STUDIES IN THE DEVELOPMENT OF CERTAIN PALEOZOIC CORALS

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ON THE ORIGIN AND DEVELOPMENT OF THE INNER WALL

Certain Paleozoic corals have been characterized by their authors as containing an inner wall which divides the corallite into an inner central and an outer annular area, the latter extending between the two walls. It has also been observed that in a number of these genera the septa extend to the center, penetrating the supposed inner wall, while in others the septa terminate in the inner wall itself. The genus Acervularia is a type of the former and Craspedophyllum[1] of the latter. The character of the inner wall in the two types is such that they can readily be differentiated even in a very cursory examination. While both genera have been considered to contain an inner wall, Edwards and Haimes as early as 1850 (*Polyp. Foss. des Terr. Paleoz.*) differentiated the two types by noting that the internal structure of Eridophyllum, which is of the Craspedophyllum type, differed from Acervularia in that the septa terminated in the inner wall, while in the latter the septa extended through the inner wall into the inner central area. They do not record having noted any difference in the structure of the inner walls themselves in the two genera.

Thin sections reveal the fact that the structure of the two types of wall are quite different and that they have an entirely different origin. The inner wall in the Craspedophyllum-Eridophyllum type is of a similar nature in texture and thickness to the septa, and occupies but a small central circular portion of the corallite.

In Craspedophyllum the diameter of the inner wall is about one-sixth to one-fifth that of the corallite. In the normal adult of this genus the inner wall has one opening, connecting the central area with the cardinal fossula. This gives to the inner wall the shape

[1] Equivalent to Thomson's Crepidophyllum, which term is used by Canadian paleontologists.

of a horseshoe, but in more specialized individuals a bridge spanning the cardinal fossula gives the inner wall a circular outline and completely separates the inner circular and the outer annular areas.

In the Acervularia type[1] the supposed inner wall is much thicker than the septa and in size about one-half the diameter of the corallite, so that even the tertiary septa take part in its formation and these as well as the secondary septa may extend into the inner central area. The supposed inner wall thus formed is not of uniform thickness, being thicker at the intersection of the septa: in some individuals the thickening from each septum is not sufficient to be in contact with the thickening from the neighboring septum, thus giving a number of openings in the wall. This is readily accounted for when it is seen that the apparent wall is formed by the lateral thickening of the septa at or near the end of the tertiary septa. When sufficient thickening of the septa occurs, they will be brought in contact, giving the appearance of an inner wall. It is evident that the supposed inner wall of this type is rather of the nature of a pseudotheca, the portion of the septa between the region of the septal thickening and the outer wall corresponding to the costae, thus differing greatly from the corals containing a true inner wall.

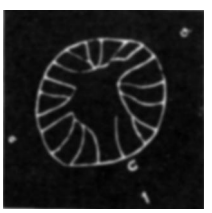

FIG. 1.—Cross-section of a young corallite of *Craspedophyllum subcaespitosum* Diameter 2mm. *a*. The alar septa. *c*. The cardinal septum. Showing the early grouping of the septa. Four openings are shown but the normal condition is three the two alar and the one at the cardinal fossula.

We may now inquire into the nature of the inner wall itself as present in such a genus as Craspedophyllum. The Devonic species, *Craspedophyllum subcaespitosum*, from the Hamilton of Thedford, Ontario, is here chosen, as it is one which is especially distinguished as showing the typical structure of the true inner wall.

The mode of origin and development can be understood by comparing a series of figures (Figs. 1–5) representing the development of the inner wall

[1] This refers to description of the type of Acervularia. In some specimens of Acervularia in this country there is no lateral thickening of the septa, and hence no indication of the supposed inner wall.

as revealed in successive sections of a single corallite. It is seen that each alar region is that at which new septa are successively added to the primary septa (Fig. 1).

The addition of new septa takes place in such a manner that the new short septa are inclined toward the older, with which they are permanently fused with their inner borders, never being detached even in the most developed stages. It is to this persistent fusion of the inner borders of the long septa that the inner wall is directly due, as will be explained presently. It is evident that the addition of new septa is the same as Duerden has found to be true in the genus Streptelasma (*Biological Bulletin*, Vol. IX, No. 1, p. 30), but that genus differs from Craspedophyllum in that the septa become free toward the close of development. It differs from the genus Hadrophyllum, as in the latter the alar pseudofossulae[1] and the pinnate arrangement of the septa are maintained in the most developed stages, whereas in Craspedophyllum the alar pseudo-fossulae become obliterated very early in the life of the individual by the formation of a dissepimental bridge, and the pinnate arrangement of the septa, with the exception of one or two septa on either side of the cardinal fossula, gives place to the more specialized radial arrangement.

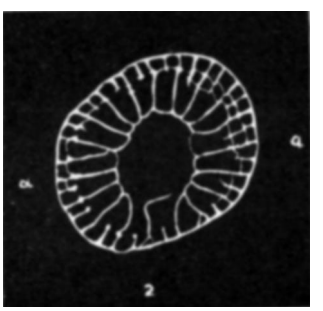

FIG. 2.—Section of same corallite 5mm higher up. Diameter 3mm. *a*. The alar septa. The cardinal fossula is connected with the inner central area.

The growth of septa in the early stages is very rapid, but the central area is always left intact never being invaded by them. This gives the septa an irregular appearance which greatly adds to the difficulty of detecting the Streptelasma mode of arrangement; the difficulty being further augmented by the tendency of the septa to arrange themselves radially and yet to remain attached with their inner borders. It is evident, that, for the septa to remain attached in this manner, only the peripheral portion can become radial at first, but this portion gradually extends inward until

[1] Grabau and Shimer, *North-American Index Fossils*, p. 48.

finally it reaches a point where it will be nearly at right angles to the inner part or attached border, which is at this time about parallel in position to the outer wall. This inner portion of each septum in this manner forms a part of the inner wall as fast as the septa become radially directed (Figs. 2, 3).

In a later section (Fig. 2) the alar pseudo-fossulae have been spanned by a dissepimental bridge which is here slightly thinner than the normal width of the inner wall. The inner wall ends in two septa, one on each side of the cardinal septum as would be expected, unless the latter should take part in the formation of the inner wall which, however, has not been observed.

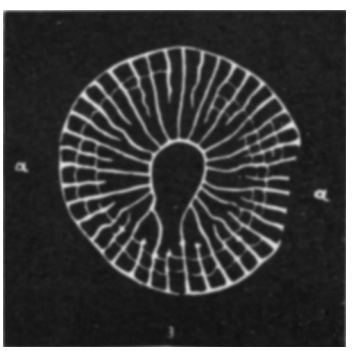

FIG. 3.—Section of same corallite taken 5mm higher up than section of Fig. 2. *a*. The alar septa. Diameter of corallite, 4mm.

In a section of a later stage (Fig. 3) the inner wall is of uniform thickness and ends in the septa nearest the cardinal fossula, as in Fig. 2. The neck between the cardinal fossula and the inner central area has become more narrow. The cardinal septum has been reduced in size to that of a tertiary septum.

This mode of development of the inner wall extends from the alar septa as initial points towards the cardinal region, and simultaneously from either side of the counter septum as another initial point toward the two alar regions. There would, therefore, be a break in the inner wall in the region of the cardinal septum, and two breaks, one at each of the alar regions where growth from the counter quadrants ceased. The two latter are early spanned by the deposition of material of a similar nature to that of the septa, thus uniting the groups and making the septal structure more firm. In Fig. 2 this growth is in the course of construction and is completed before the stage in Fig. 3 is reached, as here the wall is of uniform thickness throughout—and the "bridges" spanning the pseudo-fossulae in Fig. 2 are thoroughly incorporated. This eliminates the last trace of the

alar pseudo-fossulae, and all the septa have assumed their complete radial direction with the exception of one on either side of the cardinal fossula.

The opening in the inner wall in the region of the cardinal fossula is very persistent and remains permanently in normal individuals of the species, constituting the character of the horseshoe shaped inner wall of Craspedophyllum (Fig. 4.) In normal types it persists into the adult, but in the last stages of accelerated types it is closed. While this opening remains, the two septa on either side of the cardinal septum remain pinnate and form the ends of the incomplete wall (Fig. 3). The septa very slowly arrange themselves radially and in a similar manner to the earlier ones contribute their portion to the ends of the inner wall (compare Figs. 3 and 4). The septa on either side of the cardinal septum are now more radially arranged than in Fig. 3, and the connection between the inner central area and the cardinal fossula is more constricted. It is seen in Fig. 4 that as these two septa become radially directed, the neck connecting the cardinal fossula with the inner central area is gradually constricted until a stage is reached, as shown in Fig. 5, when this neck is spanned by a similar dissepimental bridge which early in the life of the individual cut off the connection between the alar pseudo-fossulae and the inner central area. It is evident that in further development of the individual, the cardinal fossula cannot be distinguished and to all appearance becomes similar to one of the interseptal spaces. The septa on either side of the cardinal septum have now assumed a nearly radial direction and the dissepimental bridge spans the cardinal fossula making the inner wall complete. In Fig. 5 one can clearly trace the

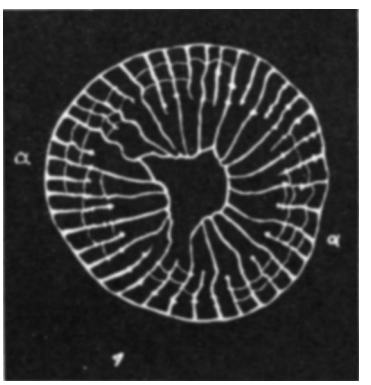

FIG. 4.—Cross-section of the same corrallite taken 5mm higher up than Fig. 3. Diameter 4mm. *a*. The alar septa. A slight irregularity of growth on the left.

order of development of the septa by their inner borders retaining a slight indication of the pinnate arrangement in the early stages. Further development of the corallite will tend to make the septa perfectly radial in direction and the inner wall, to which the primary and secondary septa are still firmly fused, assume a circular outline which is better illustrated in more specialized individuals than is shown in Fig. 5. At such a stage the true relation which exists between the inner wall and the long septa is not so evident. The former now develops quite independently of the septa, the inner borders of which may be considered as fused with the inner wall itself. The inner wall becomes circular at this stage, and it is evident that the cardinal fossula is no longer prominent. The cardinal septum has been reduced in size so as to be equal in length to a tertiary septum.

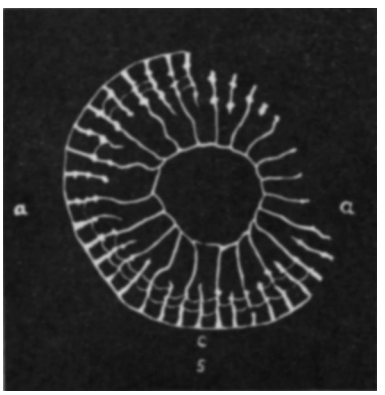

FIG. 5.—Cross-section of same corallite taken 2mm above section of Fig. 4. *a*. The alar septa. *c*. The cardinal septum. Diameter 5mm.

The tertiary septa do not appear until the secondary septa are well developed (Fig. 1. shows no tertiary septa). These differ from the primary or secondary septa in being radially arranged from their first appearance in the outer wall, and consequently their inner borders are free and can, therefore, easily be distinguished from the secondary septa. They extend one-half the distance to the inner wall before the latter is closed in the region of the cardinal septum, and this constitutes their full growth.

So far only the transverse sections at different stages have been discussed, though the longitudinal section (Fig. 6) is equally interesting. The central area is occupied by a series of tabulae the outer borders of which are fused in the inner wall, which is circumscribed by a second series of tabulae distinguished from the first series in being more delicate and more crowded. The second series of tabulae are fused with their inner borders in the inner wall, but have no con-

nection with the first series. Their outer borders extend to the innermost series of interseptal dissepiments and these dissepiments occupy the remainder of the interior to the outer wall. The carinae appear, at irregular intervals, as parallel bars extending inward and upward in an arching manner.

The essential characteristics, with the exception of the completed inner wall, are more specialized in the species *C. archiaci* from the Hamilton of Thunder Bay, Michigan. In a single corallum are found individuals representing the several stages of development. Thus are found individuals, in the young stages of which the inner wall has not appeared, others in which it is open at the cardinal septum, and still others in which it is completely closed, which is a rarer feature in this species than in *C. subcaespitosum*. When the inner wall is incomplete, the cardinal septum often extends into the inner central area (Fig. 7). This peculiarity has not been observed in any other species containing a true inner wall. When the wall is completely closed in this species, the cardinal septum extends to the dissepimental bridge which spans the cardinal fossula, becoming identical with a secondary septum with tertiary septa separating it from the other secondary septa.

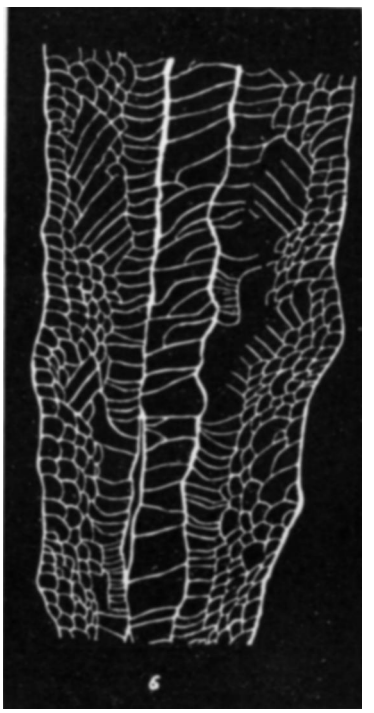

FIG. 6.—Longitudinal section of *Cras pedophyllum subcaes pitosum* showing the slight tapering of the corallite; and, from the margin toward the center: the interseptal dissepiment; the carinae; the second tabulate area; a section of the inner wall and the central tabulate area.

Closely allied to *C. archiaci* from above locality, is *Eridophyllum verneuilanum* from Columbus, Ohio, the difference in internal structure

between the two being such as might readily be expected of different individuals in the same species. This difference lies in the epithecal projections characteristic of Eridophyllum which are entirely wanting in Craspedophyllum. It seems not unlikely, therefore, that a generic relationship exists between these types. If this be so, Craspedophyllum must be considered as the ancestor. This is further substantiated in the greater specialization of *Eridophyllum verneuilanum* when compared with *Craspedophyllum subcaespitosum*. Thus the Eridophyllum is more specialized in the early expansion to normal size; in the complete inner wall which appears earlier in the life of the individual; and in the additional feature of epithecal projections. If the relationship outlined proves true, it is evident that *Eridophyllum verneuilanum* cannot be genetically related to the Siluric species, *Eridophyllum rugosum* as the latter makes its appearance before the postulated ancestor of *Eridophyllum verneuilanum*, i.e., Craspedophyllum. The characters now relied on for generic distinction being homoeomorphic, these would represent entirely distinct genera, and not as now generally considered, species of one genus. *Eridophyllum rugosum* requires further investigation, which is rendered very difficult as most material is silicified and the delicate internal structure destroyed.

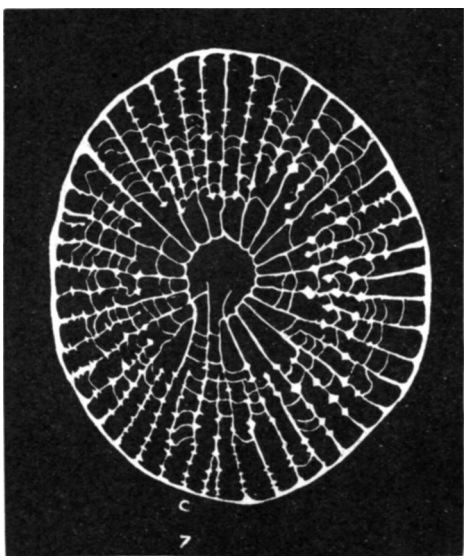

FIG. 7.—Cross-section of mature specimen of *Craspedophyllum archiaci*, showing the incomplete inner wall with the cardinal septum extending into the inner central area.

Other corals with true inner wall.—Hapsiphyllum (Simpson) and Laccophyllum (Simpson) both contain an inner wall; in the former it

is incomplete and in the latter complete. They have, however, scarcely any characteristics in common with the corals above considered. In Laccophyllum the wall is very massive and much thicker than the septa, and in both it is conical in shape, decreasing in diameter toward the tip of the corallite. This feature is reversed in the Craspedophyllum type, as in the latter the inner wall becomes smaller in diameter as the corallite develops. They are good examples of individuals in remote parallel series.

Carinae.—The carinae are not present at the early stage represented in Fig. 1, but the first series is well indicated in Fig. 2. These are formed by bar-like growths extending upward and inward in an arching manner (Fig. 6), and on corresponding sides of the septum. In transverse sections they appear as short cross-bars through the septum (Figs. 2, 5, 7). The mode of growth and the order of appearance of the carinae will be understood from the diagrammatic section, Fig. 8. The difficulty of obtaining a complete longitudinal section of a septum from a specimen is apparent as these seldom if ever develop in a true plane. The diagrammatic section is therefore based upon the development of the carinae at different stages as they are revealed by several longitudinal sections. A general idea is, however, obtained from Fig. 6, where the carinae are revealed in several places. In Fig. 8 it is seen that the tip of the corallite contains no carinae and this would therefore, represent a stage of Fig. 1, or earlier. The first carina appears at the outer wall and grows upward and inward until it finally fades away in the region of the inner wall. As soon as the room is sufficiently large between the first carina and the outer wall, the second carina begins and takes a path similar to the first. A similar direction is taken by each successive carina; all terminating in a like manner, and new ones take their places at the outer wall.

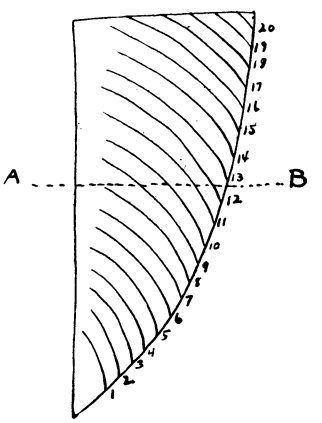

FIG. 8.—A longitudinal diagrammatic section of a septum, with ideal development of the carinæ.

It is evident that if *AB* (Fig. 8) represents a transverse section, there will be four carinae cut and in the order of their appearance these are 9, 10, 11, 12, carina number 9 being the oldest of the four, and carina number 12 the youngest. Hence the oldest carina in any transverse section is the one nearest the center, and they become successively younger toward the outer wall.

Corals with the appearance of an inner wall.—To Strombodes is attributed a rudimentary inner wall by Edwards and Haime (*Brit. Foss. Corals, Intr.*, p. lxx). It does not possess a true inner wall, however, as the coral is composed of superposed lamellae, and the fact that it contains no septa renders the presence of an inner wall impossible. The appearance of an inner wall in Phillipsastrea is the same as that in Acervularia, being formed by pseudo-thecae, and not as the true inner wall. Aulophyllum is considered by Edwards and Haime (*Polyp. Foss. des Terr. Palaeoz.*, p. 413) to contain an inner wall similar to that of Acervularia; hence, it also must be considered as not containing a true inner wall.

In Synaptophyllum (Simp.) and Schoenophyllum (Simp.) the appearance of an inner wall is attributed by their author (*Bull.* 39, *New York State Museum*, Vol. VIII, p. 212), to a thickening of the margin of the inner row of dissepiment through which the septa pass and extend with free inner borders nearly to the center. In Depasophyllum[1] the upturned outer borders of the tabulae, are fused into the lateral area of the short septa forming what appears to be an inner wall which is about two-thirds the diameter of the corallite. The septa are in no way otherwise connected with the inner wall thus formed by the tabulae, and the septa often extend with free inner borders into the central area. The wall is thus formed by the tabulae and not by the inner borders of the septa which is essential in the true inner wall.

The inner wall, as found in the coral containing a true inner wall, which I shall call "bimural corals," is defined as formed originally by the inner borders of the long septa. For this reason the long septa, with the exception of the cardinal septum, cannot extend into the inner central area in "bimural corals," by penetrating the inner wall; herein lies the distinction which differentiates it from the Acervularia type. A longitudinal thin section through the central region

[1] Grabau, *Geol. and Paleon. of the Devonic Formation of N. Michigan* (in press).

of the corallite will always disclose the two sides of the inner wall in the "bimural corals" (Fig. 6), which feature also is wanting in the Acervularia type.

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