A REVISION OF THE ZOANTHARIA RUGOSA IN THE LIGHT OF THEIR MINUTE SKELETAL STRUCTURES

By H. C. WANG, Ph.D. (Cantab)

[Plates 4 to 9]

CONTENTS

INTRODUCTION

In this communication an attempt is made to describe the minute structures of the rugose coral skeleton and to revise the classification of the Zoantharia on that basis. The paper falls into three main sections. In the first, the various structures observed in the skeleton are described and suggestions made concerning the relationships between the soft and hard parts. The conclusions arrived at are based on the investigation of a large number of thin sections in various museums and other geological institutions in Great Britain and on my own material collected in China. The second part comprises an analysis of these features, an attempted evaluation of their systematic significance, and a résumé of the evolutionary history of the rugose corals. This résumé is mainly based on a direct study of accessible material and partly on reinterpretation of the literature in the light of new observations. The third part deals with classification and the diagnoses of the suborders, families, subfamilies and genera. For each genus recognized, the genotype is cited and a diagnosis given, together with geological range and, if any, subgenera and synonyms. Only those references not contained in the *Index of Palaeozoic Coral Genera* are listed in the bibliography.

HISTORICAL REVIEW

Historical accounts of the study of corals up to the end of the previous century have been given by Ogilvie (1897) and by Počta (1902), while among later works containing comprehensive reviews may be mentioned Grove (1934), Sanford (1939), Hill (1935) and Vaughan & Wells (1943). The following is a brief sketch of the development of our knowledge concerning the Rugosa since the middle of the previous century.

The study of the Rugosa has always been influenced by that of the Scleractinia; in fact, no attempt at a historical treatment of one group could omit some account of the other.

In the classical work of Edwards & Haime (1848) it was assumed that the rules of septal insertion were valid for both groups, although one is based on a tetrameral and the other on a hexameral symmetry, but in 1869 Kunth discovered the law governing the septal insertion peculiar to most Palaeozoic corals. This had great influence on the thought of the time, and led to Haeckel's recognition in 1896 of Hexacoralla and Tetracoralla as the two main groups of Madreporaria. It should be noted that long before Haeckel's work, Lacaze-Duthiers (1872) had already shown that the elaborate rules of the cyclic introduction of septa as laid down by Edwards & Haime for the Scleractinia do not hold in some forms; on the contrary, the mesenteries and the septa are introduced in pairs in much the same way as in Rugosa. Palaeontologists have, however, since found it a convenience to treat the Rugosa and the Scleractinia as distinct groups.

Prior to the introduction of the technique of preparing thin sections, observations were necessarily confined to external characters. Thus the first revised classification after Edwards & Haime, that of Louis de Fromentel (1861), was based almost exclusively on growth forms of the corallum. During the succeeding decades many palaeontologists were engaged in describing local faunas, and the names of Lindström, Schlüter, Nicholson and Thomson suffice to recall this phase of activity. The writings of Lindström and Schlüter are remarkably precise and can still be regarded as standard works, but neither of them attempted any systematic classification. In 1873 Dybowski carried out an elaborate classification, mainly based on the characters of the endotheca. He was followed by Roemer in 1883, Gürich in 1896 and Počta in 1902. Dybowski's scheme has the advantage of supplying a complete frame into which new forms can be easily allocated, and it is perhaps this convenience that accounts for its wide acceptance up to the present time.

In the meantime Nicholson (1876) and von Koch (1881) had analyzed the method of gemmation in rugose corals, which may be calical (peripheral or central), lateral or intermural. Calical gemmation is the commonest; lateral gemmation characterizes the fasciculate forms; while intermural gemmation occurs rarely in cerioid forms.

In the later half of the previous century, as biological ideas were steadily developing, genealogical speculations had become increasingly common in the palaeontological field. In this direction Neumayr's early work of 1869 and Haeckel's genealogical tree of 1896 are outstanding examples, but Weissermel's work of 1897 was the first attempt at an extensive phylogenetic analysis.

Meanwhile the recapitulation theory of ontogenetic development was gaining ground and was greatly stimulating studies in this direction. In a series of papers published in the opening years of this century, Duerden showed that some late Palaeozoic corals (*Lophophyllidium proliferum, Cyathaxonia cynodon, Enterelasma rectum*) possess a six-septate stage. This revived the old contention of Ludwig and Pourtalès as to the primary hexameral symmetry of the Rugosa and led to the dispute between Gordon and Duerden and later between Schindewolf and Yakovlev. On the other hand, Brown had shown that the Lower Palaeozoic *Streptelasma profundum* and *S. corniculum* have no six-septate stage, and offered an interpretation of Duerden's observation in terms of acceleration of the counter quadrants, a common feature in the Rugosa. About the same time Carruthers (1906) found in *Zaphrentoides delanouei* a uniseptate (axial septum) stage, succeeded by a quadriseptate and a six-septate stage, after which there came a pause. Faurot (1909) corroborated Carruther's

discovery of the three stages in *Cyathaxonia cornu* and found, what is more important, that the minor septa were also inserted in a serial manner. The same phenomena were observed in *Semaeophyllum* by Vollbrecht in 1928 and in *Petraia* by Schindewolf in 1931. Current authors are inclined to attribute great importance to septal insertion and septal symmetry in classification of the rugose corals.

As was pointed out by Ogilvie and by Vaughan & Wells, Edwards & Haime in their great work of 1857–60 showed a thorough grasp of the structural unit of coral skeleton, the sclerodermites. They describe very clearly the building up of the skeleton as a process of successive and continuous development of the sclerodermites to form linear series (pourtrales), which coalesce in various ways and to a varying extent in the different types of the septa. The sclerodermites later became known as fibre fascicles and the pourtrales, trabeculae.

In the ninth decade of last century, detailed histological study of living corals shed much light on the mode of formation and the structure of the skeleton. Von Heider and von Koch almost simultaneously discovered the skeleton-secreting calicoblast layer of the polyp. The exact way in which the hard parts are secreted is still an open problem; it will suffice to say here that the calicoblast layer probably secreted calcareous matter through a membrane, as held by von Koch and Bourne (1897), rather than itself being converted into skeletal tissue through calcification, as advocated by von Heider and Ogilvie.

The year 1882 saw the publication of two other important papers: Koch compared the structure of the septa of '*Cyathophyllum*' sp. with that of *Caryophyllia*, and described with the utmost precision the structure of the septal spines in *Tryplasma loveni*, while Pratz described in great detail the trabecular structures of several fungioids. The importance of Koch's work cited above was justly emphasized by Ogilvie. I call special attention to his uncommonly precise description of the septal spine in *Tryplasma*. He distinguished in cross-section of the septal spine a central mass of densely crowded points surrounded by a clear zone of larger, radially arranged crystals; and, uniting these separate spines, a mass of parallel rows of crystals separated into layers by strong dark bands. The spines with radiating crystals are the holacanth of Hill, the laminated connecting tissue is the familiar lamellar tissue. Pratz's work on the fungioids marks the first extensive treatise of minute skeletal structures, and was soon followed by the work of Koby on the Cretaceous (1881–7) and Volz on the Triassic corals (1896).

Now we come to Ogilvie's work of 1897. Following the lead of von Koch, von Heider and Pratz, she made a thorough microscopic investigation of several representative coral species in great detail. In addition, she attempted an analysis and elucidation of the relation between the skeletal and soft parts, as well as a comprehensive review of the evolution of the entire group, including the Rugosa. Her main results may be briefly summarized as follows.

Ogilvie considered that the madreporarian skeleton is built up throughout by successive calcareous laminae composed of actually calcified calicoblast cells, through which calcite fibres are formed in optical continuity. The fibres are normal to the secreting surface, and every fibre fascicle, or bundle of calcite fibres with its centre of calcification, corresponds to a small pit on the secreting surface. Linear series of fibre fascicles form trabeculae, which may be variously grouped in the septum and inclined at different angles against the

wall. One growth segment of the septum consists of numerous growth parts of the numerous trabeculae, formed simultaneously at the upper edge of the invaginated aboral wall. The various patterns and the degree of porosity of the septa reflect the nature and grouping of the constituent trabeculae. The thecal structures are largely determined by the relative heights attained by the tangential (wall) and the radial (septal) parts of the polyp and the development of the edge zone. Her analysis of the various structural elements led her to the conclusion that the Madreporaria have proceeded along a line of continuous evolution since the Palaeozoic, and consequently she arranged members of both the Rugosa and the Scleractinia under the major groups of her newly established scheme.

In this connexion it is appropriate to mention that between 1870 and 1890 students of rugose corals had occasionally remarked on septal structures (e.g. Lindström 1882 and Frech 1885). The introduction of such terms as primary septa, primary streak, stereoplasm and reinforcement tissue, has caused considerable confusion, and the uncritical use of these terms is still common to-day. This was subjected to drastic criticism by Ogilvie, who maintained that from the very beginning to the last, the laying down of the skeleton has been an identical and continuous process. As I hope to show in the course of this paper, the problem cannot be altogether so easily dismissed.

It is regrettable that the results of Ogilvie's work, especially in view of their prospective applicability to the Rugosa, should have been overlooked for such a long time after publication. In 1924 Koker published a paper on the Permian corals of Timor. The state of preservation of the Timor material is excellent, and the structural details are very well shown in her plates. She distinguishes four types of septal structures differing in the complexity of the axial zone of the septa and the disposition of calcite fibres in the outer area. Some ten years later (1933) appeared Scheffen's work on the Ordovician and Silurian corals in the Oslo region. Following Wedekind, he attached much importance to the wall structures in interpreting the development of the skeleton. The merit of Scheffen's work lies in his recognition of a fibrous, in contrast to a lamellar, kind of skeleton in corals other than those of the *Tryplasma* group.

Outstanding in this series of contributions to coral palaeontology is Hill's work of 1936 dealing with the minute structures of the Silurian corals with acanthine septa. This is the first attempt since Ogilvie to trace phylogenetic relations on the basis of minute structures and to elucidate and correlate the development of different structural elements. As far as the skeletal structures themselves are concerned, Hill's important contribution is the discovery of a third kind of trabeculae, the rhabdacanth, which is a composite type of trabecula consisting of irregular aggregates of minute rods. Hill follows the earlier authors in asserting that all kinds of skeleton are fibrous, and that the dissepiments and tabulae are composed of fibres perpendicular to the surface.

In 1943 appeared Vaughan & Wells's work on Scleractinia, a very important treatise covering every possible aspect of the group and the outcome of many years' research. As far as the minute structures are concerned, however, they only reviewed previous works and did not enter much into them.

Another important work appearing in the war years is Schindewolf's monograph on the polycoelids and plerophyllids (1942). This contains many excellent plates illustrating minute structures, and discusses the taxonomy of the Rugosa as a whole, in addition to his

detailed description of the Carboniferous and Permian forms. Schindewolf recognizes that trabeulae, such as described by Volz in the Triassic corals, do not exist in the plero-phyllids. Instead, the skeleton of the latter is characterized by a lamellar structure traversed by fibre fascicles. For this lamellar and at the same time fibrous type he suggests the term *diffus-trabecula*, in contrast to *idiotrabecula* of the distinctly trabecular type. As in his earlier writings (1930, 1940) Schindewolf again advocates a primary hexameral symmetry of the Rugosa, the apparent tetrameral symmetry being the result of suppression of the counter-lateral sectors. He cites as evidence an intermediate group of early Mesozoic corals (Protoheterastraea) in which the counter-lateral sectors are only partly developed. Having thus designated the 'accelerated quadrants' as being on the cardinal instead of the counter side, and by analogy with recent Actinians, he goes further to assert that it is the counter side that should be considered as ventral, contrary to the opinion held by earlier investigators.

Regarding the relation between Scleractinia and Rugosa, he maintains that the former arose monophyletically from the plerophyllids of late Palaeozoic time.

The controversy over the common ancestry of Rugosa and Scleractinia or the descent of one from the other has been a much debated problem. The main points for consideration are the number of primary septa and the mode of septal insertion. The recognition of six instead of four protosepta carries with it as a corollary the suppression of the counter-lateral sectors. Hudson's assertion (1936) that there are only two protosepta does not really affect the view of six protosepta, since he regards KL1 and CL1 as of equal status. The occurrence of a group of corals in the early Mesozoic with transitional characters between Rugosa and Scleractinia, so far as the development of the counter-lateral sectors are concerned, seems fairly well established through the works of Frech & Volz (1891–6), Ogilvie (1896), Gerth (1919) and Schindewolf (1930, 1940, 1942). A slight acceleration of the counter-lateral minor septa is frequent in some rugose corals, and the actual occurrence of major septa in the counter-lateral sectors has been recorded in *Polycoelia* and, with less certainty, in *Pycnactis* and *Cystiphrentis*. In this connexion I may point out that in the Devonian *Digonophyllum* group, immediately beside the counter-septum (mistaken by Hill as the 'longest minor septum') are two major septa (counter-lateral), no minor septa being present in between, although the minor cycle is well developed in other sectors. It seems to me that this represents an extreme case of the suppression of the counter-lateral sectors, and is a point in favour of the presence of six primary septa. Again, in the *Plerophyllum* group with several major septa conspicuously accelerated, it is almost always the six protosepta that are first affected.

As pointed out in a previous paragraph, in some of the rugose corals both the major and the minor septa are inserted in a serial manner and some Scleractinia have also serially inserted septa. Thus it seems possible that there may be a continuous change in the fashion of septal insertion from serial to cyclic, first affecting the minor and then the major septa as well. It is true that no consistent correlation between the mode of septal insertion and the suppression of the counter-lateral sectors is indicated. These characters are not consistently progressive, but, like most other characters, affect various groups to different degrees, and for this very reason they should not be accorded too much weight in the subdivision of the group.

In view of the facts cited above and as the result of my investigation of the skeletal structures, I agree on the whole with Ogilvie that the development of the Rugosa and Scleractinia represents a more or less continuous process, and would incline to the view of direct descent rather than common ancestry as the true relation between these groups.

Concerning the subdivision of the Rugosa, I have already remarked that the current tendency has been to lay particular emphasis on septal insertion and septal symmetry. While the ontogenetic study of septal insertion and septal differentiation affords a valuable aid for the understanding of phylogenetic relations, it should be admitted that our knowledge in this respect is confined to very few genera. Furthermore, acceleration and retardation often add much to the irregularity and greatly reduce the value of such series in systematic analysis. Incidentally, it may be noted that, attaching importance to deviations in septal insertion has led Clark to establish two new genera on some very similar zaphrentoid corals from the Carboniferous of Ireland. Again, it is scarcely necessary to point to the unequal units that result from grouping those with a zaphrentoid type of insertion and those with a cyathaxonid type of insertion, as practised by Hill in her treatment of the Carboniferous coals of Scotland.

Septal symmetry or septal plan affords no surer guide to the broad subdivision of the group. A faint pinnate arrangement of the septa, especially in early stages, is probably universal in rugose corals. Such terms as zaphrentoid or streptelasmid plan have been applied so loosely that they cease to have any value at all. Thus in attaching much weight to the disposition of the septa, Grabau includes in his family Streptelasmidae such diverse · forms as *Tachyelasma* and *Arachnelasma*, forms otherwise very different from each other.

A new aspect of phylogeny and taxonomy was introduced by Lang's conception of 'trend of evolution'. Being impressed by the similar and parallel course of development of certain characters in presumably unrelated coral stocks, and recognizing the polyphyletic nature of many of the old genera, Lang sought to explain the whole matter by a 'programme evolution' of the independent characters, expressed in different lineages. By 'trend' is thus meant the more or less predestined direction of development of characters that occur repeatedly, but to varying extent, in different stocks supposed to represent genuine phylogenetic groups. This idea was first vaguely expressed by Weissermel (1897), but was fully expounded and developed by Lang (1917, 1923, 1938), who analyzed the Carboniferous corals in Great Britain and recognized eight such trends. Undoubtedly the conception of trends provides a valuable aid to phylogenetic study of corals as well as other fossil groups; it remains, however, to find some reliable characters which remain more or less constant and can be used as clues in the recognition of genuine phylogenetic groups upon which the trends operate. Among the rugose corals, it seems to me, these clues may be found to a certain extent in the minute structures of the skeleton, and to these we shall next direct our attention.

THE STRUCTURE OF THE SKELETON

A. *Lamellar and fibrous sclerenchyme and their role in the formation of the septa*

When thin transverse sections of rugose corals are examined under high magnification, two kinds of skeletal structures can usually be distinguished. The first kind consists of minute fibres of crystalline calcite, either radiating from a point or arranged in parallel rows with

reference to a plane. These fibres are roughly perpendicular to the surface of the skeleton. The second kind is composed of lamellar layers of crystalline calcareous matter separated by conspicuous dark bands, without any recognizable fibrous structure; these lamellar layers follow essentially the outline of the skeleton. The former is, generally speaking, characteristic of septal structures and usually designated as vertical or fibrous tissue; the latter is characteristic of basal and wall structures and commonly named transverse or lamellar tissue.

The distinction between fibrous and lamellar tissue noted above is very pronounced in *Tryplasma*, which has been repeatedly illustrated by authors. Investigation has revealed that these peculiar structures are not confined to *Tryplasma*, but are discernible to some degree in a great number of rugose genera. The lamellar tissue occurs not only in the wall region, but invests the trabeculae all along the septa, and also forms the essential part, and sometimes even the whole, of the septa.

In the Silurian *Syringaxon siluriense* (figure 4, plate 4), the septa are seen in transverse section to consist of a median zone of very dense, acutely pinnate, calcite fibres and a more or less continuous, investing lamellar tissue particularly developed near the wall and near the axial region. The median zone represents the longitudinal section of the horizontally disposed, usually closely superposed trabeculae. It may be broad or narrow, or absent, according as the section passes the central or the edge part of the trabeculae, or misses them entirely.

Another remarkable genus is the Carboniferous *Carcinophyllum* (figure 8, plate 4). I select these two because they are not closely related to each other and neither of them to the *Tryplasma* group. *Carcinophyllum kirsopianum* has a complex axial column and stout septa which are usually discontinuous peripherally. In transverse section the septa show successive trabecular ends consisting of radiating fibre fascicles. More or less continuous lamellar tissue invests the septa and passes into the intervening dissepiments. The trabeculae are inclined at a moderately low angle, so that in transverse section the septa show successive parts each corresponding to the obliquely cut section of one trabecula. This character is very well shown in the topotype of the genotype, now in the Geological Survey Scottish Office, and also in *C. mendipense* (holotype BM R25506).

In some other genera, the whole skeleton is composed of lamellar schlerenchyme and nowhere shows any fibrous structure, although septa are well developed (see figure 76).

In the Silurian *Onychophyllum pringlei* (figure 3, plate 4), the major septa are well developed and more dilated in the cardinal quadrants. They are composed of successive layers which can be traced from one septum to the next across the wall region and are evidently vertically and tangentially continuous.

The Carboniferous species *Zaphrentoides delanouei* (figure 1, plate 4) shows much the same kind of structure. The median plane of the septum is marked with a sharp dark line, invested on both sides by lamellar layers that bend right over the tip of the septa and across the wall. Small inward notches are sometimes developed in the lamellar tissue between the major septa, evidently representing the initial stage of minor septa.

Among other forms showing similar structures may be mentioned the Silurian *Zelophyllum* and the Lower Carboniferous *Amplexus*. In *Zelophyllum* (figures 68, 69, plate 8) the lamellar layers develop shallow inward folds and follow closely one upon another, while

in *Amplexus* (figure 6, plate 4) the short septa fork and divide into two branches, each branch bending away from the other to join the opposite branch of the neighbouring septum. In the closed loculi thus formed between the septa, the lamellar layers could be traced all the way round.

Again, in *Ceriophyllum* and many other members of the *Streptelasma* group, the septa are entirely formed of fibrous tissue and no lamellar tissue is recognizable. In short, these two kinds of sclerenchyme, the lamellar and the fibrous, may enter into the formation of the septa to a very variable extent, and either of them may be entirely absent.
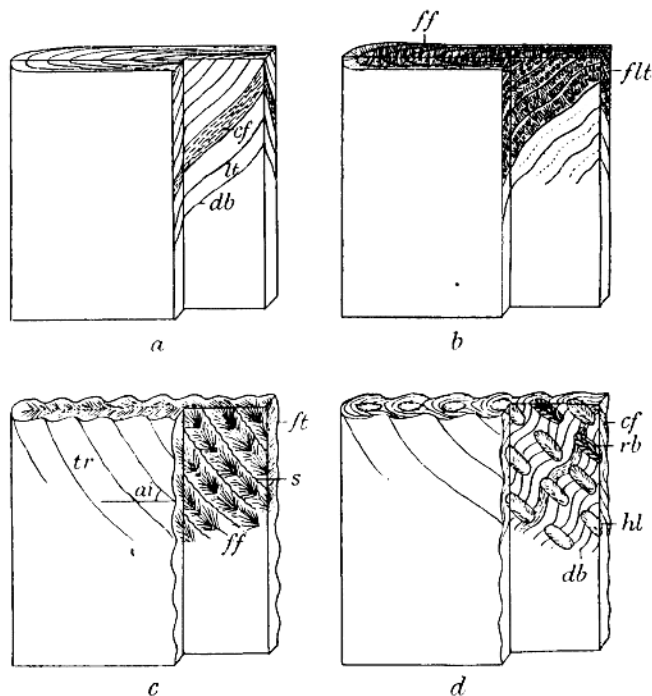

FIGURE 76. Diagram showing the structure of different types of septa. *a*, *Zaphrentoides* type; *b*, *Plero-phyllum* type; *c*, *Ceriophyllum* type; *d*, *Cystiphyllum* type. *lt*, lamellar tissue; *ft*, fibrous tissue; *flt*, fibro-lamellar tissue; *cf*, calcareous flakes; *ff*, fibre fascicles; *rb*, rhabdacanth; *hl*, holacanth; *db*, dark bands; *tr*, trabecula; *ai*, angle of inclination; *s*, suture between trabeculae.

B. *The units of lamellar and fibrous skeleton and their possible significance*

In the fibrous type of septal structure it has long been recognized that one bundle of fibres radiating from a point is the final recognizable structural unit and may be regarded as the primary unit of this type of skeleton (Ogilvie 1897, p. 235). These bundles or fibre fascicles may be grouped into composite sclerodermites or into trabeculae, or may exhibit a subparallel arrangement with their apices (centres of calcification) in the septal plane (see figure 77). In rugose corals the axial length of the individual fibre fascicles ranges from 0·05 mm. in *Columnaria* (figure 54, plate 7) to well over 0·5 mm. in *Codonophyllum* (figure 28, plate 5) and *Palaeosmilia*.

The lamellar type of skeleton is composed of lamellar layers separated by dark bands and nowhere shows fibrous structure. It has been commonly assumed that all lamellar types of skeleton are ultimately composed of fibres orientated at right angles to the lamellae (Ogilvie 1897, p. 121; Hill 1936, p. 191). In fact, so far as the rugose corals are concerned, except in the Caniniacea, to the structure of which I shall refer later on, this is certainly not the case. Under a high-power microscope, the lamellar layers are seen to be composed of calcite flakes* of subrounded shape, arranged more or less parallel to the plane of the lamellae. These flakes I take to be the primary units of the lamellar skeleton, as the fibre fascicles are of the fibrous skeleton.
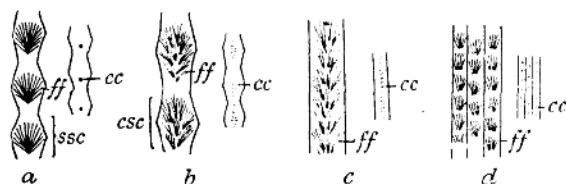

FIGURE 77. Diagram showing different types of trabeculae. *a*, *Ceriophyllum* type; *b*, *Palaeosmilia* type; *c*, *Dinophyllum* type; *d*, *Columnaria* type. *ff*, fibre fascicles; *cc*, centre of calcification; *ssc*, simple sclerodermite; *csc*, composite sclerodermite.

What is the significance of this pronounced difference between the fibrous and the lamellar sort of tissue? Von Koch, von Heider, Bourne and others have found that in present-day corals, the skeleton originates through the activity of the calicoblast layer in the ectoderm. The exact nature of the calicoblast cells and the precise method of skeletal secretion are still not fully understood. Former investigators assumed that all the different structures of the skeleton as we see them are caused by a difference in the position, either flat or pouched-up, of the secreting layer. This is expressly stated by Ogilvie (1897, p. 121) and seems to be implied by Vaughan & Wells. My observation is that corals may have well-developed septa composed entirely of lamellar tissue, or the fibrous and lamellar tissue (in sharp contrast) may occur side by side in the same septum. Moreover, these two kinds of skeleton are composed of quite different structural units; in the one case fibre fascicles, and in the other calcareous flakes. This suggests that the mere pouching up of the secreting layer does not necessarily alter the nature of the secretion itself and therefore cannot account for the difference in skeletal structures. These different structures are probably the result of a genuine variation in the secreting activity of the ectoderm, a differentiation of which we have no direct knowledge. No distinct kinds of calicoblast cells capable of producing different types of secretion are known in living corals, though juxtaposition of lamellar and fibrous tissue is also manifest in Scleractinia, as, for instance, in *Madrepora* and *Stylophyllum*. In so far as no analogy with living corals is possible, this assumed specialization of the secreting layer must remain a matter of speculation.

C. *Two different methods of the formation of fibrous sclerenchyme*

In the previous section, the distinction between the lamellar and the fibrous skeleton and their probable difference in origin have been indicated. If we examine various forms

---

* I am grateful to Dr Maurice Black who kindly examined some of my thin sections and determined the size of the calcareous flakes as probably around 0·001 mm. in thickness and 0·030 mm. in diameter.

of the *Cystiphyllum* group, we may see how the fibrous element first appeared and subsequently rose to predominance. In *Cystiphyllum omphymiforme* (figure 64 *a*, *b*, plate 8), a species with abundant lamellar tissue, the lamellar layers develop minute inward notches, in the apical part of which very slender septal spines or trabeculae sporadically occur. These minute notches may occur singly, and where they grow continuously, the trabeculae would assume the form of a holacanth; but they may also occur in aggregates, and in this case the resulting trabeculae would have in all probability the form of a rhabdacanth. The interesting point is that in this form the folds of lamellar tissue are all very shallow; well-defined, pouched parts of the ectoderm do not occur, and consequently no definite rows of trabeculae in the form of septa are discernible. In other words, the origin of the fibrous tissue is not necessarily confined to the pouched parts, but may be effected in the slightly notched flat part of the ectoderm as well.

In the Silurian cystiphyllid corals, notably those of the Middle Silurian in England, a steady increase in size and in number of the trabeculae at the expense of the lamellar tissue, roughly agreeing with the stratigraphical distribution, is well indicated. Thus starting with the Valentian *Cantrillia prisca*, in which trabeculae are very sparse and confined to the periphery, we have in succession the Woolhope Limestone form, *Cystiphyllum* sp. (SM A 15659), with short trabeculae and abundant lamellar tissue; the Wenlock Shale *Cystiphyllum* n.sp., with longer trabeculae but confined to the periphery; the Wenlock Limestone *C. siluriense*, with abundant but usually short trabeculae; and finally the Wenlock Limestone and Ludlow *C. cylindricum* and *Hedstroemophyllum* (SM A 6428), with numerous long trabeculae traversing several tabulae and contiguous with each other. Similar change may be observed in the Middle Silurian *Holmophyllum* of south China.

In the *Zaphrentoides* group the increase of trabeculae is a much slower and less pronounced phenomenon. *Z. omaliusi* (figure 2, plate 4) and *Z. enniskelleni*, both Lower Carboniferous forms resembling *Z. delanouei* externally, show occasionally a median fibrous zone in the major septa. As already noted, this median fibrous zone represents the longitudinal section of the trabeculae extending from the periphery inward; since the trabeculae are slender and comparatively few in number, transverse sections not infrequently pass through intertrabecular horizons and do not then reveal their presence at all.

However, the increase of trabeculae in the *Zaphrentoides* group can usually be traced in individual development. This is generally true with *Zaphrentoides* and related genera and is very obvious in the special group of *Rylstonia*. Thus *R. benecompacta* (figure 7, plate 4) has entirely lamellar tissue in the septa in early stages, although in the adult stage the trabeculae are sufficiently abundant as to be contiguous with each other.

Again, in a number of genera belonging to the Streptelasmacea, such as *Disphyllum* and *Codonophyllum*, the earliest stage is already marked with the predominance of trabeculae, while lamellar tissue is primarily confined to the horizontal and tangential skeleton.

It is obvious that in the *Cystiphyllum* group, trabeculae appear in advance of the development of septal folds, while in the *Zaphrentoides* group trabeculae appear relatively late in the already formed septal folds; in the *Streptelasma* group the shaping of the septa and of the trabeculae occur simultaneously. On the other hand, in all these three groups, the fibrous sclerenchyme originates at points or in concentrated areas on the ectodermal surface, flat or folded as the case may be. If these points are interrupted, the resulting

trabeculae will be short and discrete; if they are continuous but separate from each other, the trabeculae will be discrete and long; if they are numerous and confluent, the trabeculae will be long and contiguous. The fundamental point is that certain points or areas on the ectodermal surface begin to exercise a different mode of skeletal secretion, which is carried on side by side with the unspecialized part of the ectoderm.

The introduction of the fibrous sclerenchyme as sketched above is characteristic of the majority of rugose corals. Yet it is not the only way in which the fibrous character of the skeleton is achieved. In the caninids and plerophyllids, a peculiar kind of skeletal structure occurs that is both lamellar and fibrous. In both the septal and the dissepimental part, the lamellae are clearly discernible and are traversed by parallel slender fibre fascicles with their apices in the septal plane or at the base of the dissepiments. In some of the advanced forms in this group, the fibre fascicles may become elaborated and grouped together in various ways, especially in the wall region, but they never form well-shaped trabeculae. This secondary grouping, as it were, of fibre fascicles, is very well illustrated in *Verbeekiella australe* (figure 12 *a, b,* plate 4) and *Lophophyllidium wichmanni* (figure 11 *a, b,* plate 4). The peculiarity had already been noted by Koker and by Schindewolf, who suggested the term 'diffustrabecula'; in this paper I have called it the 'fibro-lamellar tissue'.

The development of this fibrous character from what was originally lamellar tissue represents a fundamentally different process from the initiation of fibrous tissue that starts at separated points. Like the fibrous tissue of the trabeculate type of septa, it probably owes its origin to a new function of the secreting layer. While in the trabecular type, the fibrous element is introduced apart from, and distinct from, the already existing lamellar tissue, in the fibro-lamellar type the fibrous character is assumed by the lamellar tissue itself. In other words, in the trabeculate type the new function of the secreting layer that produced fibrous tissue starts at isolated points which extend and coalesce afterwards, while in the fibro-lamellar type this new function is acquired more or less simultaneously all over the secreting surface.

D. *The morphology of the trabeculae and the septa*

Although trabeculae are not universally present in rugose corals, they form most distinctive features of the septa. They display regular and persistent changes and afford one of the best clues in tracing the relation between different groups. My investigation reveals that most of the characteristic features of the trabeculae as observed in the Scleractinia find their counterparts in the Rugosa. The main features of the trabeculae, i.e. their structure, disposition and mode of grouping, will be briefly described.

The component elements of trabeculae are fibre fascicles with their calcification centres. Thus the structure of the trabeculae is primarily determined by the structure and disposition of the constituent fibre fascicles. One fibre fascicle may be defined as a single bundle of calcite fibres radiating from a point (see figure 77). Where the bundles diverge widely from the centre, and the centres are widely separated, the result is a succession of reversed cones, each cone with its apex above the base of the preceding. This kind of trabecula is suggested by *Ceriophyllum* (figure 45 *a, b,* plate 7), and gives the impression that it is composed of one row of simple sclerodermites. However, the centres of radiating fibres very seldom diverge from one point (apex of the cone), but are usually grouped into a continuous series with

23-2

periodically crowded parts along the axis of the trabeculae. In this case we have composite calcification centres from which bundles of fibres diverge at various angles, as are common in the stout type of trabeculae in *Palaeosmilia* and *Codonophyllum* (figure 28, plate 5). The crowded parts with composite calcification centres form composite sclerodermites.

In *Dinophyllum involutum* (figure 30, plate 8) and *Tabulophyllum ehleri*, the fibre fascicles are long and slender and follow closely upon each other. The calcification centres are evenly distributed in a linear series along the axis of the trabecula and do not show separate sclerodermites. The slender fascicles grow freely upwards at acute angles. This kind of trabecula shows dense, acutely pinnate, fibres in both transverse and longitudinal sections.

Again, in *Entelophyllum articulatum* (figure 58, plate 7) or *Columnaria* (figure 54, plate 7), the fibre fascicles are short and slender. The calcification centres are fairly far apart and are roughly arranged in a linear series, usually deviating slightly from the axis of the trabecula. The result is successive fascicles following one upon another in a wavy course. This probably represents the simplest type of trabecula. It should be noted that the distinction between a simple and a composite sclerodermite (Vaughan & Wells 1943) is merely a matter of convenience and relativity, for in fact no sclerodermites are really simple when more than one bundle of fibres passed out from them, and the calcification centres are very rarely arranged in a single linear series.

A quite distinct type of trabecula was noticed by Hill in the *Tryplasma* group, which she calls the rhabdacanth. This is a kind of composite trabecula, in which each rod represents a small trabecula developed from one small invagination of the ectoderm. The aggregates of the rods bound by lamellar tissue in linear series forms one major trabecula. It may be mentioned in passing that when the trabeculae become excessively large, as in *Codonophyllum*, *Palaeosmilia* and *Stringophyllum* (figures 35a, b, 36, plate 6), they usually show a tendency to split into small trabeculae with their own axes of calcification. This tendency is carried to its extreme in *Schlotheimophyllum*, where each composite trabecula consists of numerous small radiating trabeculae, and is in every respect comparable with the septal tooth of *Mussa*.

Having thus surveyed the various arrangements of the fibre fascicles within the trabeculae, we may now inquire further into the habit of the trabeculae themselves. It is obvious that in the *Cystiphyllum* group, there can be no consistent direction of the trabeculae, which are short and discrete. In all the septate forms, the trabeculae are strictly speaking arranged in a fan-system, but they are nevertheless usually parallel over a considerable area, and in general they tend to be directed inwards and upwards from the wall.

In the *Zaphrentoides* type, whenever the trabeculae are developed, they are almost invariably horizontal. In *Streptelasma* and *Columnaria* and a number of other genera, almost every transition is known from horizontal (*Codonophyllum whittardi*, figure 24, plate 5) to vertical (*Entelophyllum articulatum*). It is evident that when the fan-like arrangement of the trabeculae becomes prominent, there can be no generalization as to the inclination of the trabeculae (see figure 78).

When the septa attain a considerable width, for instance in the patellate forms or in forms possessing a wide dissepimentarium, more than one fan-system of the trabeculae may be developed. In most cases the fan-systems are asymmetrical and the area of radiation is invariably near the wall. In *Acanthophyllum heterophyllum*, the separate fans are remarkably

illustrated, and in transverse section each septum shows different structures in different segments, caused by the varying angle of inclination of the trabeculae (figure 41, plate 6). A similar phenomenon may be observed in *Clisiophyllum* and *Koninckophyllum*.

In the Devonian *Phacellophyllum* (figure 47 a, b, plate 7) and *Macgeea* there is a prominent zone of trabecular divergence which coincides with one row of horseshoe-shaped dissepiments forming an inner wall. As a rule all trabeculae arise from this divergent zone, at first very slender, then expanding rapidly as they pass radially outwardly. Occasionally new trabeculae may be inserted where the fan suddenly spreads out. In *Thamnophyllum*, the trabeculae are arranged in a single series in the septal plane. The cross-section of the
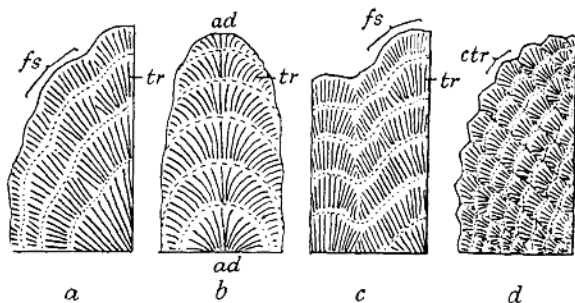

FIGURE 78. Diagram showing different grouping of trabeculae in the septum. *a, Disphyllum* type; *b, Phacellophyllum* type; *c, Acanthophyllum* type; *d, Schlotheimophyllum* type. *tr*, trabeculae; *fs*, fan-system; *ad*, area of divergence; *ctr*, composite trabeculae.

septa shows a slightly dilated zone as a result of the crowding of the trabeculae. In *Macgeea* and in advanced species of *Phillipsastraea* (figure 49, plate 7), two or three rows of trabeculae may occur in the zone of divergence and the septa become fusiform, narrowing both in the peripheral and the axial direction. As seen in transverse section, the divergent zone, with crowded and erect trabeculae, is marked by completely fused polygonal sections, each of which shows fibres radiating from the centre. Away from this conspicuous zone, in both directions, the fibres become more and more oblique as the trabeculae incline more and more away (figure 48a, b, plate 7). These features are in all respects comparable and homologous with the costae of the Scleractinia.

In coral types that possess simple slender trabeculae, complication of the septa is pursued and achieved in quite a different way. As noted above, a slight deviation of the fibre fascicles from the axes of the trabeculae is common in *Columnaria* and *Entelophyllum*. Where the trabeculae themselves are diverted from the septal plane, the septa will assume a wavy or zigzag course in transverse section. Such is the case in *E. articulatum*. Where the divergence of the trabeculae is greater, and trabeculae are numerous, they would naturally interweave and twist together in a ropy form or even produce a meshwork. The septa would have an extremely irregular and ragged surface, and every longitudinal section would cut through the projecting parts of some of the trabeculae. These features are familiar in *E. pseudodianthus* (figure 59, plate 8) and *E. prosperum*. This tendency toward the complication of the septa can be traced step by step in the series *articulatum-pseudodianthus-*

prosperum-confusum of the genus *Entelophyllum*.* Other groups showing similar trend of complication are the Devonian *Phillipsastraea* arising from *Prismatophyllum* and the Carboniferous *Aulina* and *Orionastraea* arising from *Lithostrotion*.

The primary conditions leading to this kind of complication seem to be the slenderness and abundance of the trabeculae.

Another peculiar feature worthy of notice is the flanging of the septa, so far only known in *Metriophyllum*, *Heliophyllum* and several other uncommon genera. The flanging plates proceed from the septa on both sides and are fibrous in structure. In transverse section of *Metriophyllum bouchardi* (figure 5, plate 4) the flanges are usually met with between the septa and show exactly the same structure as the latter. In *Heliophyllum* and *Eridophyllum* they are curved and arched (figure 40, plate 6) (see figure 79). Thus any plane transverse section would meet the flanges at various angles displaying different structures. The flanges themselves, at least in *Heliophyllum halli*, are composed of minute trabeculae arranged as in a septum.
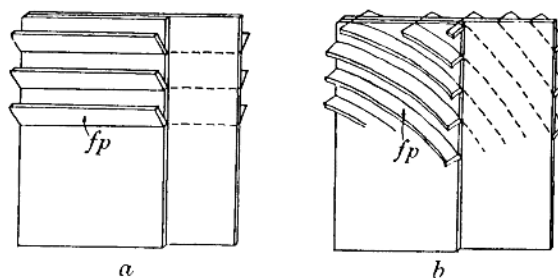

FIGURE 79. Diagram showing the structure of the flanges on the septa. *a*, *Metriophyllum* type; *b*, *Heliophyllum* type. *fp*, flanging plates.

It may be noted that the term carina has been loosely applied to any structures projecting from the septa. The *Metriophyllum* type originates, as we have seen, from plates quite distinct from the septa proper; the *Cymatelasma* type is formed by the deviation of the trabeculae from the septal plane as in *Entelophyllum*; while the *Ceriophyllum* type, the most regular of all, is produced by the expanded fibre fascicles of individual trabeculae. 'Carina' as a mere descriptive term can have little significance unless its mode of formation is indicated.

The only structural feature common in the Scleractinia, but not typically represented in the Rugosa, is the synapticula. In the Devonian *Temeniophyllum*, separate calcification centres may occasionally occur between the septa near the inner wall (figure 43, plate 6). This, however, seems never to have developed to any appreciable extent.

E. *Axial and thecal structures*

The various characters and habits of the trabeculae that determine the septal structures having been described, it remains to consider skeletal structures other than the septa.

Axial structures occupy an important place in skeleton morphology. Much has been written about the structural affinity of the column in the Scleractinia as well as in the

---

* Incidentally this kind of structure is very different from that of *Codonophyllum* (figure 28, plate 5), and I cannot agree with Dr S. Smith in linking up *Entelophyllum pseudodianthus* and *Codonophyllum truncatum*.

Rugosa. Vaughan & Wells have stated that among Scleractinia and Rugosa alike, the columella is never developed independently of the septa. In this I concur and would point out that all types of columella are fibrous in structure and can be analyzed in terms of fibre fascicles.

Morphologically, axial structures of the Rugosa may be subdivided into three categories: (1) the pseudocolumella, resulting from a twisting of the axial septal ends; (2) the columella resulting from dilatation of the counter-septum; and (3) the axial column, a broad open axial zone formed in either of these ways. In origin there are only two kinds, those formed by the axial ends of all the septa and those formed by the counter-septum alone.

The frequent upturning of the axial ends of trabeculae is a common feature in rugose corals and is perhaps only a mechanical effect of crowding. In the Devonian *Acanthophyllum* with very long septa there is a marked tendency for the trabeculae in the central region to become more erect and slender. In *A. heterophyllum* (figure 41, plate 6), an abrupt change in the inclination of the trabeculae occurs at one-fourth the distance from the centre, which produces a marked ring of discordance in transverse section. A further step in this direction of differentiation is exhibited by the Lower Carboniferous *Cyathoclisia*, in which the trabeculae in the axial area assume a wavy course, and the ring of demarcation against the outer portion of the septa becomes more pronounced. *Clisiophyllum* seems to be the end member of this series, in which a well-defined axial column formed of differentiated septal ends is finally cut off from the outer portion by the downward extension of the polypal part in the circular pit.

On the other hand, the columella in its simplest form is merely an axial extension of the counter-septum. This is typified by the Permian *Timorphyllum* and the Carboniferous *Thysanophyllum*, and is usually known as a lamellar columella. Frequently the columella is spindle-shaped, much resembling an extraordinarily large trabecula with long fibre fascicles arranged in two opposite series and converging towards both ends. At one end of such a columella, some indication of the connexion with the counter-septum can always be discerned. Typical examples are the Silurian *Dalmanophyllum* (figure 27, plate 5) and the Carboniferous *Koninckophyllum*. In some species of *Lithostrotion* (figure 53, plate 7) other major septa may join the columella, but they do not seem to have played any important part in its formation. Further complication of the columella may result from the splitting up of the fibrous tissue into slender trabeculae or septal lamellae, at first compact as in *Amygdalophyllum* and advanced forms of *Koninckophyllum*, but subsequently becoming open, with the consequent formation of tabellae, as in *Carcinophyllum* and *Waagenophyllum*. It may be noted that the open form of the elaborate columella, such as occurs in *Rylstonia* or *Carcinophyllum*, and the axial column formed by the differentiation of the axial ends of all the septa, as in *Clisiophyllum*, are not distinguishable in a section of the mature part of the coral.

Among other specially modified forms of axial structure may be mentioned *Thysano-phyllum* and the primitive species of *Lonsdaleia*, with a sort of open column structure formed by the counter-septum and arched tabellae; the few septal lamellae seem to be introduced afterwards. Another peculiar type is found in *Timorphyllum*, in some species of which the axial end of the counter-septum folds and twists about itself so as to produce a sort of meshwork. I have not had an opportunity to investigate this structure fully.

Thecal or mural structures were once used as a basis for classification of the Scleractinia. As pointed out by Grabau (1922), in the Rugosa (as opposed to the Scleractinia) it is the outer wall that forms the primary and important structural features. Ogilvie (1897) and Vaughan (1900) have both ably analyzed the various kinds of mural structures in the Scleractinia and offered interpretations in terms of space relations of the radial and tangential polypal parts. The careless use of such terms as epitheca, eutheca, pseudotheca with their derivatives epithecate wall, septothecate wall and synapticulotheca, has caused considerable confusion in the Scleractinia and still more in the Rugosa. This led Hill to discard altogether the use of these terms in the latter group, but to speak of stereozones as a general descriptive term. However, if we inquire into the different structures to which these terms were applied, the situation might not seem so confused. In both Scleractinia and Rugosa, the structure under discussion falls into two categories, the inner and the outer wall, which vary in importance. Different authors have already pointed out that the epitheca merely represents a film or a sheath formed by the retreating lip of the edge zone and should not be confused with the genuine wall structures. The application of the term epithecate wall to the lamellar kind of wall in the Rugosa is entirely due to a misconception. In the majority of rugose corals the outer wall is prominent and is continuous with the epitheca; while any kind of inner wall that may occur is of secondary origin and is usually a subsidiary structure of the septa. In the typical lamellar type of skeleton, the lamellae simply continue from one septum to the next across the wall. A suture is often discernible at the junction between the septa and the wall, probably owing to the abrupt bending of the polypal parts in these regions. This relationship is excellently shown in Nicholson's figure of *Zaphrentoides* in his *Manual* of 1889. It is hardly necessary to repeat that the lamellar layers laid down by the ectoderm in the wall and in the septa are exactly alike and result from identical processes.

In other cases, such as in *Siphonodendron* (figure 20, plate 5) and *Plerophyllum*, the peripheral ends of the septa are sharply demarcated from and wedged into the wall. Both the wall and the septa have a fibro-lamellar structure with their respective fibre fascicles abutting against each other. In some specialized forms the fibres may be zigzag in course both in the wall (*Polycoelia*) and in the septa (*Prionophyllum*). The sharp demarcation between the wall and the septa may readily be interpreted in terms of the relative heights attained by the tangential and the radial parts of the polyp. In other words, the wall of those corals with markedly exsert septa has to grow around the already existing septal ends.

In general, the wall in corals with trabeculate septa has a lamellar structure comparable with that of dissepiments and tabulae.

In all the cases related above, the outer wall represents a genuine theca, in the sense that it is laid down, and added to, from within the calice and closes the interseptal loculi on the outside. As an overhanging edge zone does not occur in the Rugosa, the deposition of the wall tissue is one-sided, and in no case are calcification centres present. I see no objection to retaining the familiar terms 'wall' and 'theca' for these structures.

When the septa are excessively thick, no room is left for the development of the outer wall, and the function of the latter is assumed by the peripheral zone of fused septal ends. To this kind of structure the term septotheca may be applied with convenience. *Codonophyllum* and *Lophophyllidium* (figure 11 *b*, plate 4) are among the conspicuous examples.

As noted above, the various kinds of inner wall are formed by the subsidiary structures of the septa. Whenever the inner walls are present and dominant, as in the Devonian Phacellophyllinae, the outer wall usually becomes degenerate or disappears altogether. Most kinds of inner-wall structures have been mentioned in connexion with the trabecular and septal structures and need not be repeated here.

Finally, a few words may be added concerning skeletal dilatation or secondary thickening. By skeletal dilatation is usually meant any kind of expansion of the skeletal parts, while secondary thickening, as the term suggests, implies something subsequently added to an already formed skeleton, presumably with structural discontinuity. There is a tendency among students to regard all lamellar skeleton as secondary, which is usually spoken of as stereome or reinforcement tissue. In such forms as *Dinophyllum involutum* or *Carcinophyllum kirsopianum*, which have a continuous median fibrous zone and investing lateral lamellar tissue in the septa, there is a clear discordance between these two kinds of structure. I believe it is partly this structure that led the old authors to speak of primary septum and secondary stereoplasm. It would seem justified, in these forms, to apply the term secondary thickening. However, in the entirely lamellar type of skeleton, no layer that is subsequently added to the septa would show any trace of discontinuity or discordance. The same applies to the fibro-lamellar type. In both these types it is impossible to distinguish between the primary and secondary skeleton, although the skeleton may be markedly thicker in one part than in another. The essential point is that, during the upward movement of the polyp, those parts that linger behind, mostly in interseptal loculi, sometimes retain active skeletal secretion and continue to add layers to the surrounding hard parts. If such parts happen to be in the form of hanging pockets, the result would be an enclosed pit lined all round by lamellar tissue. This is not infrequent in *Dinophyllum* and *Amplexus* with lamellar tissue, and in *Caninia* and *Dibunophyllum* (figure 17, plate 5) with fibro-lamellar tissue. The fact that thick septa do not occur in the peripheral region of such corals as *Phaulactis* and *Bothrophyllum*, is simply due to the cutting off of the polypal parts in this region by the continuously forming dissepiments.

Looked upon thus, it is only natural that excessive dilatation of trabeculae is comparatively rare and limited. For the trabeculae originate at the top of the polypal invagination, while any soft parts left behind at lower levels are likely to assume the more primitive function of secreting lamellar tissue.

THE SIGNIFICANCE OF THE SKELETAL STRUCTURES AND THE MAIN PHASES OF THE EVOLUTIONAL HISTORY OF ZOANTHARIA RUGOSA

Rugose corals present comparatively few characters for analysis, and little is known of the functional significance of these. Even when the functional meanings are not understood, the term 'trend', which denotes merely the orderly change of a certain character in a certain direction without necessarily implying orthogenesis, can be used with convenience and advantage. Combined with the simplicity of their structure, the corals exhibit a high plasticity, and in some cases it seems that reticulate evolution has to be taken into account even among widely separate groups. Nevertheless, the Rugosa seem to display a continuous and consistent tendency toward the achievement of a firm skeleton, and this