SPHERULITIC CRYSTALLIZATION AS A MECHANISM OF SKELETAL GROWTH IN THE HEXACORALS.

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I. Introduction.

For some years the authors of this paper had been working independently on the structure of spherulites and of corals respectively. Certain similarities in structure were noted between these organic and inorganic materials which, even at first glance, appeared to be more than superficial. It was therefore decided to collaborate in making more detailed comparisons of coralline and spherulitic structures in order to determine the degree of similarity and its possible significance.

A search of the literature revealed that although the similarity between certain aspects of coral structure and spherulitic form has already been pointed out by von Koch (1882) Bourne (1899) and Cayeux (1916, p. 416) these authors do not appear to have appreciated the significant and indeed essential part played by spherulitic crystallization in coral growth.

Comparisons of the skeletal elements of organisms with mineral substances may be based on chemical, physical, or structural features, or on some combination of these.

The fact that a chemical identity exists between certain skeletal elements and various inorganic substances is, of course, well known and only to be expected. Even when the organic materials possess in addition crystalline forms identical with those of certain specific minerals, the fact need not be regarded as especially significant. But if, in addition to identity in chemical composition and crystalline form, there is found identity in the aggregation of the constituent crystals, it would appear that a study of that particular mode of mineral growth should throw some light on the organic processes producing the identical skeletal structure.

After a close examination of the microscopic characters of the skeleton of the Hexacoralla we have concluded that these organisms have adopted spherulitic crystallization as an essential mechanism of skeletal development.

II. The Skeleton of the Hexacoralla.

(*a*) Descriptive.

The skeleton of the Hexacorals is a framework whose constituent elements are aggregates of crystalline fibres of calcium carbonate. This is generally recognised and was established chiefly by the work of von

Heider (1882), von Koch (1882), Pratz (1882), Ogilvie (1897, 1907), Bourne (1899), and Duerden (1902, 1904).

The framework is constructed of vertical skeletal elements and of horizontal skeletal elements. It is bounded on its upper surface by the soft parts from which it was formed, but elsewhere it is typically sheathed in a thin calcareous film, the epitheca.

The various parts of the skeleton of a Hexacoral are closely comparable with those of the Rugosa, recently defined and illustrated (Hill, 1935). The vertical skeletal elements are the radially arranged septa, and, in many genera, the more or less complex axial columella; the horizontal skeletal elements of the Rugosa (tabulae, tabellae and dissepiments) may, however, sometimes in the Hexacorals have their functions performed in part by modifications or outgrowths of the vertical skeletal elements—e.g., synapticulae.

Chemical analyses of Hexacoral skeletons show that on the average they are 98 per cent. $CaCO_3$, with less than 1.5 per cent. $MgCO_3$, and only a trace of $Ca_3P_2O_8$ (Clarke and Wheeler, 1924 p. 8). Sorby's researches (1879) showed that the specific gravity of both perforate and non-perforate Hexacoral skeletons was about 2.75, and he therefore concluded that they must be almost wholly aragonite, although he was not quite certain that calcite is always entirely absent. Meigen's tests (1903) on twenty zoantharian corals showed them to be aragonitic and non-magnesian, and Cullis' (1904) work on the Funafuti bore cores confirmed this.

It has been suggested that Hexacorals in the chalk and Danian of Denmark had skeletons of calcite, because they still retain the original fibrous structure (Bøggild, 1930, p. 241, and Kendall (1896, p. 790) has suggested that chemical conditions at the bottom of deep, cold seas are such that only calcite could occur in skeletons formed there.

Microscopic investigation shows that the crystalline fibres are elongate needles about 2μ in diameter. They are not arranged haphazardly in the skeletal elements, but are grouped in systems.

In true horizontal skeletal elements the fibres are arranged at right angles to the top and bottom surfaces, so that in a flat plate they are parallel, but in a curved plate they are slightly divergent—e.g., *Stylophora.* A vertical section of such a plate studied by transmitted light frequently shows a dark band at the base, which, however, is by reflected light more uniformly white than the rest. In some cases septal or columellar vestiges occur in the horizontal skeletal elements, and such vestiges have a less simple arrangement of fibres.

In the vertical skeletal elements the fibres are grouped into trabeculae, which are themselves grouped to form the septa, &c. But whereas the arrangement of fibres within the trabeculae is always approximately the same, the dimensions and arrangement of the trabeculae themselves vary from genus to genus, or from species to species. Each trabecula is a cylinder tapering convexly at the top, and consists of fibres, usually curved, directed upwards and outwards from a common axis. The fibres usually reach the surface of the cylinder somewhat obliquely, but they are at right angles in the tapering top.

The trabeculae may all be in the vertical plane of the septum, in which case they may either all be parallel, or they may diverge, those of the axial part of the septum being directed upwards and inwards, and those of the peripheral part being directed upwards and outwards.

In some cases the trabeculae may diverge laterally from the median plane of the septum to project on either side of the septum as granulations. This second type of divergence may be opposite or alternate. Combinations of these several arrangements may occur, giving in some cases very complex septa.

In a very large number of Hexacorals, the so-called Aporosa, each vertical skeletal element is formed so that the fibres of any one of its trabeculae are everywhere in contact with those of neighbouring trabeculae. In the others, the "perforate" Hexacorals, gaps are seen between the fibres of neighbouring trabeculae and sometimes the vertical continuity of a trabecula may be broken.

A lamellaton, chiefly shown by slight colour differences and degrees of opacity, is sometimes observed in vertical sections of the horizontal skeletal elements. It is at right angles to the fibres and shows no great regularity of width from one lamella to the next. The general impression obtained with the low power objective is that the fibres are continuous through the lamellations, but with the use of higher power evidence of discontinuity is to be seen at the base.

Lamellation of a similar nature is frequently visible also in the trabeculae of the vertical skeletal elements. It is everywhere at right angles to the fibres; the width of the lamellae is variable; there may be a darkening (in transmitted light) at the base of a lamella; there is an impression of continuity of the fibres of successive lamellae, but closer study shows interruptions. The axis of each trabecula is visible in transmitted light as a darker line, but by reflected light it is more densely white. The "darkening" at the axes of trabeculae and at the bases of tabulae, dissepiments, and lamellae appears to be due to excessively finely divided matter interstitial to the fibres at these places.

A very fine, even lamellation, 3μ to 6μ wide, is to be observed in the less opaque parts of most Hexacorals.

The intimate structure of the epitheca, whether fibrous or not, is unknown.*

The bleached skeletons of Hexacorals are creamy-white in colour as seen in the hand specimen, but as viewed through the microscope they appear as yellow or light brown by transmitted light.

The preceding remarks applied to the skeleton proper, as developed in each of the many sections that we have examined. Some specimens, however, show in addition to the regularly arranged aggregates of yellow crystalline fibres a discontinuous and irregular aggregation of colourless granular crystals external to the skeleton proper. These crystals are of aragonite (?) and may form scaly, vermicular, or roughly prismatic groups.

(*b*) Relation of the Madreporarian Skeleton to the Soft Parts.

It is now generally accepted that the skeleton of the Madreporaria is an exoskeleton formed by the basal ectoderm; that the ectoderm is a unilaminar sheet, in which, in general, cell boundaries are not distinguishable; and that the crystalline fibres of the skeleton arise in a colloidal matrix secreted by, but external to, the ectoderm. The soft parts are attached to the skeleton by this gel and by the sucker-like

* The work of von Koch (1882) suggests to us, however, that the epitheca may be a single sheet of minute spheres, each consisting of aragonite fibres radially arranged.

desmoidal processes which extend through the ectoderm from the mesoglaea. These conclusions have not been reached without argument, which, however, has already been sufficiently reviewed (Bourne, 1899; Duerden, 1902; Matthai, 1918; Hill, 1935, p. 484).

All vertical skeletal elements are formed in invaginations in the basal ectoderm, and all true horizontal skeletal elements are formed below the unfolded basal ectoderm between these invaginations.* The apices of the trabeculae project into smaller hollows in the septal invaginations, and the apical parts of the trabeculae are built up therein; the trabeculae are thickened from the sides of the septal invaginations. The direction of the crystalline fibres of the skeleton is always perpendicular to the surface of the ectoderm at the place and time of their addition. The direction of curvature of the vertical skeletal elements is always perpendicular to the direction of curvature of any horizontal skeletal element which abuts on to it. The calcareous fibres forming the horizontal skeletal elements are not sharply separated from those laid down at the same time on the sides of a neighbouring septum by the sides of an invagination (Hill, 1936, p. 192). It can be established from the growth lamination of the various elements that the vertical growth of a trabecula is more rapid than the vertical growth of a horizontal skeletal element, and it is deduced that upward pressure is exerted on the polyp at the tops of the invaginations. The muscular stresses developed in the base of the polyp due to the greater vertical growth of the trabeculae are thought to be relieved at the critical point to prevent rupture by the periodic release of the attachment of the skeleton to the uninvaginated base (*loc. cit.* p. 191). The base rises to a new position, in equilibrium with the stress, and a new horizontal element is begun. Thus while the upward movement of the vertical skeletal elements is continuous, that of horizontal elements is intermittent.

III. Spherulitic and Allied Structures.

(*a*) Descriptive.

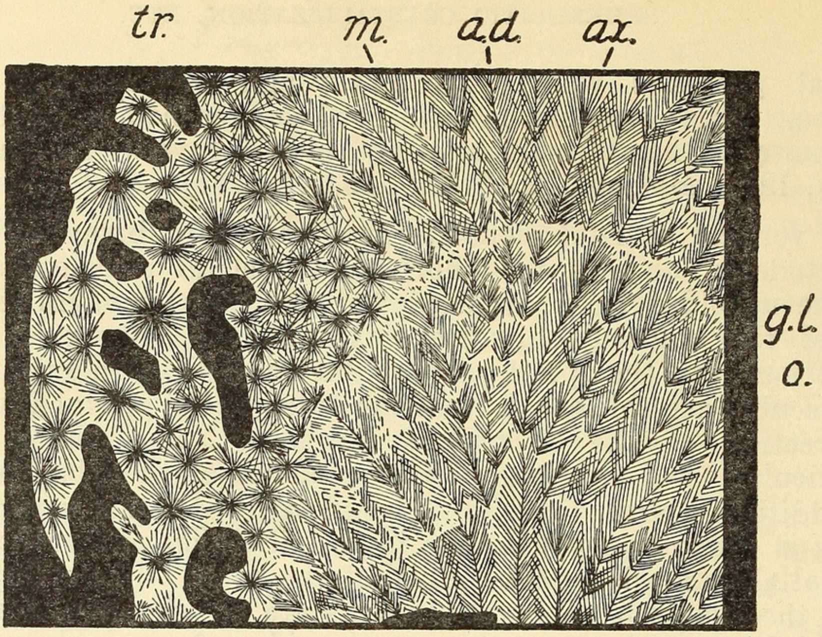
A spherulite, as originally defined, consists of "a radiating and often concentrically arranged aggregation of one or more minerals, in outward form approximating to a spheroid, and due to the radial growth of prismatic or acicular crystals in a viscous magma or rigid glass about a common centre or inclusion" (Vogelsang, 1872).† In accordance with the general practice of geologists the scope of this definition may be extended to include, in addition to radial growth about a point, divergent growth about an axis and parallel growth upon a surface and any combination of these.

Further, and in addition to such simply radial, divergent or parallel growths, other, composite, but obviously related structures are found. Such composite spherulites show the result of mutual interference between adjacent components in two types of growth that have been described as "tufted" and "plumose" respectively (Bryan, 1940, p. 46).

In the first of these types the centres from which the radial growths are directed remain fixed in their initial position and composite growth proceeds in the form of tufts, the fibres of adjacent components after initial antagonism become progressively longer and more nearly parallel,

* In some perforate Hexacorals, however, the function of the horizontal elements is wholly or in part taken over by modifications of the vertical skeletal elements.

† Cited from Holmes, 1928, p. 214.



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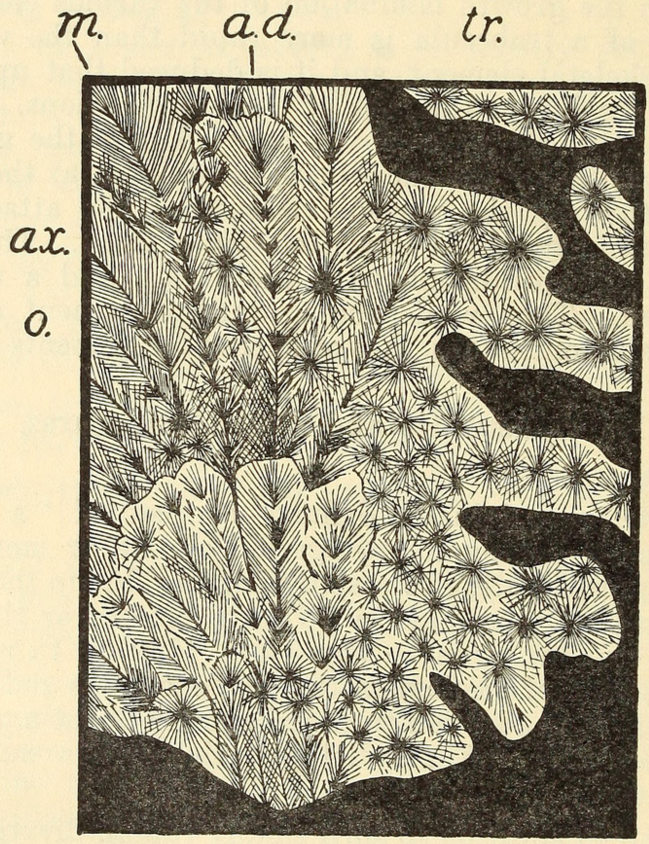

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EXPLANATION TO TEXT-FIGURES.

Each figure represents an almost vertical section through a septum of a Hexacoral, in the plane of the septum. In this species the trabeculae diverge towards the peripheral and axial edge of the septum, at *a.d.*, and they also diverge from the median plane of the septum to each septal face—i.e., they diverge into and away from the plane of the paper. Each trabecula consists of crystalline fibres of Aragonite directed upwards and outwards from its axis *ax.* Trabeculae cut transversely by the section are shown below *tr.* in each figure as radiating groups of fibres; others cut in an approximately median vertical plane are shown at *m.* in each figure as pinnate aggregates; and others again, cut obliquely, are shown opposite *o.* in each figure as fan-shaped groups of fibres. Discontinuity due to interruption in growth is shown at *g.l.*, which represents the position of the upper edge of the septum at that growth period. After Ogilvie. These figures should be compared with those illustrating various types of spherulitic growth given by Bryan in an earlier paper in this volume (Proc. Roy. Soc. Qld., LII., pp. 41-53).

and the whole structure moves toward a unity and homogeneity that resembles more and more closely simple spherulitic growth. Correspondingly the outer surface becomes more and more nearly that of a simple sphere.

In the second type the centres of radial growth move progressively outwards from their original positions, the adjacent components remain as antagonistic as when they first interfere, and the structure remains an obviously composite one with a complex outer form.

Concentric structures frequently accompany spherulitic growth. These are however by no means essential. They in no way contribute towards the radial growth, but, on the contrary, may be regarded as interruptions of it.

Such interruptions may be brought about in several ways and may be periodic or haphazard, giving rise to concentric patterns of varying degrees of regularity.

The foregoing statements apply to spherulites proper as they occur in natural rock glasses, but similar crystal aggregates dominated by radial fibrous growth are found under quite other conditions in the mineral world. It may be that in some of these the resemblance is little more than mere superficial similarity, while others may represent true homologues of the spherulites proper. Much work remains to be done to elucidate the position. Here it will be sufficient to refer briefly to a few examples typical of these analogous structures.

Of the non-metallic minerals Wavellite is perhaps the best example, while all the essential features of spherulitic structure appear to be present in some varieties of the iron ores Siderite and Haematite. Hailstones are sometimes in the form of radial aggregates. ''Spherulites'' have been formed, too, by the deposition of Aragonite in sea water.

Structures analogous to natural spherulites have also been produced artificially. They have been accidentally formed from time to time in commercial glasses. Morse, Warren, and Donnay (1932) have deliberately developed them in gels, in which medium they have succeeded in producing perfect specimens from a host of different chemical substances of every crystal system. Spencer (1925, p. 689) has grown ''spherulites'' in test tubes from supersaturated solutions of salicin containing (1) flocculated clay, (2) bentonite, (3) a gelatine-gel.

(*b*) Conditions of Spherulitic Growth.

It is difficult to state any one set of conditions that will cover the development of spherulites proper and the many inorganic structures more or less closely analogous to them. But, although one cannot define the essential conditions of spherulitic growth one may at least indicate those conditions that appear particularly favourable for its development.

Thus for the spherulites proper it is generally agreed that development is dependent upon crystallisation of highly supersaturated material in a very viscous solution. The same conditions would appear to be true for the accidental development of spherulites in artificial glasses.

Spencer (1925, p. 705) concludes with regard to spherulitic siderite in sediments that ''The radiating spherulitic form of the carbonate appears to be due to crystallisation from supersaturated solutions held within partly colloidal sediment.''

With regard to the production of artificial spherulites Morse, Warren, and Donnay have shown that they can be formed of many substances if the reacting solutions are allowed to mix by diffusion avoiding all convection. They state further that the presence of a gel appears to be highly favourable to the growth of artificial spherulites.

Schade (*fide* Bucher, 1918) has demonstrated experimentally that concretionary bodies form when a substance passes from the state of an emulsion colloid (or "emulsoid") to that of a solid, and that if the change leads to the crystalline state the resulting structure is radial if the substance is pure. Weimarn (*fide* Hedges, 1931) has advanced evidence for the conclusion that many gels contain numerous spherical aggregates of crystal fibres as essential constituents. Bradford (*fide* Spencer, 1925), too, believes that gels themselves consist of microscopic spherulites.

While not denying the possibility that closely analogous structures may be formed from ordinary solutions, it would appear from the evidence cited above that glasses, colloids, and gels present especially favourable environments for the production of spherulites. The common factor may well be as suggested by Morse, Warren, and Donnay that under such conditions convection currents are at a minimum and diffusion consequently very regular.

IV. Spherulitic Crystallization as a Factor of Skeletal Growth.

(*a*) Analogies between Skeletal Components and Spherulitic Structures.

The simplest structural unit in the skeleton of the Hexacorals is the fibre. Each fibre is composed of calcium carbonate and is crystalline in nature. More particularly, it has been established that each fibre is a single orthorhombic crystal of Aragonite. So much is generally accepted.

As has been shown above, spherulitic crystallization is a phenomenon common to many chemical substances (including calcium carbonate), and to all crystalline systems (including orthorhombic). It would appear then that there is no serious reason to exclude the possibility that the fibres of the madreporarian skeleton are essentially homologous with the crystals of a spherulite. Indeed, it is our opinion that each coralline fibre is identical in all important respects with a crystal in a spherulite.

These skeletal fibres have been interpreted by Ogilvie as bunched into aggregates that she terms fascicles, and which she regards as definite structural units. If, indeed, such fascicles exist they have no counterpart in spherulitic crystallization, but a careful study of Ogilvie's descriptions and figures and a detailed examination of our own material has failed to establish the existence of these as recognisable entities.*

In our view, the natural category next in complexity to the fibre is the trabecula. Each trabecula is an aggregate of fibres arranged about an axis. Sections transverse to the axis show a simply radial arrangement of the constituent fibres, whereas sections parallel to the axis show divergent structure. We would suggest that each trabecula is to be compared with a spherulitic growth of axiolitic type.

The aggregation of trabeculae gives rise to such skeletal elements as the septum and the columella in the manner detailed earlier in the

* One of us (Hill, 1935) found no place for fascicles in her structural analysis of the coral skeleton.

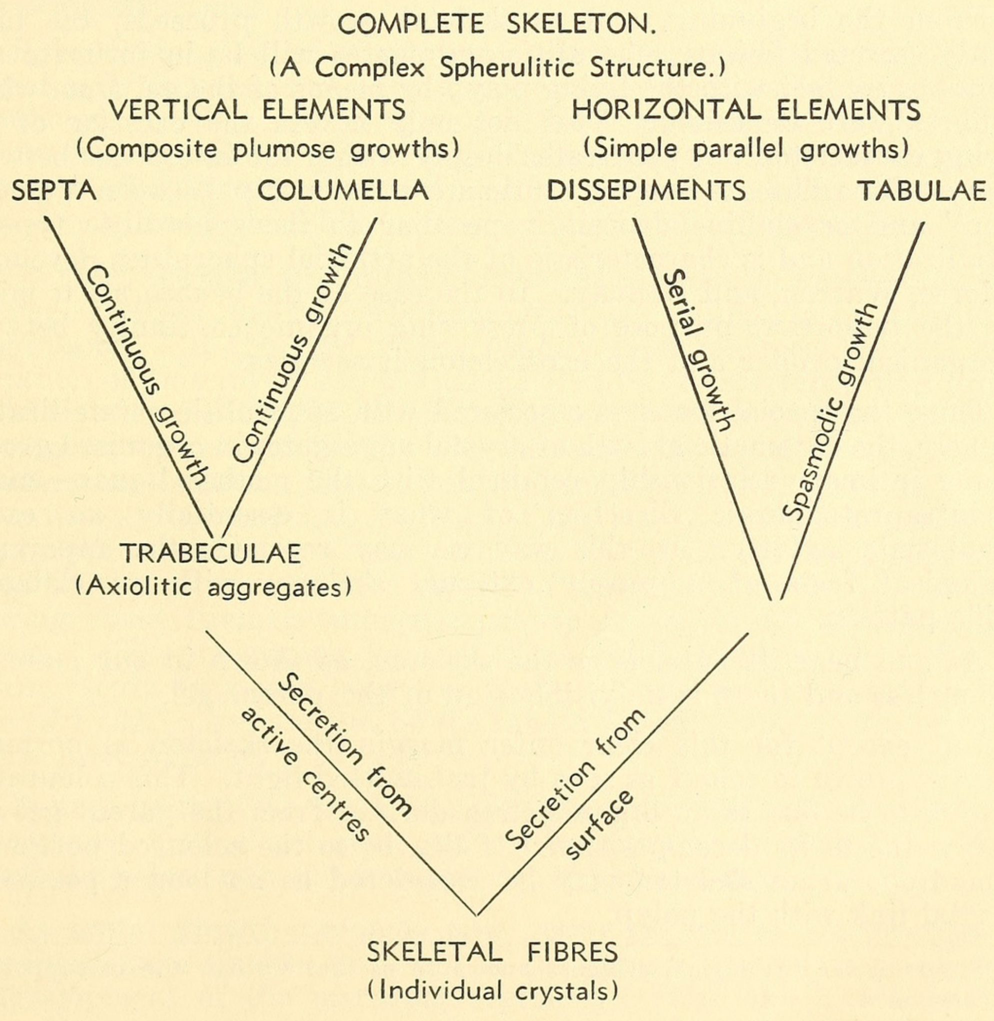
paper. It is our view that these trabecular aggregates are in all essentials closely analogous with composite spherulitic growth and more particularly with that manifestation of it that one of us has described as "plumose growth." It would thus appear that for septal growths each structural category—namely, fibre, trabecula, and septum—has its respective counterpart in spherulitic crystallization.

The columella in its complex fibrous trabeculae is closely comparable with a development of intertwined axiolitic growths.

The position with regard to the horizontal structures is somewhat different. Here the individual fibres are not aggregated into trabeculae, but appear as numerous closely parallel individuals arranged at right angles to the surfaces of the particular skeletal element of which they are units. Such pilose aggregations of fibres bear a striking resemblance to simple spherulitic growth upon a plane.

The lamellar markings and discontinuities, too, are analogous, both in appearance and relationship to the general plan, with those concentric arrangements that so frequently are found accompanying spherulitic structures.

The above conclusions are based on an examination of material especially prepared for the purpose, but it should be pointed out here that many published figures of hexacorallan skeletons, and in particular those of Ogilvie (1897), clearly and adequately demonstrate the many features in which they closely resemble spherulitic structures.



(*b*) The Growth of the Skeleton.

(i.) *General.*—Our interpretation of the development of the madreporarian skeleton in terms of spherulitic crystallization is as follows:—

In general, the whole ectodermal surface is capable of the slow exudation of a gel from which crystalline fibres of calcium carbonate are deposited in spherulitic aggregates of simply parallel character, placed at right angles to the adjacent ectoderm, thus giving rise to a pilose (carpet-like) effect.

In particular, at certain points in the ectoderm, a more concentrated production of the calcareous gel takes place.* Corresponding with each such centre, an individual spherulitic growth is initiated and maintained.

In both types of spherulitic growth development will proceed automatically and along predictable lines once the process is initiated and as long as the supply of calcium carbonate is available, but the particular spherulitic pattern on which the skeletal growth is based is determined by the number and distribution of the active centres. This pattern is not uniform for all hexacorals, but neither is it haphazard. Indeed, it is very significant and reflects the fundamental organic plan of the animal.

The centres of calcification are in general arranged in linear groups which are themselves radially disposed, but the particular arrangement of the centres in each group, as to number and position, and of the radial groups themselves, varies and is an important specific character.

From the beginning, and as skeletal growth proceeds, the more recently secreted fibrous spherulitic aggregates will be in intimate and continuous contact with the living polyp by means of the gel from which the fibres were deposited. This not only covers the exterior of the growing exoskeleton but penetrates deeply within the interstices between the crystalline fibres. Such an intimate relationship between ''mother liquor'' and crystalline deposit is peculiar to the spherulitic type of crystallization and is characteristic of the artificial spherulites developed by Morse, Warren, and Donnay. In the case of the hexacorals it might serve the important purpose of preserving organic continuity between the organism proper and the exoskeleton it secretes.

Thus, the special features associated with spherulitic crystallization —namely, the automatic growth of crystal aggregates in organised groups and the intimate relationship retained with the mother liquor—enable the intraprotoplasmic direction of what is essentially an extra-protoplasmic activity. In this way we may reconcile the apparently paradoxical facts of a purely external skeleton with an elaborate specific pattern.

At and near its outer edge the skeleton, as shown in our material, is colourless and there is no visible sign of the parent gel.

But except for this clear outer margin the skeleton is normally yellow or brown in colour as seen by transmitted light. This colouration we think to be due to an organic stain derived from the parent gel and possibly due to its decomposition. If this be so the coloured portion of the madreporarian skeleton may be considered as no longer possessing any vital link with the polyp.

* There is no histological evidence known to us that we can cite in support of this conclusion.

Superimposed on the skeleton proper there is sometimes found a discontinuous granular or scaly deposit of clear crystalline calcareous material. Such superficial deposits are non-fibrous in character and show no trace of that spherulitic organisation characteristic of the skeleton proper. Some authors have regarded these deposits as an intermediate or incipient stage in the formation of the skeleton. Our view, on the contrary, is that they are so radically different in everything except chemical content, that they could not possibly give rise directly to the skeleton proper. Indeed, the scales could only contribute to it by first disappearing in solution and afterwards being redeposited in spherulitic form.

Nevertheless, the calcareous nature of the scales and their position upon the skeleton suggest that they were derived from the same source as were the crystalline fibres of the skeleton. It appears to us that these apparently contradictory features may be reconciled if the scales are regarded as a *post-mortem* deposit. After the death of the polyp we would expect the calcium carbonate already in the extruded gel, to be thrown out of solution and deposited upon the skeleton, but not necessarily in spherulitic continuity with it.

(ii.) *Septal Growth.*—Septal growth is initiated immediately the flat disc-like planula attaches itself to its selected foundation and begins to exude calcareous gel from the original active centres. Below each such centre a fibrous spherulitic aggregate is deposited and a trabecula begun. As each trabecula develops there appears at each active centre a corresponding cupola-like recess to accommodate the upwardly projecting structure.

Spherulitic growths of adjacent trabecular centres will soon make contact and, as a result of mutual interference, composite growth will be introduced. In this manner there will be brought about the coalition of the several upwardly projecting trabeculae to form a continuous structure—the septum. Since the active centres are arranged in radial lines the septum is wall-like in shape and radial in disposition.

As the trabeculae are united to form the septum, so the corresponding cup-like recesses in the ectoderm will be united in a continuous invagination. In the past it has usually been assumed that it is the formation of this invagination that has led to the corresponding growth of the septum, the invagination forming, as it were, a mould to which the growing septum adapts itself. The converse view is, at least, worthy of consideration—namely, that the actively and positively growing septum forces its way upward into the base of the polyp, which has perforce to adapt itself. Such a view may claim on its behalf that once spherulitic crystallization is initiated, the supply of material is all that is necessary to bring about further automatic growth in continuity of the original pattern. (The suggestion by one of us (Hill, 1936, p. 191) that the growing septa impose a muscular strain on the ectoderm that is only relieved by the abandonment of the tabula follows as a natural corollary to this interpretation).

It may be that the truth lies between these two extreme views, but at least we may claim that spherulitic growth as such is a direct contributory factor in the development of the septum.

As septal growth proceeds new active centres of calcification are introduced from time to time and in accordance with the several stages of development of the maturing organism. With the introduction of each new centre a new trabecula is begun, and in this manner the septum grows in size and complexity.

Although, as has been pointed out, the chief sources of supply of the calcium carbonate are derived through the centres of calcification, exudation from the general ectodermal surface may contribute towards the enlargement of the septum.

(iii.) *Growth of Horizontal Elements.*—While the vertical elements are being developed as aggregates of trabeculae secreted from the active centres, the horizontal elements are being built up as simple parallel growths of crystalline fibres secreted by and perpendicular to the general ectodermal surface. But instead of rising continuously upon a solid foundation, as do the vertical elements, the horizontal elements have to build their own independent foundations suspended from other skeletal features. Even after such self-made foundations have been erected and spherulitic growth established this is not continuous, for, as soon as the vertical elements have reached a critical height above the horizontal structures, the polyp will be forced to abandon the latter, and the ectoderm will be lifted to a higher position and the formation of the horizontal elements will start anew.

(iv.) *The Origin of Lamellar and Concentric Features.*—The parellel or concentric bands at right angles to the general directions of spherulitic growth have numerous counterparts in spherulites proper and in similar radial aggregates. Several attempts have been made to explain such bands in inorganic structures. The more important of these explanations are, (1) that they are directly due to the presence of impurities, (Schade *fide* Bucher, 1918), (2) that they are due to radial growth temporarily outstripping the rate of supply of material (Spencer, 1925), and (3) that they represent a Liesegang effect (Mourant, 1932).

It appears to us that there remains, at least for spherulitic growths found associated with these corals, a fourth possible explanation for the lamellations—namely, that they are the direct result of variations in those organic activities responsible for the supply of substance for radial growth.

The general use of the term "growth lamellae" by Ogilvie (1897, p. 113) and others for the bands under discussion carries with it the implication that they are directly related to the variable rate or intermittent character in the growth of the living animal.

It may well be that the larger, more conspicuous and less regular bands reflect somewhat irregular growth of the organism, due possibly to seasonal and meteorological changes, as, for example, stormy weather followed by calm.

But the smaller, more delicate and remarkably regular alternations observed by us appear to call for a more precise and rhythmical control. After considering various other rhythms of small period we have arrived at the conclusion that a diurnal pulsation in the supply of $CaCO_3$ is the most feasible explanation. Rhythmic deposition of skeletal material of such a period is not improbable. Indeed, it is to be expected in view of the fact that the majority of corals are closed and quiescent during the day, and are expanded and actively feeding during the hours of darkness when, alone, zooplankton for their sustenance is abundant (Yonge, 1930, p. 55).

V. Possible Examples of the Process in other Groups.

The skeletons of the Rugosa, the Tabulata, and the Heliolitida are fibrous, and their septa are trabeculate like those of the Hexacoralla, but the arrangement of the trabeculae in the septa is simpler. Although none of these three sections is living to-day, it may be assumed by analogy with the Hexacorals that their fibrous skeletons are exoskeletons secreted by the ectoderm, and that they have been formed by spherulitic crystallization. The crystalline fibres of these corals differ from those of the Hexacorals in one respect—namely, that they are composed of calcite; and since the fibres have persisted as such from the Palaeozoic it is assumed that they were originally deposited as calcite.

Spherulitic crystallization is not general in other orders of the Anthozoa; but in the Alcyonarian *Heliopora* (Bourne, 1899) and in the Hydrozoan *Millepora* the skeleton is an exoskeleton of aragonite fibres built up by spherulitic crystallization. When calcareous skeletons occur in other Alcyonaria they are endoskeletons consisting of spicules of felted calcite needles deposited intracellularly, with strands of organic matter in the felt.

Of the foraminifera the tests of the Perforata appear to be built by planar spherulitic crystallization, for they consist in many genera of minute prisms of calcite perpendicular to the surfaces; but in the Imperforata the tests are of felted calcite needles like the Alcyonarian spicules (Sollas, 1921). In both groups the skeleton is to be regarded as an exoskeleton, and in both there is a gel-like network through the test.

In higher groups spherulitic crystallization may occasionally occur. Thus the middle or prismatic layer of the shell of some lamellibranchs may sometimes consist of prisms of calcite or of aragonite, each prism being a plumose growth of crystalline fibres, like the trabecula of a coral, but with prismatic boundaries. Bøggild has referred to this as a composite prismatic layer (Bøggild, 1930, pl. vi., fig. 6, pl. vii., fig. 1). The guard of the extinct Belemnites and the tissue of the Ostracod shell are both fibro-radiate and suggestive of spherulitic crystallization.*

VI. Conclusions.

In summary, we may say that a review of the published descriptions and the careful examination of our own material alike lead us to the conclusions that:—

(1) The skeleton of the Hexacoral is essentially a mineral aggregate.

(2) More particularly it is a fibrous aggregate in which each fibre is an individual crystal of the mineral aragonite.

(3) All the known features of the skeleton may consistently be described in terms of that type of mineral aggregation known as spherulitic crystallization.

(4) More particularly the trabeculae of hexacorals are identified with plumose aggregates in spherulites and the tabulae with pilose growths.

(5) The relation of the fibres of the Hexacoral skeleton to the colloidal matrix secreted externally by the ectoderm has its parallel in the relation of the fibres of a spherulite to its mother liquor.

* Since this paper went to press, F. W. Whitehouse has found spherulitic crystallisation in the plates of Cambrian echinoderms from north-western Queensland.

(6) The skeletal pattern is decided by the location and intensity of the ectodermal secretion.

(7) More particularly the number and position of the trabeculae are decided by the distribution of the active centres of calcification.

(8) The Hexacoral skeleton is thus due to the organic guidance of an inorganic process.

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