translation of the above - Tetradiate corals from the Lower Carboniferous of the Russian Platform, by E. Lees. National Lending Library for Science and Technology, Boston Spa, Yorkshire, England.
- DOBROLYUBOVA, T.A. 1962. In Orlov I.A. *Fundamentals of Palaeontology*, vol.2, *Porifera, Coelenterata, Vermes*. Moscow.
1971. English transl. Mercado, A., and H. Mills, L.P.S.T., Jerusalem.
- HILL, D. 1938-1941. The Carboniferous Rugose Corals of Scotland. *Palaeont. Soc. (Monogr.)* London.
- HILL, D. 1956. In Moore R.C., *Treatise on Invertebrate Palaeontology*, Part F, Coelenterata.
- KUNTH, A. 1869. Korallen des Schlieischen Kohlenkalkes. *Z. deutsch. geol. Ges.* vol.21, pp.183-220.
- LANG, W.D. 1923. Trends in British Carboniferous corals. *Proc. Geol. Ass.* vol.34, pp.120-136.
- LANG, W.D. 1938. Some further considerations on trends in corals. *Proc. Geol. Ass.* vol.49, pp.148-159.
- McCOY, F. 1849. On some new genera and species of Palaeozoic Corals and Foraminifera. *Ann. Mag. Nat. Hist.* ser. 2, vol.3, pp.1-20, 119-136.
- PINNA, G. 1972. *The dawn of life* from the series, *The world of nature* p.27, London.
- SMITH, S. The genus *Lonsdaleia* and *Dibunophyllum rugosum*. *Q. Jl. geol. Soc.*, Lond., vol. 71, pp.218-272.
- SMITH, S. 1917. *Aulina rotiformis*, gen. et sp. nov. *Phillipsastrea hennahi* (Lonsdale) and *Orionastrea* gen. nov. *Q. Jl. geol. Soc. Lond.* vol.72, pp.280-307.
- TAYLOR, F.M. 1957. *The morphology, Ontogeny and Taxonomy of certain colonial Rugose corals of Derbyshire*. Ph.D. thesis, University of Sheffield.
- TAYLOR, F.M. 1972. The Lower Carboniferous coral environments of Derbyshire and adjacent areas. *Mercian Geol.* vol. 4, No.2, pp. 81-96.
- THOMPSON, J. 1883. On the development and generic relation of the corals of the Carboniferous System of Scotland. *Proc. R. Phil. Soc., Glasgow.* vol.14, pp. 296-502.

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