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

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[Plates 4 to 9]

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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.

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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 plerophyllids. 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.

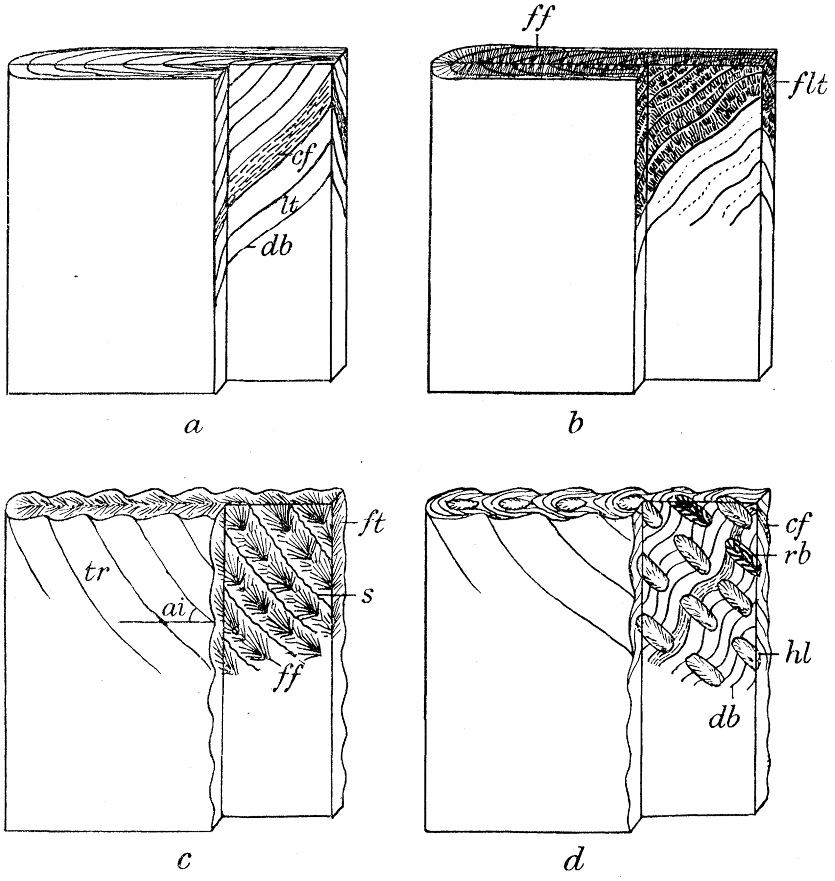

FIGURE 76. Diagram showing the structure of different types of septa. *a*, *Zaphrentoides* type; *b*, *Plerophyllum* type; *c*, *Ceriophyllum* type; *d*, *Cystiphyllum* type. *lt*, lamellar tissue; *ft*, fibrous tissue; *flt*, fibro-lamellar tissue; *cf*, calcareous flakes; *ff*, fibre fascicles; *rb*, 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.

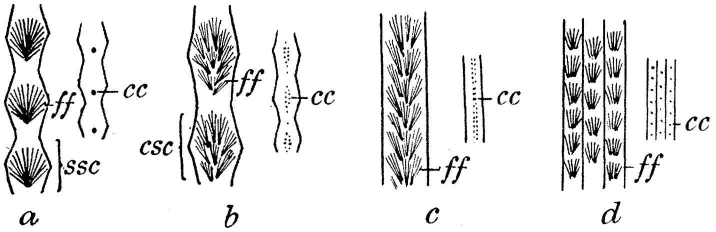

FIGURE 77. Diagram showing different types of trabeculae. *a*, *Ceriophyllum* type; *b*, *Palaeosmilia* type; *c*, *Dinophyllum* type; *d*, *Columnaria* type. *ff*, fibre fascicles; *cc*, centre of calcification; *ssc*, simple sclerodermite; *csc*, composite sclerodermite.

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

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* 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 A15659), 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 A6428), 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 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 35*a*, *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 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 48 *a*, *b*, plate 7). These features are in all respects comparable and homologous with the costae of the Scleractinia.

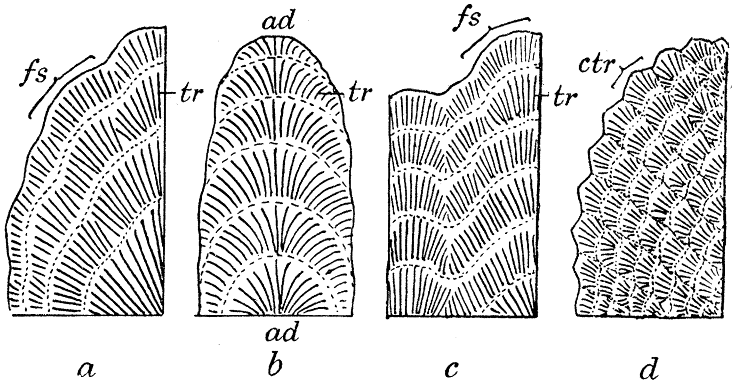

FIGURE 78. Diagram showing different grouping of trabeculae in the septum. *a*, *Disphyllum* type; *b*, *Phacellophyllum* type; *c*, *Acanthophyllum* type; *d*, *Schlotheimophyllum* type. *tr*, trabeculae; *fs*, fan-system; *ad*, area of divergence; *ctr*, composite trabeculae.

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.

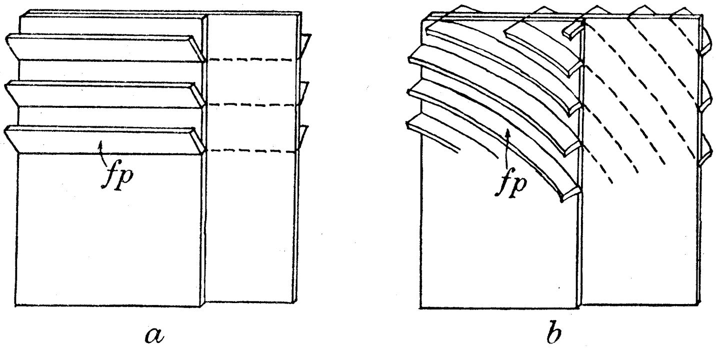

FIGURE 79. Diagram showing the structure of the flanges on the septa. *a*, *Metriophyllum* type; *b*, *Heliophyllum* type. *fp*, flanging plates.

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

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* 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 *Thysanophyllum* 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 tendency, which they evidently share with Scleractinia, may be regarded as the guiding principle in the evolution of the whole group.

Considered in this light we may proceed to investigate the ways in which this tendency is achieved within the given organization and structural pattern of the corals. We have already seen that the most fundamental change of the skeleton is from a lamellar to a fibrous structure. This probably involves a change in the mode of secretion and possibly means increased speed of formation as well as greater strength of the resulting skeleton. Again, we have distinguished two different methods by which the fibrous character is attained. It is evident that the secretion of fibrous tissue by the whole aboral surface represents a higher efficiency than localized initiation at separate points, and may be regarded as an important innovation in the history of corals, of which the Palaeozoic only saw the beginning.

In the trabeculate type of corals a further device for increasing the strength of the skeleton consists in the complication of the trabeculae that constitute the septa. It is interesting to note that in those forms in which lamellar tissue still plays an important role in forming the septa, the trabeculae generally remain smooth and show scarcely any grouping of the fibre fascicles. In the cystiphyllid group there is an increase in size and number of trabeculae, leading to compact septa; while in other groups with compact septa from the beginning, as in *Columnaria* and *Disphyllum*, the evolutionary energy is concentrated on the complication of the septa by means of different grouping and orientation of the fibre fascicles within the trabeculae or of the trabeculae themselves. This tendency is partly paralleled in corals with a fibro-lamellar kind of skeleton by the grouping of fibre fascicles. It is also obvious that the granulate or carinate kind of septa afford better anchorage for the polyp than the smooth ones.

Among structural features of less importance may be mentioned the development of axial structures. This occurs repeatedly in various coral stocks and has evidently the function of a central support. It is also manifest that the introduction of dissepiments means much convenience for the polyp to rise piecemeal and at the same time probably some economy of material as compared with more solid lamellar filling.

These features, including the complication of the septa, while evidently having a functional value, are specializations as contrasted with the fundamental change in the mode of secretion, which may be considered progressive; since the acquisition of such particular structures necessarily carries with it limitations imposed on the organism, inhibiting certain other types of further general development. Furthermore, when carried beyond a certain point, these particular trends or tendencies would appear to cease to be of benefit to the animal and sometimes even become injurious, since their excessive development may lead to extinction.

Degenerate and regressive features in the development of the coral skeleton are also common, characterized essentially by reduction in the compactness and firmness previously attained by the skeleton. Outstanding examples are the shortening of the septa, known as the Amplexoid trend, the dissociation of the septa into separate strands and basal structures, such as is found in *Naos* and *Symplectophyllum*, and the waning of the columella in a number of Permian corals. These phenomena are generally confined to highly specialized groups and are of little value in systematics.

Other features such as septal insertion and septal symmetry have already been considered in the historical account. The analysis of growth-form and method of budding in regard to colony formation has shed much light on minor systematics in the Scleractinia, but when we remember that the Rugosa are in general much less effective reef-builders, it is little wonder that research in this line should seem less promising. That colonial forms arise from simple ones is indisputable, yet it is often difficult to trace the origin of the colonial species to their simple ancestors. The difficulty is increased by the fact that perhaps in more than one case rugose corals arose from tabulate ancestors. This seems now certain in the Ordovician *Columnaria,* and very probable in some of the Silurian *Tryplasma,* the Devonian *Neospongophyllum* and the Carboniferous *Siphonodendron.*

In colonial forms, the change from fasciculate through cerioid to plocoid habit is, as pointed out by Lang, usually very rapid, and is of little systematic value; indeed, it is sometimes difficult to tell in which direction development is proceeding, especially between the fasciculate and the cerioid forms.*

Change in growth-form in the hermatypic corals has perhaps a far greater range than usually suspected. Generally speaking, growth-form in corals is essentially adaptive and may be regarded as of no more than specific value.

The main phases of rugose coral evolution

Viewed as a whole the history of the rugose corals may be divided into five phases. These phases are of course arbitrary and overlap each other considerably, especially when geographical distribution is taken into account. On the whole it can be shown that each phase is characterized by a certain dominant group or groups, with subsidiary forms usually comprising (1) remnant members of a previously dominant group, (2) members that are to rise in succeeding periods and (3) persistent stocks that undergo little or very slow change through the ages.

The first phase of coral history covers the geological period from Middle Ordovician to the lowest Silurian (Lower Llandovery) and consists in the stabilization of types of the Streptelasmacea. From Lower Silurian (Upper Llandovery) until the end of Lower Devonian, Streptelasmacea and Cystiphyllacea were both productive and played almost equal parts, each pursuing its particular course of development. This forms the second phase. The Middle and Upper Devonian saw another thriving period for rugose corals, in which certain branches of the Streptelasmacea developed to an unusual degree, while the other main groups faded gradually away one after another. In the fourth phase, that of the Carboniferous, all the main groups which had flourished in the Silurian and Devonian seas became extinct except for the persistent Zaphrentoidea, which had remained more or less unchanged since the Silurian, and the family Clisiophyllidae, probably descended from the Devonian *Acanthophyllum.* Their places were taken by the Zaphrentoidea, rising to importance for the first time, and by the new-fashioned Caniniacea.† The fifth and last phase was initiated by the rise of the Plerophyllidae, and is characterized by this latter family

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* Okulitch (1939) has recognized a change from cerioid to fasciculate habit in *Columnaria* species in the Middle and Upper Ordovician of North America.

† There is the possibility that the Caniniacea are related to the late Devonian Aulacophyllids, but they developed the fibro-lamellar kind of skeleton, which is unknown in pre-Carboniferous forms.

and some other branches of the Caniniacea; this forms the last phase of the Palaeozoic part of coral history.

The first phase may be looked upon as only a prelude to the second part which represents the acme of rugose coral development. Again, the third phase bears a strong resemblance to the second and may be regarded as its continuation with considerable readjustment and reshaping of the main constituent groups. The Lower Carboniferous witnessed the rise of groups with a distinct kind of skeleton and the waning of many important groups. The fifth phase, late Carboniferous and Permian, bears much the same relation to the Carboniferous main phase as the third (Middle and Upper Devonian) does to the Silurian main phase.

Having thus outlined the broad features, we may now enter a little more into the details of the rise and fall of the different stocks in the successive periods.

Middle Ordovician to Lower Silurian (Lower Llandovery)

It was in the quiet waters of the Middle Ordovician of North America that rugose corals first appeared. There were already two well-differentiated types, *Streptelasma* and *Columnaria*, and these remained the only two elements in the first phase of coral history. In late Ordovician, especially in Richmondian times, they abounded all around the present North Pole from central eastern Canada and the United States, Anticosti, Ellesmereland, Greenland, Scotland and Estonia to Siberia. Outside this circumpolar ring, they have been occasionally recorded from central and south-western Europe. *Streptelasma* is definitely known to occur in the Upper Ordovician in Kweichow, China.

The probable tabulate ancestry of *Columnaria* has already been alluded to. Typically *Columnaria* has a compact thin wall of lamellar tissue, with long thin septa composed of one series of slender trabeculae, and forms small colonies. The marked tendencies are towards a lengthening of the septa (*alveolata* type) and a thickening of the wall (*tamoda* type), and a change from cerioid to fasciculate habit.

The earliest *Streptelasma* of which I have studied thin sections is the Black River *S. profundum* (*Lambeophyllum*) (figure 25, plate 5). This species has a shallow calyx and very faintly developed calcite fibres in the septa, seemingly confluent with the lamellar tissue filling the interseptal loculi. Viewed as a whole, the *Streptelasma* series comprising the Black River *profundum*, the Trenton *corniculum* (figure 23, plate 5), and the Richmond *rusticum* (figure 22, plate 5) and *arcticum*, illustrates a progressive increase in size, a definite development of fibre fascicles in the septa, and the involution of the axial septal ends. By Richmondian times, diversification of the *Streptelasma* stock began to be marked. The North American *arcticum* and *rusticum* show a compaction of fibre fascicles and strengthening of the lamellar tissue, giving rise to *Dinophyllum*;* the Scottish *Streptelasma aggregatum* and *S. craigense* develop well-defined stout trabeculae and lead to *Codonophyllum*; while some unnamed species show remarkable dilatation of fibre fascicles, so as to leave no open interseptal space, and these may be ancestral to *Pycnactis*. The acceleration of the counter-septum in early stages of several species is reminiscent of the Middle Silurian *Dalmanophyllum*, though perhaps none of them bears any direct ancestral relation to it.

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* The species '*Streptelasma*' *europeanum* may also have been ancestral to *Dinophyllum*.

Lower Silurian (Upper Llandovery) to Lower Devonian

The Upper Llandovery marks the beginning of the first prolific period of the Rugosa. By this time, diversification of the *Streptelasma* stock had become already very manifest. Dinophyllidae with dense and smooth trabeculae, formed of acutely pinnate fibre fascicles and abundant lamellar tissue investing the septa, occur commonly in England,* south Norway, Gotland, the Baltic States and Siberia. *Codonophyllum* and *Pycnactis* are both very common. The former, through further elaboration of the trabeculae, led to *Schlotheimophyllum* on the one hand, and through the development of lonsdaloid dissepiments, to *Pilophyllum*† on the other. *Pycnactis* developed globose dissepiments and retained dilated septa in the axial region. This special group is very common in the upper part of the Lower Silurian, and its history appears to be much longer than was hitherto suspected.

The Columnariidae, represented only by the type genus in pre-Silurian times, now began to split up into a number of forms which were responsible for building an important part of the reefs in the Wenlock Limestone of Europe and the Niagaran Limestone of North America. Three groups are distinguishable. The first retains the simple character of uniserial trabeculae in the septa (*Spongophyllum* and *Stauria*). The second group pursued various methods in the complication of the septa by deviation, divergence and interweaving of the trabeculae as illustrated in *Entelophyllum*, *Acervularia* (figure 60*a*, *b*, plate 8) and *Arachniophyllum*, but all have the same slender trabeculae as their basic structure. It is of interest to note that in the *Entelophyllum* group, simple forms usually possess more advanced septal structures than colonial forms, and in some cases the direction of change seems to have been from the colonial to the simple rather than the reverse. A third group develops lonsdaloid dissepiments and displays a differentiation of the tabulae into an axial and periaxial series (*Strombodes* and *Spongophylloides*).

In addition to these there arose in the Lower Silurian the Cystiphyllacea. This Order is characterized by the generally short and discrete trabeculae and the abundance of lamellar tissue. Its origin is not certain, but in all probability it was derived polyphyletically from tabulate-like ancestors. In the Cystiphyllidae there is clearly a tendency towards increase in number and size of the trabeculae and a development from a diaphragmatophor (complete tabulae reaching the wall) to a cystiphor interseptal structure. These tendencies, as also the development of opercula, were pursued alike by the Cystiphyllinae with holacanth trabeculae and the Holmophyllinae with rhabdacanth trabeculae, both derived from the ancestral forms *Cantrillia* and *Tryplasma*. On the other hand, the Mycophyllidae are characterized by a well-defined peripheral zone of lamellar tissue, stout septa, and complete distant tabulae. It seems that reticulate evolution is of frequent occurrence throughout the Cystiphyllacea, especially between the *Cetophyllum* group and the *Cystiphyllum* group.

Other coral groups deserving mention are (1) the Zaphrentoidea, represented by *Syringaxon* and *Petraia*, and (2) the Disphyllidae, of uncertain origin but probably referable to the Streptelasmacea.

Concerning geographical distribution, it is clear that in Upper Llandovery and Wenlock times the main centre was still the circumpolar region. With Gotland (Wedekind 1927) as the centre, the main Wenlock and Ludlow coral faunas are practically the same from the

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* There are many unnamed *Dinophyllum* in the British Museum and the Sedgwick Museum collections.

† *Pilophyllum* is a polyphyletic genus and may also be related to the *Strombodes* group of Columnariidae.

Oslo region (Scheffen 1934) to the British Isles in the west, the Baltic States (Dybowski 1873–4), Poland (Gürich 1896) and Bohemia in the south, to the Urals (Soshkina 1937) in the east. In eastern Canada, Anticosti and the eastern United States (Foerste 1888, 1917; Greene 1898–1906; Nicholson 1875; Rominger 1876), Wenlock corals are known to be abundant, but they are still not adequately described. A preliminary survey gives the impression that the Columnariidae and the cetophyllids are well represented, while cystiphyllids and dinophyllids are relatively rare.

Tracing the Silurian deposits from eastern Europe to Asia, we first come upon a Silurian fauna, bearing a close resemblance to the boreal forms, near Constantinople (Weissermel 1939). Farther to the east, in Chinese Turkestan (Regnéll 1941), Korea (Shimuzu *et al.* 1934), central and south China (Lindström 1893; Grabau 1930, 1942; Wang 1944), the corals assume a rather different aspect. Generally speaking, the dominant groups are Holmophyllinae and specialized Cystiphyllinae with few trabeculae, possibly leading polyphyletically to *Cetophyllum*. The relative scarcity of the *Streptelasma* group and the *Columnaria* group,* as well as the early appearance of Disphyllidae, are also prominent features. The close resemblance of the forms from north Yunnan, Szechuan, Hupeh and Korea, in contrast to those from the narrow sea embayment of eastern Yunnan, is equally striking.

In the southern hemisphere, Silurian corals are known to occur in abundance in eastern Australia (Hill 1940*c*). As contrasted with China, Columnariidae flourished here, while cystiphyllids are less abundant. The lack of the Streptelasma group is also remarkable. Some *Entophyllum* species bear a close resemblance to their contemporaries in Canada and in the United States.

When the Caledonian movements set in, the picture was considerably altered, Much of north-western Europe was raised above sea-level, and marine life was driven south and east to the Bohemian Basin and the south Urals. From the Upper Ludlow to the end of the Lower Devonian (Konieprus Limestone), rugose corals lived peacefully in this Palaeotethys, but in the Middle Devonian they took another opportunity to expand. During this period, Acanthophyllinae and Mycophyllidae steadily rose to importance and were abundant from d'Erbray and Boulogne (Barrois 1889; Le Maitre 1934) in the west, to Bohemia (Počta 1902), the eastern Alps (Charlesworth 1914), Turkey (Weissermel 1939) and the south Urals (Soshkina 1937). Another part of the world where corals seem to have continued development without much disturbance was eastern Australia (Hill 1942*a*, 1943). In North America this period of coral history is not so completely understood; it seems certain that many groups were dying out at the close of Niagaran times, and the relation of the Middle Devonian Onondaga fauna to that of the Niagaran is not clear.

Middle Devonian to Upper Devonian

By the beginning of Middle Devonian times, as a result of long erosion, wide continental shelves covered with clear water again prevailed in many parts of the world, and afforded ideal conditions for the spread of coral reefs. On the Eurasian continent, the Palaeotethys with its eastern extension in the Himalayas and its northern branch in the Urals had been the persistent geosyncline, which now transgressed over parts of north-western Europe, the Russian platform and south China. Attention has already been directed to the rise of the

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* *Stauria* was recently recorded by Yin from Kweichow, China.

Disphyllidae in late Silurian and early Devonian times. The succeeding Middle and Upper Devonian period was dominated throughout by this family. Other important coral stocks are the *Ptenophyllum-Aulacophyllum* group, probably descended from the *Phaulactis* group, the *Mesophyllum-Stringophyllum* group simulating *Dinophyllum* but with dissepiments, and a special group of Cystiphyllidae, the affinity of which remains unsettled. Columnariids are represented by *Grypophyllum* and *Endophyllum*, while Zaphrentoidea became increasingly important.

Within the family Disphyllidae, the Acanthophyllinae sprang up with a number of forms at the beginning of the Middle Devonian and were common throughout Europe. All are large forms, having a wide dissepimentarium and long septa with several fan-systems of trabeculae, with involute axial ends and peripherally dissociated parts.

Two other subgroups of Disphyllidae may be distinguished, the Phacellophyllinae, and the Disphyllinae, respectively with and without a distinct area of trabecular divergence. The former group was already fairly common in the Lower Devonian (Penecke 1894), while the latter did not attain prominence until late Eifelian. Both are characterized by regular trabeculae arranged in fan-systems, with well-defined sclerodermites that give rise to regular carinae. In the Phacellophyllinae, again, the simple form *Macgeea* possesses certain advanced characters and seems to have arisen from colonial ancestors.

The *Ptenophyllum-Aulacophyllum* group, with an axial zone of dilated septa, is indistinguishable in its microstructure from *Phaulactis*. This group flourished both in North America and Europe and persisted into the Upper Devonian. The *Stringophyllum-Neospongophyllum* group, with stout and smooth trabeculae usually embedded in lamellar tissue, exactly resembles *Dinophyllum* as concerns septal structure. This is an important group in Middle and early Upper Devonian times. In the Lower and Middle Devonian there are genuine descendants of Cystiphyllidae possessing sparse holacanth trabeculae and lamellar tissue which are usually recorded as *Cystiphyllum*, *Microplasma* (Yoh 1937) and *Diplochone*. On the other hand, the *Lytophyllum* group, which is very abundant and widely distributed in the Middle Devonian, rarely shows any trabeculae, and has a skeletal structure that is neither lamellar nor exactly fibrous. This group passes on the one hand through *Zonophyllum* to *Digonophyllum*, and on the other, grades into the genuine cystiphyllids with all intermediate forms.

Two other peculiar genera that may be mentioned in this connexion are *Heliophyllum* and *Eridophyllum*. Evidence afforded by ontogenetic study points to a close affinity between *Heliophyllum* and *Aulacophyllum*, the only difference being that flanges occur in late stages in *Heliophyllum*. *Eridophyllum* bears a resemblance to *Heliophyllum* in the presence of flanges, but is evidently not related to *Aulacophyllum*. Hill has suggested affinities between *Eridophyllum* and *Entelophyllum*, and it seems that a study of the various Canadian and North American late Silurian '*Entelophyllum*' species might shed some light on the origin of *Eridophyllum*.

Regarding the minor groups of this period, the Mycophyllidae and Codonophyllidae were rapidly disappearing; Columnariidae (*Fasciphyllum*, *Grypophyllum* and *Endophyllum*) were fairly common in the Middle Devonian, but faded away in the Upper Devonian; some remnant forms of the *Streptelasma* group (*Siphonophrentis* and *Heterophrentis*) still lingered, but Zaphrentoidea were steadily gaining ground.

On the Eurasian continent, all along the belt immediately to the north of the Palaeotethys, coral reefs thrived in the Middle Devonian. From south England, north France (Barrois 1889; Le Maitre 1934, 1937), Rheinland (Wedekind 1924, 1925), Moravia (Kettnerova 1932), the eastern Alps (Schulz 1886), and the Russian Platform (Kelus 1939) to the Urals (Soshkina 1936), the Middle Devonian coral faunas are practically the same. Farther to the east, in Asia Minor (Charles 1933), Chitral, down to Burma (Reed 1908, 1930), the European stamp is still very strong. When we come to central and south China (Mansuy 1912; Yabe & Hayasaka 1916, 1920; Yoh 1937) there is an apparent change in the relative importance of the different groups. The Disphyllidae are represented almost solely by the subfamily Disphyllinae (*Ceriophyllum*, *Temeniophyllum* and colonial forms), Phacellophyllinae being practically unknown. There is also a remarkable scarcity of the *Ptenophyllum* and the *Acanthophyllum* group. Columnariids are common and the *Stringophyllum* group holds more or less the same position as in the European faunas. Cystiphyllids are also well represented.

In North America, two subprovinces are clearly discernible in Middle Devonian times, the central and east (Michigan, Ohio and eastern Canada) on the one hand, and the west (Nevada) on the other. In the central and eastern area, the main constituents are *Aulacophyllum*, *Heliophyllum*, various forms of Disphyllidae and some remnant forms of *Streptelasma* group, on the whole rather distinct from the contemporary European fauna. In the west, the Nevada Limestone has yielded (Stumm 1937, 1939) forms that strongly recall those of Europe and China.

The Middle Devonian coral fauna of eastern Australia (Hill 1940*c*, 1942*b*, 1942*c*) affords special interest in that it contains *Aulacophyllum* and *Eridophyllum* in addition to columnarids and disphyllids. It evidently represents a mixed fauna of North American and Chinese affinity, together with Upper Silurian and Lower Devonian remnant forms. When we remember that this part of the globe had remained quiet during the Caledonian orogeny, it is not surprising that most of the coral types should continue to be represented here.

Upper Devonian corals are much more restricted in their distribution and are confined to the Frasnian. In Europe they are best known in north France, the Rheinland (Walther 1928) and the Urals (Soshkina 1940); in Asia, from Chitral and Burma (Reed 1922) and parts of south China. From western Europe to Burma, the dominant forms are the Phacellophyllinae, especially *Macgeea* and *Phillipsastraea*. The disphyllid *Temeniophyllum*, and the stringophyllid *Tabulophyllum*, are also common. In south China the essential forms are the disphyllid *Ceriophyllum*, *Temeniophyllum* and large zaphrentoids. The rich Upper Devonian coral faunas of north-western Canada (Smith 1945) and Iowa (Fenton & Fenton 1938) consist of much the same elements, but the abundance of *Spongophyllum*, *Aulacophyllum** and *Ptychophyllum* is striking and unknown elsewhere.

Lower Carboniferous to Middle Carboniferous

The first phase of the Hercynian orogeny caused the extinction of many of the main rugose coral groups. The components of the Lower Carboniferous coral faunas are the persistent Zaphrentoidea, the newly established Caniniacea and the family Clisiophyllidae,

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* *Mictophyllum semidilatum* Smith is a species of *Aulacophyllum*.

perhaps the only survivor of the Streptelasmacea. The Cystiphyllacea disappeared before the Frasnian, and the Disphyllidae and the *Stringophyllum* group also died out before the close of the Devonian. In the transition fauna of the Etroeungt horizon (Frech 1885; Dehée 1929) and in Novaja Zemlja (Gorsky 1935, 1938), apart from some acanthophyllid species which probably give rise to the Clisiophyllidae, only some *Endophyllum* and possibly *Spongophyllum* seem to be present. Two other forms worth noting are the Lower Carboniferous *Aphrophyllum* from Australia (Smith 1920) which may be a survival of the Disphyllidae, and the Lower Carboniferous '*Cyathophyllum*' sp., recorded by Meriam (1942) from Oregon, which might be related to *Ptychophyllum*.

The Clisiophyllidae split into two groups early in the Tournaisian. The *Cyathoclisia-Clisiophyllum* series shows progressive specialization of the inner ends of the septa, a feature already marked in *Acanthophyllum*, leading eventually to the formation of an open axial column. The *Koninckophyllum* group, with a solid columella formed by the counter-septum, became colonial. In both groups the septa are composed of regular trabeculae which undergo various modifications in character and disposition, similar to those of the Disphyllidae in Middle Devonian times. To cite a few examples of parallel development: *Ceriophyllum* and *Koninckophyllum*, *Disphyllum* and *Diphyphyllum*, *Temeniophyllum* and *Cionodendron*, *Prismatophyllum* and *Lithostrotion*, *Phillipsastraea* and *Aulina* and *Orionastraea*. The *Koninckophyllum* group was an important reef builder of late Viséan and Namurian times.

The Zaphrentoidea, which had already attained some importance in the Devonian, began now to assume a leading position, but underwent very little change. When compared with the extent of change in other coral groups, the differences between such genera as *Zaphrentoides*, *Allotropiophyllum* (*Menophyllum*) and *Hapsiphyllum* may well be regarded as no more than subgeneric. A general increase in size, a widening of the fossula or fossulae and a strengthening of the trabeculae may be mentioned among the common lines of development. Forms with swollen septal ends (*Bradyphyllum*) also occur, but it is difficult to tell whether their origin should be looked for among contemporary zaphrentoids or in the pre-Carboniferous Metriophyllinae.*

The newly arisen Caniniacea, the skeletal structure of which is primarily lamellar, becoming fibro-lamellar, are unknown in pre-Carboniferous beds;† the Order is probably polyphyletic. While *Caninia* itself may be related to some species of *Zaphrentoides*, the colonial forms (Lonsdaleiinae) do not seem to bear any relation to pre-existing coral stocks. Within the Caniniacea, the Caniniidae are abundant throughout the Carboniferous and display a steady change from lamellar to fibro-lamellar tissue, and a grouping of the fibre fascicles into small patches. Reticulate evolution seems to be common between the *juddi* type (*Bothrophyllum*) and the *cylindrica* type (*Siphonophyllia*).

The Lonsdaleiidae first appeared in early Viséan times, reached their zenith in late Viséan and Namurian, and persisted with scarcely abated vitality into the Permian. The subgroup of the essentially simple Dibunophyllinae shows considerable complication in the grouping of the fibre fascicles and in the modification of the outer portion of the septa

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* *Cyathaxonia* with stout septa and a solid column composed of concentrically lamellar tissue, traversed by radiating fibres; might be a specialized form of the Metriophyllinae of the *Syringaxon* type.

† Busch described (1941) two species under *Caninia* from the Hamilton beds of New York. However, they seem to me to belong to the Metriophyllinae.

(*Iranophyllum*). The Lonsdaleiinae retain the simple type of septa of neatly arranged slender fibre fascicles, and develop a complex axial column, arched tabellae becoming incorporated with the counter-septum in its upward growth. Neither Waagenophyllinae nor Plerophyllidae achieved much importance before late Carboniferous and Permian. The former is represented by *Siphonodendron* alone, with simple septal structure of fibro-lamellar type and a slender solid columella. Early members of the Plerophyllidae have been reported from the Viséan in England (*Rhopalolasma*) with partly lamellar and partly fibro-lamellar tissue, but became gradually important in the late Carboniferous of eastern Europe.

In the Tournaisian the coral faunas were much more limited in distribution. Apart from the classical regions of northern France and south-western England, they were reported from central Russia (Stuckenberg 1888, 1905), Ural and Timan (Stuckenberg 1895), the Donetz Basin (Fomichev 1931), the Kirghiz Steppe (Gorsky 1932) and south China (Chu 1934; Yü 1934, 1937). The main forms are invariably Zaphrentoididae and primitive members of Caniniidae (*Uralinia* group).

The Viséan was an epoch of reef-building almost universal in extent, surpassed only by that of the Middle Devonian. A preliminary survey shows that a western or European, an eastern or Chinese and a southern or Australian province are generally distinguishable, though considerable intermingling and overlap must be admitted.

In the Viséan, the belt favourable to coral life shifted considerably to the north as compared with Devonian times. The embayment of the British Isles, northern France and Belgium does not seem to have had direct connexion with the more extensive shallow sea covering most parts of European Russia, the Urals, the eastern Alps and on the other side of the Palaeotethys the eastern Sahara (Menchikoff & Hsu 1935). Across the Atlantic the same Viséan corals occur in Nova Scotia (Lewis 1935) and eastern Canada. Over this vast area there is actually no noticeable change in the faunal aspect.

On the other hand, from Asia Minor (Kirghiz Steppe) to the east, in the main south China sea (Reed 1927; Yü 1934, 1937) and its northern extension through central China (Kansu) to Chinese Turkestan (Loweneck 1932), and possibly to Novaya Zemlja, there is a change in the relative importance of the different coral groups as marked as that already noted in Middle Devonian. Generally speaking, the Caniniidae are specially abundant and achieved large size (*Heterocaninia* and *Kweichouphyllum*); the Clisiophyllidae developed thicker septa and a complex axial column (*Auloclisia*, *Dibunophyllum vaughani densa*, *D. tingi*, etc., Yü 1934), while typical Koninckophyllidae with solid columella are unknown and typical *Dibunophyllum* with well-developed axial column are comparatively rare. Instead we get a group of intermediate forms between *Caninia* (*Bothrophyllum*) and *Dibunophyllum*, such as *Yuanophyllum* and *Arachnelasma sinense* (Yü 1934, 1937), which pass up into the Middle Carboniferous (*Koninckophyllum*, *Dibunophyllum*, Chi 1931, 1935). Asiatic reef-building forms, such as *Lithostrotion* and *Siphonodendron*, bear a close resemblance to European forms. The relative scarcity of zaphrentoid genera is remarkable, though this may be partly due to neglect of such members by investigators. *Palaeosmilia* is rare but known from China, the Khirghiz Steppe and Novaya Zemlja. Further analysis is not possible here.

The southern province covers eastern Australia (Hill 1934), Japan (Hayasaka 1924; Ozawa 1925), and the western United States, i.e. Oregon (Meriam 1942), and possibly also the Rocky Mountains (Hayasaka 1936; Kelly 1942). The outstanding features are the special koninckophyllid group, *Amygdalophyllum* and *Cionodendron*, with thick columella and septa, and *Symplectophyllum* with a peculiar mode of septal modification, together with the rarity of Clisiophyllidae and the Caniniacea as a whole. Again, the reef-building species of late Viséan times are similar to European and Chinese forms. This similarity is probably due to homeomorphic development rather than to genetic relationship.

In central and eastern America and Canada the records are less complete. Among the better known is the Chouteau (Viséan) fauna (Easton 1944*a*) consisting mostly of zaphrentoid genera having affinities with European forms.

In Namurian times there was an evident eastern and southern shift of coral life. This shift was accompanied by the rise to dominance of the caninid *Bothrophyllum* which flourished in the Moscow Basin (Dobrolyubova 1935, 1937), eastern Alps (Heritsch 1936), Urals and Timan (Stuckenberg 1895; Dobrolyubova 1936), Novaya Zemlja (Gorsky 1935, 1938), Siberia (Tolmakoff 1924, 1931) and Spitzbergen (Heritsch 1939). This dominance of the *Bothrophyllum* group seems to be universal as far as records are known (North America: Easton 1943; Jeffords 1943; South China: Yü 1934; Chi 1935). It is of interest to note that in the eastern Alps there occurred at this time a group (*Geyerophyllum* and *Carniaphyllum*) which recalls *Carruthersella* of western Europe and *Amygdalophyllum* of Australia. The persistence of forms of the Disphyllinae into Middle Carboniferous in south China has already been referred to.

Upper Carboniferous to Middle Permian

In late Carboniferous and early Permian times, the centre of coral life had again shifted. In the Eurasian continent, the Palaeotethys extended from the eastern Alps through the Himalayas to Malaya and a northern arm stretched to the Urals. This huge geosyncline continued from Malaya and the Dutch Indies to western Australia. Parts of Russia, Asia Minor and most parts of south China were at the same time flooded by epicontinental seas. In the other hemisphere, the main site of marine deposition and marine life extended from western South America (Peru, Chile) to the southern and central United States (Texas, Oklahoma and Kansas) and possibly continued to British Columbia. In both hemispheres the coral faunas were very much alike. The Clisiophyllidae had practically died out, the Caniniidae greatly declined, while the Plerophyllidae rapidly attained a leading and universal position. The Waagenophyllinae had risen to importance, and together with the persistent forms of the Lonsdaleiinae, were the essential reef-builders of the time. Some specialized members of Dibunophyllinae (*Iranophyllum*) still lingered on.

The most distinctive feature of the coral faunas under consideration is that all of them had acquired a fibro-lamellar kind of skeleton. In the Plerophyllidae the general tendency is toward a complication in the grouping of the fibre fascicles. The simplest types (*Timorphyllum* and primitive *Plerophyllum*) have subparallel fibre fascicles normal to the septal plane or the wall. In the advanced forms the fibre fascicles are grouped into arched patches which accumulate along the central part of the septa and may be variously disposed. Periodic crowding of the patches sometimes occurs, recalling the composite sclerodermites in the trabeculate type of septa (*Lophophyllidium* and advanced *Plerophyllum*). Incidentally it may be mentioned that this feature is also observable in the *Bothrophyllum* group (figure 16, plate 5). In the subfamily Lophophyllidiinae the complication of septal structures is correlated with the elaboration of the columella which changes from a compact to an open form, as illustrated by the series *Lophophyllidium proliferum-Sinophyllum wichmanni-Verbeekiella cristatum-V. australe-V. tubulosum.* The Plerophyllidae are characterized by differentiation of the six protosepta, involving sometimes some of the other major septa.

Waagenophyllinae and advanced forms of Lonsdaleiinae (*Stylidophyllum*) display on the whole similar trends in the complication of fibre fascicles. In general, the Waagenophyllinae differ from the Lonsdaleiinae in their more compact column and narrow dissepimentarium traversed by the septa, but both groups developed aphroid forms (*Polythecalia* and *Wentzellela*), and it is often difficult to distinguish those of waagenophyllid origin from those of lonsdaleiid origin.

A small Upper Carboniferous plerophyllid fauna was reported by Smith from south Wales (1930). Whether this represents a forerunner of the Plerophyllidae or is merely the contemporary of the main eastern plerophyllid fauna is not certain.

The development of the rugose corals in their last phase is almost universal. From the eastern Alps (Heritsch 1936) to the Urals (Soshkina 1925, 1928; Soshkina *et al.* 1939), from Persia (Douglas 1936) and the Salt Range (Waagen & Wentzel 1886) to Malaya, from Timor (Gerth 1921; Koker 1924) to Australia (Hinde 1890; Hill 1937, 1942), and from south China (Grabau 1922, 1928; Huang 1932; Chi 1935, 1938) to Japan (Hayasaka 1924; Ozawa 1925), Plerophyllidae, Waagenophyllinae and Lonsdaleiinae are almost equally important. Various amplexoid forms of plerophyllids and aphroid forms of lonsdaleiids are common in the Urals, while Timor furnished many peculiar forms (*Pronophyllum*, *Endothecium* and *Prosmilia*) not known elsewhere.

Plerophyllidae are known to occur in Peru (Douglas 1920, 1921), and recent works of Moore & Jeffords (1941, 1945) and Jeffords (1942, 1947) have revealed the presence of both Plerophyllidae and Waagenophyllinae in Kansas and Oklahoma.

The peculiar genus *Iranophyllum* with tertiary and quaternary cycles of septa is known only from the Permian of Persia (Douglas 1936), Indochina (Mansuy 1913, *Cyathophyllum* cf. *multiplex*) and Burma (Smith 1941).

After Middle Permian times came the biggest gap in coral history, and it was not until the early Middle Triassic that corals made their reappearance. As we have seen, all the trabeculate types died out in the Carboniferous. Lonsdaleiinae and Waagenophyllinae had passed their acme by the early Permian with the development of reef-building forms, a feature usually indicating the beginning of a decline. Indeed, the Plerophyllidae was the only group left still retaining high vitality at the close of the Palaeozoic era. Thus if we are to derive the Scleractinia from the Rugosa, Schindewolf's suggestion that they represent the monophyletic descendants of the Plerophyllidae seems to be acceptable.

CLASSIFICATION

Having described the structure of rugose corals in some detail, and reviewed the main phases in their evolution, I now turn to the classification of these Zoantharia. Any zoological classification should meet two needs: a practical one which provides the systematist with the means of easy reference and the allocation of species, and a theoretical one which will so far as possible express the phylogenetic relationship between the different groups.

In devising the present scheme, I have laid special emphasis upon the genera. The sense and scope defined by a genus will, I hope, provide the worker with a useful guide. The arrangement of genera under higher categories must of necessity be a matter of personal opinion. In evaluating the validity of genera I have adopted the more conservative attitude, that is, I am inclined to 'lump' rather than to 'split'. Out of more than 430 generic names proposed for the Rugosa, I have recognized 116 genera and 46 subgenera. It should be noted that my subgenera are all good morphological genera, and their retention is desired for stratigraphical purposes. The families and subfamilies are not used in the same sense as in any previous works, and I have endeavoured to make them represent real phylogenetic groups; while, within the groups, the genera may be only horizontal stages arrived at by parallel and related lineages. This phylogenetic grouping is of course sometimes impracticable, especially as reticulate evolution seems to be present. The diagnoses of genera and of higher groups have been made as concise as possible. Characters common to a higher category are not always repeated in the diagnoses of its constituent members. Subgenera are very briefly defined. No comment is made under the main categories. I hope this deficiency will be supplemented by the tables of evolution (pp. 245, 246) and by the text in the section on evolutional history.

1. Suborder ZAPHRENTOIDEA

Small solitary corals, skeleton lamellar, septa composed of a few horizontal trabeculae embedded in lamellar tissue, or composed of lamellar tissue only. Wall lamellar and thick, epitheca present, no dissepiments. Silurian-Permian.

Family I. Zaphrentoididae

As for the Suborder.

(*a*) Subfamily Zaphrentoidinae

Small solitary corals, prominent fossula or fossulae, septa composed of a few trabeculae or entirely of lamellar tissue, no dissepiments. Silurian-Permian.

(1) *Zaphrentoides* Stuckenberg, 1895 (figures 1, 2, plate 4).

Genotype: *Zaphrentis griffithi* Edwards & Haime, 1851. Lower Carboniferous.

> Curved ceratoid or trochoid corallum, long major septa, prominent narrow cardinal fossula and rudimentary minor septa, tabulae complete, slightly domed. Lower Carboniferous-Permian.

Synonyms: *Trochophyllum* Edwards & Haime, 1850; *Phryganophyllum* de Koninck, 1872; *Amplexi-Zaphrentis* Vaughan, 1906; *Zaphrentula* Bulkhovitinova, 1915; *Craterophyllum* Tolmakoff, 1931; *Neozaphrentis* Grove, 1935.

(2) *Menophyllum* Edwards & Haime, 1850.

Genotype: *M. tenuimarginatum* Edwards & Haime, 1850. Tournaisian.

> Like *Zaphrentoides*, but of large size, corallum rarely trochoid, prominent cardinal and alar fossulae, major septa in cardinal sectors usually confluent through lamellar tissue. Lower Carboniferous-Permian.

Synonyms: *Fasciculophyllum* Thomson, 1883; *Triplophyllum* Simpson, 1900; *Meniscophyllum* Simpson, 1900; *Caenophyllum* Clark, 1926; *Heptaphyllum* Clark, 1924; *Allotropiophyllum* Grabau, 1928.

(3) *Hapsiphyllum* Simpson, 1900.

Genotype: *Zaphrentis calcariformis* Hall, 1882. Middle Devonian.

> Like *Zaphrentoides*, with a very wide cardinal fossula, nearly all the septa coalescent at the fossula wall and reinforced by lamellar tissue. Middle Devonian-Lower Carboniferous (Viséan).

Synonyms: *Clinophyllum* Miller, 1891; *Verneuilia* Stuckenberg, 1895.

(4) *Onychophyllum* Smith, 1930 (figure 3, plate 4).

Genotype: *O. pringlei* Smith, 1930. Lower Silurian.

> Small trochoid corallum with deep calice, septa composed entirely of lamellar tissue, more dilated in cardinal sectors, two of the protosepta join at centre in early stage. Lower Silurian.

(*b*) Subfamily Metriophyllinae

Small solitary corals, septa of roughly radial symmetry and composed of horizontal trabeculae swollen at inner ends and reinforced by lamellar tissue. Middle Silurian-Middle Carboniferous.

(1) *Syringaxon* Lindström, 1882 (figure 4, plate 4).

Genotype: *Cyathaxonia siluriense* McCoy, 1850. Silurian.

> Small ceratoid or subcylindric corallum, major septa contiguous at inner ends through investing lamellar tissue, and forming inner wall, minor septa short and contratingent, counter-lateral minor septa longer than others, tabulae divided into an inner horizontal series and outer inclined series. Middle Silurian-Middle Devonian.

Synonyms: *Permia* Stuckenberg, 1895; *Laccophyllum* Simpson, 1900; *Enallophyllum* Greene, 1901; *Alleynia* Počta, 1902; *Barrandeophyllum* Počta, 1902.

Subgenus *Duncanella* Nicholson, 1874.

Subgenotype: *D. borealis* Nicholson, 1874. Silurian.

> *Syringaxon* with entirely lamellar septa and faintly dilated axial ends.

(2) *Metriophyllum* Edwards & Haime, 1850 (figure 5, plate 4).
Genotype: *M. bouchardi* Edwards & Haime, 1850. Devonian.

> Small trochoid corallum, septa with horizontal flanges, major septa reaching axis, slightly swollen at inner ends, minor ones short except the counter-lateral, tabulae thin and inclined to the periphery, no dissepiments. Middle Devonian-Lower Carboniferous.

Synonyms: *Lindströmia* Nicholson & Thomson, 1876; *Lophelasma* Simpson, 1900; *Stereolasma* Simpson, 1900.

(3) *Cyathaxonia* Michelin, 1847 (tentatively referred here).
Genotype: *C. cornu* Michelin, 1847. Tournaisian.

> Small trochoid to subcylindric corallum, septa thick, both major and minor inserted in serial manner, composed of fibre fascicles not grouped into trabeculae, prominent columella composed of concentric lamellae traversed by radiating fibres, tabulae thin, complete and distant, no dissepiments. Lower Carboniferous.

Subgenus *Cyathocarinia* Soshkina, 1928.
Subgenotype: *C. tuberculata* Soshkina, 1928. Carboniferous.

> *Cyathaxonia* with carinate septa of the flanging-plates type.

(4) *Bradyphyllum* Grabau, 1928.
Genotype: *B. bellecostatum* Grabau, 1928. Middle Carboniferous.

> Trochoid corallum, major septa reaching or nearly reaching axis, reinforced by lamellar tissue and sometimes swollen, minor septa rudimentary, tabulae numerous and convex, no dissepiments. Carboniferous.

Synonym: *Rotiphyllum* Hudson, 1942.

(*c*) Subfamily Petraiinae

Small solitary corals, septa composed entirely of lamellar tissue and grouped into several series, minor septa contratingent, wall thick. Silurian-Carboniferous.

(1) *Petraia* Munster, 1839.
Genotype: *P. radiata* Munster, 1839. Silurian.

> Small trochoid or subcylindric corallum with deep calice, thick lamellar wall, septa thin and wavy, major septa coalescent in groups and meeting at centre, minor contratingent, tabulae rare. Silurian-Middle Devonian.

Synonyms: *Orthophyllum* Počta, 1902; *Paterophyllum* Počta, 1902; *Asthenophyllum* Grubbs, 1936; *Stewartophyllum* Busch, 1941.

Subgenus *Ditoechelasma* Simpson, 1900.
Subgenotype *Petraia fanninganum* Safford, 1869. Devonian.

> Ceratoid to cylindrical *Petraia* with numerous tabulae and anastomosing axial structure.

(2) *Heterophyllia* McCoy, 1849.
Genotype: *H. grandis* McCoy, 1849. Lower Carboniferous.

> Slender cylindrical corallum, flexuous septa contratingent with each other, wall thick, tabulae domed. Carboniferous.

Synonym: *Cystelasma* Miller, 1891.

(3) *Hexaphyllia* Stuckenberg, 1904.

Genotype: *H. prismatica* Stuckenberg, 1904. Carboniferous.

Six-sided prismatic corallum, six flexuous septa meeting at centre and protruded through the thick wall as costae, tabulae domed. Carboniferous.

(*d*) Subfamily Amplexinae

Small solitary corals, septa short, composed entirely of lamellar tissue, tabulae complete and distant. Silurian-Carboniferous.

(1) *Amplexus* J. Sowerby, 1814 (figure 6, plate 4).

Genotype: *A. coralloides* J. Sowerby, 1814. Lower Carboniferous.

Trochoid corallum, septa short, forked and diverted to connect with each other, tabulae flat and distant. Carboniferous.

Synonym: *Bordenia* Greene, 1911.

(2) *Amplexoides* n.g.

Genotype: *Amplexus appendiculatus* Lindström, 1883. Silurian.

Small trochoid to subcylindrical corallum, septa short, with low ridges developed on the distant and complete tabular floors. Silurian.

Synonym: *Strobilasma* Scheffen, 1933?.

(3) *Fletcheria* Edwards & Haime, 1851.

Genotype: *F. tubifera* Edwards & Haime, 1851. Silurian.

Slender fascicular corallites, rarely simple, thin lamellar wall, very few short and slender trabeculae projecting horizontally from wall, complete distant tabulae, no dissepiments. Silurian-Middle Devonian.

Synonyms: *Pycnostylus* Whiteaves, 1884; *Placophyllum* Simpson, 1900; *Cylindrophyllum* Yabe & Hayasaka, 1915 (*Yabeia* Lang, Smith & Thomas, 1940); *Synamplexus* Grabau, 1928.

(*e*) Subfamily Carcinophyllinae (tentatively referred here)

Solitary corals with prominent columella structure formed by the counter-septum, septa composed of stout trabeculae at moderate angle of inclination and embedded in lamellar tissue. Carboniferous.

(1) *Rylstonia* Hudson & Platt, 1927 (figure 7, plate 4).

Genotype: *R. benecompacta* Hudson & Platt, 1927. Viséan.

Cornute or cylindro-cornute corallum, prominent columella splitting into septal lamellae and tabellae in late stages, septa composed of lamellar tissue in early stages but of stout trabeculae in late stages, minor septa short, tabulae steeply inclined to the periphery, dissepiments may occur. Lower Carboniferous.

Synonym: *Hettonia* Hudson & Anderson, 1928.

(2) *Carcinophyllum* Thomson & Nicholson, 1876 (figure 8, plate 4).

Genotype: *C. Kirsopianum* Thomson, 1880. Lower Carboniferous.

Like *Rylstonia* but of larger size, well-developed lonsdaleioid dissepiments, elaborate open axial column and very thick septa composed of stout trabeculae. Carboniferous (Viséan-Uralian).

Synonym: *Axophyllum* Edwards & Haime.

2. Suborder CANINIACEA

Solitary and colonial corals, skeleton fibro-lamellar, septa composed of fibre fascicles not grouped into trabeculae, axial structures common. Lower Carboniferous-Permian.

Family I. Plerophyllidae

Solitary corals, septa composed of fibre fascicles, wall thick, no dissepiments except in specialized members. Lower Carboniferous-Permian.

(*a*) Subfamily Lophophyllidiinae

Solitary corals, columella usually prominent, fibre fascicles in septa grouped in various ways in advanced forms. Upper Carboniferous-Permian.

(1) *Lophophyllidium* Grabau, 1928 (figures 9, 10, 11*a*, *b*, plate 4).

Genotype: *Cyathaxonia proliferum* McChesney, 1860. Upper Carboniferous.

> Small curved ceratoid corallum, septa thick, composed of fibre fascicles perpendicular to the septal plane in young stages but variously disposed in adult stages, minor septa short, columella composed of long fibre fascicles, occasionally open in advanced forms, tabulae domed, no dissepiments. Upper Carboniferous-Permian.

Synonyms: *Sinophyllum* Grabau, 1928; *Malonophyllum* Okulitch & Albritton, 1937; *Leonardophyllum* Moore & Jeffords, 1941.

Subgenus *Lophamplexus* Moore & Jeffords, 1941.

Subgenotype: *L. eliasi* Moore & Jeffords, 1941. Permian.

> *Lophophyllidium* with reduced columella.

Subgenus *Lophocarinophyllum* Grabau, 1922.

Subgenotype: *L. acanthiseptum* Grabau, 1922. Upper Carboniferous.

> *Lophophyllidium* with carinate septa probably of flanging-plates type.

Synonym: *Lophotichium* Moore & Jeffords, 1945.

(2) *Verbeekiella* Gerth, 1921 (figure 12*a*, *b*, plate 4).

Genotype: *Verbeekia permica* Penecke, 1908. Permian.

> Conical or trochoid corallum, septal structure like *Lophophyllidium*, large open axial column, numerous incomplete domed tabulae, no dissepiments. Permian.

Synonym: *Zelaeophyllum* Heritsch, 1936.

(3) *Timorphyllum* Gerth, 1921.

Genotype: *T. wanneri* Gerth, 1921. Permian.

> Trochoid or ceratoid corallum, septa thin, composed of fibre fascicles perpendicular to septal plane, counter-septum conspicuously larger, minor septa short, tabulae numerous and domed, no dissepiments. Upper Carboniferous-Permian.

Synonyms: *Soshkineophyllum* Grabau, 1928; *Stereostylus* Jeffords, 1947.

(*b*) Subfamily Plerophyllinae

Solitary corals, several of the major septa conspicuously larger than the rest, fibre fascicles grouped in various ways in advanced species, dissepiments may occur in specialized members. Lower Devonian-Permian.

(1) *Pentaphyllum* de Koninck, 1872.

Genotype: *P. armatum* de Koninck, 1872. Carboniferous.

Small ceratoid corallum with deep calice, C 2A, 2KL,* large, septa composed of lamellar tissue only, minor septa rudimentary, tabulae few, no dissepiments. Middle Devonian-Upper Carboniferous.

Synonyms: *Oligophyllum* Počta, 1902; *Cryptophyllum* Carruthers, 1919; *Pseudocryptophyllum* Easton, 1944?.

(2) *Plerophyllum* Hinde, 1890.

Genotype: *P. australe* Hinde, 1890. Permian.

Small curved ceratoid corallum, C, 2A, 2KL large, septa composed of fibre fascicles grouped into arched patches in the septal plane, tabulae numerous and domed, no dissepiments, wall may be degenerate. Permian.

Synonym: *Timorosmilia* Koker, 1924.

Subgenus *Rhopalolasma* Hudson, 1936 (figure 13, plate 4).

Subgenotype: *R. tacheblastum* Hudson, 1936. Tournaisian.

Primitive *Plerophyllum* with partly lamellar and partly fibro-lamellar tissue.

Synonyms: *Disophyllum* Tolmakoff, 1924; *Claviphyllum* Hudson, 1942; *Kinkaidia* Easton, 1944; *Empodesma* Moore & Jeffords, 1945.

Subgenus *Tachyelasma* Grabau, 1922.

Subgenotype: *T. cha* Grabau, 1922. Permian.

Plerophyllum with K reduced in early stage.

Synonyms: *Ufimia* Stuckenberg, 1895; *Hexalasma* Soshkina, 1928.

Subgenus *Prionophyllum* Schindewolf, 1942.

Subgenotype: *P. crassoseptatum* Schindewolf, 1942. Permian.

Plerophyllum with K reduced in early stages and with zigzag fibres in the septa.

Subgenus *Pleramplexus* Schindewolf, 1940.

Subgenotype: *P. similei* Schindewolf, 1940. Permian.

Plerophyllum with shortened and less swollen septa.

Synonym: *Pentamplexus* Schindewolf, 1940.

(3) *Calophyllum* Dana, 1846.

Genotype: *Turbinolia donatiana* King, 1848. Permian.

Small ceratoid corallum, C, 2A, K large, fibre fascicles perpendicular to septal plane, tabulae few, no dissepiments. Lower Carboniferous-Permian.

Synonyms: *Polycoelia* King, 1849; *Gerthia* Grabau, 1928.

Subgenus *Tetralasma* Schindewolf, 1942.

Subgenotype: *T. quadriseptata* Schindewolf, 1942. Lower Carboniferous.

Primitive *Polycoelia* with an entirely lamellar kind of skeleton.

Synonym: *Weissermelia* Schindewolf, 1942 (*non Weissermelia* Lang Smith & Thomas, 1940).

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* For septal notation, see Hudson (1935).

(4) *Endothecium* Koker, 1924.

Genotype: *E. apertum* Koker, 1924. Permian.

Small ceratoid corallum, septa stout, differentiation not apparent, an inner wall composed of patches of fibre fascicles developed in late stages, tabulae few, no dissepiments. Permian.

(5) *Prosmilia* Koker, 1924.

Genotype: *P. zaphrentoides* Koker, 1924. Permian.

Curved to ceratoid or subcylindrical corallum, rejuvenescence common, septa thin and long, C, 2A, K large, fibre fascicles grouped in various ways near the wall, tabulae numerous and domed, well-developed lonsdaleioid dissepiments. Permian.

(6) *Duplophyllum* Koker, 1924.

Genotype: *D. zaphrentoides* Koker, 1924. Permian.

Ceratoid corallum, septa long, major reaching axis, slightly swollen, minor contratingent, fibre fascicles parallel in inner portion of septa, variously grouped near the wall, tabulae domed, no dissepiments. Permian.

(7) *Lytvelasma* Soshkina, 1925 (tentatively referred here).

Genotype: *L. asymmetricum* Soshkina, 1925. Permian.

Turbinate or ceratoid corallum, thick septa, contiguous in young stages, fibre fascicles perpendicular to septal plane, major septa reaching the centre, minor short, a cardinal fossula may be present, tabulae distant, no dissepiments. Upper Carboniferous-Permian.

Synonym: *Euryphyllum* Hill, 1937?.

(8) *Amplexicarinia* Soshkina, 1928.

Genotype: *A. muralis* Soshkina, 1928. Permian.

Small trochoid corallum, septa short and bent to meet each other, forming complete or incomplete inner wall, septa composed of fibre fascicles, tabulae complete and few, divided by the inner wall into an inner and an outer series, no dissepiments. Permian.

Synonym: *Paralleynia* Soshkina, 1928.

(9) *Homalophyllum* Simpson, 1900.

Genotype: *H. angulus* (Rominger), 1876. Devonian.

Calceoloid corallum, septa reaching centre, peripheral zone contiguous, septal structure like *Plerophyllum*. Devonian.

Family II. CANINIIDAE

Solitary, rarely weakly compound corals, skeleton fibro-lamellar except in primitive forms, pronounced cardinal fossula, tabulae numerous, wall thin, dissepiments mostly present. Lower Carboniferous-Permian.

(1) *Caninia* Michelin *in* Gervais, 1840.

Genotype: *C. cornucopiae* Michelin, 1847. Tournaisian.

Small trochoid corallum, lamellar to fibro-lamellar skeleton, septa not reaching axis, open fossula with aborted cardinal septum, tabulae complete and flat, down-turned at periphery, dissepiments absent or only developed in late stages. Lower Carboniferous-Permian.

Synonyms: *Cyathopsis* d'Orbigny, 1849; *Para-caninia* Chi, 1937; *Faviphyllum* Hall, 1852.

(2) *Bothrophyllum* Trauchold, 1879 (figure 16, plate 5).

Genotype: *B. conicum* Trauchold, 1879. Upper Carboniferous.

Trochoid or cylindrical corallum, septa not quite reaching axis, composed of fibre fascicles grouped into patches in septal plane, wide tabularium and narrow dissepimentarium, weak open fossula, tabulae arched and close together, down-turned near periphery. Lower Carboniferous (Viséan)-Permian.

Synonyms: *Faviphyllum* Hall, 1852; *Rossophyllum* Stuckenberg, 1888; *Pseudocaninia* Stuckenberg, 1888; *Pseudozaphrentoides* Stuckenberg, 1904; *Caninophyllum* Lewis, 1929; *Caninella* Gorsky, 1938; *Vesiculophyllum* Easton, 1944.

Subgenus *Timania* Stuckenberg, 1895.

Subgenotype: *T. schmidti* Stuckenberg, 1895. Carboniferous.

Large *Bothrophyllum* with long septa grouped into series and with narrow dissepimentarium.

Subgenus *Lophophrentis* Chi, 1935.

Subgenotype: *L. trilobatum* Chi, 1935. Middle Carboniferous.

Bothrophyllum with short thin septa grouped into series and with a weak axial structure.

(3) *Gshelia* Stuckenberg, 1888.

Genotype: *G. rouilleri* Stuckenberg, 1888. Upper Carboniferous.

Phacelloid corallites, septa not reaching axis, fibre fascicles perpendicular to septal plane, equally thickened in tabularium, minor septa short, few dissepiments. Carboniferous (Viséan)-Uralian.

Synonyms: *Craterophyllum* Barbour, 1911; *Barbouria* Lang, Smith & Thomas, 1940; *Peetzia* Tolmakoff, 1924; *Tschussovskenia* Dobrolyubova, 1935; *Caninostrotion* Easton, 1943.

(4) *Heterocaninia* Yabe & Hayasaka, 1920.

Genotype: *H. thalotabulatum* Yabe & Hayasaka, 1920. Carboniferous.

Large cylindrical or trochoid corallum, numerous long septa, prominent cardinal fossula, fibre fascicles perpendicular to the septal plane, thickened in cardinal sectors, numerous globose dissepiments, incomplete arched tabulae passing into tabellae. Lower Carboniferous.

Synonyms: *Yabeella* Yü, 1931; *Kweichouphyllum* Yü, 1931; *Clisiophyllites* Löweneck, 1932.

(5) *Siphonophyllia* Scouler *in* McCoy, 1844 (figure 14, plate 4).

Genotype: *S. cylindrica* Scouler, 1844. Lower Carboniferous.

Large trochoid corallum, septa composed of lamellar to fibro-lamellar tissue, major septa reaching the axis, minor short, both dilated, closed cardinal fossula with aborted cardinal septum, tabulae flat or concave, large lonsdaleioid dissepiments. Carboniferous.

Subgenus *Uralinia* Stuckenberg, 1895.

Subgenotype: *U. multiplex* Stuckenberg, 1895. Upper Carboniferous.

Siphonophyllia with irregular lonsdaleioid dissepiments and asymmetrically disposed septa.

Synonym: *Pseudouralinia* Yü, 1931.

Subgenus *Cystiphrentis* Yü, 1931 (figure 15, plate 5).

Subgenotype: *C. kolaohoensis* Yü, 1931. Lower Carboniferous.

Small *Siphonophyllia* with discontinuous septa in adult stage and with ill-defined lonsdaleioid peripheral zone.

(6) *Keyserlingophyllum* Stuckenberg, 1895.
Genotype: *K. obliquum* Stuckenberg, 1895. Upper Carboniferous.

Large trochoid corallum, septal structure like Siphonophyllia, septa long, reaching axis and grouped into four series, with four prominent fossulae, narrow lonsdaleioid zone, tabulae close together and flat. Upper Carboniferous.

Synonym: *Humboldtia* Stuckenberg, 1895.

Family III. LONSDALEIIDAE

Solitary and colonial corals, skeleton dominantly fibro-lamellar, axial column prominent, wall thin, dissepiments numerous. Lower Carboniferous-Permian.

(*a*) Subfamily Dibunophyllinae

Solitary and weakly compound corals, septa composed of fibre fascicles perpendicular to septal plane but variously disposed in advanced forms, column open, septa reaching periphery. Lower Carboniferous (Viséan)-Permian.

(1) *Dibunophyllum* Thomson & Nicholson, 1876 (figure 17, plate 5).
Genotype: *D. muirheadi* Thomson & Nicholson, 1876. Viséan.

Large trochoid to subcylindrical corallum, numerous long major septa, wide complex axial column with a median plate, few septal lamellae and numerous tabellae, septa composed of fibre fascicles slightly dilated in tabularium. Lower Carboniferous (Viséan)-Upper Carboniferous.

Synonyms: *Histiophyllum* Thomson, 1879; *Rhodophyllum* Thomson, 1874.
Subgenus *Arachnelasma* Grabau, 1922.
Subgenotype: *A. sinense* Grabau, 1922. Viséan.

Dibunophyllum with suppressed minor septa and not well-defined axial column.

Synonym: *Yuanophyllum* Yü, 1931.

(2) *Corwenia* Smith & Ryder, 1926 (figure 18, plate 5).
Genotype: *Lonsdaleia rugosa* McCoy, 1849. Viséan.

Phacelloid corallites, septa thin, composed of fibre fascicles perpendicular to septal plane, axial column weak, numerous dissepiments. Lower Carboniferous (Viséan)-Lower Permian.

Synonym: *Yatsengia* Huang, 1932.

(3) *Iranophyllum* Douglas, 1936.
Genotype: *I. splendens* Douglas, 1936. Permian.

Large trochoid to subcylindrical corallum, long septa occasionally with tertiary and quaternary cycles, composed of fibre fascicles variously disposed or split up into longitudinal dissepiments, axial column as in *Dibunophyllum*, tabulae and dissepiments numerous. Permian.

(4) *Gangamophyllum* Gorsky, 1938.
Genotype: *G. boreale* Gorsky, 1938. Carboniferous.

Large trochoid to subcylindrical corallum, septal structure like *Dibunophyllum*, inner portion of septa dilated, outer portion interrupted by lonsdaleioid dissepiments, large axial column composed of dilated involute septal lamellae and tabellae without well-marked median plate. Carboniferous.

(*b*) Subfamily Lonsdaleiinae

Colonial corals with open axial column and wide lonsdaleioid dissepiments. Carboniferous-Permian.

(1) *Lonsdaleia* McCoy, 1849 (figure 19, plate 5).

Genotype: *L. duplicata* Martin, 1809. Viséan.

Phacelloid or cerioid corallites, wide-open complex column with median plate, formed by the counter-septum and arched tabellae, well-developed lonsdaleioid dissepiments, septa composed of fibre fascicles perpendicular to septal plane. Lower Carboniferous (Viséan)-Permian.

Synonyms: *Axinura* Castlenau, 1843; *Actinocyathus* d'Orbigny, 1849; *Acrocyathus* d'Orbigny, 1849; *Stylidophyllum* de Fromentel, 1861; *Arachnastraea* Yabe & Hayasaka, 1916; *Diphystrotion* Smith & Lang, 1930.

Subgenus *Lithostrotionella* Yabe & Hayasaka, 1915.

Subgenotype: *L. unicum* Yabe & Hayasaka, 1915. Permian.

Lonsdaleia with narrow dissepimentarium and with simple axial column.

Synonym: *Stelechophyllum* Tolmakoff, 1933.

Subgenus *Polythecalia* Yabe & Hayasaka, 1916.

Subgenotype: *P. confluens* Yabe & Hayasaka, 1916. Permian.

Plocoid *Lonsdaleia* with very wide irregular dissepimentarium.

Synonyms: *Cystiphora* Yabe & Hayasaka, 1916; *Lonsdaleiastraea* Gerth, 1921; *Protolonsdaleiastraea* Gorsky, 1932.

(2) *Thysanophyllum* Nicholson & Thomson, 1876.

Genotype: *T. orientale* Nicholson & Thomson, 1876. Lower Carboniferous.

Phacelloid or cerioid corallites, septa lamellar or fibro-lamellar in structure, counter-septum conspicuously larger, forming a weak axial structure with arched tabellae, well-developed lonsdaleioid dissepiments. Lower Carboniferous.

(*c*) Subfamily Waagenophyllinae

Small colonial corals, compact and complex axial column, usually narrow dissepimentarium. Lower Carboniferous-Permian.

(1) *Siphonodendron* McCoy, 1849 (figure 20, plate 5).

Genotype: *S. aggregatum* McCoy, 1849. Lower Carboniferous.

Small phacelloid corallites, septa comparatively few, composed of perpendicular fibre fascicles, prominent axial column composed of long fibre fascicles radiating outwardly and upwardly, tabulae distant, tent-shaped, dissepiments few or absent. Lower Carboniferous.

Synonyms: *Schoenophyllum* Simpson, 1900; *Cystidendron* Schindewolf, 1927; *Stylostrotion* Chi, 1935.

(2) *Waagenophyllum* Hayasaka, 1924 (figure 21, plate 5).

Genotype: *Lonsdaleia indica* Waagen & Wentzel, 1886. Permian.

Phacelloid corallites, septa composed of fibre fascicles grouped into patches, compact axial column with median plate, numerous conical tabellae and steeply inclined tabulae from the periphery, dissepiments few or absent. Upper Carboniferous-Permian.

Subgenus *Wentzelella* Grabau (1931 *in* Chi, 1932 *in* Huang).
Subgenotype: *Lonsdaleia salinaria* Waagen & Wentzel, 1886. Permian.

Cerioid *Waagenophyllum* with well-developed dissepimentarium.

Subgenus *Heritschia* Moore & Jeffords, 1941.
Subgenotype: *H. girtyi* Moore & Jeffords, 1941. Permian.

Large phacelloid *Waagenophyllum* with wide dissepimentarium, flat tabulae and almost compact axial column.

Synonym: *Lonsdaleoides* Gerth, 1916?.

3. Suborder STREPTELASMACEA

Solitary and colonial corals, skeleton predominantly fibrous, septa composed of compact trabeculae or of contiguous fibre fascicles not clearly grouped into trabeculae. Middle Ordovician-Carboniferous.

Family I. STREPTELASMIDAE

Solitary, rarely weakly compound corals, septa composed of stout trabeculae (except in primitive forms) undergoing various modifications, tabulae domed, dissepiments present only in advanced forms. Middle Ordovician-Middle Devonian.

(1) *Streptelasma* Hall, 1847 (figures 22, 23, plate 5).
Genotype: *S. corniculum* Hall, 1847. Ordovician.

Trochoid to subcylindrical corallum, narrow cardinal fossula, bilateral symmetry of septa apparent, septa thick, reaching axis, composed of contiguous fibre fascicles not grouped into trabeculae, with denticulate inner edge and more or less invested with lamellar tissue near the periphery, tabulae convex, no dissepiments. Middle Ordovician-Middle Devonian.

Synonym: *Cionelasma* Simpson, 1900?.

Subgenus *Lambeophyllum* Okulitch, 1938 (figure 25, plate 5).
Subgenotype: *Streptelasma profundum* Conrad, 1843. Ordovician.

Small primitive *Streptelasma* with few tabulae, septa composed of calcite fibres confluent with lamellar tissue filling interseptal loculi.

Subgenus *Palaeophyllum* Billings, 1858.
Subgenotype: *P. rugosum* Billings, 1858. Middle Ordovician.

Phacelloid *Streptelasma* with well-defined trabeculae in the septa.

Subgenus *Kiaerophyllum* Wedekind, 1927.
Subgenotype: *K. kiaeri* Wedekind, 1927. Lower Silurian.

Streptelasma with anastomosing axial structure formed by denticulate inner edges of septa.

Synonym: *Grewingkia* Dybowski, 1873?.

Subgenus *Dybowskia* Wedekind, 1927 (*Brachyelasma* Lang, Smith & Thomas, 1940).
Subgenotype: *D. prima* Wedekind, 1927. Lower Silurian.

Amplexoid *Streptelasma*.

Synonym: *Rhegmatophyllum* Wedekind, 1927.

(2) *Siphonophrentis* O'Connell, 1914 (figure 26*a*, *b*, plate 5; figure 70, plate 9).

Genotype: *Caryophyllia gigantea* Lesueur, 1821. Middle Devonian.

Large cylindrical corallum, septa stout, structure as in *Streptelasma*, bilateral symmetry septa apparent, tabulae complete and domed, distinct siphonofossula, no dissepiments. Middle Devonian.

(3) *Dalmanophyllum* Lang & Smith, 1939 (figure 27, plate 5; figure 71, plate 9).

Genotype: *Cyathaxonia dalmani* Edwards & Haime, 1851. Upper Silurian.

Small trochoid or ceratoid corallum, very thick contiguous septa, major not reaching axis, minor very short, composed of subparallel stout trabeculae at low angle of inclination, large columella composed of long fibre fascicles, formed by counter-septum, tabulae thin and suppressed, no dissepiments. Middle Silurian-Upper Silurian.

(4) *Codonophyllum* Wedekind, 1927 (figures 24, 28, plate 5).

Genotype: *Streptelasma milne-edwardsi* Dybowski, 1873. Silurian.

Trochoid or cylindrical corallum, rarely compound, bilateral symmetry of septa apparent, septa thick and contiguous in peripheral region, major septa long and reaching axis, minor short, composed of very stout trabeculae, sclerodermites composite, fan-system of trabeculae pronounced, tabulae domed, close and incomplete, no dissepiments. Upper Ordovician-Upper Silurian.

Synonym: *Patrophontes* Lang & Smith, 1927.

Subgenus *Circophyllum* Lang & Smith, 1939 (*Rhysodes* Smith & Tremberth, 1927).

Subgenotype: *R. samsugnensis* Smith & Tremberth, 1927. Silurian.

Phacelloid *Codonophyllum* with complete and distant tabulae.

(5) *Pilophyllum* Wedekind, 1927 (figure 29, plate 5).

Genotype: *P. keyserlingi* Wedekind, 1927. Middle Silurian.

Subcylindrical to cylindrical corallum, septal structure like *Codonophyllum*, but developing lonsdaleioid dissepiments. Silurian.

(6) *Schlotheimophyllum* Smith, 1945.

Genotype: *Fungites patellatus* Schlotheim, 1820. Middle Silurian.

Large patellate corallum with reflexed calical platform and a central boss, septa thick and contiguous in peripheral region, composed of large composite trabeculae each forming a small fan-system of small trabeculae, inner portion of septa as in *Codonophyllum*, major septa reaching axis and involute, tabulae incomplete and close together, highly convex. Middle Silurian-Lower Devonian.

Synonyms: *Vesicularia* Rominger, 1876; *Cystiphorolites* Miller, 1889.

Subgenus *Chlamydophyllum* Počta, 1902.

Subgenotype: *C. obscurum* Počta, 1902. Lower Devonian.

Schlotheimophyllum with complete and distant tabulae.

Subgenus *Nevadaphyllum* Stumm, 1937.

Subgenotype: *N. masoni* Stumm, 1937. Middle Devonian.

Schlotheimophyllum with prominent narrow fossula, long involute septa and convex vesicular tabellae.

(7) *Chonophyllum* Edwards & Haime, 1850.

Genotype: *Cyathophyllum perfoliatum* Goldfuss, 1826. Silurian.

Large patellate corallum, septal structure like *Schlotheimophyllum* but reduced to separate segments on successive tabular floors. Middle Silurian-Middle Devonian.

(8) *Craterophyllum* Foerste, 1909.

Genotype: *C. volcanicum* Foerste, 1909. Silurian.

Large patellate corallum with reflexed calical border, outer portion of septa split into separate strands and small tabellae, inner portion of septa degenerate. Silurian.

Synonyms: *Briantia* Barrois, 1889; *Naos* Lang, 1926; *Pseudochonophyllum* Soshkina, 1937.

(9) *Plasmophyllum* Dybowski, 1873 (tentatively referred here).

Genotype: *Cyathophyllum goldfussi* Edwards & Haime, 1851. Devonian.

Trochoid corallum, very thick contiguous septa breaking up into separate sections on successive floors and composed of very stout erect composite trabeculae. Middle Devonian.

Synonym: *Stereophyllum* Schlüter, 1889.

Family II. DINOPHYLLIDAE

Solitary and colonial corals, septa composed of smooth stout trabeculae at a low angle of inclination, fibre fascicles long and acutely pinnate, lamellar tissue well-developed and investing the septa. Lower Silurian-Middle Devonian.

(1) *Dinophyllum* Lindström, 1882 (figures 30, 31, plate 6; figure 72, plate 9).

Genotype: *D. involutum* Lindström, 1882. Silurian.

Large trochoid or ceratoid corallum, prominent cardinal fossula, major septa reaching axis and involute, composed of stout trabeculae with acutely pinnate fibre fascicles at a low angle of inclination and invested with lamellar tissue, tabulae convex, no dissepiments. Middle Silurian-Lower Devonian.

Subgenus *Heterophrentis* Billings, 1875 (figure 32, plate 6; figure 73, plate 9).

Subgenotype: *H. spatiosa* Billings, 1875 (=*H. prolifica* Billings, 1858). Devonian.

Dinophyllum with septa withdrawn from the axis and with less convex tabulae.

Subgenus *Scenophyllum* Simpson, 1900.

Subgenotype: *Zaphrentis conigera* Rominger, 1876. Middle Devonian.

Cylindrical *Dinophyllum* with strongly arched tabulae forming an axial structure.

Subgenus *Lamprophyllum* Wedekind, 1927.

Subgenotype: *L. degeeri* Wedekind, 1927. Silurian.

Dinophyllum with septa which have withdrawn from the axis and with dissepiments.

(2) *Neospongophyllum* Wedekind, 1922 (figures 33–4, plate 6).

Genotype: *N. variable* Wedekind, 1922. Middle Devonian.

Small phacelloid corallites, rarely simple, septa few and thick, major reaching axis, minor very short or rudimentary, composed of stout trabeculae at low angles of inclination and embedded in lamellar tissue, tabulae flat and concave, dissepiments lonsdaleioid. Middle Devonian-Upper Devonian.

Synonyms: *Loepophyllum* Wedekind, 1925; *Lyliophyllum* Kelus, 1939.

(3) *Stringophyllum* Wedekind, 1921 (figures 35*a*–*b*, 36, plate 6).

Genotype: *S. normale* Wedekind, 1921. Middle Devonian.

Large trochoid to subcylindrical corallum, septal structure like *Neospongophyllum*, bilateral symmetry prominent, major septa long, minor discontinuous, tabulae incomplete and deeply concave, dissepiments irregular and large. Lower and Middle Devonian.

Synonyms: *Schizophyllum* Wedekind, 1925; *Diversophyllum* Sloss, 1939.

(4) *Mesophyllum* Schlüter, 1889 (figure 37, plate 6).

Genotype: *M. defectum* Schlüter, 1889. Middle Devonian.

Large trochoid to cylindrical corallum, bilateral symmetry of septa apparent, septa composed of stout smooth trabeculae at a low angle of inclination and more or less discrete, invested with lamellar tissue, incomplete tabulae and numerous dissepiments. Middle Devonian.

Synonyms: *Cosmophyllum* Vollbrecht *in* Wedekind, 1922; *Atelophyllum* Wedekind, 1922; *Lekanophyllum* Wedekind, 1922; *Hemicosmophyllum* Wedekind, 1925; *Dialytophyllum* Wedekind, 1925; *Arcophyllum* Marcov, 1926.

(5) *Nalivskinella* Soshkina, 1941 (tentatively referred here).

Genotype: *N. profundum* Soshkina, 1941. Middle Devonian.

Ceratoid corallum, major septa stout, minor rudimentary, tabulae flat and complete, lonsdaleioid dissepiments developed in a late stage. Middle Devonian.

Family III. PYCNACTIDAE

Solitary corals, bilateral symmetry of septa apparent, septa composed of long, acutely disposed fibre fascicles not grouped into trabeculae, dissepiments developed in advanced forms. Lower Silurian-Upper Devonian.

(1) *Pycnactis* Ryder, 1926.

Genotype: *Hippurites mitratus* Schlotheim, 1820. Silurian.

Trochoid corallum, very thick contiguous septa with distinct bilateral symmetry, prominent cardinal fossula, major septa nearly reaching axis, minor very short, tabulae suppressed, no dissepiments. Silurian.

Synonyms: *Cymatelasma* Hill & Butler, 1936.*

(2) *Phaulactis* Ryder, 1926 (figure 38, plate 6).

Trochoid to subcylindrical corallum, apparent symmetry of septa, septa thin in dissepimentarium and thick in tabularium, usually invested with lamellar tissue and composed of acutely pinnate fibre fascicles, tabulae flat, usually suppressed. Silurian.

Synonyms: *Mesactis* Ryder, 1926; *Lycophyllum* Wedekind, 1927; *Lycocystiphyllum* Wedekind, 1927: *Hemicystiphyllum* Wedekind, 1927; *Desmophyllum* Wedekind, 1927; *Semaeophyllum* Vollbrecht, 1928; *Hercophyllum* Jones, 1936.

(3) *Aulacophyllum* Edwards & Haime, 1850.

Genotype: *Caninia sulcata* d'Orbigny, 1850. Middle Devonian.

Large trochoid corallum, bilateral symmetry of septa apparent, prominent fossula, dilatation of septa confined to tabularium, tabulae close together and incomplete, dissepiments globose. Devonian.

Synonyms: *Hallia* Edwards & Haime, 1850; *Coelophyllum* Hall, 1883; *Odontophyllum* Simpson, 1900.

Subgenus *Papiliophyllum* Stumm, 1937.

Subgenotype: *P. elegantulum* Stumm, 1937. Middle Devonian.

Aulacophyllum with septa which have withdrawn from the axial and also the peripheral region.

Synonym: *Eurekaphyllum* Stumm, 1937.

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* *Cymatelasma corniculum*, the genotype, is a species of *Pycnactis*; *Cymatelasma multiseptatum* is *Dinophyllum involutum*; *Cymatelasma carinatum* is a species of *Spongophylloides*.

(4) *Ceratophyllum* Gürich, 1896 (figure 39, plate 6; figure 74, plate 9).

Genotype: *C. typus* Gürich, 1896.

Large curved trochoid to cylindrical corallum, bilateral symmetry of septa apparent, prominent fossula, counter-lateral sectors entirely suppressed, dilatation of fibre fascicles confined to axial region in the adult stage, numerous incomplete tabulae and globose dissepiments. Devonian.

Synonyms: *Digonophyllum* Wedekind, 1923; *Ptenophyllum* Wedekind, 1923; *Mochlophyllum* Wedekind, 1923; *Glossophyllum* Wedekind, 1924; *Zonodigonophyllum* Vollbrecht, 1926; *Enteleiophyllum* Walther, 1928; *Pseudocosmophyllum* Wedekind & Vollbrecht, 1932; *Uralophyllum* Soshkina, 1936.

(5) *Heliophyllum* Hall MS. *in* Dana, 1848 (figure 40, plate 6).

Genotype: *Strombodes helianthoides* Goldfuss, Hall, 1843. Devonian.

Simple or weakly compound corals, septa in young stages composed of acutely pinnate fibre fascicles, in adult stages dilated in the tabularium, thin in dissepimentarium, with numerous curved flanges, dissepiments globose. Middle Devonian.

Subgenus *Billingsastraea* Grabau, 1917.

Subgenotype: *Phillipsastraea verneuili* Edwards & Haime, 1851. Devonian.

Thamnastraeoid *Heliophyllum.*

(6) *Zonophyllum* Wedekind, 1924 (tentatively referred here).

Genotype: *Z. duplicatum* Wedekind, 1924. Middle Devonian.

Small cornute corallum, septa very thick and contiguous in early stages, breaking into separate segments in the late stage except in axial region, interseptal structure cystiphor. Middle Devonian.

Synonyms: *Legnophyllum* Wedekind, 1924; *Pseudozonophyllum* Wedekind, 1924; *Pseudomicroplasma* Soshkina, 1941.

(7) *Acrophyllum* Thomson & Nicholson, 1876.

Genotype: *Clisiophyllum oneidense* Billings, 1859. Middle Devonian.

Large trochoid or ceratoid corallum, septa composed of dilated, acutely pinnate fibre fascicles in young stages, dilatation of septa confined to tabularium or disappearing in adult stages, steeply inclined dissepiments, highly convex tabulae giving rise to an axial structure. Middle Devonian.

Family IV. Disphyllidae

Solitary and colonial corals, septa composed of trabeculae in one or more fan-systems, dissepiments present. Middle Silurian-Upper Devonian.

(*a*) Subfamily Acanthophyllinae

Solitary and weakly compound corals, septa composed of broad fan-systems of trabeculae which may undergo various modifications, bilateral symmetry of septa pronounced, dissepiments numerous. Upper Silurian-Upper Devonian.

(1) *Acanthophyllum* Dybowski, 1873 (figure 41, plate 6).

Genotype: *Cyathophyllum heterophyllum* Edwards & Haime, 1851. Middle Devonian.

Large trochoid corallum with long major and minor septa composed of several fan-systems of trabeculae, trabeculae in inner portion erect and slender, those in outer portion undergoing various modifications, tabulae close together and with a median notch, dissepiments numerous and globose. Upper Silurian-Upper Devonian.

Synonyms: *Mesophylloides* Wedekind, 1923; *Dohmophyllum* Wedekind, 1923; *Astrophyllum* Wedekind, 1924; *Rhopalophyllum* Wedekind, 1924; *Stenophyllum* Wedekind, 1925.

Subgenus *Xystriphyllum* Hill, 1939.

Subgenotype: *X. dunstani* Etheridge, 1911. Middle Devonian.

Cerioid *Acanthophyllum.*

Subgenus *Eddastraea* Hill, 1942*d.*

Subgenotype: *Phillipsastraea grandis* Dun *in* Benson, 1918. Middle Devonian.

Plocoid *Acanthophyllum.*

Subgenus *Tortophyllum* Sloss, 1939.

Subgenotype: *T. cycticum* (Winchell), 1866. Middle Devonian.

Trochoid to subcylindrical *Acanthophyllum* with axially convex incomplete tabulae forming a calical boss. Middle Devonian.

(2) *Ptychophyllum* Edwards & Haime, 1850.

Genotype: *P. stokesi* Edwards & Haime, 1850. Upper Silurian.

Large trochoid, sometimes patellate corallum, septal structure like *Acanthophyllum,* major septa long and involute at axis, minor usually degenerate, thus producing herring-bone dissepiments, tabulae incomplete and domed. Middle Silurian-Upper Devonian.

Synonyms: *Trematophyllum* Wedekind, 1924; *Sparganophyllum* Wedekind, 1924; *Mictophyllum* Lang & Smith, 1939.

(*b*) Subfamily Disphyllinae

Solitary and colonial corals, septa composed of trabeculae without any marked area of divergence, fibre fascicles variously arranged in trabeculae, tabulae flat, dissepiments globose. Middle Silurian-Upper Devonian.

(1) *Disphyllum* de Fromentel, 1861.

Genotype: *Cyathophyllum caespitosum* Goldfuss, 1826. Middle Devonian.

Phacelloid corallites, major septa not quite reaching axis, minor short, trabeculae subparallel, moderately inclined, sclerodermites mostly simple, tabulae differentiated into a flat axial and an inclined periaxial series, dissepiments numerous and globose. Middle Silurian-Upper Devonian.

Synonyms: *Cylindrophyllum* Simpson, 1900; *Schlüteria* Wedekind, 1922; *Megaphyllum* Soshkina, 1941; *Ceratinella* Soshkina, 1941.

(2) *Prismatophyllum* Simpson, 1900.

Genotype: *Cyathophyllum rugosum* Edwards & Haime, 1851. Middle Devonian.

Cerioid corallites, septal structure like *Disphyllum,* but may be carinate, dissepimentarium wide, tabulae incomplete, differentiated into axial and periaxial series. Middle Devonian and Upper Devonian.

Synonyms: *Hexagonaria* Gürich (=*Hexagoniophyllum* Gürich), 1896; *Polyphyllum* de Fromentel, 1861.

(3) *Temeniophyllum* Walther, 1928 (figures 42, 43, plate 6).

Genotype: *T. latum* Walther, 1928. Middle Devonian.

Simple or weakly phacelloid, interseptal structure like *Disphyllum,* septal trabeculae stout, forming more than one fan-system, contiguous periphery or at inner wall, fibre fascicles may occur in interseptal loculi at inner wall. Middle Devonian and Upper Devonian.

Synonyms: *Kunthia* Schlüter, 1885.

Subgenus *Charactophyllum* Simpson, 1900 (figure 44*a*, *b*, plate 7).

Subgenotype: *Campophyllum nanum* Hall & White, 1872. Upper Devonian.

Temeniophyllum with trabeculae forming a sharp curve near the periphery.

(4) *Ceriophyllum* Wedekind, 1923 (figures 45*a*, *b*, 46, plate 7).

Genotype: *C. heiligensteini* Wedekind, 1923. Middle Devonian.

Trochoid or ceratoid corallum, septa numerous, major reaching the axis, trabeculae regularly inclined, sclerodermites well separated and expanding periodically, thus producing regular carinae, tabulae close together and incomplete, dissepiments numerous and globose. Middle Devonian and Upper Devonian.

Synonym: *Spinophyllum* Wedekind, 1923.

(5) *Cyathophyllum* Goldfuss, 1826.

Genotype: *C. dianthus* Goldfuss, 1826. Middle Devonian.

(6) *Aphrophyllum* Smith, 1920 (tentatively referred here).

Genotype: *A. hallense* Smith, 1920. Viséan.

Large weakly phacelloid corallites, septal structure like that of *Temeniophyllum*, lonsdaleioid dissepiments well developed. Lower Carboniferous (Viséan).

(*c*) Subfamily Phacellophyllinae

Colonial and solitary corals, trabeculae with a marked area of divergence, fibre fascicles variously grouped. Lower Devonian-Upper Devonian.

(1) *Phacellophyllum* Gürich, 1896 (figure 47*a*, *b*, plate 7).

Genotype: *Lithodendron caespitosum* Goldfuss 1826. Devonian.

Phacelloid corallites, short septa composed of slender trabeculae with an area of divergence coinciding with one row of horseshoe dissepiments, tabulae complete and distant. Lower Devonian-Middle Devonian.

Synonyms: *Synaptophyllum* Simpson, 1900; *Peneckiella* Soshkina, 1941.

Subgenus *Thamnophyllum* Penecke, 1894.

Subgenotype: *T. stachei* Penecke, 1894. Lower Devonian.

Primitive *Phacellophyllum* with horseshoe dissepiments not yet well developed and with very short septa.

Subgenus *Trapezophyllum* Etheridge, 1899.

Subgenotype: *T. elegantulum* (Dun), 1898. Devonian.

Cerioid *Phacellophyllum* with long septa.

(2) *Macgeea* Webster, 1899 (figure 48*a*, *b*, plate 7).

Genotype: *Pachyphyllum solitarium* Whitfield, 1873. Upper Devonian.

Trochoid to cylindrical corallum, major septa not reaching axis, with an area of trabecular divergence coinciding with horseshoe dissepiments, trabeculae with composite sclerodermites, tabulae close and incomplete, outer rows of globose dissepiments. Middle Devonian (Givétian)-Upper Devonian (Frasnian).

Synonym: *Pexiphyllum* Walther, 1928.

(3) *Phillipsastraea* d'Orbigny, 1849 (figure 49, plate 7).
Genotype: *Astraea hennahi* Lonsdale, 1840. Devonian.

Plocoid corallum, septa composed of erect slender trabeculae, deviating from septal plane and variously reduced, with a marked area of divergence, tabular area narrow, dissepiments irregular and numerous. Lower Devonian-Upper Devonian.

Synonyms: *Pachyphyllum* Edwards & Haime, 1850; *Medusaephyllum* Roemer, 1855; *Smithia* Edwards & Haime, 1851; *Pseudoacervularia* Schlüter, 1881; *Haplothecia* Frech, 1885; *Radiastraea* Stumm, 1937.

Family V. CLISIOPHYLLIDAE

Solitary and colonial corals, septa composed of compact subparallel trabeculae at a moderate angle of inclination, axial structure prominent, dissepiments present. Carboniferous.

(*a*) Subfamily Clisiophyllinae

Solitary corals, septa numerous, bilateral symmetry apparent, long narrow fossula, axial column formed by differentiation of axial ends of all the major septa. Lower Carboniferous.

(1) *Palaeosmilia* Edwards & Haime, 1848.
Genotype: *P. murchisoni* Edwards & Haime, 1848. Lower Carboniferous.

Large solitary, rarely compound corals, numerous long major and minor septa composed of subparallel compact trabeculae with composite sclerodermites, long key-hole fossula, numerous arched incomplete tabulae and globose dissepiments. Lower Carboniferous.

Synonym: *Campophyllum* Edwards & Haime, 1850.

(2) *Cyathoclisia* Dingwall, 1926.
Genotype: *C. tabernaculum* Dingwall, 1926. Lower Carboniferous.

Solitary large corallum, numerous long major and minor septa, inner portion of major septa composed of very slender and erect trabeculae, sharply demarcated against outer portion, axial tabellae arched, dissepiments numerous and globose. Lower Carboniferous.

(3) *Clisiophyllum* Dana, 1846 (figure 50, plate 7).
Genotype: *C. keyserlingi* McCoy, 1849. Lower Carboniferous.

Curved trochoid to subcylindrical corallum, like *Palaeosmilia* in septal structure, minor septa short, axial column composed of slender erect trabeculae and arched tabellae, tabulae flat, sloping away from the axial region. Lower Carboniferous-Middle Carboniferous (Namurian).

Synonyms: *Auloclisia* Lewis, 1927; *Clisaxophyllum* Grabau *in* Chi, 1931.

(4) *Cyathaxonella* Stuckenberg, 1895.
Genotype: *C. gracilis* Stuckenberg, 1895. Lower Carboniferous.

Small trochoid corallum, septal structure and axial column like *Clisiophyllum*, septal lamellae in axial column few in number, no dissepiments. Lower Carboniferous (Viséan).

Synonym: *Cravenia* Hudson, 1928.

(5) *Aulophyllum* Edwards & Haime, 1850.

Genotype: *A. fungites* (Fleming), 1828. Viséan.

Curved trochoid to subcylindrical corallum, numerous major and minor septa composed of dilated fibre fascicles not clearly grouped into trabeculae, markedly cuspidate column with anastomosing septal lamellae and tabellae, tabulae sloping down to the periphery, dissepiments numerous and globose. Lower Carboniferous (Viséan)-Middle Carboniferous (Namurian).

Synonym: *Cyclophyllum* Duncan & Thomson, 1867.

(*b*) Subfamily Koninckophyllinae

Solitary and colonial corals, bilateral symmetry of septa not apparent, trabeculae slender to moderate in size, solid columella formed by the counter-septum alone, wall thin, dissepiments present. Carboniferous.

(1) *Koninckophyllum* Thomson & Nicholson, 1876* (figure 51, plate 7).

Genotype: *K. magnificum* Thomson & Nicholson, 1876. Viséan.

Curved trochoid to subcylindrical corallum, rarely compound, trabeculae slender and subparallel, columella solid, composed of long fibre fascicles, sometimes degenerate, numerous arched tabulae and globose dissepiments. Carboniferous (Tournaisian-Namurian).

Synonyms: *Lophophylloides* Stuckenberg, 1904; *Eostrotion* Vaughan, 1915; *Carinthiaphyllum* Heritsch, 1936; *Koninckocarina* Dobrolyubova, 1937.

(2) *Amygdalophyllum* Dun & Benson, 1920.

Genotype: *A. etheridgei* Dun & Benson, 1920. Viséan.

Large trochoid to subcylindrical corallum, numerous long major and minor septa composed of stout trabeculae which may undergo various modifications in the peripheral part, large solid columella composed of compact septal lamellae, numerous incomplete tabulae and steeply inclined dissepiments. Carboniferous (Viséan-Uralian).

Synonyms: *Echigophyllum* Yabe & Hayasaka, 1924; *Carniaphyllum* Heritsch, 1936.

(3) *Cionodendron* Benson & Smith, 1923.

Genotype: *C. columen* Benson & Smith, 1923. Viséan.

Phacelloid corallites, septa thick, composed of stout trabeculae at a moderate angle of inclination, large solid columella, complete tabulae and globose dissepiments. Lower Carboniferous.

(4) *Carruthersella* Garwood, 1913 (figure 52, plate 7).

Genotype: *C. compacta* Garwood, 1913. Viséan.

Trochoid or subcylindrical corallum, rarely compound, septa composed of stout trabeculae, well-defined lonsdaleioid dissepimentarium, large solid columella. Carboniferous (Viséan-Uralian).

Synonym: *Geyerophyllum* Heritsch, 1936.

Subgenus *Cionophyllum* Chi, 1931.

Subgenotype: *C. dibunum* Chi, 1931. Viséan.

Small *Carruthersella* with thin septa.

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* I have seen the specimen labelled as *Lophophyllum konincki* in the Mus. d'Hist. Nat. Paris, which is a zaphrentoid coral with weak columella (see Hill 1938–40, p. 86), evidently not congeneric with *Koninckophyllum magnificum*, the genotype of *Koninckophyllum*.

(5) *Nagatophyllum* Ozawa, 1925.

Genotype: *N. satoi* Ozawa, 1925. Lower Carboniferous.

Large trochoid to subcylindrical corallum, numerous long septa splitting into strands and tabellae as in *Naos*, prominent anastomosing axial column, incomplete tabulae and numerous dissepiments. Lower Carboniferous.

Synonym: *Symplectophyllum* Hill, 1934.

(6) *Lithostrotion* Fleming, 1828 (fig. 53, plate 7).

Genotype: *L. strictum* Fleming, 1828. Carboniferous.

Phacelloid or cerioid corallites, septa composed of very slender subparallel trabeculae, solid columella formed by elaboration of counter-septum, tabulae complete, tent-shaped, dissepiments few. Carboniferous (Viséan-Namurian).

Synonyms: *Nematophyllum* McCoy, 1849; *Lasmocyathus* d'Orbigny, 1849; *Chonaxis* Edwards & Haime, 1852; *Petalaxis* Edwards & Haime, 1852; *Fisherina* Stuckenberg, 1904; *Dorlodotia* Salée, 1920; *Cystistrotion* Schindewolf, 1927.

(7) *Diphyphyllum* Lonsdale, 1848.

Genotype: *D. concinnum* Lonsdale, 1848. Carboniferous.

Phacelloid corallites, septa composed of slender trabeculae as in *Lithostrotion*, columella weak or absent, tabulae flat or slightly arched, dissepiments numerous. Lower Carboniferous.

Synonyms: *Stylastraea* Lonsdale, 1845; *Nemistium* Smith, 1928; *Donophyllum* Fomichev, 1939.

(8) *Aulina* Smith, 1916.

Genotype: *A. rotiformis* Smith, 1916. Viséan.

Phacelloid to plocoid corallites, septa composed of slender erect trabeculae usually deviating from septal plane, axial ends of septa deviate to connect with each other, thus forming an aulos, tabulae divided into an outer and an inner series, numerous globose dissepiments. Carboniferous (Viséan-Namurian).

(9) *Orionastraea* Smith, 1916.

Genotype: *O. phillipsi* (McCoy) Smith, 1916. Viséan.

Plocoid corallites, septa composed of slender erect deviating trabeculae reduced in various ways, columella weak or absent, dissepiments numerous and irregular. Lower Carboniferous (Viséan).

Synonyms: *Cystiphorastraea* Dobrolyubova, 1935; *Ivanovia* Dobrolyubova, 1935.

(10) *Paralithostrotion* Gorsky, 1938 (tentatively referred here).*

Genotype: *P. jermolaevi* Gorsky, 1938. Carboniferous.

Slender phacelloid corallites, one row of inclined dissepiments, slightly dilated septa, minor septa rudimentary, weak columella and concave tabulae. Carboniferous.

Family VI. COLUMNARIIDAE

Colonial and solitary corals, skeleton predominantly fibrous, septa composed of very slender trabeculae which may be variously modified and grouped, bilateral symmetry of septa not apparent. Middle Ordovician-Upper Devonian.

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* *Paralithostrotion* shows a marked resemblance to *Neospongophyllum* of the Devonian except for the columella. I have included it in the *Koninckophyllinae* temporarily, pending further knowledge about its skeletal structure.

(*a*) Subfamily Columnariinae

Colonial and solitary corals, septa mostly composed of one row of subparallel trabeculae, dissepiments present only in advanced forms. Middle Ordovician-Upper Devonian.

(1) *Columnaria* Goldfuss, 1826 (figure 54, plate 7).

Genotype: *C. sulcata* Goldfuss, 1826. Middle Devonian.

Massive cerioid corallites, septa thin and variable in length, composed of one row of inclined slender trabeculae, tabulae complete and flat, wall thick, dissepiments occur very occasionally. Middle Ordovician-Middle Devonian.

Synonyms: *Favistella* Hall, 1847; *Cyathophylloides* Dybowski, 1873; *Loyolophyllum* Chapman, 1914.

(2) *Stauria* Edwards & Haime, 1850.

Genotypes: *Madrepora favosa* Linnaeus, 1758. Silurian.

Phacelloid or cerioid corallites, septal structure like *Columnaria*, four major septa larger than the others and joined at centre, minor septa short, tabulae incomplete, dissepiments very rarely occur. Silurian.

Synonym: *Decaphyllum* French, 1885.

Subgenus *Ceriaster* Lindström, 1883.

Subgenotype: *C. calamites* Lindström, 1883. Silurian.

Stauria with five major septa larger than others and joined at centre.

(3) *Eridophyllum* Edwards & Haime, 1850.

Genotype: *E. seriale* Edwards & Haime, 1850. Middle Devonian.

Phacelloid corallites, connected with each other by periodic calical expansion, septa thin, with curved flanges as in *Heliophyllum*, tabulae divided into axial and periaxial zones by an inner wall formed by deviation of inner septal ends, numerous globose dissepiments. Silurian-Devonian.

Synonyms: *Craspedophyllum* Dybowski, 1873; *Crepidophyllum* Nicholson, 1876; *Schistotoechelasma* Stewart, 1938.

Subgenus *Astraeophyllum* Nicholson & Hinde, 1874.

Subgenotype; *A. gracile* Nicholson & Hinde, 1874. Silurian.

Slender *Eridophyllum*, septa thin, reaching axis, flanges and inner wall rarely developed, tabulae distant and complete, no dissepiments.

(4) *Fasciphyllum* Schlüter, 1885 (figure 55, plate 7).

Genotype: *Fascicularia conglomeratum* Schlüter, 1880. Devonian.

Phacelloid corallites with thick lamellar wall, septa short, composed of slender trabeculae, tabulae flat, one row of large dissepiments occurs in interseptal loculi. Silurian-Devonian.

Synonym: *Densiphyllum* Dybowski, 1873?.

(5) *Grypophyllum* Wedekind, 1922 (figure 56, plate 7).

Genotype: *G. denkmanni* Wedekind, 1922. Middle Devonian.

Simple or phacelloid corals, septa long and thin, composed of slender trabeculae deviating from the septal plane, close tabulae, numerous dissepiments. Lower Devonian-Middle Devonian.

Synonyms: *Neostringophyllum* Wedekind, 1922; *Leptoenophyllum* Wedekind, 1925; *Moravophyllum* Kettnerova, 1932; *Radiophyllum* Hill, 1942?.

Subgenus *Lyrielasma* Hill, 1939 (figure 57*a*, *b*, plate 7; figure 75, plate 9).
Subgenotype: *Cyathophyllum subcaespitosum* Chapman, 1925. Devonian.

Grypophyllum with trabeculae markedly deviating from the septal plane.

(6) *Vepresiphyllum* Etheridge, 1920.
Genotype: *V. falciforme* Etheridge, 1920. Devonian.

Cerioid corallites, septa short, composed of one row of wavy trabeculae strongly deviated from the septal plane, deeply concave tabulae, no dissepiments. Devonian.

(*b*) Subfamily Entelophyllinae

Colonial and solitary corals, septa composed of one or more rows of erect trabeculae which may be grouped in various ways, dissepiments numerous. Middle Silurian-Middle Devonian.

(1) *Entelophyllum* Wedekind, 1927 (figure 58, plate 7; figure 59, plate 8).
Genotype: *Cyathophyllum articulatum* Wahlenberg, 1821 [1819]. Upper Silurian.

Phacelloid or simple corals, numerous long thin septa composed of slender trabeculae which may deviate from the septal plane, or interweave so as to produce a ropy appearance, tabulae differentiated into an axial domed series and periaxial concave series, dissepiments numerous and globose. Upper Silurian-Lower Devonian.

Synonyms: *Xylodes* Lang & Smith, 1927; *Neocystiphyllum* Wedekind, 1927; *Ptilophyllum* Smith & Tremberth, 1927 (*Weissermelia* Lang, Smith & Thomas, 1940); *Petrozium* Smith, 1930; *Tenuiphyllum* Soshkina, 1937.

(2) *Acervularia* Schweigger, 1819 (figure 60*a*, *b*, plate 8).
Genotype: *Madrepora ananas* Linnaeus, 1758. Silurian.

Cerioid or phacelloid corallites, trabeculae forming a distinct area of divergence, tertiary septa may occur in large species, tabulae flat, complete or incomplete, dissepiments numerous in advanced forms. Silurian.

Synonyms: *Diplophyllum* Hall, 1851; *Rhabdophyllum* Wedekind, 1927.

(3) *Arachniophyllum* Dana, 1846.
Genotype: *Acervularia baltica* Schweigger, partim Lonsdale (non *Acervularia baltica* Schweigger), 1819. Middle Silurian.

Irregular astraeoid low-spreading corallum, very wide dissepimentarium, narrow central lumen, septa normal in axial region only, breaking up into segments and strands as successive tabular floors. Middle Silurian.

Synonyms: *Darwinia* Dybowski, 1873; *Nicholsonia* Schlüter, 1885; *Zonophyla* Hill, 1940.

(*c*) Subfamily Endophyllinae

Solitary and colonial corals, septa composed of slender trabeculae deviating from the septal plane, well-developed lonsdaleioid dissepiments, tabulae differentiated into axial and periaxial series, lamellar tissue near wall region. Middle Silurian-Upper Devonian.

(1) *Spongophylloides* Meyer, 1881.

Genotype: *S. schumanni* Meyer, 1881. Silurian.

Trochoid to subcylindrical corallum, septa composed of relatively stouter trabeculae arranged in broad fan-systems and deviating from the septal plane, usually invested with lamellar tissue near boundary between tabularium and dissepimentarium, dissepiments lonsdaleioid, tabulae close and concave. Silurian.

Synonym: *Actinocystis* Lindström, 1882.

(2) *Strombodes* Schweigger, 1819 (figure 61*a*, *b*, plate 8).

Genotype: *Madrepora stellaris* Linnaeus, 1758. Silurian.

Phacelloid corallites, expanding at intervals to connect with each other, septa composed of one row of trabeculae interrupted by lonsdaleioid dissepiments developed in expanded parts, tabulae close together and domed. Silurian.

Synonyms: *Donacophyllum* Dybowski, 1871; *Cyphophyllum* Wedekind, 1927.

Subgenus *Grabauphyllum* Foerste, 1917.

Subgenotype: *G. johnstoni* Foerste, 1917. Silurian.

Cerioid *Strombodes*.

(3) *Endophyllum* Edwards & Haime, 1851 (figure 62, plate 8).

Genotype: *E. bowerbanki* Edwards & Haime, 1851. Devonian.

Simple or compound corals, septal structure like *Spongophylloides*, lonsdaleioid peripheral zone wide, tabulae differentiated into an axial domed, and periaxial concave series. Lower Devonian-Upper Devonian.

Synonyms: *Blothrophyllum* Billings, 1859; *Sinospongophyllum* Yoh, 1937; *Tabulophyllum* Fenton & Fenton, 1924; *Apolytophyllum* Walther, 1928.

Subgenus *Sanidophyllum* Etheridge, 1899.

Subgenotype: *S. davidis* Etheridge, 1899. Lower Devonian.

Phacelloid *Endophyllum* with short slender septa.

(4) *Spongophyllum* Edwards & Haime, 1851.

Genotype: *S. sedgwicki* Edwards & Haime, 1851. Devonian.

Phacelloid or cerioid corallites, septal structure like *Columnaria*, trabeculae a little stouter, one or more rows of lonsdaleioid dissepiments developed, tabulae close together and concave. Upper Silurian-Upper Devonian.

Synonym: *Battersbya* Edwards & Haime, 1851.

Subgenus *Neomphyma* Soshkina, 1937.

Subgenotype: *N. originata* Soshkina, 1937. Upper Silurian.

Phacelloid or solitary *Spongophyllum* with wide lonsdaleioid zone and slender septa.

4. Suborder CYSTIPHYLLACEA

Solitary or colonial corals, septa composed of discrete trabeculae embedded in lamellar tissue. Lower Silurian-Middle Devonian.

Family I. Cystiphyllidae

Solitary or colonial corals, trabeculae generally short, never quite contiguous, tabulae complete or passing into cystiphor tabellae. Lower Silurian-Middle Devonian.

(*a*) Subfamily Cystiphyllinae

Solitary, occasionally weakly compound corals, trabeculae mostly holacanth. Lower Silurian-Middle Devonian.

(1) *Tryplasma* Lonsdale, 1845 (figure 63, plate 8).

Genotype: *T. aequable* Lonsdale, 1845. Silurian.

Simple or phacelloid corals, septa composed of rows of discrete holacanth or rhabdacanth trabeculae embedded in lamellar tissue, tabulae complete, no dissepiments. Lower Silurian-Middle Devonian.

Synonyms: *Pholadophyllum* Lindström, 1871; *Acanthodes* Dybowski, 1873; *Cyathopaedium* Schlüter, 1889; *Spiniferina* Penecke, 1894; *Aphyllum* Soshkina, 1937.

(2) *Cystiphyllum* Lonsdale, 1839 (figure 64*a*, *b*, plate 8).

Genotype: *C. siluriense* Lonsdale, 1839. Middle Silurian.

Trochoid, ceratoid or cylindrical corallum, the whole lumen filled with cystose tabellae, numerous discrete short holacanth trabeculae developed on successive floors and embedded in lamellar tissue. Middle Silurian-Middle Devonian.

Synonym: *Conophyllum* Hall, 1851.

Subgenus *Hedströmophyllum* Wedekind, 1927 (figure 65, plate 8).

Subgenotype: *H. articulatum* Wedekind, 1927. Silurian.

Cystiphyllum with very numerous trabeculae traversing more than one tabella.

Subgenus *Yassia* Jones, 1930.

Subgenotype: *Spongophyllum enorme* Etheridge, 1913. Silurian.

Cerioid *Cystiphyllum* with well-differentiated tabular zone.

Synonym: *Crinophyllum* Jones, 1932.

(3) *Diplochone* Frech, 1886.

Genotype: *D. strictum* Frech, 1886. Middle Devonian.

Ceratoid or subcylindrical corallum, trabeculae very few, lamellar tissue weak, tabular zone well developed. Middle Silurian-Middle Devonian.

Synonym: *Cayugaea* Lambe, 1901.

(4) *Microplasma* Dybowski, 1873 (figure 66*a*, *b*, plate 8).

Genotype: *M. gotlandicus* Dybowski, 1873. Silurian.

Phacelloid, rarely simple corals, few holacanth trabeculae embedded in lamellar tissue and few large arched tabellae. Silurian-Middle Devonian.

(5) *Cetophyllum* Wedekind, 1927.

Genotype: *C. elegantulum* Wedekind, 1927. Middle Silurian.

Turbinate corallum with frequent rejuvenescence and rootlets, septa composed of slender holacanth trabeculae embedded in lamellar tissue on successive floors, well-differentiated tabularium and lonsdaleioid dissepimentarium. Silurian.

Synonyms: *Heterolasma* Ehlers, 1919; *Docophyllum* Wedekind, 1927.

Subgenus *Tabularia* Soshkina, 1937.

Subgenotype: *T. turiensis* Soshkina, 1937. Silurian.

Primitive *Cetophyllum* without well-developed dissepimentarium.

(6) *Calceola* Lamarck, 1799.
Genotype: *Anomia sandalina* Linnaeus, 1771. Devonian.

Calceoloid corallum with one flat side, semicircular operculum, compact lamellar sclerenchyme, tabellae incomplete and arched. Upper Silurian-Middle Devonian.

Synonyms: *Rhytidophyllum* Lindström, 1883; *Platyphyllum* Lindström, 1883; *Rhizophyllum* Lindström, 1886.

(7) *Lytophyllum* Wedekind, 1924 (tentatively referred here).
Genotype: *L. marginatum* Wedekind, 1924. Middle Devonian.

Trochoid, subcylindrical or ceratoid corallum, compact sclerenchyme developed on successive floors, splitting up into segments, rarely showing trabeculae. Middle Devonian.

Synonyms: *Paralytophyllum* Wedekind, 1925; *Plagiophyllum* Wedekind, 1925; *Nardophyllum* Wedekind, 1925; *Scoliophyllum* Wedekind, 1937; *Cystiphylloides* Yoh, 1937.

(8) *Rhapidophyllum* Lindström, 1882.
Genotype: *R. constellatum* Lindström, 1882. Silurian.

Cerioid or phacelloid corallites, trabeculae long and developed in the whole lumen, tabulae incomplete and concave, no dissepiments. Silurian-Lower Devonian.

Synonyms: *Polyorophe* Lindström, 1882; *Storthygophyllum* Weissermel, 1894; *Xiphelasma* Smith & Lang, 1930; *Stortophyllum* Wedekind, 1927; *Baeophyllum* Hill, 1940.

(*b*) Subfamily Holmophyllinae

Solitary, occasionally compound corals, trabeculae mostly rhabdacanth. Middle Silurian-Upper Silurian.

(1) *Rhabdocyclus* Lang & Smith, 1939.
Genotype: *Palaeocyclus fletcheri* Edwards & Haime, 1851. Silurian.

Turbinate or trochoid corallum, long rhabdacanth trabeculae embedded in lamellar tissue which lines the wall, few complete distant tabulae, no dissepiments. Silurian.

Synonym: *Acanthocyclus* Dybowski, 1873.

(2) *Cantrillia* Smith, 1930.
Genotype: *C. prisca* Smith, 1930. Silurian.

Simple trochoid corallum, wall thick, composed of lamellar tissue with few holacanth or rhabdacanth trabeculae, tabulae complete and distant. Silurian.

(3) *Holmophyllum* Wedekind, 1927 (figure 67*a*, *b*, plate 8).
Genotype: *H. holmi* Wedekind, 1927. Silurian.

Simple, rarely compound corals, trabeculae stout, rhabadcanth, embedded in lamellar tissue, tabellae cystose, more or less differentiated into peripheral and tabular zones. Silurian.

Subgenus *Gyalophyllum* Wedekind, 1927.
Subgenotype: *G. angelini* Wedekind, 1927. Silurian.

Holmophyllum with compact contiguous trabeculae on successive floors and with more or less differentiated tabularium.

(4) *Goniophyllum* Edwards & Haime, 1851.

Genotype: *Turbinolia pyramidalis* Hisinger, 1831. Silurian.

Pyramidal corallum with four opercula, septa composed of compact stout trabeculae embedded in lamellar tissue, tabellae arched and incomplete. Silurian.

Subgenus *Araeopoma* Lindström, 1883.

Subgenotype: *A. prismaticum* Lindström, 1883. Silurian.

Goniophyllum without fully developed opercula.

Synonym: *Proaraeopoma* Ting, 1937.

Family II. MYCOPHYLLIDAE

Solitary, rarely compound corals, septa thick and contiguous, composed of stout trabeculae embedded in lamellar tissue or of lamellar tissue only, tabulae complete and distant, no dissepiments. Middle Silurian-Lower Devonian.

(1) *Zelophyllum* Wedekind, 1927 (figures 68–9, plate 8).

Genotype: *Z. intermedium* Wedekind, 1927. Silurian.

Small simple corallum, rarely phacelloid, septa composed entirely of lamellar tissue, fused together along the whole length, tabulae complete and distant. Middle Silurian-Upper Silurian.

(2) *Pseudamplexus* Weissermel, 1894.

Genotype: *Zaphrentis ligerensis* Barrois, 1889. Lower Devonian.

Large trochoid corallum, septa contiguous, composed of rhabdacanth trabeculae embedded in lamellar tissue, complete and wide tabulae. Lower Devonian.

Synonym: *Pselophyllum* Počta, 1902.

(3) *Mycophyllum* Etheridge, 1894.

Genotype: *M. crateroides* Etheridge, 1894. Upper Silurian.

Large trochoid corallum with wide calical platform and reflexed border, septal structure like *Pseudamplexus*, tabulae complete and distant. Middle Silurian-Lower Devonian.

Synonyms: *Aspasmophyllum* Römer, 1880?; *Pseudomphyma* Wedekind, 1927.

INCERTAE SEDIS

(1) *Calostylis* Lindström, 1868.

Genotype: *C. cribraria* Lindström, 1868. Silurian.

Simple or compound corals, septa breaking into trabecular strands joining with those of the neighbouring septa so as to produce a meshwork, tabulae feeble, skeletal structure not clearly known. Silurian.

Subgenus *Helminthidium* Lindström, 1882.

Subgenotype: *H. mirum* Lindström, 1882. Silurian.

Simple *Calostylis* with anastomosing septa and with tabulae entirely suppressed.

(2) *Enterelasma* Simpson, 1900.

Genotype: *Streptelasma stricta* Hall, 1874. Devonian.

Ceratoid corallum, rejuvenescence common, thick carinate septa contiguous in peripheral zone and anastomosing in axial zone, numerous incomplete flat tabellae. Devonian.

INDEX TO CLASSIFICATION

PROBLEMATICA, STRUCTURE UNKNOWN

Porpites Schlotheim, 1820; *Baryphyllum* Edwards & Haime, 1850; *Combophyllum* Edwards & Haime, 1850; *Hadrophyllum* Edwards & Haime, 1850; *Microcyclus* Meek & Worthen, 1868; *Dipterophyllum* Römer, 1883; *Xenocyathellus* Bassler, 1937.

GENERIC NAMES ALLOWED TO LAPSE, NOT FIGURED, INSUFFICIENTLY DESCRIBED, OR NO LONGER TRACEABLE

Campsactis Rafinesque & Clifford, 1820; *Peripaedium* Ehrenberg, 1834; *Ellipsocyathus* d'Orbigny, 1849; *Anisophyllum* Edwards & Haime, 1850; *Polydilasma* Hall, 1851; *Canophyllum* Dybowski, 1873; *Elasmophyllum* Hall, 1882; *Palaeocyathus* Foerste, 1888; *Edaphophyllum* Simpson, 1900; *Retiophyllum* Počta, 1902; *Mictocystis* Etheridge, 1908; *Helenterophyllum* Grabau, 1910; *Depasophyllum* Grabau, 1922; *Stratiphyllum* Scheffen, 1933; *Tyria* Scheffen, 1933; *Phragmophyllum* Scheffen, 1933; *Stegophyllum* Scheffen, 1933; *Diplophyllum* Soshkina, 1940.

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Description of plates 4 to 9

Abbreviations

BM	British Museum (Natural History), London.
SM	Sedgwick Museum, Cambridge.
GUP	Geological Collection, University of Peking, China.
GS	Geological Survey and Museum, London.
SS	Collection of Dr Stanley Smith, Bristol University.
AV	Collection of the late Dr A. Vaughan, Bristol University.

Plate 4

Zaphrentoididae, Plerophyllidae, Caniniidae

Figure 1. *Zaphrentoides delanouei* (Edwards & Haime), × 12. Transverse section. BM R 19601. Lower Carboniferous, Dublin, Ireland. Compare Carruthers 1908, figure 6, plate V.

FIGURE 2. *Z. omaliusi* (Edwards & Haime), × 12. Transverse section. BM R 19592. Same horizon and locality. Compare Carruthers 1908, figures 1–3, plate IV.

FIGURE 3. *Onychophyllum pringlei* Smith, × 24. Transverse section (cardinal sectors) showing contiguous septa and shallowly bent lamellar layers. GS M 726. Lower Silurian, Shropshire, England. Compare Smith 1930, p. 299, figure 2.

FIGURE 4. *Syringaxon siluriense* (McCoy), × 12. Transverse section. SM A 7554*b*. Silurian, Salop, England. Compare Butler 1935, plate II.

FIGURE 5. *Metriophyllum bouchardi* Edwards & Haime, × 12. Transverse section showing three septa and one flange. BM R 16263. Upper Devonian, Ferques, France. Compare Smith 1945, figure 12, plate I.

FIGURE 6. *Amplexus coralloides* Sowerby, × 9. Transverse section showing the branching-off of septa to join each other. AV I 3. Lower Carboniferous, Bristol Region, England.

FIGURE 7. *Rylstonia benecompacta* Hudson & Platt, × 12. Transverse section. BM R 25566. Lower Carboniferous, Rylstone, Yorks, England. Compare Hudson and Platt 1927, figure 2, plate I.

FIGURE 8. *Carcinophyllum simplex* Garwood, × 12. Transverse section showing three major septa and part of the axial column. GS 63939. Lower Carboniferous, Meanthop, Arnside, Cumberland, England. See Garwood 1912, figures 3, 4, plate XLVIII.

FIGURE 9. *Lophophyllidium proliferum* (McChesney), × 12. Transverse section showing periodical crowding of arched patches of fibre fascicles in the septa. SM A 7733. Upper Carboniferous, Spring Field, Illinois, U.S.A.

FIGURE 10. *L. wichmanni* (Rothpletz), × 12. Transverse section showing the splitting up of the septa into 'longitudinal dissepiments' in the peripheral region. BM R 32989. Permian, Soempek, Timor.

FIGURE 11. The same, × 12. BM R 32988. Permian, Soempek, Timor. (*a*) Septa showing secondary grouping of fibre fascicles in the peripheral region. (*b*) Part of columella showing patches of fibre fascicles.

FIGURE 12. *Verbeekiella australe* (Beyrich), × 12. BM R 32579. Permian, Toenioen, Eno, Timor. (*a*) Septa with long fibre fascicles. (*b*) Part of axial column showing favositoid structure in the central and radiating fibre fascicles in the outer part.

FIGURE 13. *Rhopalolasma granulata* (Thomson), × 12. Transverse section showing the partly lamellar and partly fibrous structure of the septa. SM A 9501. Lower Carboniferous, Cross Fell, Cumberland, England.

FIGURE 14. *Siphonophyllia cylindrica* Scouler, × 12. Two septa showing the slender parallel fibre fascicles contiguous with the dilated dissepimental parts. AV II 117. Lower Carboniferous (D 2), Avon section, Bristol, England. Compare Lewis, 1927, plates XVI, XVII.

Plate 5

Caniniidae, Lonsdaleiidae, Streptelasmidae

FIGURE 15. *Cystiphrentis kolaohoensis* Yü, × 12. Transverse section showing the parallel fibre fascicles contiguous with the dilated dissepimental parts. SM A 8154*e*. Lower Carboniferous, Hsianghsiang, Hunan, China. Compare Yü 1937, figures 1–8, plate I.

FIGURE 16. *Bothrophyllum* sp., × 12. Transverse section showing the periodical crowding of patches of fibre fascicles. GUP 47001. Upper Carboniferous, Tapanchio, Kunming, Yunnan, China.

FIGURE 17. *Dibunophyllum bipartitum* (McCoy), × 12. Transverse section showing the subparallel fibre fascicles and the splitting up of septa into 'longitudinal dissepiments'. SM A 1971*g*. Lower Carboniferous, Derbyshire, England. Compare Hill 1938–40, figures 15–20, plate II.

FIGURE 18. *Corwenia rugosa* (McCoy), × 12. Transverse section. SM E 12756. Lower Carboniferous, Ayrshire, Scotland. Compare Smith & Ryder 1926, figure 2, plate V.

FIGURE 19. *Lonsdaleia floriformis* (Martin), × 12. Transverse section showing the parallel fibre fascicles in the septa and in the wall. SM A2359. Lower Carboniferous (Viséan), Derbyshire, England. Compare Smith 1916, figure 1, plate XIX.

FIGURE 20. *Siphonodendron irregulare* (Phillips), × 24. Transverse section showing septa with parallel fibre fascicles wedged in the wall. BM R15369. Lower Carboniferous (Viséan), Wrington, Somerset, England.

FIGURE 21. *Waagenophyllum indicum* (Waagen & Wentzel), × 12. Transverse section showing secondary grouping of fibre fascicles near the wall. SM A4610. Permian, Salt Range, India. Compare Smith 1935, figure 5, plate VIII.

FIGURE 22. *Streptelasma rusticum* Billings, × 12. Tangential section showing the arrangement of fibre fascicles in the septa (no trabeculae). SM A3452*f*. Upper Ordovician, Wayesville, Ohio, U.S.A. Compare Cox 1936, figures 11–13, plate II.

FIGURE 23. *Streptelasma corniculum* Hall, × 12. Transverse section showing the fibrous septa and the lamellar tissue near the wall. SM A7861. Middle Ordovician, Trenton Limestone, Cornwall, Ontario, Canada. See Cox 1937, figure 2*a*, *b*, plate I.

FIGURE 24. *Codonophyllum whittardi* (Smith), × 12. Longitudinal section passing through one septum, showing well-defined trabeculae at low angle of inclination. SM A7593*c*. Silurian, Shropshire, England. See Smith, 1930, figures 9–14, plate XXVIII.

FIGURE 25. *Lambeophyllum profundum* (Conrad), × 12. Transverse section showing the indistinct fibrous character of the septa confluent with the interseptal lamellar tissue. SM A7849*d*. Middle Ordovician, Deborah Formation, Minnesota, U.S.A.

FIGURE 26. *Siphonophrentis gigantea* (Lesueur), × 12. SM H4395*e–f*. Middle Devonian, Indiana, U.S.A. See figure 70, plate 9. (*a*) Transverse section. (*b*) Tangential section showing long fibre fascicles in the septa not grouped into trabeculae.

FIGURE 27. *Dalmanophyllum dalmani* (Edwards & Haime), × 12. Transverse section showing long fibre fascicles in the septa and in the columella. SM A13609*e*. Upper Ordovician, Ringerike, Norway. See figure 71*a*, *b*, plate 9.

FIGURE 28. *Codonophyllum truncatum* (Linnaeus), × 12. Transverse section. SM A8043. Silurian, Shropshire, England. Compare Smith & Tremberth 1929, figure 7, plate VIII.

FIGURE 29. *Pilophyllum* sp., × 12. Transverse section showing the elaborate fibre fascicles. BM R24289. Silurian, Gotland.

Plate 6

Dinophyllidae, Pycnactidae, Disphyllidae

FIGURE 30. *Dinophyllum involutum* Lindström, × 12. Transverse section showing the fibrous trabeculae embedded in the lamellar tissue. SM A15228*e*. Silurian, Saugh Hill Group, Girvan, Scotland.

FIGURE 31. *Dinophyllum* sp., × 12. Transverse section. SM A8569*e*. Middle Devonian, Hamilton Group, N.Y., U.S.A. See figure 72*a*, *b*, plate 9.

FIGURE 32. *Heterophrentis prolifica* Billings, × 12. Transverse section. SM H4394*d*. Lower Devonian, Ohio, U.S.A. See figure 73*a*, *b*, plate 9.

FIGURE 33. *Neospongophyllum isactis* (Frech), × 12. Transverse section showing stout trabeculae embedded in lamellar tissue. GUP 43131. Middle Devonian, Poshi, Yunnan, China.

FIGURE 34. *Neospongophyllum suni* n.sp., × 12. Longitudinal section showing stout trabeculae consisting of numerous minute trabeculae. GUP 43190. Middle Devonian, Sierh, Yunnan, China.

FIGURE 35. *Stringophyllum primaevum* n.sp., × 12. GUP 40026–7. Middle Devonian, Poshi, Yunnan, China. (*a*) Transverse section showing the separate trabeculae. (*b*) Longitudinal section showing trabeculae at low angle of inclination.

FIGURE 36. *Stringophyllum* sp., × 12. Longitudinal section showing stout composite trabeculae consisting of numerous minute trabeculae. SM H169*e*. Devonian, Newton, England.

FIGURE 37. *Mesophyllum yunnanense* n.sp., × 12. Transverse section showing separate trabeculae. GUP 42041. Middle Devonian, Poshi, Yunnan, China.

FIGURE 38. *Phaulactis glevensis* (Ryder), × 12. Transverse section showing long fibre fascicles in the inner zone of dilated septa. SM A15286. Middle Silurian, Wenlock Limestone, Gloucestershire, England. Compare Ryder 1926, figures 1–6, plate X.

FIGURE 39. *Ceratophyllum* sp., × 12. Transverse section showing the long fibre fascicles in the inner dilated zone of the septa. SM A15070. Middle Devonian, Eifel, Germany. See figure 74*a*, *b*, plate 9.

FIGURE 40. *Heliophyllum halli* Edwards & Haime, × 12. Transverse section showing sections of the curved flanges. BM R29383. Middle Devonian, Ontario, Canada. Compare Smith 1945, figure 3, plate XXXVIII.

FIGURE 41. *Acanthophyllum heterophyllum* (Edwards & Haime), × 12. Transverse section showing different structures in different segments of the septa as a result of the varying angle of inclination of the trabeculae. SM A9075*e*. Middle Devonian, Eifel, Germany.

FIGURE 42. *Temeniophyllum crassiseptatum* n.sp., × 12. Transverse section showing the confluent fibre fascicles in the inner wall. GUP 43054. Middle Devonian, Poshi, Yunnan, China.

FIGURE 43. *Temeniophyllum complicatum* n.sp., × 12. Transverse section showing separate fibre fascicles developed in the inner wall. GUP 40055. Same horizon and locality.

Plate 7

Disphyllidae, Clisiophyllidae, Columnariidae

FIGURE 44. *Charactophyllum nanum* (Hall & White), × 12. SM A9695*d*, *e*. Upper Devonian, Rockford, Indiana, U.S.A. Compare Smith 1945, figures 7, 8, plate I. (*a*) Transverse section. (*b*) Longitudinal section showing the elbow folding of the trabeculae.

FIGURE 45. *Ceriophyllum heiligensteini* Wedekind, × 12. GUP 40071–2. Middle Devonian, Poshi, Yunnan, China. (*a*) Transverse section, showing the trabecular carinae. (*b*) Longitudinal section showing the well-defined trabeculae.

FIGURE 46. *Ceriophyllum conicum* n.sp., × 12. Longitudinal section. GUP 43037. Same horizon and locality.

FIGURE 47. *Phacellophyllum caespitosum* (Goldfuss), × 12. SM A7739*e*–*f*. Middle Devonian, Eifel, Germany. Compare Lang & Smith, 1935, figures 1, 2, plate XXV. (*a*) Transverse section showing the costae-like outer portion of the septa. (*b*) Longitudinal section showing the area of trabecular divergence.

FIGURE 48. *Macgeea gallica* Lang & Smith, × 12. SM A6957*d*, *e*. Upper Devonian, Ferques, France. Compare Lang & Smith 1935, figures 4–12, plate XXXVII. (*a*) Transverse section showing the cross-sections of the trabeculae. (*b*) Longitudinal section showing the area of trabecular divergence.

FIGURE 49. *Phillipsastraea exigea* Lambe, × 12. Transverse section showing the costae-like outer portion of the septa. SM A14630*a*. Upper Devonian, Trout River, Canada. Compare Smith 1945, figures 3–6, plate XXI.

FIGURE 50. *Clisiophyllum keyserlingi* McCoy, × 12. Transverse section showing the slender fibrous septa. SM A2353*a*. Lower Carboniferous, Derbyshire, England. See Hill 1938–40, figures 1–10, plate I.

FIGURE 51. *Koninckophyllum dianthoides* (McCoy), × 12. Transverse section showing the slender trabeculae deviating from the septal plane. SM A2387*d*. Lower Carboniferous, Arnside, Cumberland, England. Compare Hill 1938–40, figure 14, plate IV.

Figure 52. *Carruthersella compacta* Garwood, × 12. Transverse section showing the elaborate fibre fascicles in the septa. GS 63914. Lower Carboniferous, Arnside, Cumberland, England.

Figure 53. *Lithostrotion junceum* (Fleming), × 9. Transverse section showing the fibrous septa and columella and the lamellar wall. SS 28003. Lower Carboniferous (Viséan), Melmerby Scar Limestone, Melmerby, England. Compare Hill 1938–40, figures 3–8, plate IX.

Figure 54. *Columnaria gotlandica* Edwards & Haime, × 12. Transverse section showing the slender fibrous septa arising from the lamellar wall. BM R 26165. Silurian, Faro, Gotland.

Figure 55. *Fasciphyllum conglomeratum* Schlüter, × 12. Transverse section showing the slender fibrous septa arising from the lamellar wall. BM R 23294. Middle Devonian, Paffrath, Cologne, Germany. Compare Lang & Smith 1935, p. 548, figures, 6, 7.

Figure 56. *Grypophyllum normale* Wedekind, × 12. Transverse section showing the slender fibrous septa and the lamellar wall. GUP 42123. Middle Devonian, Poshi, Yunnan, China. Compare Wedekind 1925, figures 25, 26, plate XIV.

Figure 57. *Lyrielasma* sp., × 12. SM A 9100*c*, *d*. Middle Devonian, Eifel, Germany. See figure 75*a*, *b*, plate 9. (*a*) Transverse section showing the slender trabeculae deviating from the septal plane. (*b*) Longitudinal section showing the high angle of inclination of the trabeculae.

Figure 58. *Entelophyllum articulatum* (Wahlenberg), × 12. Transverse section showing the slender trabeculae slightly deviating from the septal plane. SM A 6773. Middle Silurian, Much Wenlock, Wenlock, England. Compare Smith & Tremberth 1929, plate VII.

Plate 8

Columnariidae, Cystiphyllidae, Mycophyllidae

Figure 59. *Entelophyllum pseudodianthus* (Weissermel), × 12. Transverse section showing the interwoven slender trabeculae in the septa. SM A 15177. Middle Silurian, Much Wenlock, England. Compare Smith & Tremberth 1929, figures 3, 4, plate VIII.

Figure 60. *Acervularia ananas* Linnaeus, × 12. BM R 28889. Middle Silurian, Wenlock Limestone, Shropshire, England. Compare Smith 1945, figure 4*a*, *b*, plate XXX. (*a*) Transverse section showing the slender trabeculae forming clusters in the outer and the inner wall. (*b*) Longitudinal section showing the area of trabecular divergence in the inner wall.

Figure 61. *Strombodes stellata* Linnaeus, × 12. BM R 23955. Middle Silurian, Visby, Gotland. Compare Smith 1945 figures 1, 2, plate XXIX. (*a*) Transverse section showing the slender trabeculae slightly deviating from the septal plane. (*b*) Longitudinal section showing the angle of inclination of the trabeculae.

Figure 62. *Endophyllum annulatum* n.sp., × 12. Transverse section showing the slender trabeculae slightly deviating from the septal plane and the dissociated trabecular segments of the minor septa. GUP 42105. Middle Devonian, Poshi, Yunnan, China.

Figure 63. *Tryplasma paucitabulatum* (Schlüter), × 12. Transverse section showing the short trabeculae embedded in the lamellar tissue. SM A 8635*c*. Middle Devonian, Eifel, Germany. Compare Schlüter 1881, figures 1–4, plate VI.

Figure 64. *Cystiphyllum omphymiforme* Grabau, × 12. Middle Silurian, Maokeshan, Maolungtien, Jungshan, Yunnan, China. (*a*) Transverse section (GUP 45075) showing the initiation of slender trabeculae in the lamellar tissue. (*b*) Longitudinal section (GUP 45083) showing the same.

Figure 65. *Hedströmophyllum weissermeli* Wedekind, × 10. Transverse section showing the holacanth trabeculae embedded in the lamellar tissue. SS 30001. Middle Silurian, Gotland. Compare Wedekind 1927, figures 3, 4, plate XXI.

Figure 66. *Microplasma gotlandica* Dybowski, × 9. Middle Silurian, Gotland. (*a*) Transverse section (SS 11001) showing the slender trabeculae in the wall. (*b*) Longitudinal section (SS 20001) showing the same.

FIGURE 67. *Holmophyllum tungchuanense* n.sp., × 12. GUP 45087–8. Middle Silurian, Choukeng, Hueitze, Yunnan, China. (*a*) Transverse section showing the stout rhabdacanth trabeculae interrupted by the dissepiments. (*b*) Longitudinal section showing the same.

FIGURE 68. *Zelophyllum primaevum* n.sp., × 12. Transverse section showing the lamellar structure of the contiguous septa. GUP 47051. Middle Silurian, Nanchangkou, Yingtsuiya, Yentsin, Yunnan, China.

FIGURE 69. *Zelophyllum lindström* n.sp., × 12. Transverse section showing the shallow folding of the lamellar layers in the septa. GUP 45069. Middle Silurian, Siaohyatien, Takuan, Yunnan, China.

Plate 9

Streptelasmidae, Dinophyllidae, Pycnactidae, Columnariidae

FIGURE 70. *Siphonophrentis gigantea* (Lesueur), × 2. SM H4395*e*. See figure 26*a*, plate 5.

FIGURE 71. *Dalmanophyllum dalmani* (Edwards & Haime), × 2. See figure 27, plate 5. (*a*) Transverse section, early ephebic stage. SM A13609*c*. (*b*) Transverse section, ephebic stage. SM A13609*d*.

FIGURE 72. *Dinophyllum* sp., × 2. See figure 31, plate 6. (*a*) Transverse section. SM A8569*e*. (*b*) Longitudinal section. SM A8569*d*.

FIGURE 73. *Heterophrentis prolifica* Billings, × 2. See figure 32, plate 6. (*a*) Transverse section, early ephebic stage. SM H4394*d*. (*b*) Transverse section, ephebic stage. SM H4394*c*.

FIGURE 74. *Ceratophyllum* sp., × 2. See figure 39, plate 6. (*a*) Transverse section. SM A15070*e*. (*b*) Longitudinal section. SM A15070*f*.

FIGURE 75. *Lyrielasma* sp., × 2. See figure 57, plate 7. (*a*) Transverse section. SM A9103*b*. (*b*) Longitudinal section. SM A9103*c*.

TABLE 1. STRATIGRAPHICAL DISTRIBUTION OF THE FAMILIES AND SUBFAMILIES OF ZOANTHARIA RUGOSA

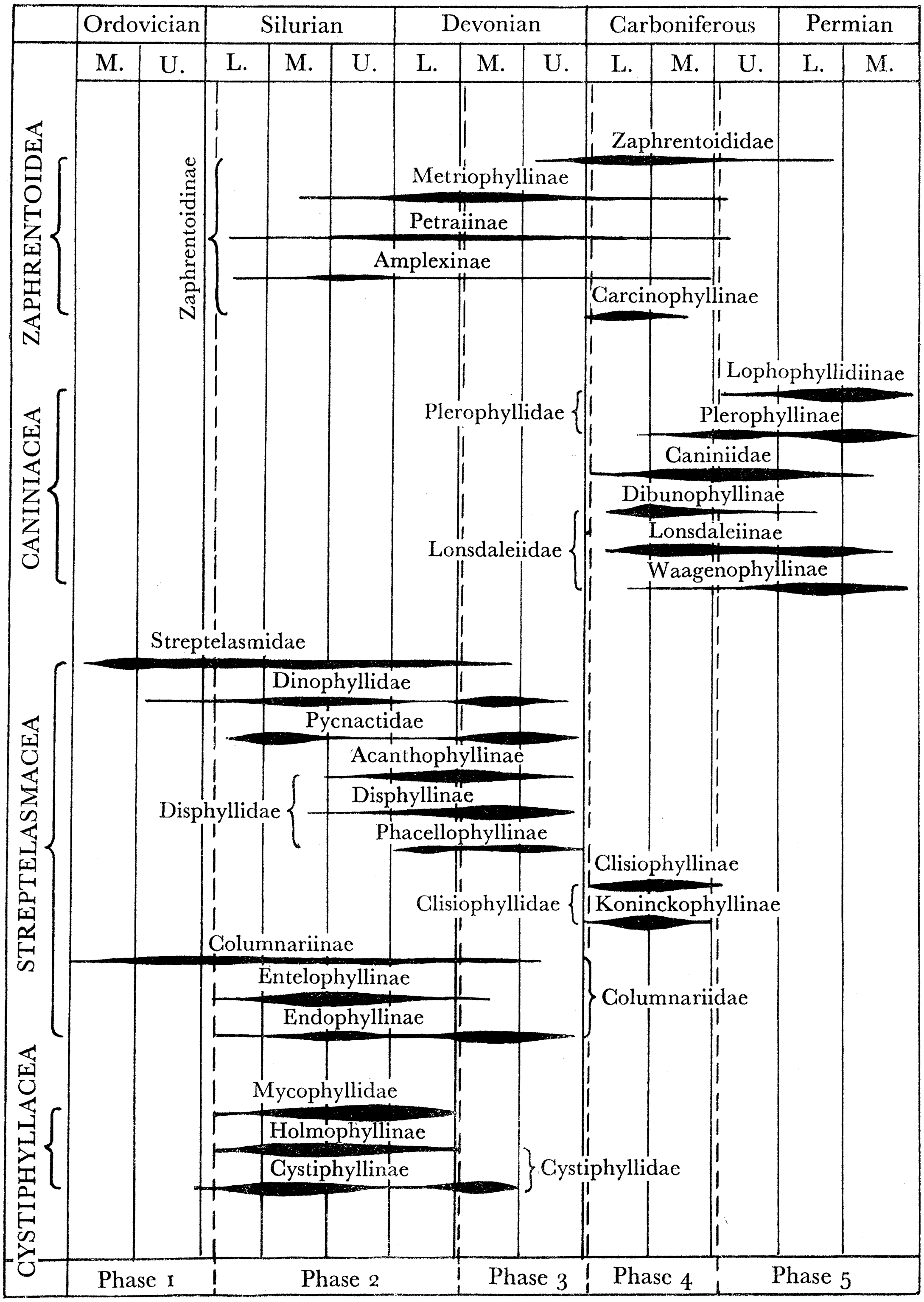
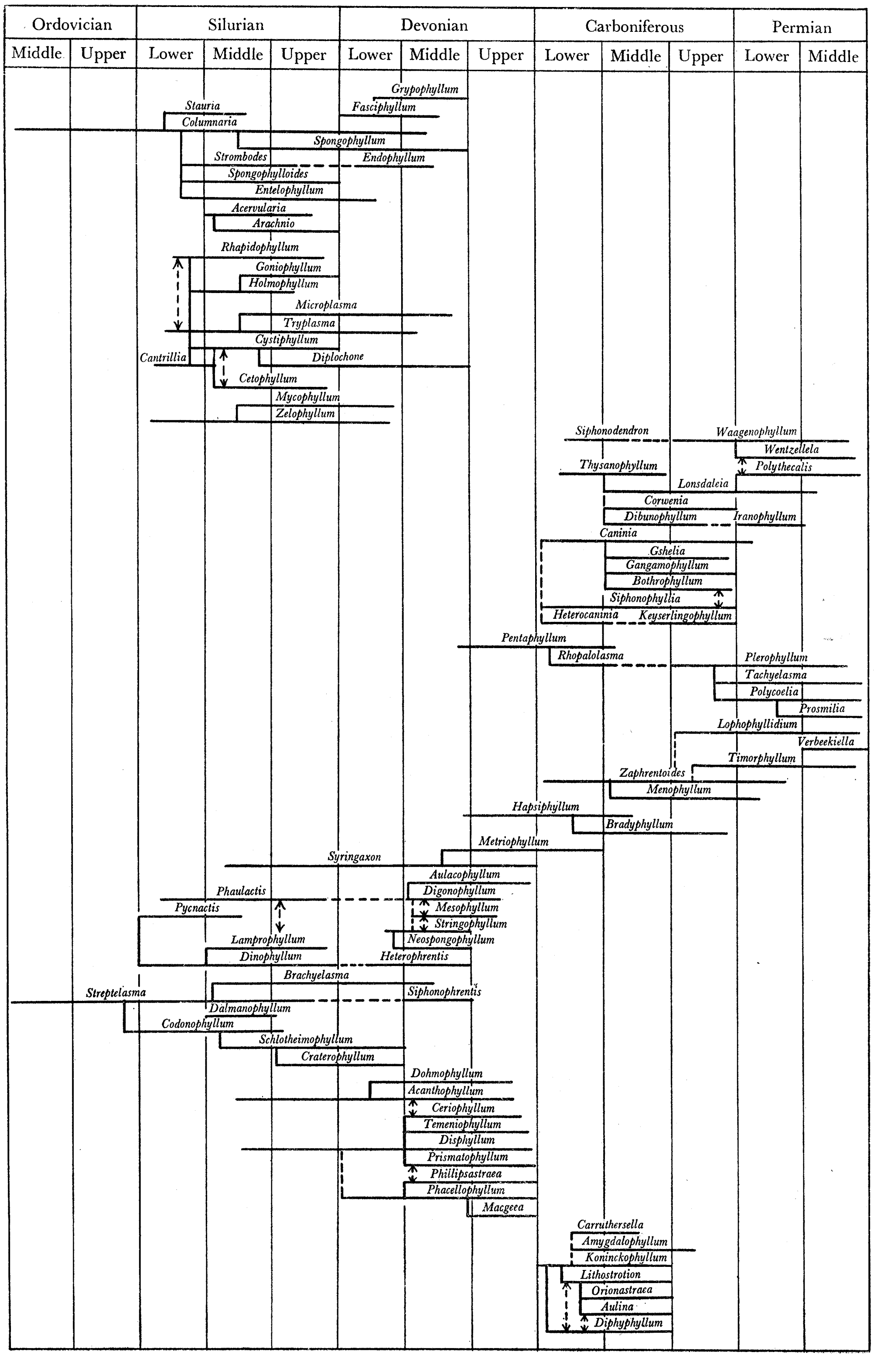
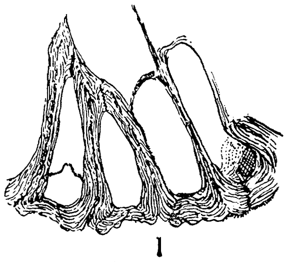


TABLE 2. STRATIGRAPHICAL DISTRIBUTION OF SOME IMPORTANT RUGOSE CORAL GENERA AND SUBGENERA

Horizontal solid line: stratigraphical range.
Vertical solid line: probable genetic relationship.
Horizontal dotted line: probable descent.
Vertical dotted line: possible genetic relationship.
Vertical dotted line with arrows on both ends: probable reticulate evolution.





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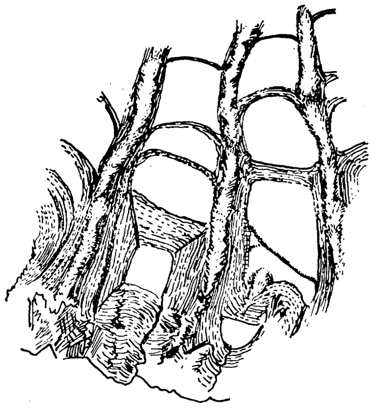

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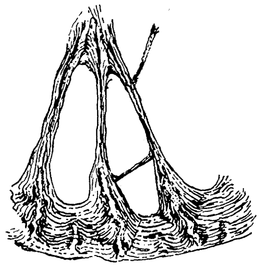

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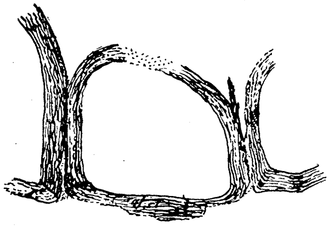

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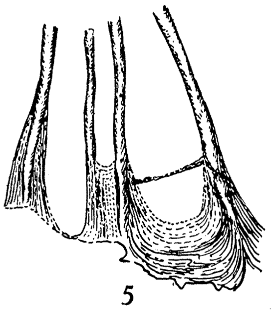

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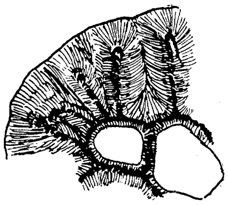

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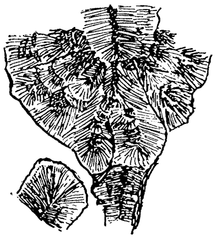

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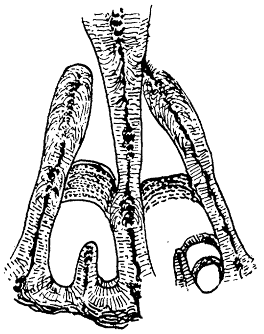

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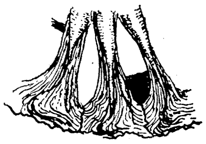

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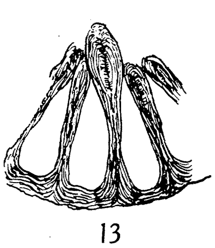

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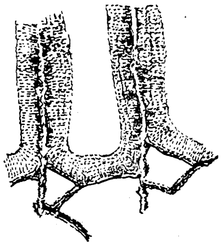

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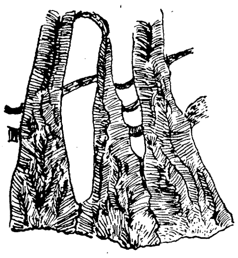

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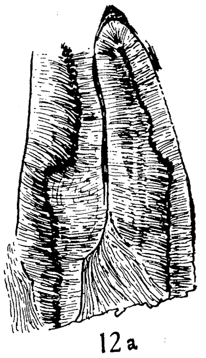

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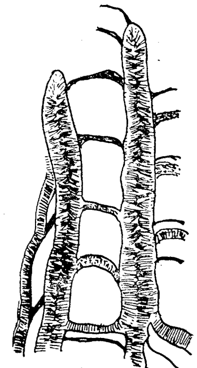

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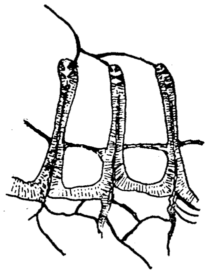

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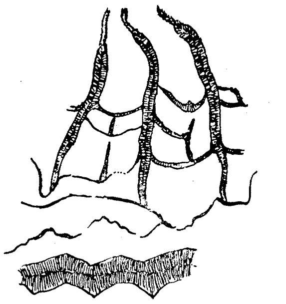

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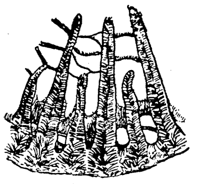

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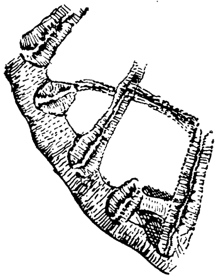

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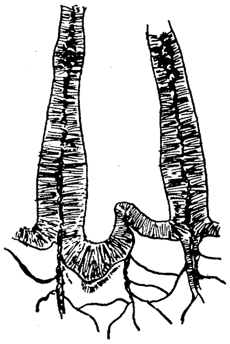

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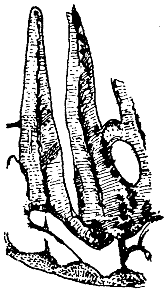

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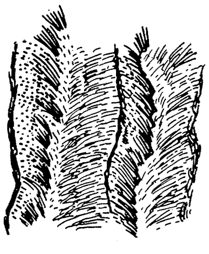

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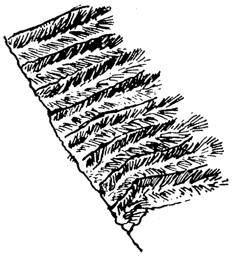

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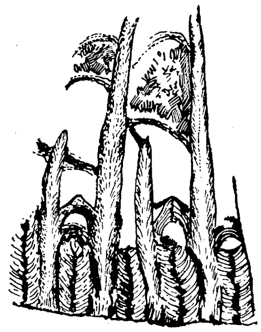

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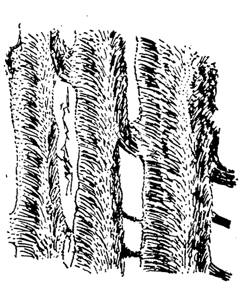

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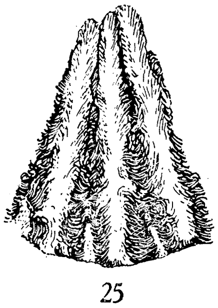

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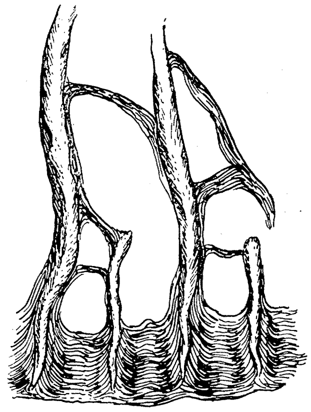
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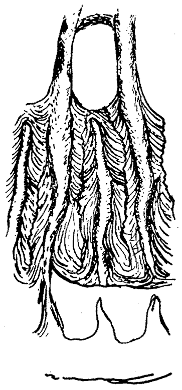
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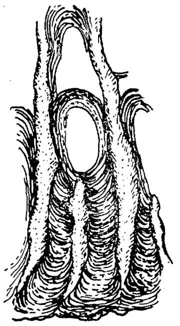
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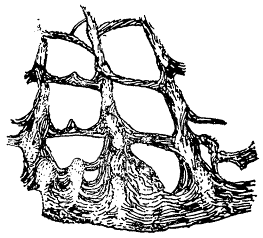
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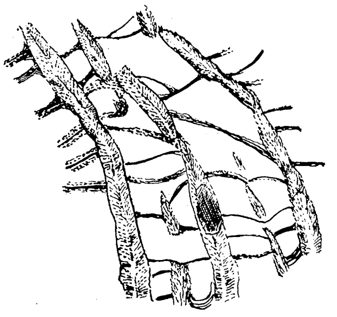
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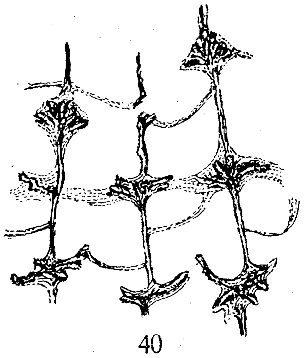
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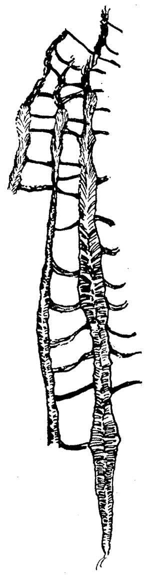
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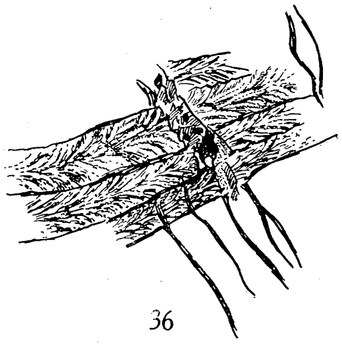
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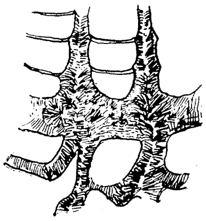
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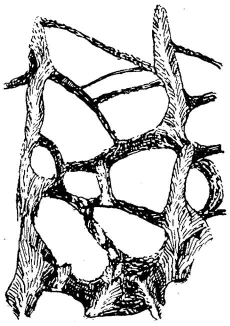
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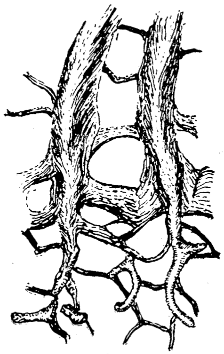
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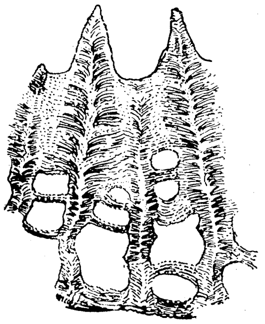
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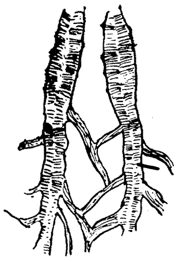
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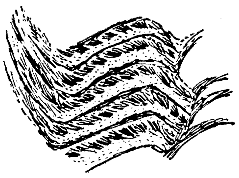
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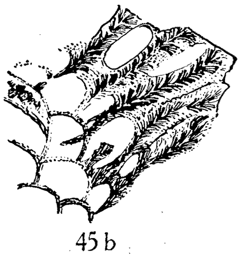
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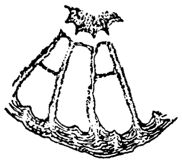
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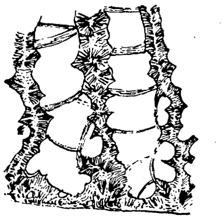
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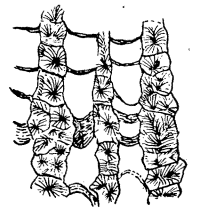
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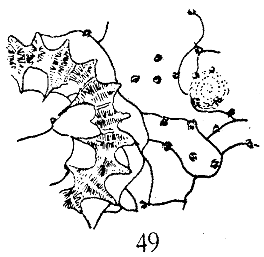
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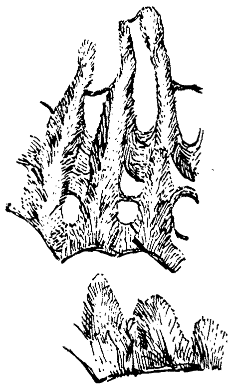
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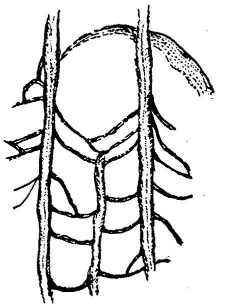
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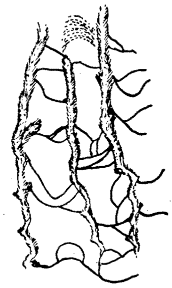
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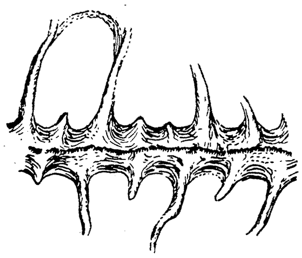
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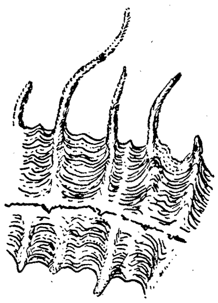
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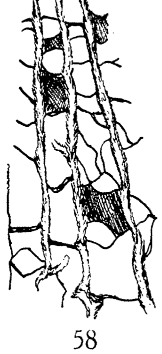
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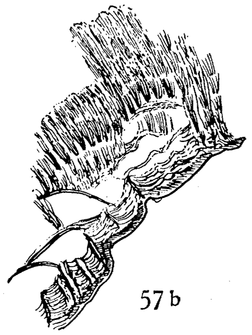
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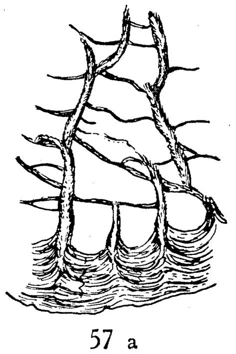
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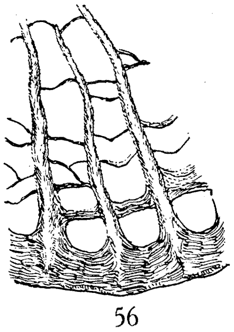
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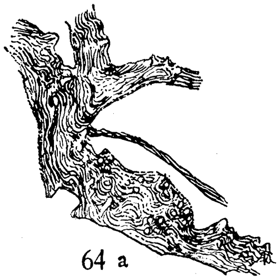
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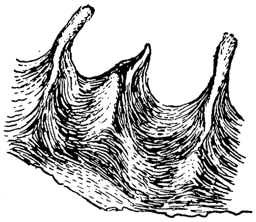
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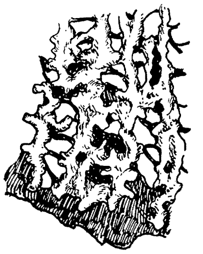
60 b


64 b


65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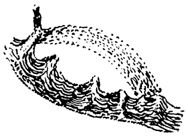
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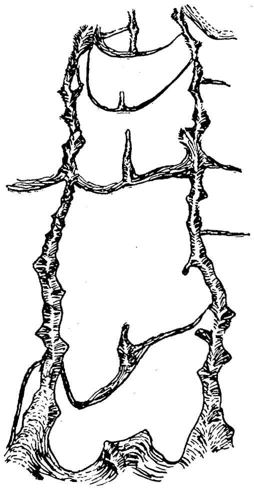
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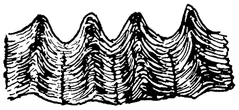
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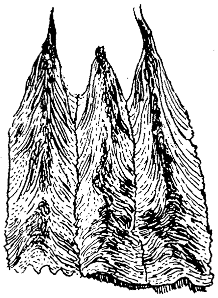
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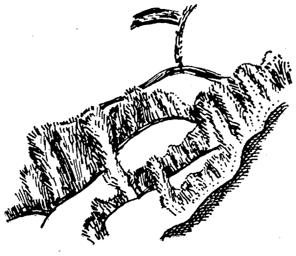
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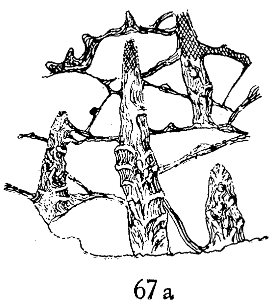
67 b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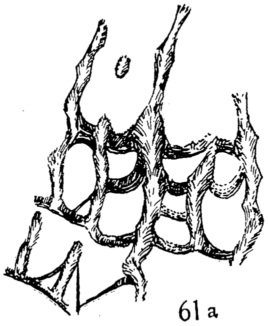
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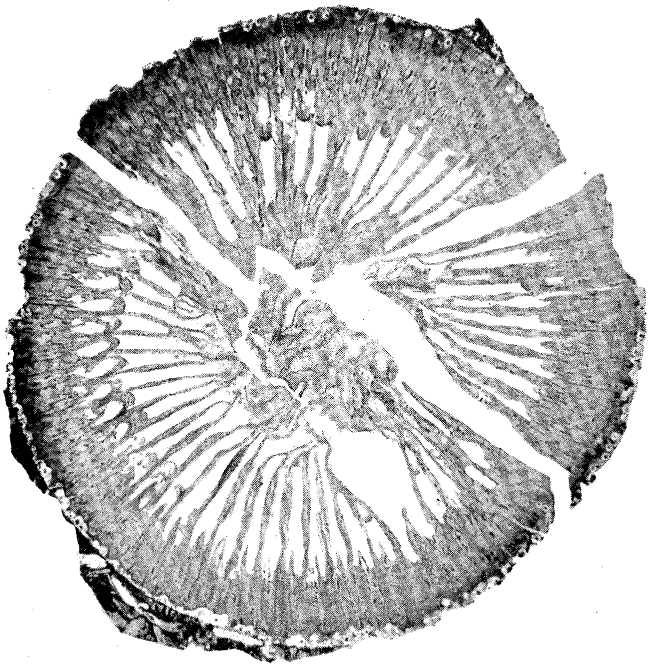

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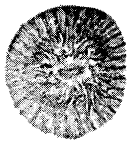

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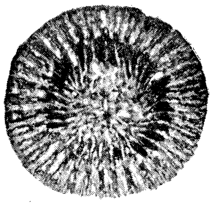

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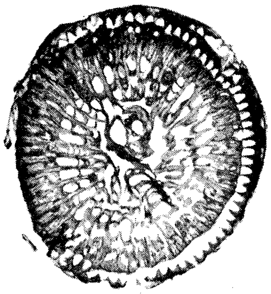

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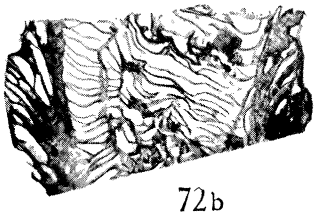

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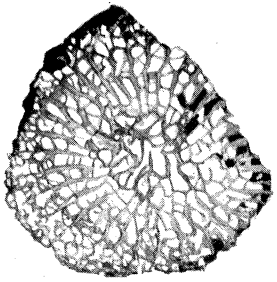
73 b



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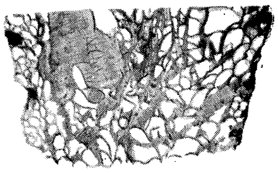

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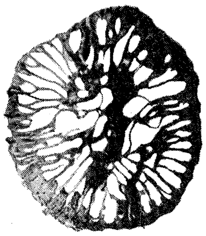

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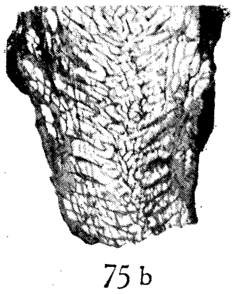
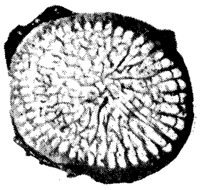


75 b



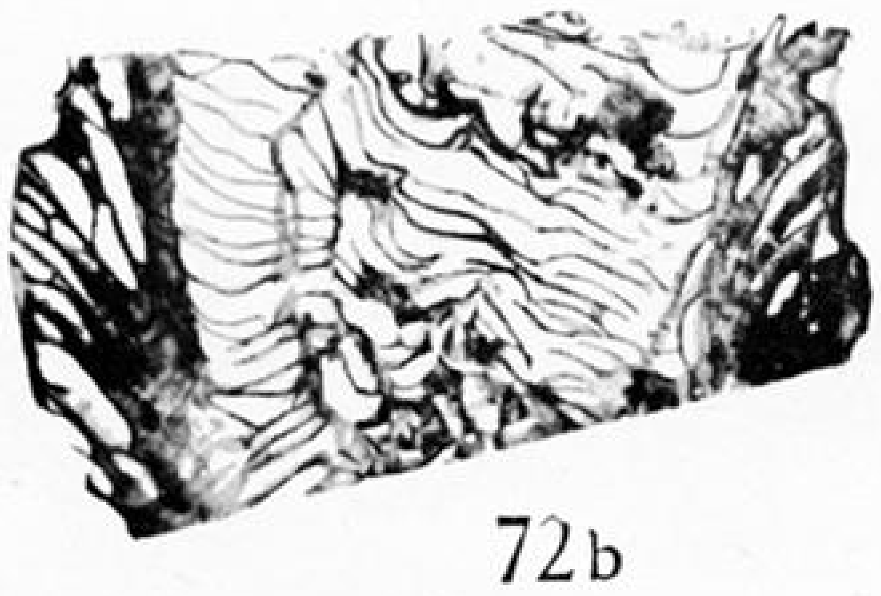
75 a

70

71 a

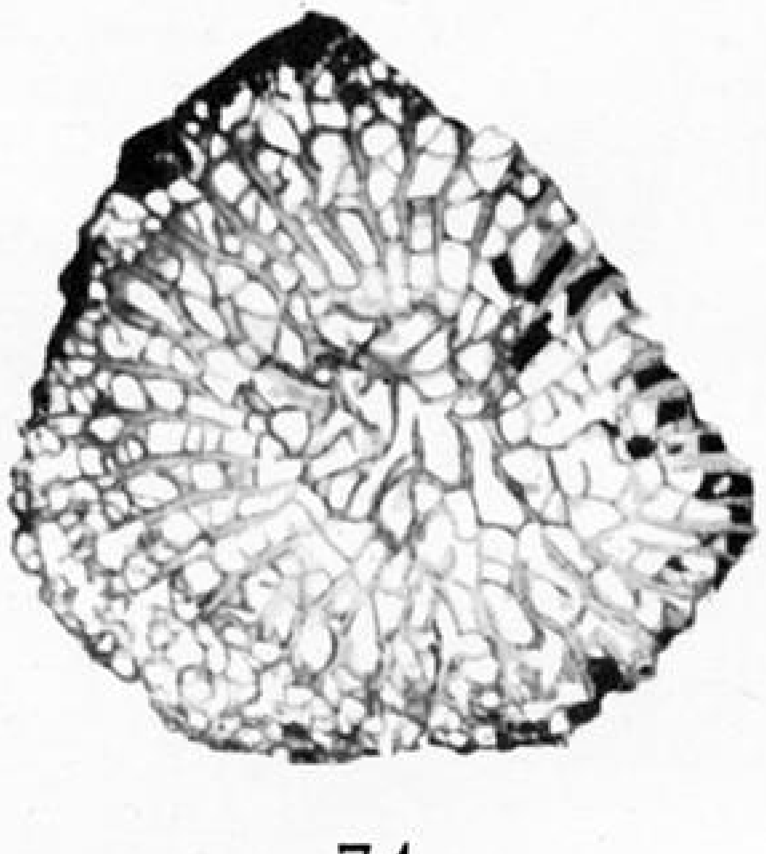
71 b

72a



72b

73 b



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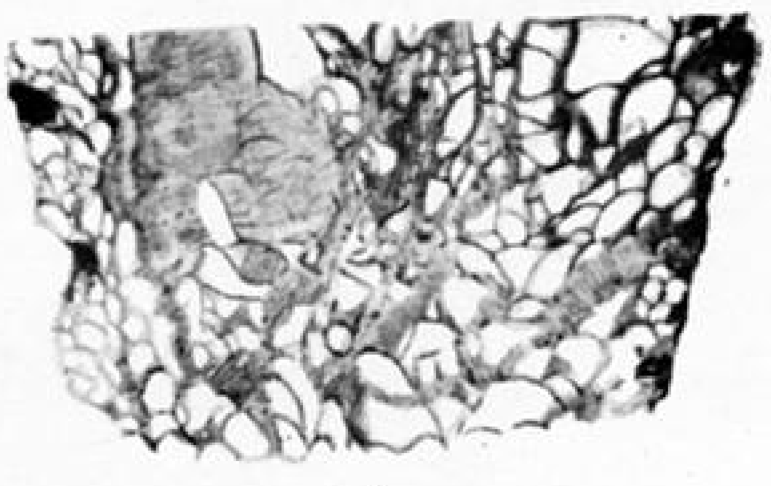

74 b

73 a

75 b

75 a

Plate 9

Streptelasmidae, Dinophyllidae, Pycnactidae, Columnariidae

FIGURE 70. *Siphonophrentis gigantea* (Lesueur), × 2. SM H 4395*e*. See figure 26*a*, plate 5.

FIGURE 71. *Dalmanophyllum dalmani* (Edwards & Haime), × 2. See figure 27, plate 5. (*a*) Transverse section, early ephebic stage. SM A 13609*c*. (*b*) Transverse section, ephebic stage. SM A 13609*d*.

FIGURE 72. *Dinophyllum* sp., × 2. See figure 31, plate 6. (*a*) Transverse section. SM A 8569*e*. (*b*) Longitudinal section. SM A 8569*d*.

FIGURE 73. *Heterophrentis prolifica* Billings, × 2. See figure 32, plate 6. (*a*) Transverse section, early ephebic stage. SM H 4394*d*. (*b*) Transverse section, ephebic stage. SM H 4394*c*.

FIGURE 74. *Ceratophyllum* sp., × 2. See figure 39, plate 6. (*a*) Transverse section. SM A 15070*e*. (*b*) Longitudinal section. SM A 15070*f*.

FIGURE 75. *Lyrielasma* sp., × 2. See figure 57, plate 7. (*a*) Transverse section. SM A 9103*b*. (*b*) Longitudinal section. SM A 9103*c*.