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FINE SKELETAL STRUCTURES IN RUGOSA

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§ Abstract

Instead of the term "micro-structure", "fine skeletal structure" here purposefully defined means tissues of skeletal elements composing corallites observable under microscope at low magnification.

This paper will present the result of observation of those structures in very concised form, although the author has made detailed study on a fairly large number of corals, ranging from the Ordovician to Permian in age.

Next, the mechanism of skeletal formation and the significance of skeletal patterns will be fully interpreted. Further, secondary deforma-

tion and evolutionary trends of fine structure will be brought into consideration. Finally, the taxonomic importance of fine skeletal structures in rugosa will be briefly discussed.

§ Introduction

The writer began his study on Palaeozoic corals in 1956 under Professor M. MINATO of Hokkaido University. In the course of his study, he became aware that most forms treated by him retain fine structures in almost every skeletal element of corallites so well as to be observable in detail.

Such structures, the writer thinks, should be accordingly also precisely described in a description of species, like other morphological features of corals. Then such questions arose as the following: Are there many diverse forms in these fine structures in rugosa? If so, is there any definite relationship discernable between some types of fine structure and mega-structures of corallites? Suppose there is change in the fine structures through the ages, is it possible in reality to perceive any evolutionary trends in the skeletal morphology of corallites in harmony with the fine structures? Did fine structure have intimate relationship concerned with the function of skeletal secretion in the soft body, although the latter can be seen no more at present.

To give an answer to those questions, the writer has devoted himself to a study of nearly all species of rugosa having ever been described in Japan: he finally found there are at least two forms in respect to the fine structure of septa in those corals. He tentatively called those forms A and B type respectively. This finding was briefly stated in a footnote in an earlier paper (1959).

Then the writer tried to make thorough investigation on literatures of corals, desiring to discover former studies in the same line concerning the fine or micro-structures of corallites. He learned that there had been done much important work in this regard prior to him. Especially those papers published by HILL (1936), SCHINDEWOLF (1942), and by SCHOUPPÉ and STACUL (1955) have been a great inspiration to him. The writer also became aware of WANG's paper (1950); he worked out the same subject on the same line with the writer. Unfortunately, this paper was unavailable to him until 1959 when he moved to study in London.

Meanwhile, the British Council Scholarship in 1959 provided the writer an opportunity to study numerous coral type materials in Britain. He was also fortunate enough to make detailed observation on fine skeletal

structures of many corals from all over the world, under the kind supervision of Dr. H. D. THOMAS at the British Museum of Natural History.

Under kind suggestion by Dr. H. D. THOMAS and Prof. D. HILL of the University of Queensland, the writer would like here to present the result of his observations and his interpretation of the fine structures in rugosa.

It is urgently needed to accumulate data on various forms of rugosa as to their fine skeletal structures, so that firm bases might be established in rugose coral taxonomy. The writer sincerely hopes that the present work could provide a sort of stimulus to the said line of future research in rugose corals.

§ Acknowledgements

The writer wishes to express his hearty thanks to Prof. M. MINATO of the Hokkaido University for kind guidance given to the present study. He first introduced the writer to the study of corals. He then recommended him to the British Council for a scholarship which afford an opportunity to study many type specimens in Britain. He also critically read the present paper in manuscript.

Dr. H. DIGHTON THOMAS of the British Museum has given valuable criticism and encouragement to the present study. He warmly supervised the writer's study at the British Museum during the writer's tenure of the British Council Scholarship.

The writer also wishes to record his indebtedness to the authorities of the following institutions for permission to examine materials under their care, as well as their help to the present study in various ways: The British Museum of Natural History; Geology Department of Bristol University; Royal Scottish Museum; The Hunterian Museum of Glasgow University; Department of Geology of the University of Aberdeen; Geological Survey of Great Britain; The Imperial College of Science and Technology in London; Sedgwick Museum of Cambridge; Department of Geology of Tokyo University; Department of Palaeontology of Tohoku University; and the Department of Geology and Mineralogy of the Tokyo University of Education.

Prof. D. HILL of the University of Queensland, Dr. K. KANMERA of Kyushu University, Mr. J. LAFUSTE in Paris and Dr. C. L. FORBES of the Sedgwick Museum kindly discussed the present subject with the writer.

The staff of the Department of Geology and Mineralogy of Hokkaido University, and the Department of Palaeontology of the British Museum of Natural History helped the writer's study in various ways.

To all of them the writer's most cordial thanks are offered.

§ Historical review on study of "micro" structure of corals.

Prior to the adoption of the microscope, taxonomic study of corals had to be entirely based on their external characters. Works by FROMENTEL (1861) and D'ORBIGNY (1849) are examples. EDWARDS and HAIME authorities of corals at that time, published comprehensive monographical works on this group of organisms (1857), based on their observations mainly on weathered or broken surfaces of corals, for the inspection of the internal characters of them. They utilized polished cross sections as well. However adoption of thin section technique and wide use of the microscope have become good devices for every branch of biology and brought brilliant results. HEIDER's, BOURNE's and КОЧ's studies in the 1880s all followed this stream.

КОЧ (1882) was the first who described fine skeletal structures in rugosa in studying a coral now known as *Tryplasma loveni* with acanthine septa. A number of microscopic investigations appeared then in monographic studies on Mesozoic, Cenozoic corals and also, on some Palaeozoic forms. PRATZ (1882), КОBY (1881) and VOLZ (1896) were the authorities on the former corals, while FRECH (1885), WAAGEN (1887), STRUVE (1898) and SCHÄFER (1889) described fine structures of the latter. But the most important work was a systematic study of fine skeletal structures of scleractinia by OGILVIE (1886), who considered the mechanism of their formation, and recognized their important role in phylogeny both in rugosa and in scleractinia. Her work is so meritorious as to be called the climax of the first epoch of this line of coral study.

In spite of her remarkable study, it was followed by a general slackening in the field of coral study, especially as to the fine skeletal structure, when the mode of septal insertion seems to have been much appreciated in the study of corals. GRABAU's study on Palaeozoic corals (1922) in general includes terminology and considerations on some fine structures of tabulae and dissepiments. In 1924 КОКЕР, who studied Permian corals of Timor, recognized "fibro-lamellar" type of septa and gave an unique interpretation of the skeletal formation. LANG found a peculiar type of septal structure in the genus *Naos* in 1926. SCHEFFEN's work on Silurian rugosa of Norway appeared in 1933; in that paper he first recognized fine structures as a phylogenetic criterion although his description in this respect was not satisfactory. Study of Palaeozoic corals became rather active in 1930s. BUTLER (1935) described "microstructures" of *Syring-*

axon, and HILL (1934) noted "microstructures" of septa of *Symplectophyllum* (Pl. II, fig. 2). The septa of those corals are all of trabecular type. It was VOJNOVSKY-KRIEGER who first remarked zig-zag structure of septa in Zaphrentid coral in 1934. GROVE reviewed (1934) coral studies including microstructures. HILL in her comprehensive terminology for rugose corals (1935), briefly reviewed studies of microstructure. Also HILL's study on Silurian corals with acanthine septa in 1936 furnished a sort of model in investigation of trabecular septa setting standards of how to treat such fine structures in taxonomy. HILL and BUTLER first reported on a result of recrystallization in septa of *Cymatelasma* in 1936. WEDEKIND rather precisely defined some skeletal structures of rugosa including fine structures and revised the former classification of corals in this regard so as to be applicable to microstratigraphy. In 1938 HILL described fine structures of some Carboniferous corals. SANFORD's review of rugosan families in 1939 was based on works by GRABAU, HILL and WEDEKIND, especially in respect to fine structure of skeleton. In 1939 SLOSS noted septal dilation in some American Devonian corals. SMITH (1940) found a curious type of septa in Burmese *Iranophyllum*. SCHINDEWOLF studied wall structure in Heterophyllids in 1941, and he (1942) gave descriptions on many Polycoelias and Plerophyllids together with a detailed consideration of fine structures of skeleton. Further, he discussed the mechanism of formation of microstructures and their significance. He proposed a term "diffuso-trabecular" for "fibro-lamellar" septa, in distinguishing it from "trabecular" type. Although KOKER (1924) started the study on fine structure of "diffuso-trabecular" type, SCHINDEWOLF set fundamentals of the study of this type of septa, which have been followed by WANG (1950), SCHOUPPÉ and STACUL (1955). In 1941, BRYAN and HILL published an interesting paper on the mechanism of skeletal formation in scleractinia, which is readily applicable to rugosa. They clearly demonstrated the aspect of mineral deposition in the mechanism of skeletal formation of the organic body of corals.

The comprehensive study of scleractinia made by VAUGHAN and WELLS in 1943 is quite remarkable because of their adoption of fine skeletal structure as the basis of classification in family rank. EASTON (1944) in his study of Chouteau corals gave terminology including some explanations on fine skeletal structures of rugosa. SMITH (1945) in his description of Devonian corals of Canada specially remarked on some microstructures, and gave concrete terminology with review on many Silurian and Devonian coral genera. ROZKOWSKA (1946) also described fine structure in some Polish Silurian corals. Thus terminates the second

epoch of study which is best represented by the works of HILL, SCHINDEWOLF, VAUGHAN and WELLS.

In 1950 WANG, being inspired by THOMAS, published his systematic study on fine skeletal structures of the entire group of rugosa. This marks the beginning of the third epoch of study. Synthesizing the results of authorities, WANG outlined nearly all fine structures of corallites hitherto known in rugosa and directly applied them to classification of rugosa. He recognized four fundamental types of septa representing four sub-orders of rugosa, placing stress on his 'lamellar' structure. This ambitious attempt has been met, however, some unnatural sorting of diverse forms. LECOMPTE (1952) employed fine structure as the basis of family classification in *Traité de Paléontologie*, tome 1. In 1952, ALLOITEAU in the same volume proposed a new classification of scleractinia, which was presented in very elaborate form in 1957. He also treated "microstructures of septa" as important biocharacters in scleractinia. Besides, he recognized a new type of septa, namely "granular" type, yet the writer would disagree with him because of its secondary nature. ROZKOWSKA (1953 & others) and SOSHKINA (1952) have shown many excellent figures illustrating fine skeletal structures of Devonian corals. In the current study of corals, fine structure has come lately to be described more in detail, although such structures have not yet been fully accepted in general as taxonomic characters. Those works by SCHOUPPE (1955), SUTHERLAND (1958), FONTAINE (1961), OLIVER (1960) and SANDO (1961) may be on this line of research for example.

Especially the studies by SCHOUPPE and STACUL on well preserved Permian corals from Timor are remarkable. They made important observations on the fine structure of corals, mainly of "fibro-lamellar" type and gave an interpretation of the mechanism of their formation and its significance. SUTHERLAND (1958) called the zig-zag structure "chevron structure".

There have been several contributions to the study of the mechanism of the skeletal formation in scleractinia, and recently GOREAU (1959) published his observations.

In short, the old method of observation solely from the outside of the corallum has been gradually replaced by the study of internal structures in using thin sections, and there is now a tending to note fine structures of skeleton itself. Also the mechanism of skeletal formation has been interpreted to some extent. Studies of fine structures in rugosa and in scleractinia have progressed side by side. It seems now to be a current view that there is no essential difference in fine skeletal structure between

rugosa and scleractinia.

It was 1902, when a Japanese Palaeozoic coral, *Lonsdaleia akasakensis*, was first described by YABE. Since then, many forms or faunules have been described. However there were few papers in which fine skeletal structures are dealt with. In this respect, the first record was a description of *Pseudopavona* by YABE, SUGIYAMA and EGUCHI (1943). Based on their experiences in study of scleractinia, they gave special attention to well differentiated trabeculae in septa of *Pseudopavona* found in the middle Carboniferous. They considered the coral to be a Palaeozoic representative of "hexacoral" partly because of somewhat peculiar nature of trabeculae. The classification has been followed by MINATO (1955), YOKOYAMA (1957) and KAWANO (1959). However, as will be explained later, the fine structure now under consideration is nothing but a common feature found in many forms of corals. The writer agrees with KANMERA (1961) in the consideration that *Pseudopavona* is not a "hexacoral". In 1947 MINATO described fibrous structure in spindle like columella of *Arachnolasma* from the Kwanto Mountains. Similar structure is also shown in *Siphonodendron nakazawai* MINATO & KATO (1957). MINATO (1943) remarked on septal dilation in *Kueichouphyllum*. MINATO (1955) described "septal grating" in his new genus *Taisyakuphyllum*. This is a good example of trabecular septa in which each trabecula is clearly differentiated. MINATO and KATO (1957) described "fibro-lamellar" type of septa in "*Clisiophyllum* aff. *maccoyanum* THOMSON" (Plate I, fig. 3). In 1959 KATO distinguished two types of septal structure not only amongst Japanese Carboniferous corals but also in all rugosa. YAMAGIWA (1960) mentioned the septal grating in *Taisyakuphyllum*. KANMERA (1961) described and figured fine septal structures of *Clisiophyllum subramosum* and some other forms of Carboniferous corals. In truth, his illustrated septal structures correspond to the writer's A and B types but he perhaps regarded them to be essentially the same in character, because he termed all of them "trabecular".

At the end of this chapter, fine structure of tabulata will be briefly mentioned. STRUVE (1898) may be the first to have recognized lamellar wall in *Syringopora* (Plate III, figs. 1-2), and a trabecular one in *Chaetetes*. There was a work by LINDSTRÖM on Heliolitids (1882). NICHOLSON published his comprehensive study on tabulata in 1879. Later SMYTH (1929) described fine structure of *Palaeacis*, and SWANN (1947) studied wall structure of *Favosites*. LEMAITRE (1954) applied "holacanthine" to spiny projections in tabulata. BUEHLER (1955) and HAMADA (1957) investigated the wall structure of Halysitids. CHUDINOVA (1959)

distinguished two groups of *Thamnoporoids* on the basis of an ill assumption that the lamellar walls are essentially different from the fibrous walls. Various types of "micro-structures" in tabulata are summarized by SOKOLOV (1955) and HILL and STUMM (1956). However, there seems never to have been presented any systematic treatment on fine structures of tabulata.

§ Consideration upon the mechanism of the skeletal formation in rugose corals.

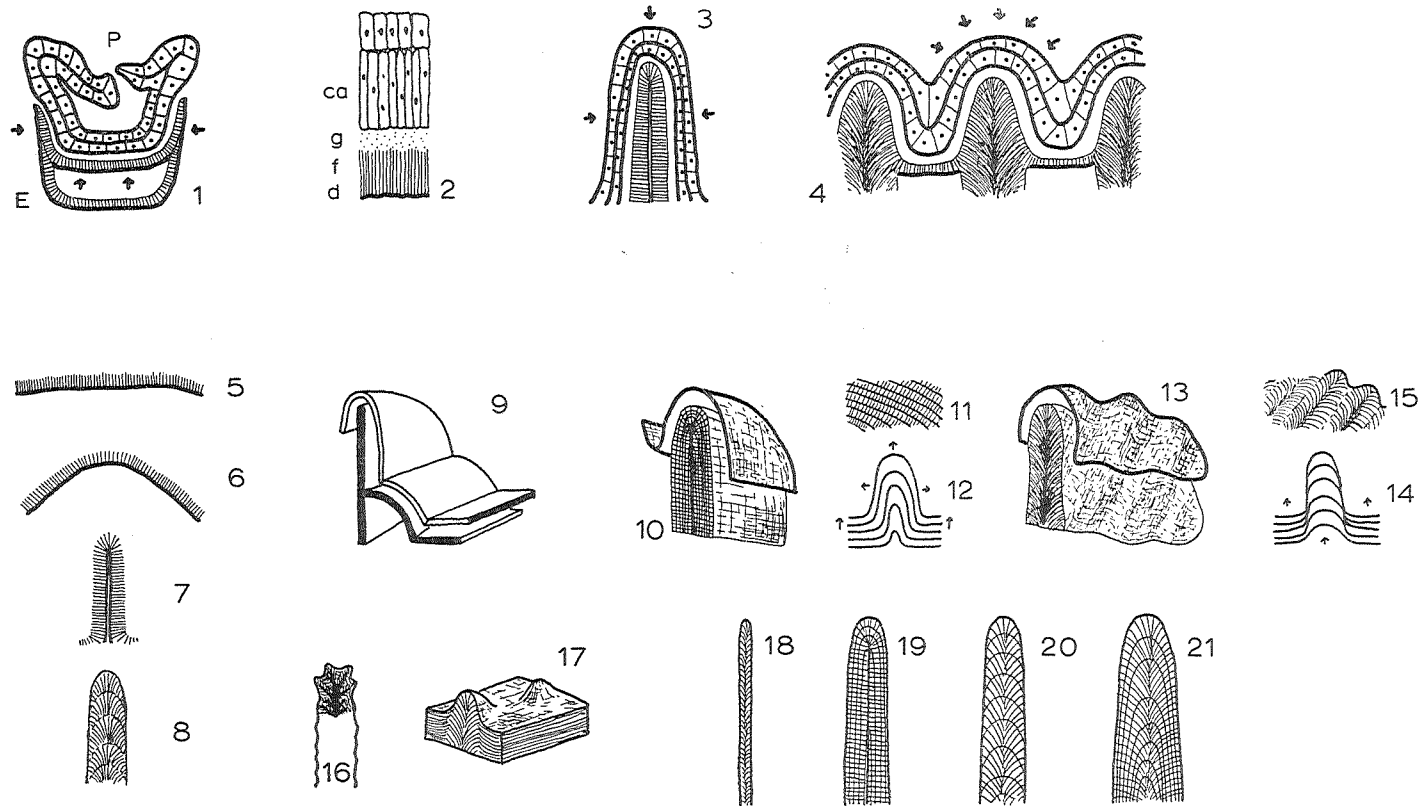
After having worked on fine skeletal structures in rugosa, the writer reached the following interpretation upon mechanism of their formation.

In rugosa every skeletal element is composed mainly of fibrous calcium carbonate, which in all probability is calcite. Fine skeletal structures are so well preserved in many forms of rugose corals that the original form of calcium carbonate in this group might be considered to be stable calcite rather than aragonite. Indeed no aragonite has ever been detected in rugosa skeleton. Besides it is believed that there is no sign of mineral transformation from aragonite to calcite in the skeleton of the Palaeozoic organisms so far as the writer is aware. These fibres are all arranged to be perpendicular to the surface of the coral skeleton, and are also optically normal in relation to the surface. In other words, the optical axis of each fibrous calcite is in the same direction as the elongation of fibres. Hence when they are observed between crossed nicols the straight extinction can be readily recognized to the plane of coral skeleton and to the plane perpendicular to it.

The coral skeleton in Palaeozoic rugosa is surely an exoskeleton, since the formation of fibrous calcite is observed to have taken place radially to the central, polypal cavity now known as the calice, within a wall as the outer limitation of their formation (Text-figure 1-1). There can be seen no signs of fibre formation that may be thought entirely to have been within soft body tissue. Because of the nature and the arrangement of fibres which are in reality one-sided with dark lines on the outer side of skeleton, the skeletal formation should be one-sided. The writer would like to call this "unilateral deposition".

In scleractinian corals it seems to have been already firmly established that the skeleton is an exoskeleton secreted by calicoblast layer. A concept that the precipitation of calcium carbonate within the calicoblast layer as claimed by OGILVIE (1886), can not be believed to be the case, although HAYASHI (1937) detected Ca^{++} in this body layer. GOREAU's (1959)

Text-figure 1
Mechanism of deposition of fibres and the formation of skeletal elements.



Text-fig. 1. Mechanism of deposition of fibres and the formation of skeletal elements.

1. Diagram showing relationship between living polyp and coral skeleton. P: Polyp E: Exoskeleton Arrows indicate the direction of the deposition of fibres.
2. Diagram showing mechanism of fibre formation from soft body layer. ca: calicoblast layer g: gel layer f: fibres d: dark line
3. Diagram showing bilateral deposition of fibres forming platy septum.
4. Diagram showing bilateral deposition of divergent fibres to form septa as well as horizontal tabulae.
5. & 6. Flat or domed skeleton formed by unilateral deposition from unfolded part of basal ectoderm.
7. & 8. Skeletons owing to the bilateral deposition of fibres from the folded part of ectoderm.
9. Diagram showing the differentiation of skeletal elements owing to the forms of folding types of basal ectoderm.
10. Block diagram of a septum showing fibro-normal type structure. Thick folded plane indicates the form of basal ectoderm.
11. Median vertical section of a fibro-normal septum. Growth lines and fibres are shown.
12. A figure schematically indicating the direction and the mode of growth in the fibro-normal septa.
13. Block diagram of a trabecular septum. Covering shown by a thick line is the form of basal ectoderm.
14. A figure indicates the mode of growth in common trabecular septa.
15. Median vertical section of a trabecular septum.
16. Transverse section of a rhabdacanthine septum.
17. Block diagram of monacanthine septa and lamellar structure.
18. Slender septum. The median portion of diffuso-trabecular or semi-trabecular septa is of this type.
19. Transverse section of a fibro-normal septum showing growth lamellation which is a mark of lateral growth. Dilation.
20. Common trabecular septum.
21. A figure showing lateral growth in trabecular type of septum. A case in dilated septa.

recent diagram well demonstrates the current interpretation upon the skeletal formation in scleractinia in which aragonite is introduced (Text-figure 1-2). Outside of the calicoblast layer there seems to be a gel layer between the skeleton and body layer. Through this gel layer CaCO_3 precipitates as skeleton, resulting in being left as a fibrous structure.

The mechanism of skeletal formation in rugosa may be readily comparable to that of scleractinia, although aragonite is common in the latter but quite lacking in the former. Furthermore any forms of costae, septotheca and other skeletal elements which are very common in scleractinia never develop in the wall of rugosa, owing to the different type of polypal covering.

Now, let it be presumed that the ectodermal layer in rugosa which secreted skeletons might have been flat or folded in various ways. If this layer were flat, the skeleton also has to be flat. If domed, arched skeleton should have been formed. This is as will be later considered, the method of formation of so-called horizontal elements in coral skeleton (Text-figures 1-5 & 6). When this layer is so strongly and acutely folded that it forms a sheath in which plate-like skeleton may have been originated, the depositional mechanism can be accordingly called bilateral. In fact this type of bilateral deposition of calcareous fibres is the method by which so-called vertical elements are formed (Text-figs. I-3 & 7).

A different type of bilateral deposition is recognizable in a skeleton in which a different kind of arrangement of fibres is to be seen. When little dome or folded ectodermal layer continuously secretes fibrous calcite, a plate results which consists of fibres divergent to the median plane of the said plate (Text-fig. I, 4 & 8).

Close observation of coral skeleton reveals that fibres are essentially the same both in vertical and horizontal skeletal elements as it is above stated. That is to say, there is no marked difference between fibres constructing horizontal elements and those of vertical ones. Growth lines cut across these fibres are observable to be entirely continuous from one skeletal element to the other. Hence, it is easily understood that there is no fundamental difference between the mechanism of skeleton formation in horizontal element and that of the vertical one. Differentiation of these skeletal features can only have originated from the difference of the types of ectodermal folding (Text-figs. I-4 & 9).

Also another sort of difference between these two elements should be here mentioned. Deposition in vertical element continuously occurs but the thing is different in horizontal element. Why the latter is different is chiefly due to the sudden leaping up of an unfolded part of ectodermal

layer, which results in new and following formation of horizontal elements such as tabulae and dissepiments (Text-fig. I-1). As explained above, the mechanism of skeletal formation itself can be said to be rather simple instead of highly complicated on basis of the appearance of corallites in some species. In the writer's observation there is not any fundamental difference discernible between fine structures of rugosa and those in scleractinia, as well as even in the tabulata.

§ Various types of septal structure.

† Introductory remarks on septal structure

The writer proposes now to deal further with the fine structure of septa, which is the most fundamental skeletal element characterizing rugosa.

Essentially all septa are fibrous in their internal construction. Fibres are commonly arranged at right angle to the surface of septum, which is presumably parallel to the ectodermal layer.

In one type of septa, a median dark line is visible under microscope at the centre of septum and fibres are all perpendicular to it. Figures 10~12 in text-figure 1 show the structure of this kind of septum which the writer calls "fibro-normal" (= *A* type of the same writer in 1959). Fibres seem to grow directly from the median dark line. Septa grow laterally as well as upwardly. In median vertical section of this type of septa, growth lines and fibres perpendicular to the former are clearly seen.

On the one hand, as a consequence of gentle doming or folding of basal ectoderm, divergent fibres are formed to make up a septum (Text-figure 1, 13~15). This doming also occurs in the direction of septal elongation, so that the distal end of septum or basal ectoderm looks like a series of cone-like invaginations. Hence the divergent fibres are also seen in median vertical section. Each cone-like invagination of basal ectoderm secretes a fairly large pillar with domed top, which is a trabecula. Septa made up of these trabeculae are said to be trabecular; they correspond to *B* type of the writer.

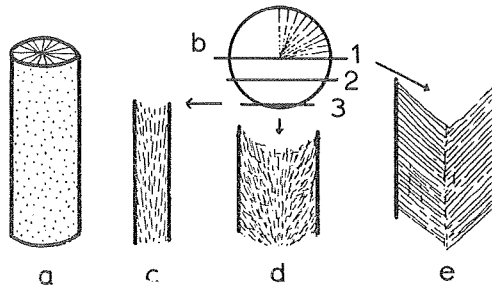
BRYAN and HILL explained the origin of trabeculae as spherulitic crystallization of calcium carbonate. However, the mechanism of skeletal secretion itself can be regarded as simple as the writer has already explained in the preceding chapter. The differentiation of skeletal elements comes solely from the different modes of folding, or invagination

of basal ectoderm. Trabecular and fibro-normal types are fundamental types of skeletal construction, and may be apt to be considered as representing different orders and so on. As will be explained later, there are, however, many transitional types linking those two, and also there is recognizable an evolutionary trend from trabecular to fibro-normal septa.

In a slender septum, the structure is fine trabecular. And the medial portion of a fibro-normal and the other types of septa is perhaps trabecular, because they must have been formed of rounded end of basal ectoderm. Lateral growth or expansion is very common even in trabecular septa, which in their extremities infinitely approach to the form of fibro-normal septa (Text-fig. 1, figs. 18~21).

Trabecular and fibro-normal types look so different that it may be possible to select them as fundamental characters in rugosa; WANG once took this line. But every coral lineage or stock has potential to adopt any kind of septal construction. Indeed the morphological change from trabecular to fibro-normal is believed to have taken place in different coral lineages. One thing, however, must be kept in mind. It is the very fact that the septal structure does not change essentially throughout ontogeny.

To say it again, trabecular and fibro-normal types in septa may be certainly regarded to be two major fundamental fine structures. Nevertheless such structures cannot be employed as good criteria for classification of rugosa as WANG once adopted. In doing so, one may step into so-called horizontal (artificial) classification instead of natural one.



Text-fig. 2. The mode of appearance of fibres in sections. a: a single trabecula: b. transverse section of a trabecula showing positions of longitudinal sections: c & d. tangential section of a trabecula: e. median vertical section of a trabecula.

† Special remarks on trabeculae

- a) Mode of appearance of trabecula in thin sections.

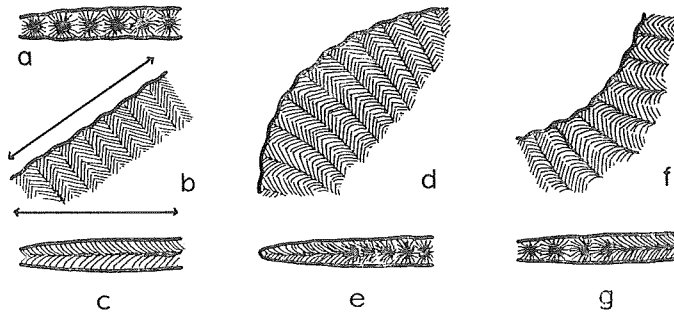
It must be borne in mind that trabeculae appear to be different depending on different cut angles. Otherwise, one can not discuss the true patterns of fine structures desiring to use them as taxonomic bio-characters.

In fibro-normal type, the thing is quite simple. If thin sections are cut at right angle to septa in any direction, one always gets fibro-normal feature in sections. If the section is cut tagentially, that means cutting numerous fibres, the general appearance seems to show a dark, moire structure with fine black dots in detail. In median vertical section of a septum growth lines as well as radiating fibres are seen. If septa are obliquely cut, the median dark line is visible at the centre, with oblique sections of fibres and growth lines on both sides of it.

In trabecular septa, however, the circumstance is somewhat complicated. A single trabecula, being ideally cylindrical, shows radially arranged fibres in it in the view from the top. In median vertical section of a trabecula, feather like arrangement of fibres is visible. In other words, fibres are directed from the centre of trabecula outward as well as upward. When it is seen from outside, the surface of a trabecula must be spotted by numerous edges of these fibres. Figure *d* in text-fig. 2 is a tangential section of a trabecula, and fibres are gently diverging. Further excentric section of figure *c* shows nearly parallel fibres of a trabecula. Oblique section of a trabecula naturally shows elliptical outline, and fibres are radiating. As the oblique angle becomes sharp, the appearance of the section infinitely approaches that of the feather like type in median vertical section.

Figure *b* in text-fig. 3 shows median vertical section of a septum, in which trabeculae are parallel. If this is cut transversely, dark centres of fibre radiation in trabecula are seen to be arranged in a row as in fig. *a*. When the section is cut obliquely, divergent fibres from the central line are seen as in normal trabecular type, as the consequence of the continuation of obliquely cut fibres.

As will be discussed later on, there are many types of vertical arrangement of trabeculae, but here the writer picks out two cases of convex and concave arrangement of trabeculae with their appearances in sections. These vertical arrangements of trabeculae are seen clearly to be related to the form of the upper end of a septum, when these are cut transversely, a part being cut obliquely and a part cut transversely. Thus the appearances shown in figures *e* and *g* in text-fig. 3 will be attained. These fine structural patterns, of course, cannot be treated separately, as the essential type is only trabecular in both of them.



Text-fig. 3. The mode of appearance of fibres in sections.

- a. cross section of a septum showing distinct trabeculae in which centres of calcification are observable.
- b. median vertical section of a septum in which trabeculae are arranged parallel.
- c. transverse section of a septum in which divergent fibres are seen, owing to the oblique cutting of trabeculae.
- d. median vertical section of a septum in which trabeculae are subparallel and convex upward.
- e. transverse section of a septum shown in *d*.
- f. median vertical section of a septum in which trabeculae are arranged subparallel, and concave upward.
- g. transverse section of a septum shown in *f*.

One may even obtain reversed divergence of fibres by a special direction of cut from a simple trabecular septum. However, as will be shown later, a special group may be defined by characteristic vertical arrangement of trabeculae.

b) Dimensions of trabeculae.

As to the dimensions of trabeculae, the matter has been least investigated. In 1936 HILL described acanthine septa, and stated that the diameter of a "monacanth" is about 0.5 mm, that of rhabdacanth is also 0.5 mm with 0.05 mm diameter of rods constructing rhabdacanth, and that of "holacanth" 2 mm. WANG in 1950 stated that the diameter of trabeculae ranges from 0.05 mm in *Columnaria* to 0.5 mm in *Kodonophyllum* and *Palaeosmilia*. He set lamellar structure as a skeletal unit, which is composed of calcite flakes. He also said that the dimensions of that flake are 0.001 mm thick and 0.03 mm in diameter, after BLACK's measurement. Recently ALLOITEAU (1957) specially remarked on the dimensions of trabeculae and stated that it varies from 0.5 mm in *Pseudoseris* to 0.01 to 0.015 mm in Caryophyllidae, Amphiastraeidae, and in Turbinolidae.

According to the writer's study the diameters of trabeculae in corals

are as follows, although the measurement has been done only in trabecular type.

Silurian

<i>Acanthocyclus fletcheri</i> (E. et H.)	rhabdacanth	0.5 mm
	rods	0.05
	holacanth	0.2
	mono-rhabdacanth	0.3
<i>Acanthocyclus transiens</i> HILL	trabecula	0.1
	rhabdacanth	0.2
<i>Acanthocyclus</i> aff. <i>transiens</i> HILL	rhabdacanth	0.2-0.4
	rods	0.03
<i>Arachnophyllum diffluens</i> (E. et H.)	spine	0.1
<i>Schlotheimophyllum patellum</i> (SCHLOTHEIM)		
	rods	0.1
<i>Cystiphyllum cylindricum</i> LONSDALE	monacanth	0.2
<i>Cystiphyllum</i> sp.	„	0.1
<i>Hedstroemophyllum tenue</i> WANG	„	0.15
<i>Kodonophyllum truncatum</i> (LINN.)		
= <i>Strephodes vermiculoides</i> M'COY	trabecula	0.7
<i>Streptelasma whittardi</i> SMITH	„	0.25-0.3
<i>Tryplasma flexuosa</i> (LINN.)	spine	0.1

Devonian

<i>Cyathophyllum ceratites</i> GOLDFUSS		0.1-0.15
<i>Grypophyllum schwellmense</i> WEDEKIND		0.5
<i>Macgeea gallica</i> LANG et SMITH		0.3
<i>Stringophyllum</i> sp.	trabecula	0.6
	single fibre	0.03-0.05
<i>Tabulophyllum erraticum</i> FENTON et F.	trabecula	0.1
<i>Phillipsastraea hennahi</i> (LONSDALE)	composite	1.8
<i>Phillipsastraea</i> cf. <i>intercellulosa</i>		0.25

Carboniferous

<i>Palaeosmilia murchisoni</i> E. et H.		0.2-0.4
<i>Syringopora geniculata</i> (PHILLIPS)	spine	0.1
<i>Syringopora</i> sp.		0.1

Multi-trabecular septa are thickened considerably especially in their peripheral parts. For example, in *Schlotheimophyllum patellum*, the thickness of a septum reaches up to 2.5 mm, although this is actually composed of sclerenchyme and numerous "holacanth"-like rods in it. The feature is similar to that of rhabdacanthine type.

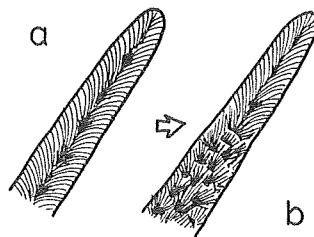
Generally speaking, septa in corals with so-called stereo-zone are rather thick. *Kodonophyllum* is an example of this case, a septum of which is composed of a single series of trabeculae, which attain as much as 0.7 mm in maximum thickness. Each trabecula shows somewhat compressed appearance in cross section.

In cases of corals with acanthine septa, the measurement of trabeculae is rather easy.

As can be seen in the above list, the diameter of a single trabecula ranges from 0.1 to 0.5 mm. A rhabdacanth has the same size, but rods constructing it are of 0.03 to 0.05 mm in size. This value of measurement is similar to the size of fibres in some *Stringophyllum*. In general, trabecular diameter is about 0.1 to 0.5 mm. Especially large examples of trabeculae are observed in *Macgeea*, *Streptelasma*, *Grypophyllum* and in *Palaeosmilia*. In the case of rods in rhabdacanthine type, fibres of simple trabecular type and rods in multi-trabecular type, the diameter of them ranges from 0.03 to 0.05 mm. The smallest unit of the skeleton must be comparatively finer fibres, which build up rods of 0.03~0.05 mm, and these rods again are bundled to make up trabeculae of 0.1~0.5 mm in size.

Each trabecula is typically curved cylindrical, and fairly long, but the length of them the present writer has not yet studied.

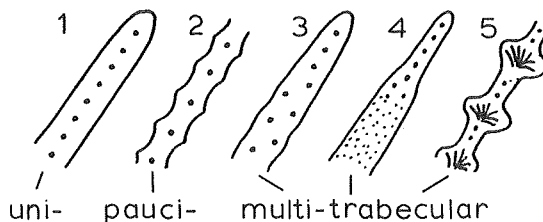
It has not yet been clarified whether any significant relationships exist between trabecular size and stratigraphical change in trabeculae.



Text-fig. 4. Diagrams showing progressive change from uni-trabecular to multi-trabecular.

c) Trabecular arrangement in transverse section.

Usually a septum consists of a series of vertically fused trabeculae. However, aggregation of a number of trabeculae occurs in the thick part of septa, especially in peripheral parts. Here, the writer calls the former "uni-trabecular", while the latter "multi-trabecular". Uni-trabecular to multi-trabecular septa are the morphology of continuous nature



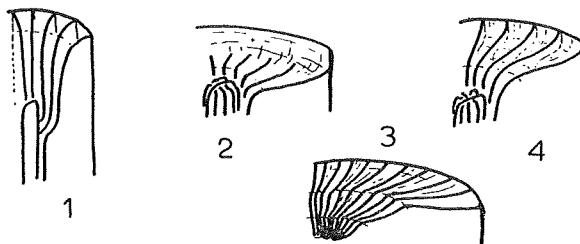
Text-fig. 5. Diagrams showing the arrangement of trabeculae in transverse section. Each dot represents a centre of calcification of a trabecula.

(Text-fig. 4, figs. a~b).

The lateral side of each trabecula more or less expands, and the side of a septum gives somewhat wavy look. The case is called "pauci-trabecular" (= pseudo-synapticular). Sometimes the arrangement of trabeculae in one row shows some disorder, or trabecular alternation. These are transitional cases from uni- to multi-trabeculae (Text-fig. 5, figs. 1~5).

In *Naos* numerous rods like trabeculae are seen at the periphery of a septum. These rods are smaller than the proper trabeculae. In *Helio-phyllum* well known yard arm type of carinae seems to be actually a bunch of rhabdacanthine type trabeculae. In fact externally recognized forms of carinae may actually be a dislocation of trabeculae, or the swelling of trabeculae, or they could be a composite trabecula internally.

In Ordovician specimens, trabecular septa are always uni-trabecular, but in Silurian they are much complicated, and multi-trabecular type appears. But even in multi-trabecular type of septa the construction is not necessarily composite throughout the ontogeny of a coral. Usually



Text-fig. 6. Septal forms & calicular view.

1. deep calice of *Siphonodendron*.
2. shallow calice of *Lonsdaleia* with margin free from septa.
3. moderate calice of *Dibunophyllum*.
4. widely opened calice of *Palaeosmilia*.

the younger stage of the coral has uni-trabecular septa. In a single septum, the axial portion may be uni-trabecular, while the peripheral portion may be multi-trabecular. For example in *Acervularia* a single series of trabeculae becomes triple at the periphery. In *Entelophyllum* the peripheral part of a septum is carinated and further become cribriform to make a sort of mesh work near the wall. In *Naos* the peripheral part of a septum shows irregular aggregation of fine dots, which are slender trabeculae. These examples of multi-trabecular septa are quite common among Silurian and Devonian corals, but not so much so in Carboniferous and Permian corals. Devonian examples are *Chonophyllum*, and *Pselophyllum*, while in Carboniferous there are *Nagatophyllum*, *Symplectophyllum*, *Palaeosmilia* and *Taisyakuphyllum* (Plate 2, figs. 1 & 2). *Iranophyllum* and *Lophophyllidium* are Permian examples.

The complexity of trabecular arrangement is an interesting subject in its stratigraphical and the ontogenetical changes. However, these changes are, as in the case of lonsdaleoid dissepiments, potentials in various corals, and may best be considered as trends. Hence corals with multi-trabecular septa are not necessarily closely related with each other. For example *Chonophyllum* type and *Symplectophyllum* type of septa are very alike each other, but they could never be classified into one group judging from the other characters.

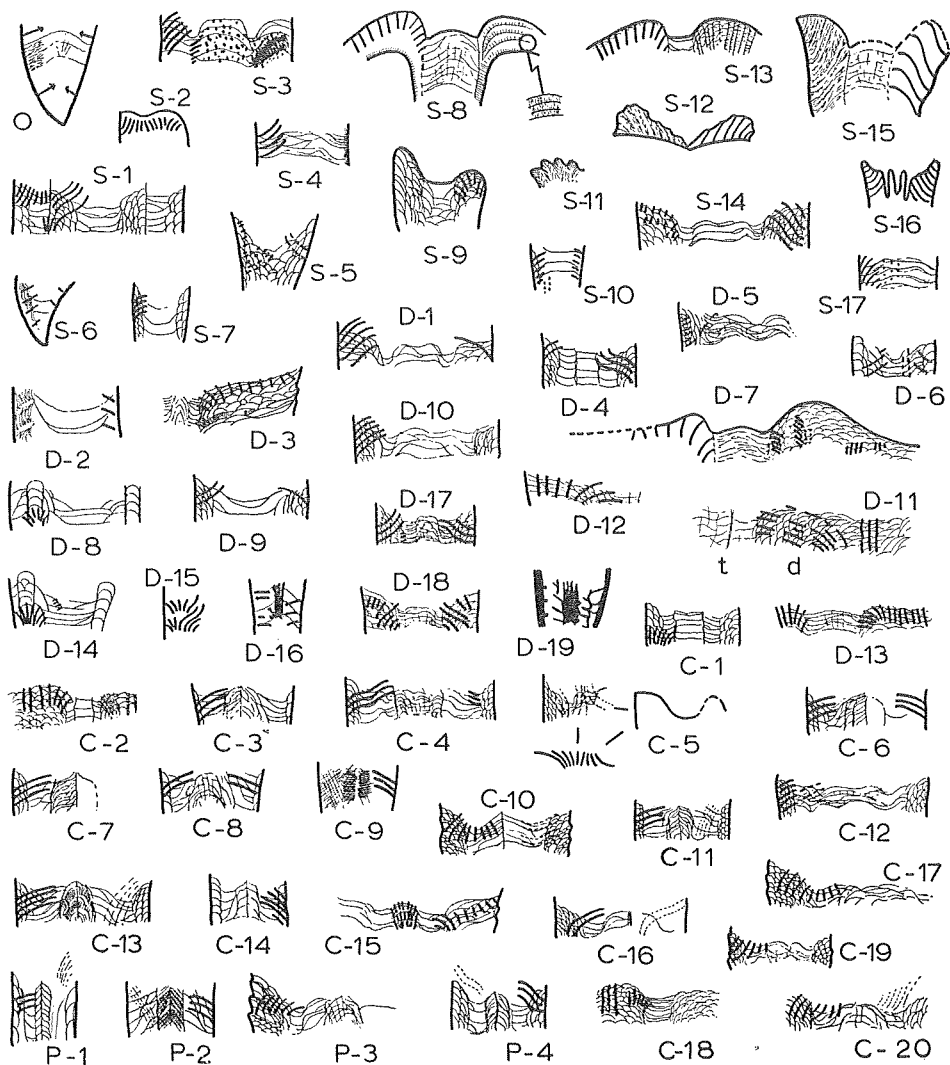
d) Vertical arrangement of trabeculae.

The vertical arrangement of trabeculae has not been fully remarked by workers. Only in such remarkable Devonian forms as *Macgeea*, illustrations have been made to show fan-shaped arrangement of trabeculae in vertical sections (SOSHKINA, ROZKOWSKA and SCHOUPPE).

Generally, trabeculae grow upward from the inner side of the wall, but their angle to the wall and the degree of their length vary case by case. They are sometimes horizontal, rarely inclined downwards as well as inward. In text-figure 7 the writer tried to show the vertical arrangement of trabeculae and their inclination as it appears in longitudinal sections of corals of different periods. Not only forms with trabecular septa but also forms with diffuso-trabecular septa are shown in the figure so as to illustrate the direction of fibre growth in them.

When the trabeculae do not fuse with each other, they are found to have either denticulate or perforate septa. Many examples are known of acanthine septa, in which each trabecula is commonly spiny, short, and straight. There are, however, some examples, in which the trabeculae are convex upward (S-17) or concave upward (D-6).

Trabecular inclination and their vertical arrangement are schemati-



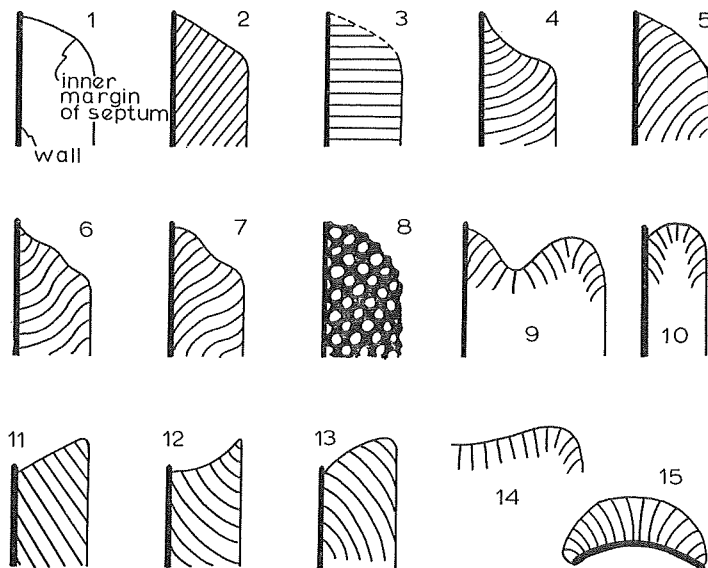
Text-fig. 7. Diagrams showing vertical arrangements of trabeculae in various forms of rugose corals. Thick line indicates the inclination and arrangement of trabeculae. Fine dotted line indicates growth line. t: tabularium, d: dissepimentarium.

Explanation of text-fig. 7.

O-1.	<i>Streptelasma craigense</i> M'COY	D-14, 15.	<i>Macgeea gallica</i> LANG et SMITH
S-1, 2.	<i>Acervularia ananas</i> (LINN.) var. <i>truncata</i> (WAHL.)	D-16, 19.	<i>Metriophyllum bouchardi</i> E. et H.
S-3.	<i>Calostylis denticulatus</i> (K.)	D-17.	<i>Hexagonaria boloniensis</i> (BLAINVILLE)
S-4.	<i>Columnaria sulcata</i> M'COY	D-18.	<i>Prismatophyllum prisma</i> LANG et SMITH
S-5.	<i>Cystiphyllum cylindricum</i> LONS.		
S-6.	<i>Cantrillia prisca</i> SMITH	C-1.	<i>Aulina horsefieldi</i> SMITH et YÜ
S-7.	<i>Holmophyllum simplex</i> LEWIS	C-2.	<i>Aulina rotiformis</i> SMITH
S-8.	<i>Chonophyllum patellatum</i> (SCHLOTH.)	C-3.	<i>Auloclisia mutata</i> LEWIS
S-9.	<i>Goniophyllum pyramidale</i> (HISINGER)	C-4.	<i>Aulophyllum fungites</i> (FLEMING)
		C-5.	<i>Amygdalophyllum</i> sp.
S-10.	<i>Xiphelasma tubulata</i> (SCHLOTH.)	C-6.	<i>Clisiophyllum rigidum</i> LEWIS
S-11, 12.	<i>Palaeocyclus porpites</i> (LINN.)	C-7.	<i>Clisiophyllum delicatum</i> SMITH
S-13.	<i>Naos pagoda</i> (SALTER)	C-8.	<i>Cyathoclisia tabernacula</i> DINGWALL
S-14.	<i>Entelophyllum pseudodanthum</i> (WEISS).	C-9.	<i>Cyathaxonia rushiana</i> VAUGHAN
		C-10.	<i>Koninckophyllum</i> ?
S-15.	<i>Kodonophyllum truncatum</i> (LINN.)	C-11.	<i>Dibunophyllum monense</i> LEWIS
S-16.	<i>Syringaxon siluriense</i> (M'COY)	C-12.	<i>Cyathophyllum aquigranense</i>
S-17.	<i>Tryplasma loveni</i> (EDWARDS et HAIME)		FRECH
D-1.	<i>Hexagonaria inequalis</i> (H. & W.)	C-13.	<i>Koninckophyllum praecursor</i>
D-2.	<i>Tryplasma</i> sp.		HOWELL
D-3.	<i>Chonophyllum</i> sp.	C-14.	<i>Lithostrotion arundineum</i> ETHER.
D-4.	<i>Eridophyllum archaci</i> (BILLINGS)	C-15.	<i>Koninckophyllum columatum</i>
D-5.	<i>Cyathophyllum aquigranense</i> FRECH		GEORGE
		C-16.	<i>Lithostrotion columnare</i> ETHER.
D-6.	" <i>Fasciophyllum conglomeratum</i> (SCHLOTH.)"	C-17.	<i>Palaeosmilia murchisoni</i> E. et H.
		C-18.	<i>Orionastraea edmondsi</i> HUDSON
D-7.	<i>Dohmophyllum helianthoides</i> (GOLDFUSS)	C-19.	<i>Palaeosmilia fornix</i> HUDSON
		C-20.	<i>Palaeosmilia regia</i> (PHILLIPS)
D-8.	<i>Thamnophyllum multizonatum</i> REED	P-1.	<i>Waagenophyllum indicum</i> (W. et W.)
		P-2.	<i>Verbeekiella wichmanni</i> (ROTH-PLETZ)
D-9.	<i>Cylindrophyllum</i> sp.		
D-10.	<i>Disphyllum goldfussi</i> (GEINITZ)	P-3.	" <i>Clisiophyllum</i> " <i>tumulus</i> SALTER
D-11, 12.	<i>Mesophyllum maximum</i> SCHLOTH.	P-4.	<i>Wentzelella socialis</i> (MANSUY)
D-13.	<i>Phillipsastrea pengellyi</i> E. et H.		

cally outlined in text-figure 8. In curved trabeculae, there are cases which are concave or convex upward, and further sigmoidal sometimes because of a complication of the former two types. An especially noted form is the so-called divergent arrangement as in *Macgeea*.

As noted above already, the upper end of a septum is affected largely by the vertical arrangement of trabeculae in it. The relationship is also illustrated in text-fig. 8 (See also text-fig. 6). In most corals the upper end of a septum is situated below the upper margin of the wall, but in such corals as *Macgeea* that has divergent, fan-shaped trabe-



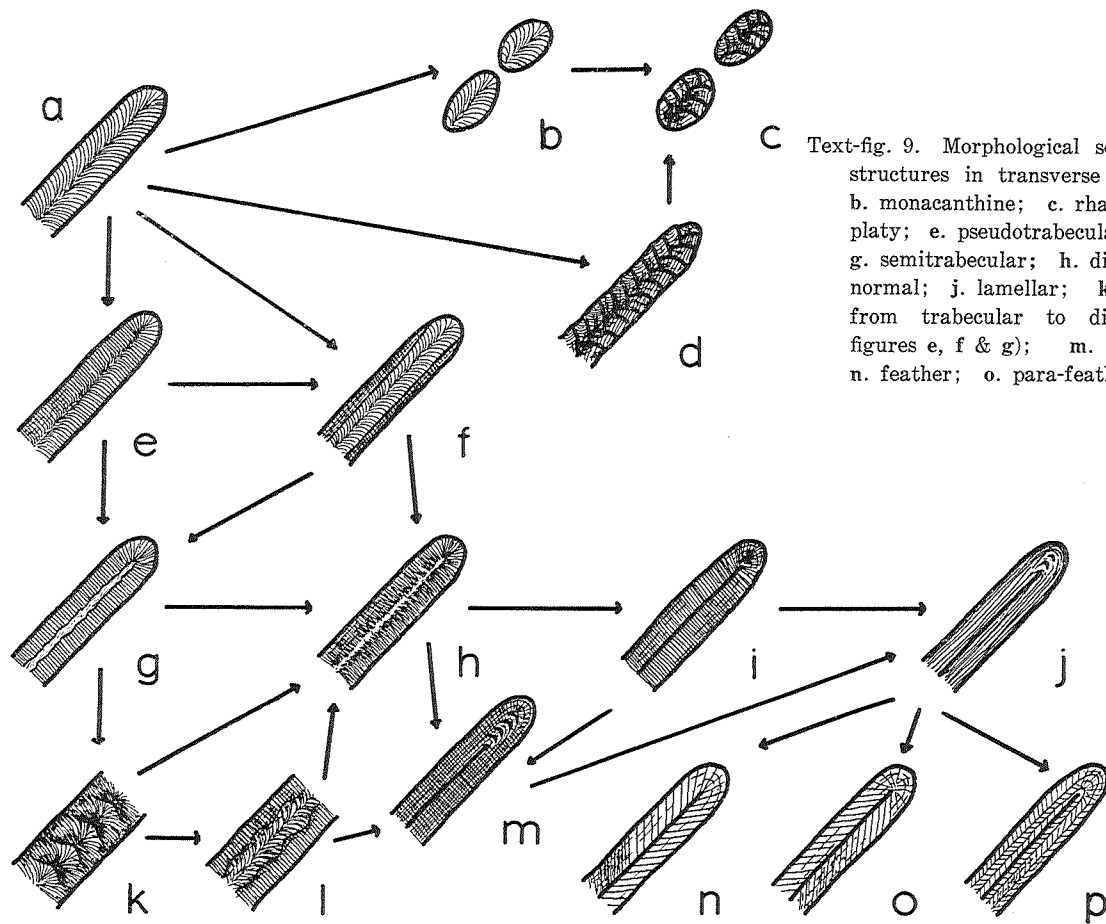
Text-fig. 8. Types of trabecular arrangement. Vertical section of a septum in which various types of trabecular arrangement are shown.

1. index diagram; 2. straight upward; 3. horizontal; 4. concave upward; 5. convex upward; 6. sigmoidal; 7. reversed sigmoidal; 8. mesh work (perforate); 9. complex; 10. fan shaped; 11.~13. downward; 14. vertico-fan shaped; 15. fan shaped.

culae, the upper ends of septa are elevated beyond the upper limit of the wall. The feature reminds one of a scleractinian character.

Now the question is how these vertical arrangements of trabeculae may be useful in the practical classification of Palaeozoic corals. As can be seen in D-17 trabeculae are simple, concave upward in part, but they are sigmoidal in another part of the same corallite. In D-9 trabecular inclination varies concave to convex in different corallites of the same species. Thus the fine detail of these vertical arrangements of trabeculae seems to be a not very reliable character in the classification. But roughly speaking, the general pattern of trabecular arrangement is not so variable at all. And, to some extent such patterns may be considered to be of some importance.

As the writer described in the preceding chapter, there are certain trends in fine structure appearing in the transverse sections of septa which are applicable to the classification. Naturally the trabecular arrangement is essentially three dimensional, so, patterns of trabecular arrangement showing in transverse section only may lead one to the



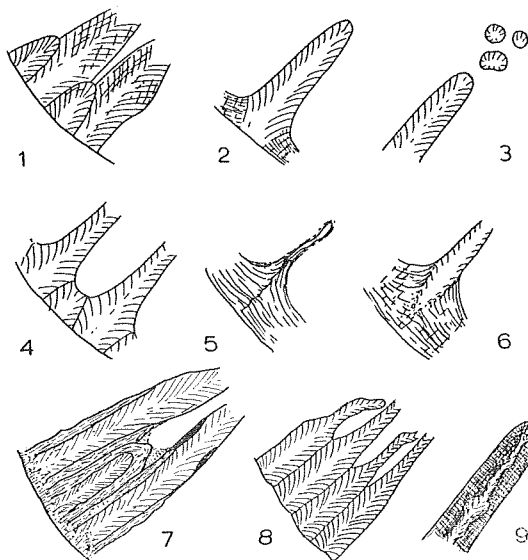
Text-fig. 9. Morphological series of types of septal structures in transverse sections. a. trabecular; b. monacanthine; c. rhabdacanthine; d. rhabdoplasty; e. pseudotrabeular; f. lamellotrabeular; g. semitrabeular; h. diffusotrabeular; i. fibro-normal; j. lamellar; k. & l. transitional forms from trabecular to diffusotrabeular (compare figures e, f & g); m. fibro-lamellar (clathrate); n. feather; o. para-feather; p. zigzag structure.

misconception of three dimensional arrangement of them. Types in transverse sections are only the result defined by the inclination of vertical arrangement of trabeculae and the angle at which septa are cut. The same type of vertical arrangement of trabeculae excepting for their inclination may give significantly different patterns in transverse section. In this regard, the vertical arrangement of trabeculae is related to the types of true septal structures in transverse section as biocharacters.

In short, the writer could recognize many types of vertical arrangement in trabeculae; notice should be taken of the mode of vertical arrangement of trabeculae, in connection with their appearances in transverse sections.

† Various types of septal structure.

There are many forms in the septal construction in rugosa, which

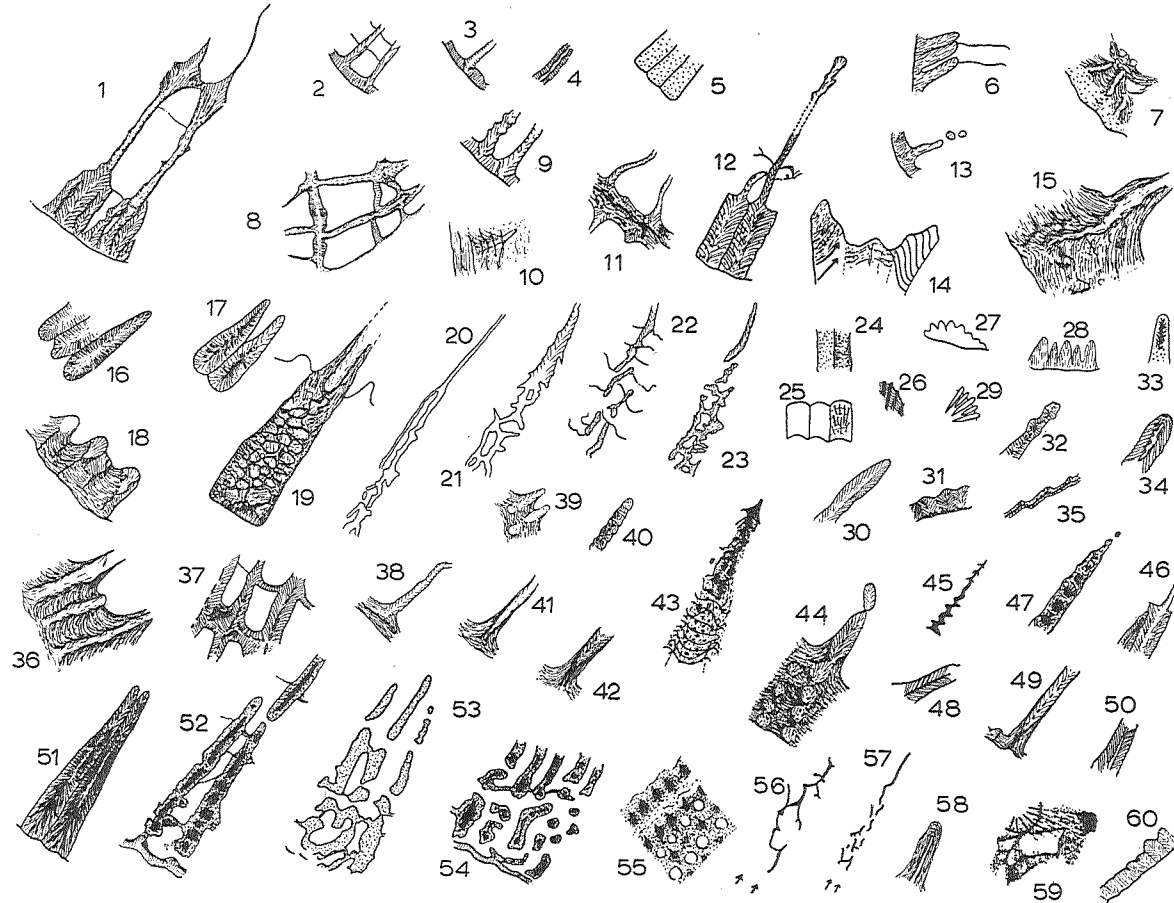


Text-fig. 10. Diagrams showing fine structures of septa and walls in Ordovician rugose corals.

- 1 & 4. *Lindströmia subduplicata* M'COY
- 2, 5 & 6. *Lindströmia laevis* N. et H.
- 3. *Grewingkia* sp.
- 7. *Streptelasma corniculum* HALL
- 8. *Streptelasma aggregatum* N. et H.
- 9. *Streptelasma robustum* WHIT.

All are in transverse section.

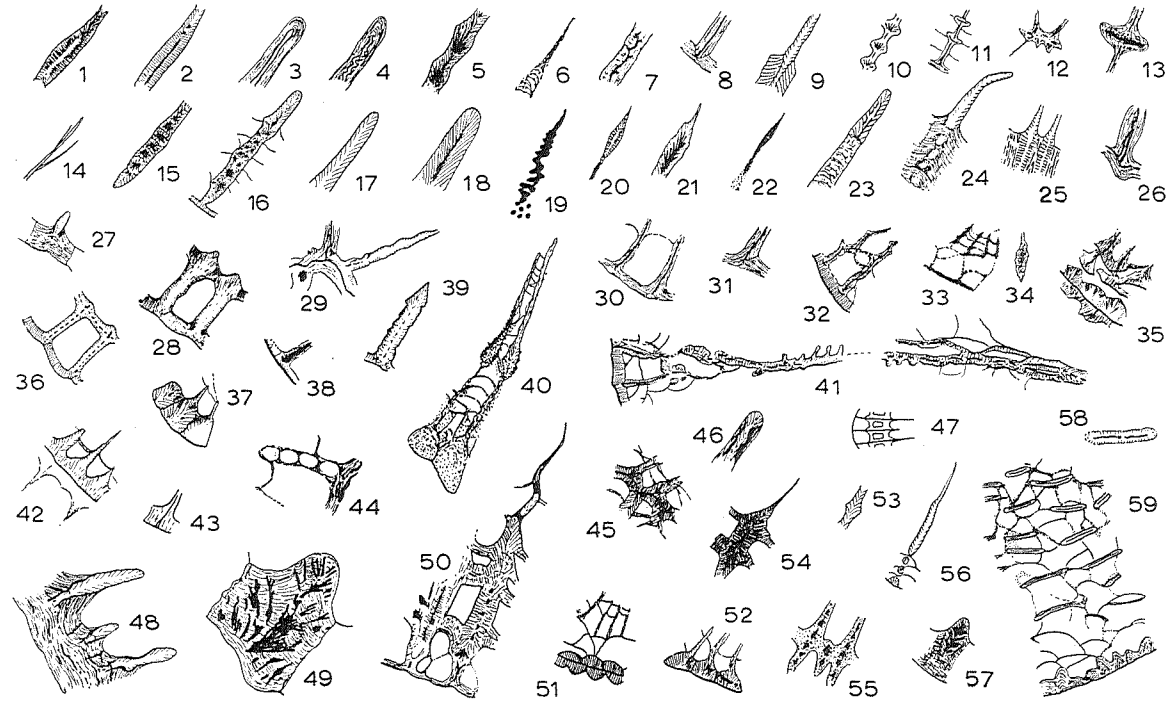
Text-fig. 11. Diagrams showing fine structures of septa and walls in Silurian rugose corals.



Explanation of text-fig. 11.

- 1, 2 & 37. *Acervularia ananas truncatus* (WAHL.)
- 3 & 4. *Acervularia exigua* LANG et SMITH
5. *Chonophyllum* sp.
- 6 & 13. *Tryplasma flexuosum* LONSDALE
- 7 & 39. *Cystiphyllum cylindricum* LONS.
8. *Acervularia ananas singularis* L. et S.
9. *Acervularia densa* SMITH et LANG
10. *Cantrillia prisca* SMITH
- 11 & 38. *Columnaria gotlandica* E. et H.
- 12 & 14. *Kodonophyllum truncatum* (LINN.)
15. *Dinophyllum hisingeri* (E. et H.)
- 16, 27-32. *Palaeocyclus porpita* (LINN.)
17. *Thamnophyllum reclinatum* HILL
18. *Syringaxon siluriense* (M'COY)
19. *Kodonophyllum* sp.
- 20-23. *Entelophyllum pseudodianthus* (WEISS.)
- 24-26. *Mucophyllum crateroides* ETH.
- 33, 46. *Acanthocyclus transiens* HILL
34. *Plasmophyllum brevilamellatum* M'COY
35. *Spongophylloides grayi* (E. et H.)
36. *Dinophyllum* sp.
40. *Goniophyllum pyramidale* (HISINGER)
41. *Dalmanophyllum* sp.
42. *Lindströmia hisingeri* E. et H.
43. *Naos pagoda* (SALTER)
44. *Tryplasma tubulata* (SCHLOTHEIM)
45. *Ptylophyllum lindströmi* SMITH et TREMBARTH
47. *Grewingkia kiaeri* (WEDEKIND)
48. *Mesactis glevensis* RYDER
49. *Streptelasma aquisulcata* M'COY
50. *Ketophyllum obturata* BUTLER
51. *Schlotheimophyllum* sp.
- 52-55. *Calostylis denticulatum* (KIERULF)
- 56-57. *Phaulactis augusta* (LONSDALE)
58. *Ptycholopas* sp.
59. *Ptychophyllum* sp.
60. *Streptelasma whittardi* SMITH

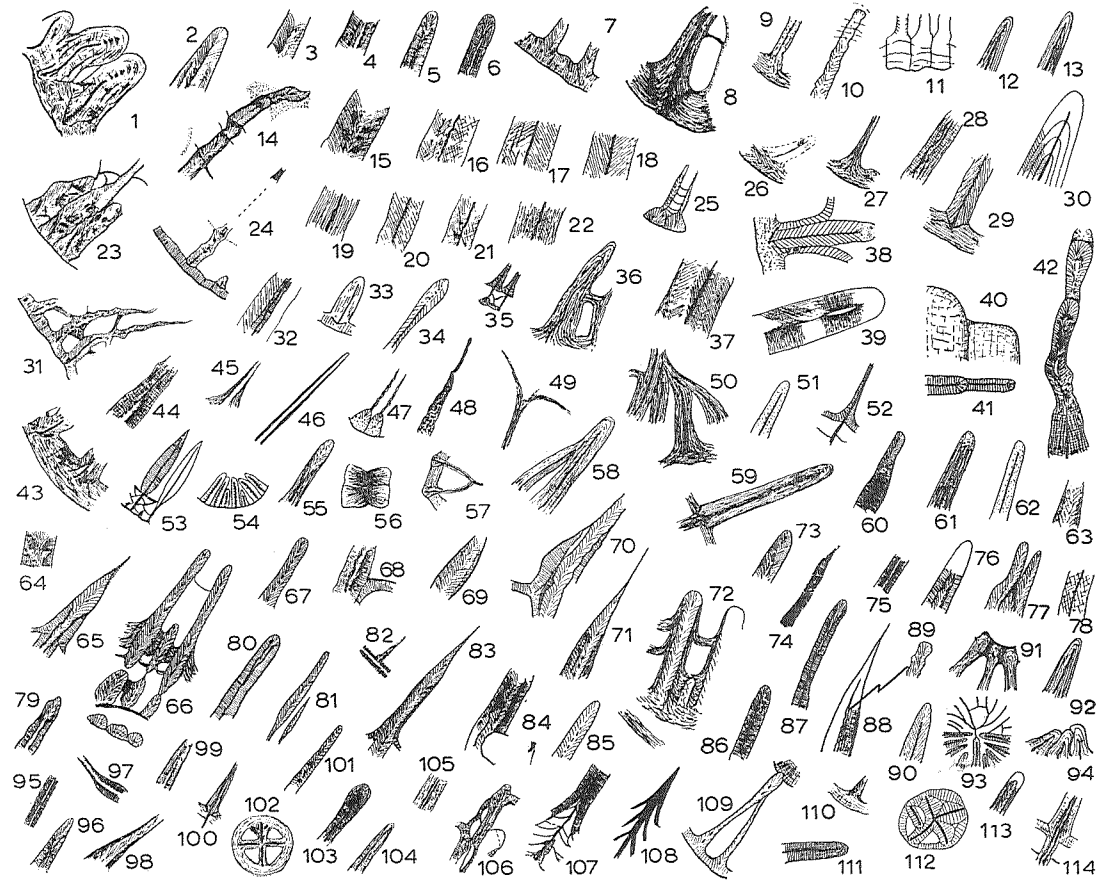
Text-fig. 12. Diagrams showing fine structures of septa and walls in Devonian rugose corals.



Explanation of text-fig. 12.

- 1 & 2. *Acanthophyllum heterophyllum* (E. et H.)
3. *Acrophyllum oneidaense* (BILLINGS)
4. *Amplexus* sp.
5. *Keriphyllum conicum* WANG
6. *Chonophyllum perfoliatum* E. et H.
7. *Aulacophyllum sulcatum* (D'ORB.)
8. *Cyathophyllum* sp.
9. *Dinophyllum* sp.
- 10-13. *Heliophyllum halli* E. et H.
14. *Lyrielasma* sp.
- 15-16. *Macgeea gallica* L. et S.
17. *Indet.*
18. „
- 19-20. *Phillipsastraea pengellyi* E. et H.
21. *Phillipsastraea vesiculosa* SMITH
22. *Prismatophyllum pentagonum* (GOLDFUSS)
23. *Pselophyllum bohemicum* (BARRANDE)
24. *Tabulophyllum erraticum* F. et F.
25. *Temeniophyllum poshiense* WANG.
26. *Zaphrentis corniculum* (LESUEUR)?
27. *Tryplasma paucitabulata* (SCHLÜTER)
- 28 & 36. *Diplophyllum caespitosum* HALL
- 29 & 39. *Hexagonaria inequalis* (H. et W.)
- 30 & 31. *Depasophyllum adnetum* GRABAU
32. *Eridophyllum arundinaceum*
- 33 & 34. *Phillipsastraea cincta* SMITH
35. *Endophyllum abditum* E. et H.
37. *Battersbyia* sp.
38. *Acanthophyllum dermontensis* ETH.
40. “*Cyathophyllum*” *helianthoides* GOLDFUSS
41. *Mesophyllum maximum* SCHLÜTER
- 42 & 43. *Columnaria sulcata* GOLDFUSS
44. *Stringophyllum* sp.
45. *Prismatophyllum quadrigeminum arcticum* (MEEK)
46. *Charactophyllum novum* (H. et W.)
47. *Phacelophyllum trigemme* (QUENSTEDT)
48. “*Amplexus*” *tortuosus* PHILLIPS
49. “*Amplexus*” sp.
50. *Thamnophyllum multizonatum* REED
- 51-52. *Spongophyllum cyathophylloides* ETH.
53. *Disphyllum goldfussi* (GEINITZ)
54. *Phillipsastraea macouni* R. et H.
55. *Acervularia coronata* E. et H.
56. “*Cyathophyllum*” *dammoniense* LONSDALE
57. *Amplexus* sp.
- 58-59. “*Cyathophyllum*” *dammoniense* LONSDALE”

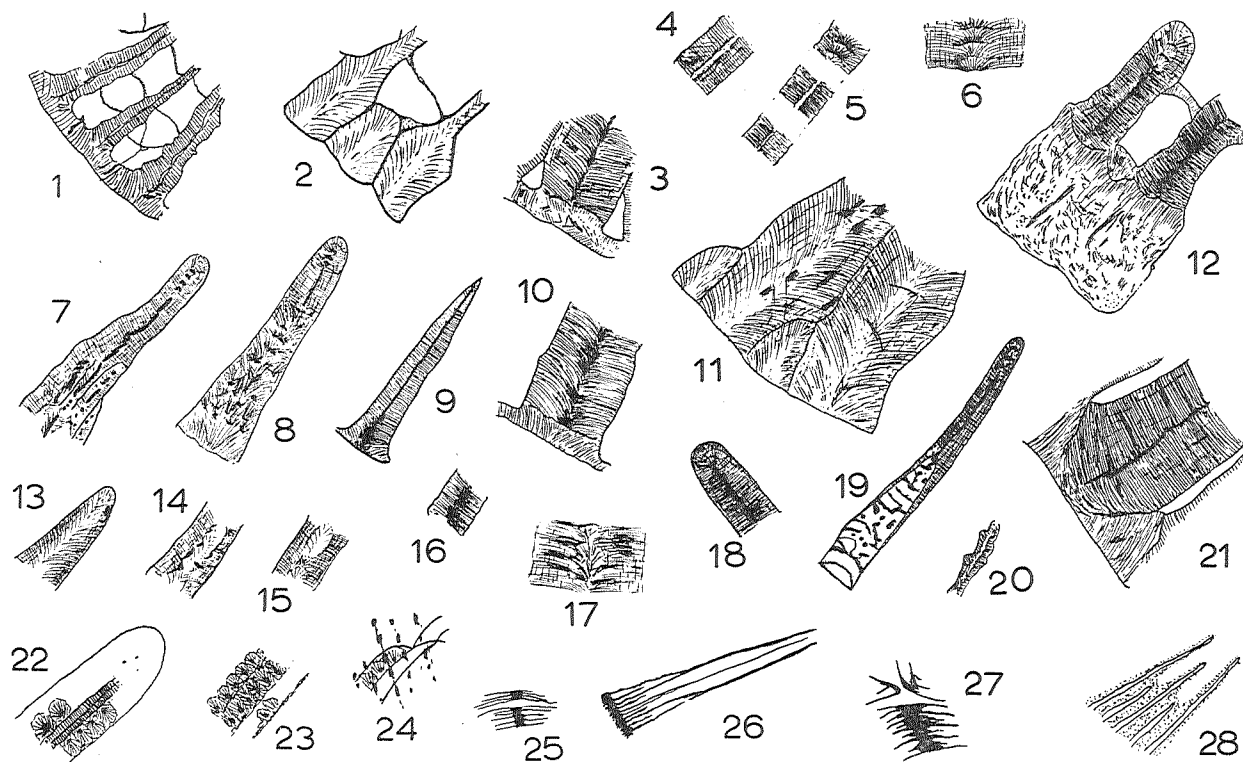
Text-fig. 13. Diagrams showing fine structures of septa and walls in Carboniferous rugose corals.



Explanation of text-fig. 13.

- 1, 2. *"Amplexus" pustulosus* HUDDLESTON
- 3-7, 14. *Aulophyllum fungites* (FLEMING)
8. *Claviphyllum eruca* (M'COY)
9. *Zaphrentis delepini* VAUGHAN
- 10, 11. *Zaphrentis konincki* E. et H.
- 12, 13. *Zaphrentis enniskilleni* E. et H.
15. *Caninophyllum patulum* (MICHELIN)
- 16-22. *Caninia cornucopiae* MICHELIN
23. *Amygdalophyllum* sp.
24. *Corwenia rugosa* (M'COY)
25. *Amygdalophyllum inopinatum* (ETHERIDGE)
26. *Zaphrentis enniskilleni derbiense* LEWIS
- 27, 28. *Zaphrentis omaliusi ambigua* CARR.
29. *Zaphrentis enniskilleni ashfelense* LEWIS
30. *Zaphrentis enniskilleni* E. et H.
31. *Aulina horsefieldi* SMITH et YÜ
32. *Caninia benburbensis* LEWIS
33. *Caninia amplexoides* (WILMORE)
34. *Lophophyllidium proliferum* (MCCHESNEY)
35. *Cystophrentis kolaohoensis* YÜ
36. *Amplexizaphrentis* sp.
37. *"Amplexus" pustulosus* HUDDLESTON
38. *Zaphrentis oystermouthensis* VAUGHAN
39. *Siphonophyllia hettonensis* WILMORE
- 40-42. *Rotophyllum costatum* (M'COY)
43. *Auloclisia mutata* LEWIS
44. *Bothrophyllum patulum* (MICHELIN)
45. *Carcinophyllum vaughani* SALEÉ
46. *Diphyphyllum lateseptatum* M'COY
47. *Palaeosmilia murchisoni* E. et H.
48. *Symplectophyllum mutatum* HILL
49. *Amplexus coralloides* SOWERBY
50. *Zaphrentis delanouei* E. et H.
- 51, 52. *Stylastraea inconferta* LONSDALE
53. *Caninia calophylloides* (HOLTEDAHL)
54. *Caninia juddi* var. *cumbrensis* LEWIS
55. *"Lophophyllidium"* sp.
56. *Palaeosmilia murchisoni* E. et H.
57. *Heterophyllia ornata* M'COY
58. *Zaphrentis amplexoides* WILMORE
59. *Lonsdaleia* sp.
60. *Lonsdaleia laticlavata* SMITH
61. *Lonsdaleia* sp.
62. *Lonsdaleia duplicata* (MARTIN)
63. *Clisiophyllum ingletonense* VAUGHAN
- 64-66. *Koninckophyllum columatum* GEORGE
67. *Koninckophyllum divisum* LEWIS
68. *Koninckophyllum* sp.

69. *Koninckophyllum praecursor* HOWELL
- 70-71. *Koninckophyllum scarlettense* LEWIS
72. *Carcinophyllum mendipense* SIBLY
73. *Clisiophyllum* aff. *maccoyanum* THOMSON
74. *Dibunophyllum* sp.
75. *Dibunophyllum bipartitum* (M'COY)
- 76-77. *Cyathoclisia tabernaculum* DINGWALL
78. *Siphonophyllia* sp.
79. *Koninckophyllum interruptum* N. et T.
80. *Koninckophyllum* sp.
81. *Cionodendron columen* BENSON et SMITH
82. *Lithostrotion maccoyanum* E. et H.
83. *Clisiophyllum delicatum* SMITH
84. "Clisiophyllid"
85. *Clisiophyllum* sp.
86. *Dibunophyllum* sp.
87. *Dibunophyllum* aff. *muirheadi* N. et T.
- 88-89. *Caninia juddi* (THOMSON)
90. *Caninia cornucopiae* MICHELIN
91. *Permia caverna* HUDSON
92. *Rhopalolasma bradbournensis* HUDSON
93. *Cryptophyllum enorme* HUDSON
94. *Rylstonia benecompacta* H. et P.
95. *Nemistium edmondsi* SMITH
96. *Siphonodendron* aff. *martini* nr. *caswellense* HOWELL
97. *Diphyphyllum lateseptatum* M'COY
98. *Siphonodendron junceum* FLEMING
99. *Diphyphyllum lateseptatum* M'COY
100. *Thysanophyllum pseudovermiculare* (M'COY)
101. *Orionastraea radiata* (MARTIN)
102. *Zaphrentis phillipsi* E. et H.
103. *Claviphyllum hillae* H. et F.
104. *Allotropiophyllum tuberculatum* (THOMSON)
105. *Caninia recurvata* (THOMSON)
106. *Stimoniphyllum slimonianum* (THOMSON)
107. *Caninia juddi* THOMSON
108. *Caninia elegantula* (THOMSON)
109. *Cyathaxonia cornu erecta* H. et F.
110. *Siphonodendron junceum* (FLEMING)
111. *Fasciculophyllum carruthersi* HILL
112. *Cryptophyllum hibernicum* CARRUTHERS
113. *Rylstonia benecompacta* H. et P.
114. *Siphonodendron scoticum* (HILL)



Text-fig. 14. Diagrams showing fine structures of septa and walls in Permian rugose corals.

- | | |
|---|--|
| 1, 5, & 6. <i>Waagenophyllum indicum</i> (WAAGEN et WENTZEL) | 19. <i>Iranophyllum spongifolium</i> SMITH |
| 2. <i>Verbeekiella cristata</i> (GERTH) | 20. <i>Waagenophyllum virgalense</i> (WAAGEN et WENTZEL) |
| 3, 9 & 10. <i>Lytvelasma cainodon</i> (DEKONINCK) | 22, 23 & 24. <i>Timania</i> sp. |
| 4. <i>Caninia</i> sp. | 25 & 26. <i>Lonsdaleiastraea</i> sp. |
| 7, 8 & 12. <i>Lophophyllidium wichmanni</i> var. <i>elongatum</i> WANG | 27. <i>Wentzelella maoria</i> LEED |
| 11, 14, 15, 16, 17, 18 & 21. " <i>Dibunophyllum</i> " <i>australe</i> BEYRICH | 28. <i>Trachypsammia dendroides</i> GERTH |
| 13. <i>Verbeekiella rothpletzi</i> GERTH | |

are illustrated in Text-figures 10 to 14 period by period (Plates I~III).

Septa in rugosa may be classified into the following tabular scheme according to their external features.

continuous	-smooth:	both sides of septa may be smooth, but axial or upper edges may be weakly undulated.
	-pseudo-synapticular:	sides of septa undulated and the swelled portion may be coalesced with the corresponding parts of the neighbouring septa.
	-carinate:	flange like projections are on the sides of septa.
	-denticulate (fused acanthine):	the internal edges of septa may be denticulated.
discontinuous or unfused septa	-amplexoid:	
	-lonsdaleoid:	
	-acanthine:	septa are represented by spiny projections which may appear on the wall (phaneroacanthine), or may be embedded in other tissue (crypto-acanthine).
	-perforate:	

In the fine structure, various types are also discernible among corals. They are briefly explained as follows (Text-fig. 9).

trabecular: As the result of oblique cutting trabeculae fibres are seen to be arranged divergently from the median part of a septum. Dark spots representing the centre of calcification of trabeculae may be present.

monacanthine: Trabeculae are separated.

holacanthine: The internal feature is structureless owing to the recrystallization. Original structure is small monacanthine. Rods constructing rhabdacanthine or multi-trabecular septa are of this type.

rhabdo-trabecular: A special kind of multi-trabecular septa, which consist of numerous composite rods or holacanth embedded in sclerenchyme or lamellar structure. Rhabdo-trabecular septa may be platy (rhabdo-platy), or acanthine (rhabdacanthine).

pseudo-trabecular: Outer portions of divergent fibres normal to the median plane become larger, and trabecular features become less well differentiated.

lamello-trabecular: Dilated portion of trabecular septa may be lamellar as well as clathrate in consequence of trabecular uniting.

semi-trabecular: Median portion of a septum remains trabecular, while the peripheral portions are fibro-normal.

diffuso-trabecular: Fibres are perpendicular to the surface of a septum, although some sort of bundling is still visible. Median portion of a septum is seen to be light in colour and both sides

of this light layer there are two dark lines sometimes.

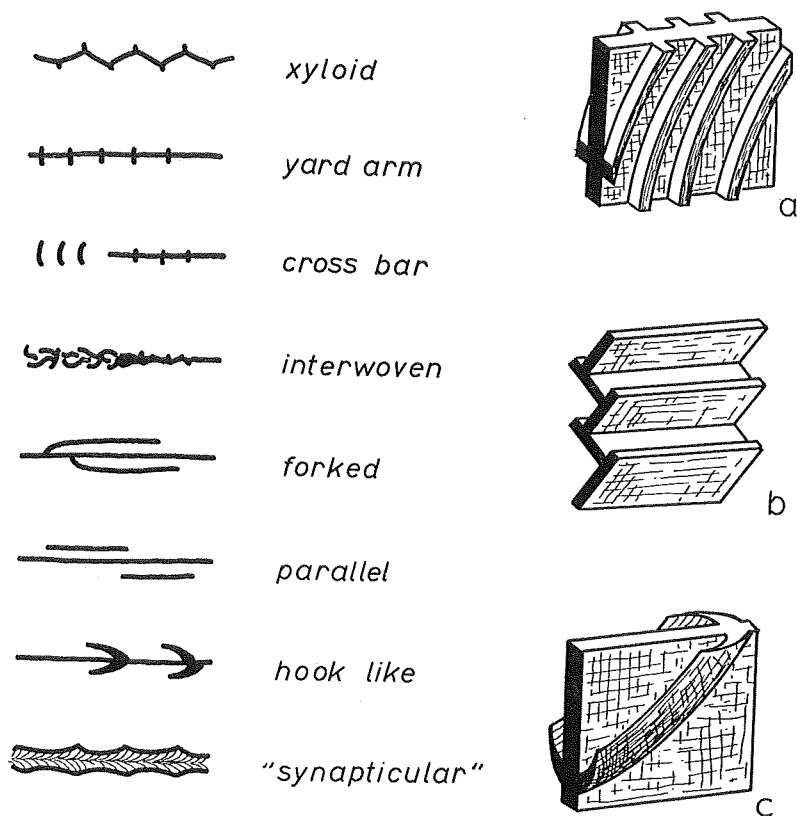
fibro-normal: Fibres are perpendicular to the median dark line.

fibro-lamellar (clathrate): Growth lamellation is added to the fibro-normal type.

lamellar: Septa are made up of lamellae parallel to the median dark line.

feather like: Feather like lines occur oblique to the median dark line.

para-feather like: Reversed pattern of the form above.



Text-fig. 15. Types of carinae.

a: Diagram of limb-like carinae which appear as yard arm carinae both in transverse and longitudinal sections.

b: Diagram showing vertically zigzag carinae. In transverse section it may be parallel, but xyloid in longitudinal section.

c: Diagram showing drain type carinae which are seen to be hook-like in transverse or in longitudinal section.

Left hand figures show various types of carinae in transverse sections.

zigzag (chevron): Numerous oblique lines are confined to space between growth lines so as to form zigzag pattern as a whole.

massive: Structureless platy septa which correspond to holacanthine type.

granular: Numerous granules are seen in massive septa. The type has been known hitherto only in scleractinia.

These various types of fine structure of septa are purely morphological, superficial, and are to be combined with the external forms of septa as above tabulated. They are not necessarily types independent of each other but interchange morphologically from one to the other. Some of them are proved to be of secondary nature, and by no means essential in the classification.

Brief remarks on carinae.

Carinae are projections on both sides of a septum, like foldings or flanges. The origin of carinae is either swelling or displacing of trabeculae. The inclination and the curvature of carinae directly indicate the length, and growth of trabeculae. In uni-trabecular septa, each trabecula is swollen to form undulations on the sides of septa. Sometimes the centres of trabeculae are arranged alternately, thus they make lateral projections on the sides of septa. It is convenient to classify them by their external morphology, and many specific terms were already proposed for forms of carinae.

The writer's scheme is as follows (see Text-figure 15):

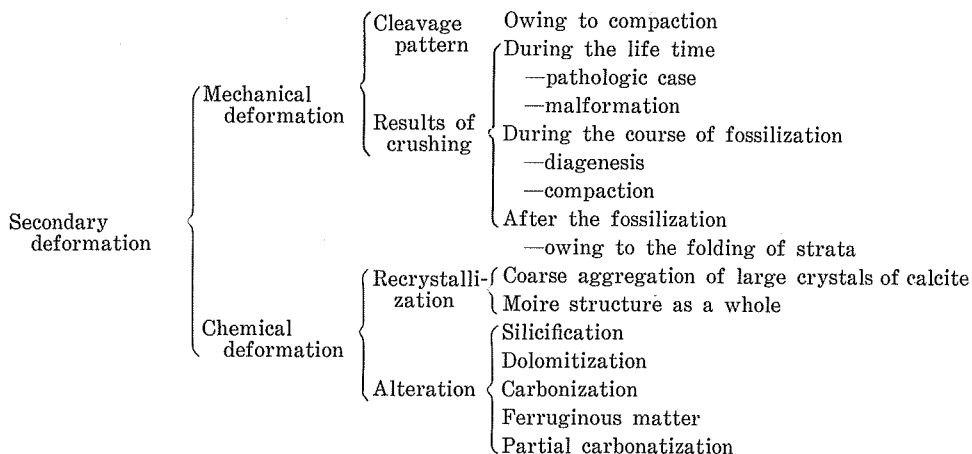
{	limb like type	{	trabeculae inclined downward	{	xyloid	
					{	yard arm
			trabeculae inclined upward	{	xyloid	
					{	yard arm
{	drain like	{	septa waving vertically		parallel	
			flanges are nearly horizontal-hook like or forked			
			transverse carinae= cross bar carinae			
			tubercles			

† On the secondary deformation of septal structure

When septal structure is considered, one should take into account their secondary deformation of primary structure through or after fossilization, because only primary and fundamental forms of septal structure ought to be considered as taxonomic characters. Up to the present, this secondary change in skeletal structure seems to be largely overlooked. As a result, there are cases when some sort of secondary structure has been given some taxonomic significance.

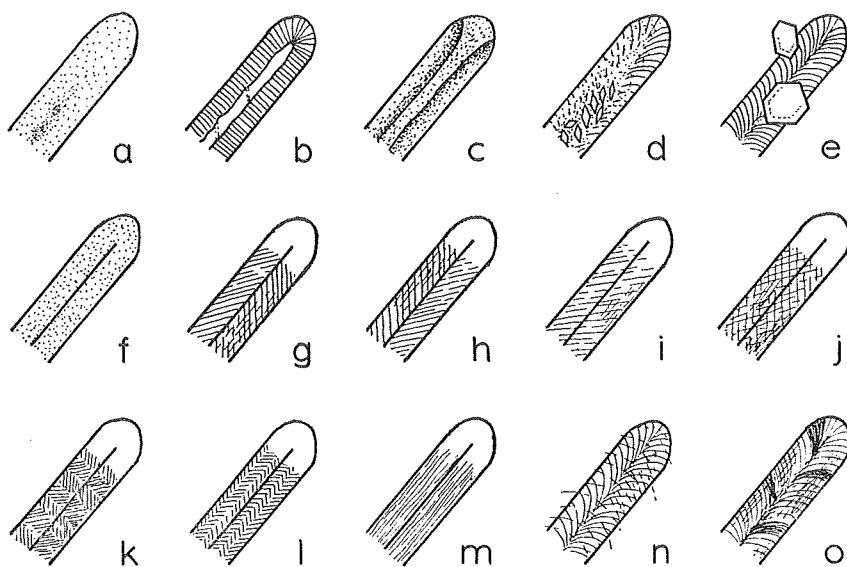
As far as the writer is aware, the first remark on secondary features of skeleton was made by HILL and BUTLER (1936) on the septa of *Cymatelasma*. Their example is a case like figs. *b* & *c* in text-figure 16. This is simply a result of recrystallization in semi-trabecular or in lamello-trabecular septa, in which fibrous parts are obscured by recrystallization.

The writer attempts to classify the secondary deformation in septa (also applicable to the other organs) as follows.



The term “deformation” may sound improper, because the thing is that the internal structure of septa has been changed from its primary state. But since no other suitable words are readily available, the writer employed the term “deformation”.

Various types of secondary deformation are shown in text-figure 16. Figures *a-e*, *n*, *o* are cases in trabecular septa, while figures *f-m* are in fibro-normal type. Cases *a-f* show effects of recrystallization and those caused by alteration. Figure *a* shows that fibrous structure disappears altogether as a result of recrystallization, and only spots which are relicts of the centres of calcification in former trabeculae are seen at the median part of septa. In figure *b* axial, only the trabecular part is obscured, otherwise fibrous structure is retained in semi-trabecular type. Figure *c* is a case of lamello-trabecular septa loose fibrous structure, leaving dark boundary lines between axial part and “stereoplasmic” dilated portion. In figure *d*, the axial part is partially altered by crystals of dolomite, and in *e* large crystals of calcite grow in the manner of intrusion, but the remainder part still shows trabecular structure. Figure *f* is a case where the entire fibres are lost by recrystallization except



Text-fig. 16. Secondary deformation in septal structure. Figures a to f show the effects of recrystallization and alteration, while figures g to o show the effects of cleavages. See text for the more detailed explanations.

for the central dark line.

In fibro-lamellar and in fibro-normal septa, fibres have sometimes vanished, leaving only growth lines clearly visible. This is perhaps due to a sort of obscuration, presumably of some chemical nature. Although lamellar structure has long been considered to be a genuine fine skeletal structure in rugosa, the writer is inclined to believe that it is secondary in nature, because in a well preserved specimen of forms previously believed to have lamellar structure clearly shows fibrous structure, at least in parts. And fibres are normal to lamellae which are believable to be growth lamellae. In many instances growth lamellation is seen with normal fibres, thus they make clathrate pattern for which the term "fibro-lamellar" has been already applied. There are corals in which fibres are partially disappearing, although growth lamellation is still clearly visible.

WANG (1950) actually thought that the lamellar structure is one of the essential types of skeletal construction, citing the measurement of calcite flake by BLACK, and which was supposed to be an unit constructing lamellation. The writer failed to detect any genuine flakes in this lamellation, which is indeed made up of growth lines cutting through neighbouring fibres. Between crossed nicols, straight extinction is clearly

recognizable in fibro-normal type of septa as well as in lamellar type. One should keep in mind that fibres of septa are in fact fibrously elongated crystals of calcite which may be treated from the view point of its mineralogical aspect. Lamellar structure is, according to the writer's opinion, also nothing but an effect of some sort of obscuration in skeletal structure of fibro-normal type. Figure *m* is an example of lamellar septa.

Now, figures *g* to *l* show some oblique patterns, and special names previously proposed for some of them. However, they are all cleavage patterns owing chiefly to the most conspicuous cleavage in mineral calcite, $10\bar{1}1$. Optically, straight extinction is still recognizable in each of these cleavage patterns under crossed nicols, regardless of these oblique structures. Moreover, in some of these oblique structure fibrous as well as lamellar structures are left here and there. And sometimes, cleavages are crossed with each other. These oblique cleavages often occur within the limit of lamellae, thus they make a zigzag pattern. This structure has been specially noted by certain workers, some of whom thought that they are taxonomically important. Nobody ever succeeded in explaining why this structure has been formed. However, there is no regularity in this zigzag structure which varies even within a corallite. They are known in many of such otherwise unrelated forms as *Amplexus*, *Plerophyllum*, *Caninia*, *Lophophyllidium* and "*Zaphrentis*". Further, optically, the extinction angle in this kind of structure is either normal or parallel to the median plane of the septum. And this is the same thing in fibro-normal type. Thus the oblique pattern or zigzag pattern does suggest that they are due to cleavages in calcite. $10\bar{1}1$ cleavage in calcite is 45 degrees.

Tilted angle of the cleavage is less than 45 degrees in septa owing to cut directions of thin sections, and is explained as corresponding to the angle of $10\bar{1}1$ cleavage in calcite. Fibrous calcite which made up the septa is needle like crystal, of which the axis is normal to the growth plane that is represented by the surface of septa or the median dark line. One more thing may be mentioned. Those corals with zigzag structure are often found in shaly facies in which they are likely to have been under compaction pressure through geologic time. In conclusion, oblique pattern or zigzag structure in septa of rugosa are not genuine characters but they are of secondary nature, thence they have no taxonomic value.

Cleavage pattern is also detectable in common trabecular septa. In this case, cleavages are semicircular as the fibres of septa are in form divergent to the direction of septa. The case is shown in fig. *n* (also plate I, fig. 4).

Figure 6 is not easily explicable, in which a part of septum is darkened by some sort of recrystallization.

† Evolutional trends in septal structure through geologic time.

The first appearance of rugosa is in Ordovician time when already fairly rich coral faunas are known to have existed. Being represented by Streptelasmids the fine structure of septa in Ordovician corals is practically of all trabecular type in which only one series of trabeculae occurs. Otherwise modifications of trabecular septa are known. Hence it might be considered that a trabecular septum is the fundamental septal structure in rugosa. Main types are shown in Text-figure 10. Septa are all platy, but trabeculae are sometimes axially separated so as to form axial lobes, which show the relationship to the perforate group of corals in Silurian time. No carinate septa are known amongst Ordovician rugosa. The laterally expanded part of a septum becomes lamellar in some cases.

In Silurian, rugose corals flourished with numerous species (Text-fig. 11). The essential type of fine septal structure is also of trabecular type but in elaborated forms. Acanthine septa appeared commonly and rhabdacanthine type has been found. Uniserial arrangement of trabeculae in Ordovician corals turns up to become multi-trabecular in many Silurian corals, parallel to the development of marginarium. There are reported the third order or even fourth order of septa in some Silurian corals. However, these are nothing but modified multi-trabecular septa. In multi-trabecular type, trabeculae in peripheral parts of septa often tend to become a crowd of rods which are like to acanthine trabeculae, "holacanth". Vertically, the arrangement of trabeculae also varies considerably in Silurian corals. Sigmoid, concave, complex and fan-shaped arrangement can be recognized among them. Peculiar forms are Calostylids in which perforate septa and cribriform axial columns are to be seen. Carinae are often present, and the xyloid type is the commonest.

In Devonian, many forms are after the stream of Silurian forms (Text-fig. 12). Especially early Devonian forms are not very much different from the Silurian forms. The essential type of septa is still trabecular. Acanthine and rhabdacanthine septa are continued. But in general appearance, the modification of fine structure makes Devonian corals variable in respect to septal construction. Representative forms are Pachyphyllids in which horse-shoe dissepiments are characteristic. And trabeculae are vertically arranged in fan shape in these forms. Horizontal carinae appear in *Metriophyllum* and in *Lyriellasma*. Other representatives are

Cystimorphs. At the end of this period, lamellar type of septa appeared in some Ampexoid corals from North America, and acanthine forms disappear altogether.

In Carboniferous period, the general appearance of coral fauna changes considerably from that of Devonian. Although Devonian elements are entering into the early Carboniferous coral fauna, newly introduced columellated forms rapidly multiply and become dominant. Later the group extended into Permian. Trabecular type of septa is still to be seen. But diffuso-trabecular or fibro-normal type is newly introduced, by which and by the axial structures, Carboniferous corals are being characterized. Divergency in the mode of septal construction is reduced to be much simpler in comparison to the Devonian corals. Carinae are by no means common in the Carboniferous corals. Representatives of Carboniferous corals are Clisiophyllids and Caninids. Clearly differentiated tertiary septa are detectable in a species of *Cyathoclisia*. Lamellar septa are also very common amongst Zaphrentids, partially because of their occurrence in shaly facies in which mechanical and chemical deformation are very likely to appear (Text-fig. 13).

In Permian fibro-normal septa are dominant, axial structure maintains its importance, and there occur third or even fourth order of septa in some forms. Representative forms of Permian corals are Plerophyllids and Waagenophyllids. Acanthine septa are very rarely reported, but their structures are still waiting to be analytically explained. A peculiar type of multi-trabecular septa is known in *Iranophyllum*, and multi-trabeculation is not uncommon in *Lophophyllidium* or in other forms. Finally rugosa ends at the end of Permian completing its history (Text-fig. 14).

The following trends can be deduced in the development of septal structures ontogenetically or phylogenetically. The structural tendency from uni-trabecular to multi-trabecular is evolutionary as well as ontogenetical. Uni-trabecular type starts in Ordovician time and multi-trabecular type in Silurian. But this tendency occurs in various divergent coral lineages as a trend, so that it is not reasonable to group those types into one. The oldest known type of septa is trabecular which becomes pseudo-trabecular in losing clear trabecular differentiation. Then it gradually tends to be diffuso-trabecular in which no trabecular differentiation can be seen. Later fibro-normal septa appear, which may be clathrate (fibro-lamellar), or lamellar or even zigzag (chevron) in structure owing to the later transformation. Acanthine type might follow a different line of evolution. Trabecular splitting could be one trend

and the reverse, that is the trabecular fusion, may also be a trend. Rhabdacanthine type is not always confined to the acanthine group but is to be found in the other types of septa. The series from "monacanthine" to rhabdacanthine seems to exist in some corals (See Text-fig. 9). Vertically, straight convex or concave arrangement of trabeculae tends to become sigmoidal or divergent. This is an ontogenetical trend as well as the rough tendency through geologic time. The number of septa is also a developmental factor. Minor septa already appeared in Ordovician corals and tertiary septa in Silurian. But again this is a developmental factor, cannot be taken into account in grouping corals with the presence of a certain order of septa.

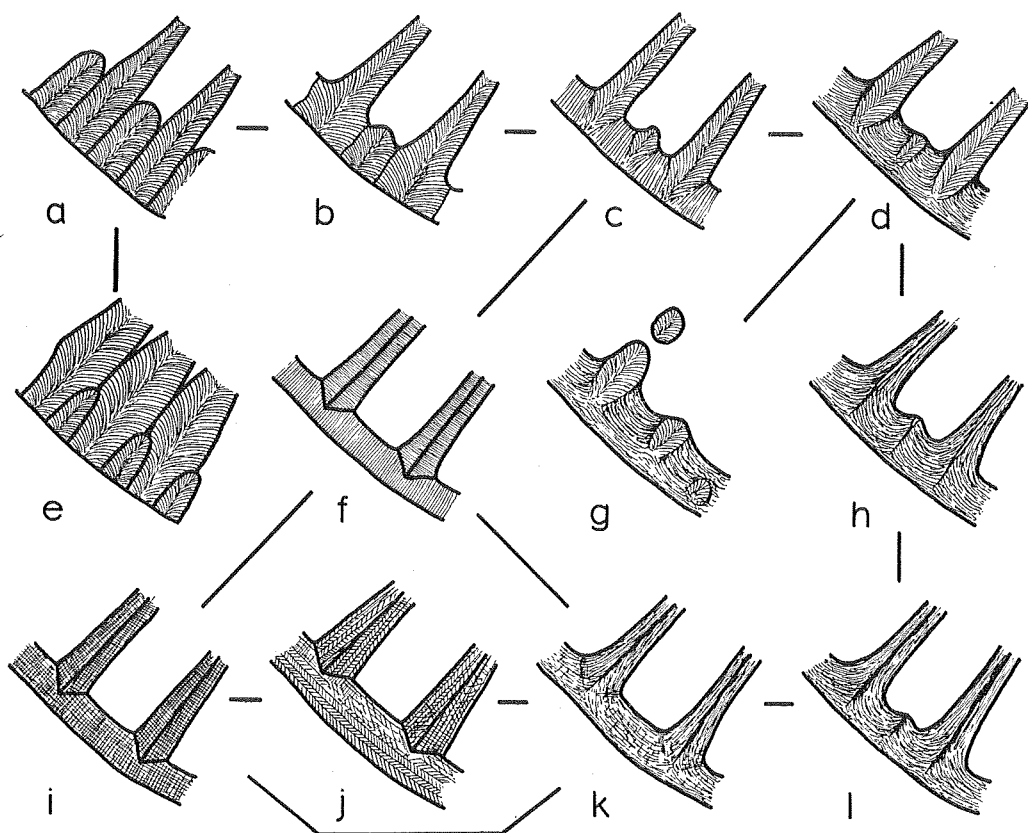
§ Other elements of skeletal construction

† Horizontal elements

So-called horizontal elements are tabulae and dissepiments. Both are situated roughly at right angles to the growth direction of coral, and are formed by flat or unfolded part of basal ectoderm. The reason why the differentiation between tabulae and dissepiments takes place and whether these organs are physiologically significant are difficult problems. But ontogenetically or phylogenetically tabulae are first formed, then dissepiments are introduced. In any case, there lies a dark line at the base of skeleton, and fibres are again perpendicularly arranged to it. As in the case of septa, these fibres may be seen to be lamellar, fibro-lamellar, or even cut obliquely by cleavages. But essentially the whole structure is fibrous, and there is no fundamental difference in all cases of the structure. Types of tabulae arrangement such as complete, incomplete, uparched, horizontal, concave, clino-tabulae and so on, have nothing to do with fine structure. The case is very much the same also in dissepiments. In this regard, fine structure in horizontal elements is very simple. The mechanism of formation of these horizontal elements is so-called planar control, or "blanket type" of spherulitic crystallization of BRYAN and HILL, and is uni-lateral deposition. An axial tabella which is an element in construction of the axial column is also a horizontal element with the same fine detail.

Now the wall has often been considered as a vertical element. However, according to the writer's opinion, this is also an exo-skeleton due to uni-lateral deposition although it occupies a vertical position in a corallum. It is convenient to treat it as a horizontal element in the

mode of fine structure, although the word "horizontal" may not be suitable for it. As is described above, wall as an element in corallite structure is a result of uni-lateral deposition, however, as a matter of fact it is closely related to the formation of septa and also it can be said that the two are actually mutually transformable from one into the other. There have been some attempts made to classify walls morphologically, but observations have rarely been described on fine structures of walls. And also there has been practically no consideration published on the morphological relationship between various types of walls. As in septa, many types of fine structure can be observed in wall. And these are also interchanged gradually from one form to the other, so it is



Text-fig. 17. Morphological series of wall structures in rugose corals. a. "septotheca"; b. "stereowall"; c. fibrous; d. lamellar; e. "keilsepten"; f. fibro-normal; g. lamellar; h. lamellar; i. fibro-lamellar; j. zigzag (chevron); k. fibro-lamellar; l. lamellar. In figures a, b & e, wall is not differentiated from septa, but note the lateral coalition of septa.

possible to recognize morphological series among them. The writer's scheme is shown in Text-figure 17.

In the first place, walls are not differentiated from septa, but are formed by lateral coalition of the latter. So-called "Keil-septen", stereowall and septotheca in rugosa are all in this category. Then fibrous wall is formed to connect the marginal part of corallites between each septum. Thus this fibrous wall may tend to be lamellar, fibro-normal or zigzag in form. Although morphological series is recognizable among these forms of wall, the types *a* to *e* are already to be seen in Ordovician forms, and are continued until Permian, while type *g* enters in Silurian, and types *h*, *k* and *l* in Devonian. All types are known in Carboniferous onward. Hence, walls can be said to be developed in connection with septal structures with little significance in stratigraphy by themselves. Ontogenetically, so-called "Keil-septen" or septotheca are often discernible in early stages of corals. So, it may be concluded in some forms that the differentiation of wall from septa occurs later than the introduction of the latter, according to the ontogenetical as well as stratigraphical observations.

Now consideration should be given to walls in compound corals as simple forms just described above. In fasciculate corals, the boundary wall of a corallite is separated from a neighbouring one, and its mode and structure are the same as those in simple forms. But in cerioid forms, each corallite becomes polygonal owing to their lateral compaction, and calcareous fibres secreted from two neighbouring corals are arranged at right angles towards the junction place between the two corallites. This junction may be shown as a transparent space, or dark line. So, the appearance of wall in compound corals is just the same as in the case of bilateral deposition in vertical elements. Walls thus formed may be smooth or crenulated internally owing to the septal affections upon them at the peripheral parts of the corals. In many forms of cerioid and plocoid corals, walls look like an aggregation of trabeculae. This is interpreted as follows. Crenulated wall sometimes show the bunching of fibres which become divergent to form trabecular appearance. Peripheral parts of septa often present this kind of trabecular appearance, which is in fact trabecular. The junction of two opposite trabeculae of two neighbouring corallites becomes a wall. Lateral contiguation of these trabeculae in a series at their most swollen parts makes the thick appearance of wall. Vertical trabecular divergence should therefore occur at the point of junction of two opposite, but in fact continuous septa. Confluent septa in plocoid forms are thus formed. Peculiar occurrence

of a so-called canal is explained as a gap in these septa in coagulation. As above described, so-called thick wall thus can be histologically different from thin wall which is comparable to fibro-normal structure in septa.

The writer would briefly comment on supporting process at this occasion. Talon, stolon, elbow, and rootlet are terms hitherto proposed for various kinds of this projection outside of a corallite. The projection has been observed to be either "connecting" or "rudiciform". Functionally the process may have supported the corallite in some way or other to make coral stand up in suitable position for collecting food or something else, against wave action or hard substratum for attachment. Elbow and talon are only the swelling out of a dissepimentarium either to support the corallite against the another one, or to attach it to the substratum at the base of the coral. Stolon and connecting process are laterally expanded tubes outside of corallite. In *Waagenophyllum*, they are hollow tubes occurring from tabularium, extending through the marginarium. This appeared as a canal in cerioid *Parawentzelella*. In many forms of "stolon" the external end of the process is closed, so that it only makes contact with the other corallites so as to support the corallite. But a canal is really a connecting organ between two neighbouring corallites. Presumably fibres are arranging perpendicularly to the surface of a stolon tube. So they can be treated as a horizontal element. Some rudiciform processes or rootlets in *Tryplasma* or in *Ketophyllum* are the same sort of hollow tube or stolons as above mentioned, which extend downwards towards the substratum.

† Vertical elements

Septa, columella, median plates, septal lamellae and an axial column itself are those elements which construct axial structure in rugosa. Among them details about septa and their related organs have been described above. Here vertical elements other than septa are considered. As in septa, the characteristic feature in vertical elements is that they are entirely formed within a corallite and are the product of bilateral deposition of fibres from basal ectoderm. The simplest form of axial structure is a columella which is merely a plate; the typical one is supplied by *Lophophyllidium*. In this form the axial end of a counter septum extends to the centre of the corallite, swells up and forms a columella. But as the origin of the axial structure, there is known a case of the extension of the cardinal septum instead of the counter. In any case, its fine structure is the same as that in septa, and the mechanism of skeletal formation is also thought to be the same.

In *Siphonodendron*, *Arachnolasma*, and *Koninckophyllum* the columella is more or less continuous to the cardinal and counter septa. And its central portion swells to make spindle shaped columella, the centre of which there exists a dark line. Both sides of this dark line fibres are arranged at right angles to it. Dark line often shows bright appearance at the centre between two dark lines instead of one. Fibres also show bunching in some cases. The case of *Lophophyllidium* is interpreted as the axial swelling of the counter septum. All these single solid columellae are produced by an axial invagination of basal ectoderm (Text-fig. 18, figs. f & g).

One more type of solid columella is found in *Cyathaxonia*. In cross section radiating fibres from the centre of the axial columella and concentric growth lines are clearly observable. In longitudinal section, perpendicular fibres on domed tabulae are successively continued to form solid pillar-like columella. This looks like a serial deposition from domed basal ectoderm. It certainly is comparable to a very large single trabecula (Text-fig. 18, fig. h).

Of the complex type of axial structure, the axial column in general is the commonest. There are usually a median plate, axial tabellae and septal lamellae in an axial column, but there seem to be many sorts of differentiation of these organs. One example is that of *Dibunophyllum* in which a median plate has fibro-normal structure, and is originated from the axial septum, i.e. the cardinal counter continuation. Septal lamellae have the same structure, and were originally the axial elongation of major septa. Tabellae, as has been mentioned in the preceding chapter, are the axial differentiation of tabulae, facing their concave sides outward as well as upward. Thus they construct an axial column, which is in fact the complication or elaboration of bilateral deposition type. A median plate has a tendency to degenerate in some coral lineages.

On the other hand there is another type of axial column. That is commenced by a single, solid columella of *Amygdalophyllum*, which is superficially very similar to that in *Lophophyllidium*. But in the former type of columella, the central portion is seen to be bright, and around it radial fibres are arranged. This is a structure readily comparable with the trabecular type in septal construction. In *Amygdalophyllum*, the inside of the columella is compact, it does not show any sort of differentiation. However, this type of column gradually tends to split into bundles to form septal lamellae, of which the structure is also trabecular. As the septal lamellation proceeds, a solid column becomes vesiculated by axial tabellae which face their convex sides outward and

upwards. Such fundamental construction of this type of axial structure looks quite similar to that of *Dibunophyllum*. Then axial tabellae become dominant to an extent to clear all stereoplastic deposits from the column, and septal lamellae become weaker and weaker. The series is diagrammatically shown in text-figure 18 (figs. *a-e*), and is believed to represent both ontogenetical as well as phylogenetical changes in some Japanese Carboniferous corals.

Even if the axial structure is seen to be a simple rod externally, the internal structures may be different as in Cyathaxonid, Lophophyllid or Amygdalophyllid, although they can be transformable and interchangeable from one to the other. But the writer thinks it desirable that one should consider not only the external features but also internal structure in reflection of the mechanism of skeletal formation. In this regard, the above three types of rods can be considered different as the forms of basal ectoderm should at least morphologically be distinguishable from one another.

A special sort of axial structure is sought in the organ called axial lobes. The structure seems to provide a morphological series from Ordovician *Streptelasma*, *Kiaerophyllum* to *Grewingkia*, and possibly to Silurian Calostylids. The structure is nothing but a trabecular differentiation splitting at its extremity at the axial parts of septa. When the doming of tabulae in the centre of a corallite is combined with this trabeculation, such axial lobes are formed. So-called sclero-columella of GRABAU seems to be of this category. Amoeba-like multi-trabecular feature of this axial lobe is really an axial coagulation of septa in a form of irregular mesh work.

The writer's scheme for morphological types of axial structure in tabulated form is as follows.

structure typically fibro-normal	-	Lophophyllidiid columella (rhopaloid swelling of the axial end of the counter septum)
	-	Arachnolasmid columella (spindle-like swelling at the centre of the axial septum)
	-	Dibunophylloid column (distinct axial column with a median plate)
	-	Verbeekielloid column (axial column without definite median plate)
structure typically trabecular	-	Cyathaxonoid columella (simple axial rod consists of radiating fibres)
	-	Amygdalophylloid column (compact, sometimes bundled axial rod)
	-	"Clisaxophylloid" column (septal lamellae are present in varied degree)
	-	Streptelasmid column (irregular mesh work)

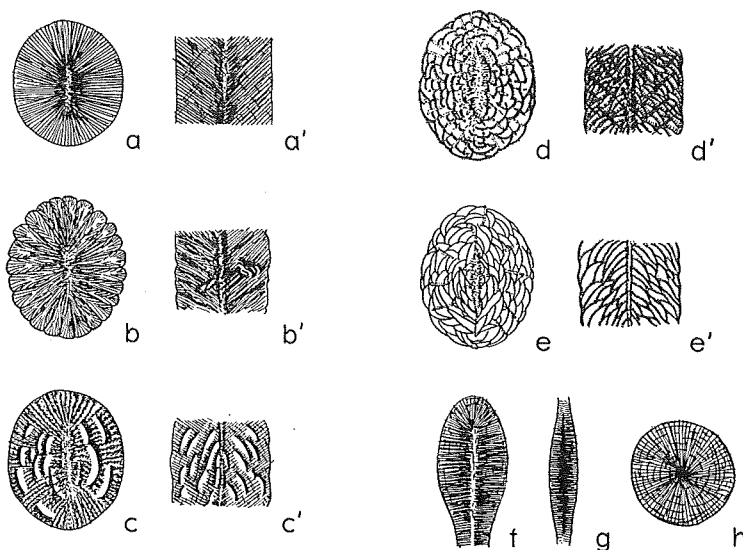
General trends within the axial structure are also tabulated as follows:

axial column: median plate→addition of septal lamellae→axial col-

umn→degeneration of median plate→“caninoid trend”.

solid axial columella: simply fibrous→multi-trabecular→bunching of fibres→replacement by tabellae→vesicular appearance.

In short, axial structure is an important character in rugosa. Simplification and complication of structure are both reckoned to be trends. They can be traced as an indicator in phylogenetic treatment or arrangement of rugose corals. The inconsistency of the axial structure may be checked by other characters such as dissepimentarium or septal structure.



Text-fig. 18. Types of axial column.

- a: Amygdalophylloid column in transverse section showing radially fibrous and compact nature in the column. a': Longitudinal section.
- b: Amygdalophylloid column in which fibres are grouped into bundles. b': Vesicular tabellae appear in longitudinal section.
- c: Transverse section of "Clisaxophylloid" column in which axial tabellae become distinct. c': Longitudinal section of the same.
- d: "Clisaxophylloid" column showing septal lamellae completely differentiated, giving reticulo-vesicular pattern together with axial tabellae. d': Longitudinal section of d.
- e: Transverse section of "Clisaxophylloid" column in which septal lamellae become obscure, so that general appearance tends to become vesicular. e': Longitudinal section of the "vesicular" type column.
- f: Lophophyllidiid columella. g: Arachnolasmid columella.
- h: Cyathaxonoid columella in transverse section.

§ Mutual relationship between various skeletal elements.

Fine structure of each element has been explained separately so

far. Now the writer proposes to deal with these elements in respect to their relationship with each other.

As to the vertical elements, there are three sorts of junction between septa and wall as shown in text-figure 19, a-f. When the upright growth of septa and wall is well balanced, the peripheral end of each septum intrudes into the wall in wedge-like form, and common growth lines are running through septa and wall, which indicate that they grow laterally and upward simultaneously. This is so-called dilation. If the septal growth to the wall is hindered, septa are seen to abut on the "dilated" wall, so that the root of the septal wedge in the wall becomes shallow. Is there any case in rugosa in which septa grow faster than the wall? There are some cases as in *Macgeea*, *Palaeosmilia* and Porpitids that the septal ends are elevated up beyond the plane of wall limit. But this is due to the fan shaped arrangement of trabeculae in vertical series; the balance between the septal growth and wall is still maintained at the part of their junction (See text-fig. 6).

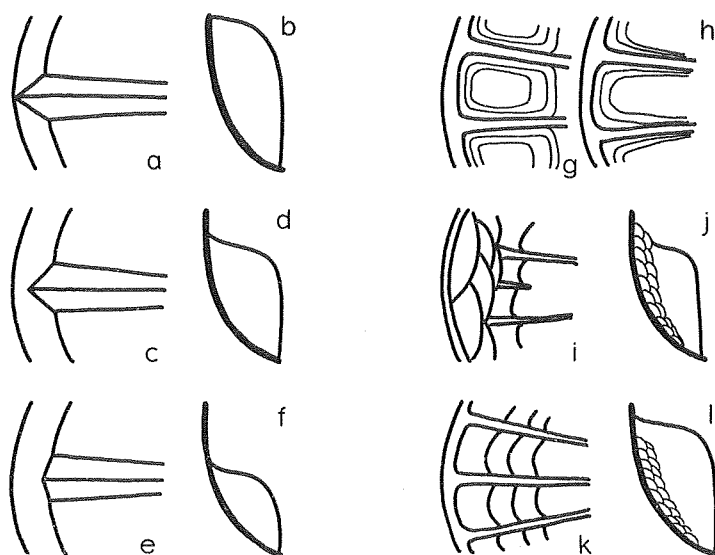
When the septal growth to the wall is well hindered, lonsdaleoid dissepiments occur between septa and wall. Lonsdaleoid dissepiments can, in this case, be regarded as a sort of inner wall, to which the relationship with septa forms the junction as above described. But the fact that the dilation of septa is normally much greater than that of the inner margin of lonsdaleoid dissepiments may be kept in mind for further consideration on it.

Then comes the relation between tabulae and septa. This relationship is also applicable to the relation between tabulae and wall, tabulae and axial structure. As its function limits, tabulae are never formed prior to septal formation. If such a thing does occur, that means the formation of septa is completely masked by tabulae from the basal part of ectoderm. There are two kinds of tabulae abutment. One is to abut simply on the other vertical elements such as septa. The other relation is that fibres of tabulae are connected to the lateral expansion of septa and other vertical elements. The former is the case in which tabulae formation occurs backward from the septal upgrowth and there is a gap of calc-secretion between the flat part and invaginated part of basal ectoderm. The latter case is often observed in many corals in which vertical elements grow upward as well as laterally, and their tissue is seen to continue to that of tabulae.

Incidentally the way of inclination of tabulae can be easily checked by looking at fibres of tabulae carefully, even if transverse sections only are available. Whether the growth direction of fibres in tabulae is

orienting towards the centre of the corallite with dark line on the side or else could decide either the tabulae are inclined towards the centre or not. If tabulae are flat, they are theoretically either not appearing in cross section at all or only dark aggregation of cut edges of fibres making up the tabulae. This method of determination of the inclination of tabulae in transverse section is simply that fibres of tabulae are sited on which side of the dark line.

The relationship between septa and dissepiments is just as in the first case of septa and tabulae. But as has been stated above, dissepiments are often formed prior to the formation of septa near the wall. This is of course, the lonsdaleoid dissepiment above mentioned. A so-called septal crest on the inner side of lonsdaleoid dissepiments in transverse section is not a spine-like process but cut edges of external portion



Text-fig. 19. Relationship between septa, wall & dissepiments. Figures a, c, e, g, h, i, and k are transverse sections of peripheral portions of corals. Walls are shown at the left hand side.

Figures b, d, f, j and l are longitudinal sections of septa with walls (thick lines) at the left hand and dissepiments in some case. In a and b the growth rates of septa and wall were well balanced. In c and d wall is formed faster than the septal formation. In e and f septa are well behind the rapid up-growth of wall, so that septa appear to be only abutting on the wall. In g tabulae are inclined outward, while in h they inclined inward. Figures i and j show the relationship between septa, wall and dissepiments in lonsdaleoid peripheral zone. Figures k and l show the same relationship in normal type of coral in which dissepiments are concentric.

of septa; it is formed on gently tilted, coarse lonsdaleoid dissepiments (Text-figure 19, j & i).

There are of course other cases of contact relationship between organs not mentioned above. However, nothing particular has been investigated upon them, but one case may be mentioned here. The formation of axial structure is normally earlier in comparison to the axial elongation of major septa. So, the relationship is also that of one abutting on the other. But cases have been known where axial portion of septum is elongated to meet the others at the centre of the corallite so as to form an axial structure. In this case, as the axial structure is usually elevated on the calicular floor, trabeculae are probably arranged in reversed fan shape. When septal lamellae become independent of septa, their conjugation is mere abutting, with opposite trabecular divergence.

§ Taxonomic value of "fine structure" in rugosa

Commonly fine skeletal structures are fairly well preserved in many forms of Palaeozoic rugosa. The reason for that may have something to do with the original form of fibres which are of calcite so as to escape later transformation owing to their stability. And this makes the feature valuable in classification.

"Fine structure" may reflect the true systematic position of a coral because of the essential nature of its formation. So, it may be possible to check homoeomorphy by using this character as a lineage tracer. Even if corals are observed in fragmental state, their taxonomic position can be estimated according to the minute nature of fine structure. However, recrystallization may prevent correct identification in this regard, and also thin sections are needed in study. But these can not be said to be unpractical, because we are really aiming at a natural classification, not a practical sorting.

Some examples of classification with special reference to fine structure may be mentioned here. HILL (1936) discussed the phylogeny of palaeocyclusids in tracing the types of acanthine septa in some Silurian corals. She used acanthine septa as specific characters, however, these can be generic because of the successive changes in fine structure may be considered to be of generic significance when their effects are accumulated. Thus her series from *Acanthocyclus* to *Tryplasma* includes phylogenetic change in generic rank.

SCHINDEWOLF (1942) once based his new subgenus, *Prionophyllum* on the zigzag nature of its fibres in septa. But this is, as the writer

noted above, a mere secondary feature, and can not have any status in classification, other than only descriptive significance.

WANG (1950) thought fine structures are useful in rugosan taxonomy. The writer fully agrees with him in this regard, but not as to the extent that WANG pushed the idea to an extremity. The consideration on inter-formal relationship between types of fine skeletal elements does not permit their use as fundamentally as WANG advocated.

LECOMPTE (1952) included some forms with multi-trabecular septa into one family, Chonophyllidae. But this treatment is not necessarily suitable, because the nature is a developmental one, and appears in divergent lineages as a trend.

FONTAINE (1961) considered his *Khmerophyllum* as different from *Lophophyllidium* on the basis of the multi-trabecular type of columellar structure in the former. Again this is naturally not a stable character especially in *Lophophyllidium*, so the genus may have subgeneric status at best.

In classification in practice, no single biocharacter can be overwhelmingly important over the another. Fine skeletal structures also should not be considered alone, but in good combination with the other biocharacters of rugosa. Also no definite taxonomic status can be given to any certain character. For example, lonsdaleoid dissepiments are a characteristic feature in some families but is merely an unstable character in others in which they only appear sporadically here and there. But generally speaking fine skeletal structure, especially of septa, can be regarded as a family rank character, but various forms can occur even in the same corallite of some group.

The writer will next consider some instances of Carboniferous corals as to their septal as well as axial structures and their application to the classification specifically.

Cravenia HUDSON was included in the family Timorphyllidae by HILL in 1956, however, the writer thinks it is a true clisiophyllid even if it lacks dissepiments. Septa of Timorphyllids are typically fibro-normal, while they are trabecular in *Cravenia*. Further, *Cravenia* has a distinct axial column, but there is none in Timorphyllid. *Cravenia* also closely resembles the younger stage of clisiophyllids, and the development of dissepimentarium is ontogenetic as well as phylogenetic in this group of coral. So, *Cravenia* should be placed in Clisiophyllidae rather than in Timorphyllidae.

There are some form groups known in *Caninia* sensu lato. There are, for example *Siphonophyllia*, *Caninia cornucopiae* group, *Caninia*

cornucopiae group of HUDSON, *Caninia concava* group, *Caninophyllum*, *Caninia subibicina* group, *Caninia minor* group and so forth. In *Siphonophyllia* septa are fibro-normal but the genus has distinct lonsdaleoid dissepiments. In *Caninia cornucopiae* septa may be fibro-normal, but not in HUDSON's forms in which septa are trabecular or pseudotrabecular. *Caninia concava* has been proved to be a diphymorph of *Koninckophyllum interruptum* in which septa are semi-trabecular or diffuso-trabecular. *Caninophyllum* has trabecular septa. *Caninia subibicina* also has trabecular septa as well as a clisiophyllid concentric dissepimentarium. *Caninia minor* has semi-trabecular septa. These facts when combined with the others suggest that the so-called *Caninia* is not a genuine group but consists of several divergent stocks which have only a caninimorph tendency in common.

Carcinophyllum (correctly it should be known as *Axophyllum*) is often regarded as a lonsdaleoid. But in reality, it has semi-trabecular or lamello-trabecular septa, while septa of *Lonsdaleia* are typically fibro-normal. The difference also lies in the mode of the initiation of axial column in the two forms. In *Lonsdaleia* the axial elongation of the counter septum becomes an axial structure, while according to the writer's preliminary investigation, the axial structure is originated from the cardinal septum in *Carcinophyllum*. Thus proves that these two genera belong to different stocks, although superficial resemblance between the two can not be denied.

Commonly septa of Carboniferous "*Zaphrentis*" are fibro-normal, very often lamellar or even zigzag in structure. But in "*Zaphrentis*" *konincki* or in "*Z.*" *delepinii*, septa are trabecular. This may also be a sufficient basis for separation of these two from the other Zaphrentids. Indeed stratigraphical, ontogenetical and histological research on "*Z.*" *konincki* suggests that the species may be related to *Palaeosmilia murchisoni*.

Cerioid *Lithostrotion* is a very commonly known group of Carboniferous corals, which have almost exclusively trabecular septa although they are slender. The genus *Stylastraea* LONSDALE has been often regarded to be a diphymorph of *Lithostrotion*, and is synonymous to *Diphystrotion*. But the genus has the sign of fibro-normal septa and is certainly congeneric with *Protowentzelella*, with which and with some others they might form a new family.

Fasciculate forms of "*Lithostrotion*" have been broadly considered to be a mere genomorph of cerioid *Lithostrotion*. But actually both forms occur together within the same lithofacies which presumably shows no environmental difference. The same internal characters are also not

directly found in the corresponding occurrence of the other form. Further, in many *Siphonodendron* (fasciculate "*Lithostrotion*"), septa are diffuso-trabecular, although they may be trabecular in some early forms. These facts do suggest that two genera may have shared a common ancestor, but they developed different lineages of either fasciculate or cerioid character, steps being traceable from trabecular to diffuso-trabecular septa in *Siphonodendron*.

The other example is the genus *Kueichouphyllum*. The genus was originally established as a subgenus of *Palaeosmilina*. But the two are really very different with each other. *Kueichouphyllum* shows typical diffuso-trabecular or fibro-normal septa, while they are trabecular in *Palaeosmilina* as is mentioned elsewhere. *Kueichouphyllum* really stands much closer to *Heterocaninia* from which the former only differs in its long minor septa. *Heterocaninia* is common in the central province of East Asia such as Hunan and central Japan. On the other hand *Kueichouphyllum* is known mainly from the southern province extending from Northeast Japan, Southwest Japan, South China and Viet Nam, Tianshan as far as Turkey. These two genera are both considered to be representatives of the Upper Viséan *Yuanophyllum* zone in East Asia. The genus *Yuanophyllum* is, incidentally, a northern element. The writer would rather place *Kueichouphyllum* as a subgenus of *Heterocaninia*. HILL included *Kueichouphyllum*, *Heterocaninia*, *Palaeosmilina*, *Amygdalophyllum* and *Cyathoclisia* into the same family. But the writer would group the former two into one, *Palaeosmilina* to Palaeosmiliidae, *Amygdalophyllum* to Amygdalophyllidae and the last one to Clisiophyllidae.

HAYASAKA once described *Waagenella omiensis* from central Japan. The precise systematic position of this species has not yet been firmly settled. Some place it in *Waagenophyllum*, some in *Corwenia*. But the actual septal structure of this form is distinctly trabecular, so that it differs from both *Waagenophyllum* or *Corwenia*. It is really close to the "*Clisaxophyllum*" *awa* group, and to the clisiophyllids in general.

Corwenia vaga is the oldest known form of the genus. But there is some evidence that it may be an early representative of *Koninckophyllum* in respect to stratigraphical occurrence as well as its fine structure though the point is not fully understood yet.

A specimen, B.M.R. 15289 is remarkable because of a cerioid *Lithostrotion* is intergrowing with a fasciculate *Siphonodendron*. The former has lonsdaleoid modification, of a form previously known as *Petalaxis*. Septa are trabecular and corallites are polygonal in this form. Corallites of *Siphonodendron* are round in cross section, and septa are diffuso-

trabecular in contrast to the former. *Petalaxis* may have grown later to incorporate a former colony of *Siphonodendron* in this case.

Dibunophyllum and *Clisiophyllum* are both thought to belong to the same family. The distinction between the two is sometimes difficult. However *Dibunophyllum* typically shows diffuso-trabecular septa, while *Clisiophyllum* shows trabecular septa. Although there are known some intermediate forms, the differentiation between the two is fairly clear in respect to fine septal structure.

Lastly one more genus will be mentioned. *Kakwiphyllum* SUTHERLAND reported from Canada possesses sagging tabulae which are a not uncommon character in Devonian corals but do not occur in Carboniferous ones, although there are some instances such as *Vesiculophyllum* and *Enygmophyllum*. SUTHERLAND compared his genus with a Devonian *Stringophyllum bipartitum*, however, the former provides fibro-normal septa, while the latter shows trabecular ones. So they may not be related at all.

Now the general taxonomic value of fine structures will be considered.

As it has been assumed that there is no essential difference within the mechanism of skeletal formation in each element, the idea that fine structures are readily applicable to the actual classification of rugosa may be thought to be incorrect. However, actually structural difference has been introduced by the differentiation of basal ectoderm. This function of basal ectoderm or its differentiation should have been related to an essential living action in rugosa. Hence, fine structures become useful in the actual classification, and the structures should be given, at least the same sort of importance as the mode of septal insertion.

Among them, septal structures are important, and similar septal structure may possess family rank significance in classification. But such structures cannot represent suborder or order, because of morphological transition recognized among forms. Classification should be based upon the combination of all or some of these skeletal elements. Septal structure may be stable throughout a group, or may be variable even in a single corallite. However, different kinds of septa cannot normally be placed in the same family. In this matter the writer means that trabecular, pseudo-trabecular, acanthine, diffuso-trabecular and fibro-normal septa are usually significantly different. Change in trabecular arrangement from uni- to multi-trabecular has generic significance in some instances, but appears even in one and the same species as a trend. Vertical arrangement of trabeculae is not to be used solely, but it controls the mode and appearance of forms of fine septal structures. Patterns

of carinae are a specific character, but generic in many cases. Wall structure is related with septal structure, but is not to be considered by itself. Juncture relationship between elements has considerable significance, as it has close connection with the forms of calicular floor. It has at least specific importance, or even more than that, especially in the common case of lonsdaleoid dissepiments. Also patterns of axial structure have more than specific value. Columns and columellas of Lophophyllidiid, Arachnolasmid, Cyathaxonoid, Amygdalophylloid and "Clisaxophylloid" are particularly of generic importance.

§ Conclusions

1. The unit which constructs skeletons of rugose corals is a fibre of calcite.

2. Fibres are formed outside of presumed soft body layer perpendicularly to it. This mechanism of fibre formation does not differ in the parts of the skeleton.

3. Owing to the folding pattern of "soft body layer" or ectoderm, differentiation in the mode of aggregation of fibrous calcite took place. These fine skeletal structures could be classified into several different types, though every possible transitional form may be expected between these types.

4. Two major types of skeletal structure are discernible. They are trabecular and fibro-normal. The distinction of these types can also be applied to the classification of fine structures of skeletons of both tabulata and scleractinia.

5. There can be recognized stratigraphical change in these types of fine structure, namely from trabecular to fibro-normal.

6. The most important skeletal structures are those of septa, and the patterns of fine structure in them are also to be found in the other skeletal elements.

7. Alleged lamellar, granular and zigzag structures are all proved to be of secondary nature owing to some sort of deformation or other, not to be considered as primary skeletal structures, and have no taxonomic or other importance at all.

8. Fine skeletal structures are extremely useful in tracing true lineages from one to another within divergent forms of corals. Thus they possess stratigraphic value as well.

9. Complete description of a species of coral and well established systematics should be accompanied by descriptions of fine structures not

only for the sake of completeness but also because of the firm taxonomic basis in doing so.

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The above bibliography is intended to cover literature on corals with special interest in their fine skeletal structures. This list also includes works not mentioned in the text, but to which reference is made.

Explanation of
Plate I

Explanation of plate I

(All figures 51 times natural size.)

Figure 1: *Neokoninckophyllum nipponense* KATO

Transverse section showing diffuso-trabecular to fibro-normal type septa and cut edges of tubulae. The Carboniferous Ichinotani Formation. Ichinotani, Fukuji, Gifu Prefecture.

Figure 2: *Heterocaninia* sp. nov.

Transverse section showing the same character as above stated. Horizon and locality are also same as above.

Figure 3: "*Clisiophyllum*" aff. *maccoyanum* THOMSON

Transverse section showing typical diffuso-trabecular septum and its junction with tabulae. Nagaiwa Formation. Nagaiwa, Kesen Gun, Iwate Prefecture.

Figure 4: "*Clisaxophyllum*" sp. nov.

Transverse section showing trabecular septa with very fine, semi-circular cleavages. Akiyoshi limestone group. Tobinosu, Oda, Yamaguchi Prefecture.

1



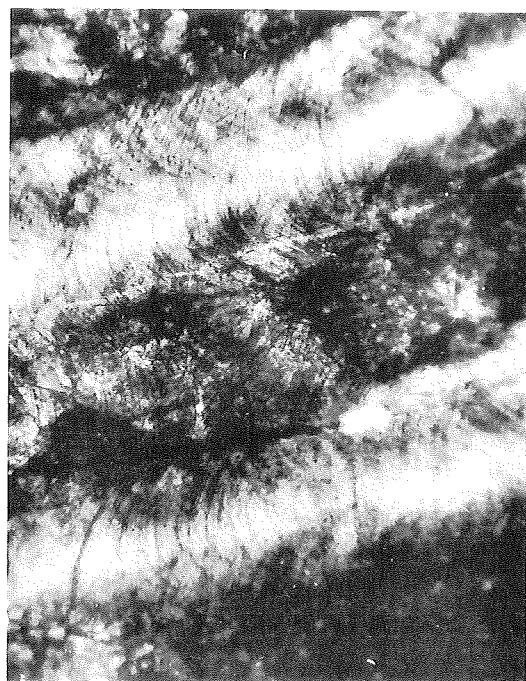
2



3



4



Explanation of
Plate II

Explanation of plate II

(All figures ten times natural size.)

Figure 1: *Palaeosmilia murchisoni* (EDWARDS et HAIME)

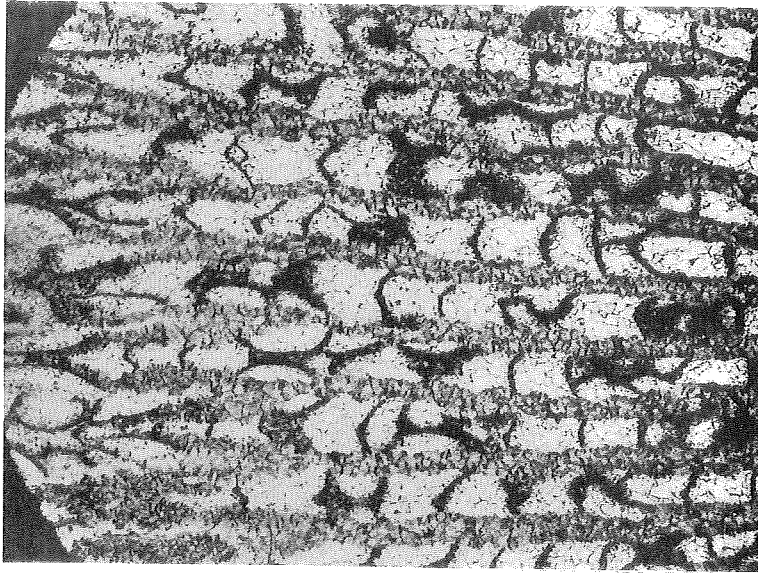
Transverse section showing multi-trabecular aspect in septa within the dissepimentarium. S. M. E. 15861

Figure 2: *Symplectophyllum mutatum* HILL

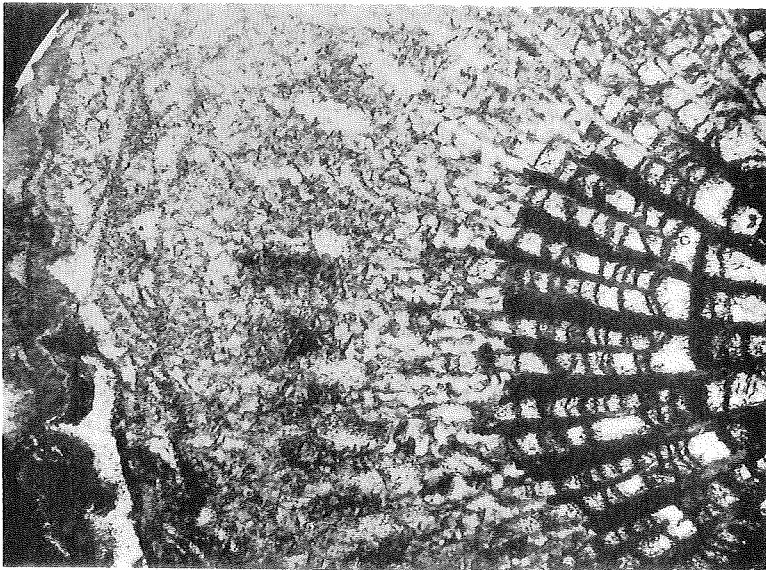
Transverse section of the peripheral part of corallite showing multi-trabecular aspect, so-called naotic character in septa. S. M. A. 5471

Photos by Dr. C. L. FORBES, Cambridge.

1



2



Explanation of
Plate III

Explanation of plate III

(All figures ten times natural size.)

Figure 1: *Syringopora geniculata* (PHILLIPS)

Transverse section.

Figure 2: *Syringopora geniculata* (PHILLIPS)

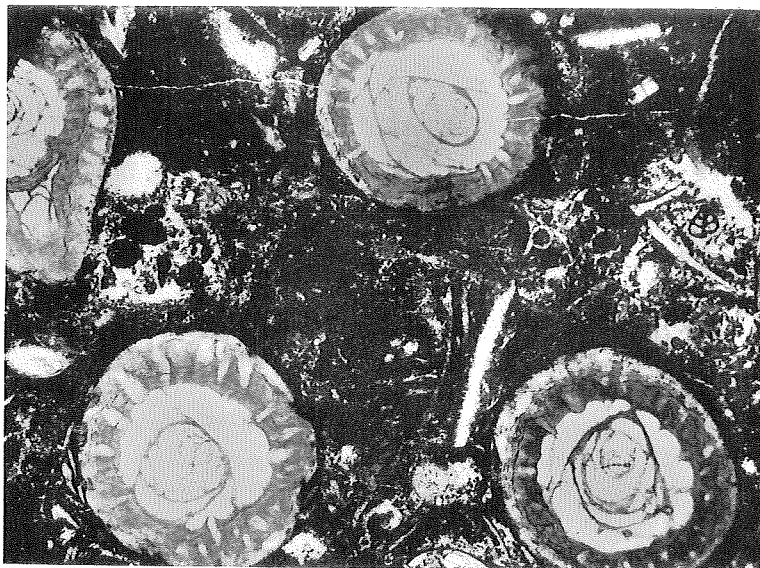
Longitudinal section. S. M. E. 14701, D₁ limestone. Ling Gill, Cum beck, 3 mls. north of Horton in Ribblesdale, Yorkshire.

Figure is erroneously inverted.

Showing "septal spines" in "lamellar" wall.

Photos by Dr. C. L. FORBES, Cambridge

1



2

