Art. VII.—*Studies on Early Stages in Paleozoic Corals;** by C. E. Gordon.

The group of the Anthozoa has been the object of careful and detailed study for many years. The discovery that these organisms were really animals enlisted the attention of many investigators during the latter years of the eighteenth century. As first defined, the group included the Hydroid polyps, Bryozoa and Sponges; forms now known to be quite distinct. In 1828 Milne-Edwards showed that the "Sea-mat" and allied forms possessed a definite mouth and anus. Later the Sponges were made a distinct class, and finally the Hydroid types were firmly established as a distinct division of the Cœlenterates. "The anatomy and classification of the group thus purged of intruders were placed on a firm basis by the classical works of Dana and of Milne-Edwards and Haime (1857)." Since then studies in the development, comparative anatomy, and histology of the Anthozoa have contributed to a further and more exact knowledge of the group, although much remains that is yet doubtful and obscure. Especially is this true of the extinct Anthozoa of Paleozoic time: the Rugosa of Milne-Edwards and Haime, the Tetracoralla of Hæckel.

Since with these extinct forms only the hard parts are preserved, the study of relationships and mode of development is exceedingly difficult, and all conclusions on these points are necessarily, to a greater or less degree, matters of conjecture and inference. Several investigators, however, have endeavored to show the relationship of these extinct types to modern forms. How far they have succeeded in doing this is still a matter of dispute.

In so far as the plan of structure, which should be understood to mean the plan of growth from the earliest stages, can be proved to be similar to that of modern forms, just so far can relationships be assumed. Here we recognize that an inference can be drawn from a study of the hard parts, for example, the arrangement of the septa in corals. This arrangement is such that a reasonable assumption may be made as to their order of appearance. The difficulty must lie in securing specimens well adapted to show primitive characters with respect to the plan of growth of these septa.

With modern corals the order of appearance of the mesenteries is made of prime importance, and since the septa follow the mesenteries, the endeavor to classify the fossil forms has

* The studies embodied in this paper were carried on in the Paleontologic Laboratory of Columbia University, New York City.

been on the order of appearance of the septa, so far as could be inferred by a careful study of early stages. It is by no means true, however, that the early stages of all fossil forms will give us the clue to the phylogeny of the group. It frequently happens that certain individuals represent a specialized condition and are, on that account, not suitable for working out their own life history, which could be interpreted only by a careful comparative study of many individuals. This specialized condition may result from an acceleration in development of certain ancestral characters resulting in a premature appearance of certain stages which normally belong somewhat later in the animal's life, and which obscure the early conditions by their premature development; again, certain characters are retained longer than usual and are prolonged to the obliteration of later stages, for the appearance of which the life of the animal is not long enough. In interpreting the structural characteristics of any species the possibility of specialization must not be overlooked. Among forms somewhat removed in geological time from the ancestral stock, one must look for types in which acceleration, or retardation, or both, have been important factors in altering early ancestral conditions, and have produced new species, or varieties, according to one's choice of designation.

It is not within the province of man to say where, or in what parts, these modifications are to take place when only natural conditions operate to produce them. They are to be looked for anywhere, and it is reasonable perhaps to expect them in parts which have taken on new physiological importance, or have ceased to have such importance, as responses to certain conditions. Instances are numerous which forcibly illustrate the principles of acceleration and retardation. The genera Cyathophyllum and Heliophyllum are distinguished by the presence in the latter of carinae. But sections of certain Heliophyllums (*Heliophyllum halli*) show the carinae appearing very late in the life of the individual.* Up to the time of their appearance they are not to be distinguished from Cyathophyllum. In other individuals the carinae appear so early as entirely to obliterate the Cyathophyllum stage. It is clear that here are two types originating from a common ancestor, which had both a Cyathophyllum and a Heliophyllum stage, the latter being a late ephebic character. One retained the Heliophyllum stage as an ephebic character, and is to be regarded as a retarded type. The other became accelerated until the carinae stage became established as a nepionic character. It is apparent that here are two distinct types, each

* "Hamilton Group of Thedford, Ontario," Shimer and Grabau; Bull. Geol. Soc. Amer., vol. xiii, pp. 167-168.

having a Cyathophyllum ancestor, but that acceleration has produced in one case a distinct type in which the Cyathophyllum stage is either lost, or is of such short duration that it escapes notice.

In attempting to arrive at some definite conclusion as to the ancestral condition of any fossil group, or as to whether any particular plan of structure in fossil forms is a primitive one or not, one must not ignore these facts so obviously illustrated in many groups that have been carefully and successfully studied. In the absence of proof that the specimens in hand are primitive, or that they illustrate a primitive condition, of which one must always be in doubt, one must in order to meet the first requirements of a safe premise select a type most likely to be primitive, and this must be done on the basis of chronogenesis. A type occurring late in geological time, at least a considerable time subsequent to the earliest occurrence of a type at all similar, is likely to be far from primitive, in all respects at least, and at all events is not a safe type for study. But a specimen selected on the basis of its early appearance in geological time may be presumed to give the most primitive conditions which it is possible to obtain until an earlier form which is favorable for study can be secured.

Dr. J. E. Duerden has attempted to show by studies based on *Lophophyllum proliferum* that it is unnecessary to "account for a primitive tetramerism" in the Rugosa.* He would, on the basis of his studies, consider the quadripartite symmetry as a secondary development erected on a primitive hexameral arrangement of the primary septa; and by the development of the secondary septa, according to his interpretation of the primary condition, he finds the Rugosa, in so far as *L. proliferum* may be representative, most closely related to the modern Zoantheæ. In this paper I am not so much concerned with establishing the relationship of the Rugosa as with discussing the probable number of the primary septa in these forms. Certain studies which I have undertaken seem to indicate that there is still good ground for believing that the tetrameral plan is a primitive one.† Moreover, a careful study of the diagrams in Duerden's paper has raised the question if after all they may not illustrate a primitive tetrameral arrangement of the main septa.

It will be necessary in order to make as full a comment as seems desirable on Duerden's studies of Lophophyllum to reproduce a few of his figures.

* Johns Hopkins University Circular, January 1902; Annals and Magazine of Natural History, May 1902.

† For valuable suggestions and criticisms in carrying on these studies the writer is deeply indebted to Dr. Amadeus W. Grabau.

In figure 1 we have a

"transverse section, through the tip of the corallum. The dark median lines of only six primary septa are present, but the outlines of the septa as a whole are not clearly determinable, their surfaces being fused throughout. The two median septa are represented by a continuous line, while the other four septa are arranged as an upper bilateral pair and a lower bilateral pair. Of the six primary interseptal spaces the two upper are slightly smaller than the others. By interseptal spaces may be here understood the interval between the dark lines of two contiguous septa; the septa are so broad as to occupy the whole of the calicinal cavity, leaving no interseptal loculi."

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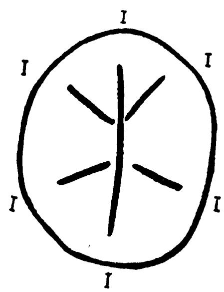

FIGURE 1. *Lophophyllum proliferum.* Transverse section through the tip of the corallum. After Duerden.

The author explains that the terms "upper" and "lower" are used merely for convenience and have no morphological significance. I wish here to call attention to Duerden's observation that the two upper "primary" (of Duerden's figures) interseptal spaces are smaller than the others, as this fact lends some support to a different interpretation of the figures from that which Duerden had given and which I presently wish to discuss.

"In all the figures the upper border corresponds with the convex side of the coral, and the lower with the concave border; the primary septa are indicated by the Roman numeral I, and the later septa by the letters A-D, according to their order of appearance within the four primary interspaces."

The reader's attention is again called to the exact language of the author, as great stress is laid by him upon the development of these septa in four primary interseptal spaces, which according to him do not represent the whole number, but only four out of six such spaces. I think another interpretation may be given to this early arrangement as exhibited in the apical section studied by Duerden.

In figure 2, which is a transverse section through the tip of another corallum taken comparatively a little higher than in the case of figure 1, two new septa are making their appearance, apparently as a unilateral pair. This is probably to be explained as a case of slightly unequal growth, as Duerden remarks. The dark tadpole-shaped spaces represent the interseptal loculi and partly indicate the boundaries of the septa. The dotted line in all the figures marks the outline of the actual section.

Figure 3 represents a transverse section of a third corallum taken a little higher than in the previous sections. Duerden remarks that the six primary septa are recognizable by their greater size. The outlines of the septa are indicated in the figure by the thin marginal lines and the oval interseptal loculi. The two median septa are now distinct from one another and the upper is larger than the lower. Duerden indicates that the former is

"thereby already recognizable as the main or chief septum."

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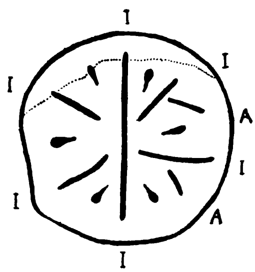

FIGURE 2. *L. proliferum.* Section through the tip of a second corallum; a little higher than in figure 1. After Duerden.

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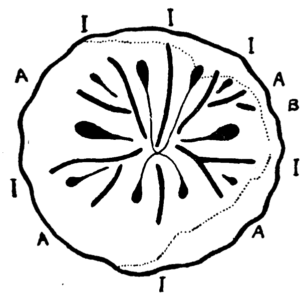

FIGURE 3. *L. proliferum.* Section of a third corallum from a still higher level. After Duerden.

He also makes the important observation that the

"upper primary interseptal spaces are much narrower than the middle and lower interspaces. Within each of the latter an additional septum (A) has appeared, and within the middle, right interspace the rudiment of a second additional septum (B) occurs. No new septa are ever developed within the two upper interseptal spaces."

Figures 4 and 5 are easily interpreted with respect to what has already been explained concerning the structural features of previous figures. Figures 6 and 7 will be referred to again.

The reader's attention is now directed to figures 8, 9, 10 and 11, which are Duerden's diagrams reproduced again, but this time inverted. This has been done for the sake of easier comparison. In figure 8 it will be noticed that what are now the upper lateral septa are, as indicated by the dark lines, more nearly at right angles with the median than are the lower ones, while the median dark lines of the lower ones in this figure (upper in Duerden's) have a proximity to the median dark line which is at this stage very noticeable and suggestive.

Before entering upon a further discussion of the diagrams obtained by inverting Duerden's figures, I wish to call attention to the possibility, which I have suggested above, of a specialized condition in *Lophophyllum proliferum.* Lophophyllum is a Carbonic type. It occurs comparatively late in the geological history of the Rugosa. It may, therefore—I should say rather, it must, therefore—have been somewhat

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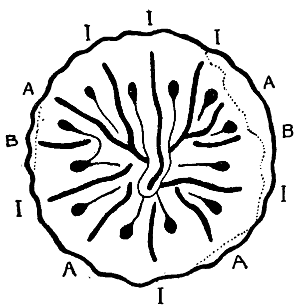

FIGURE 4. *L. proliferum.* Section from same specimen as in case of figure 3, but a little further from the apex. After Duerden.

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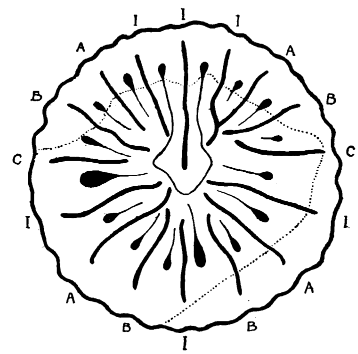

FIGURE 5. *L. proliferum.* Section of same corallum as before from about the middle of its length. After Duerden.

modified from an earlier condition. Whether this modification took place in the arrangement or order of appearance of the septa there is no absolute means of ascertaining, while one cannot gainsay the possibility that either acceleration, or retard-

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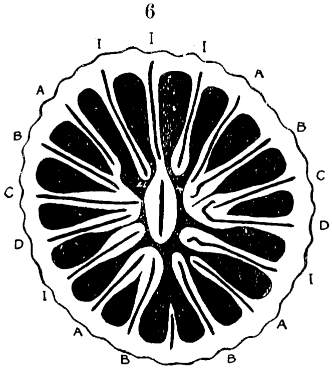

FIGURE 6. *L. proliferum.* Section from upper part of the same corallum as before. After Duerden.

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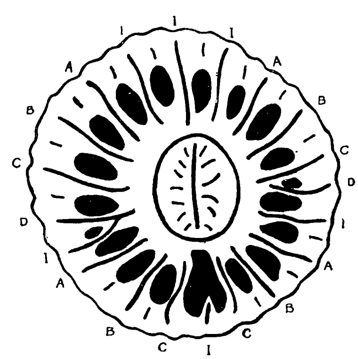
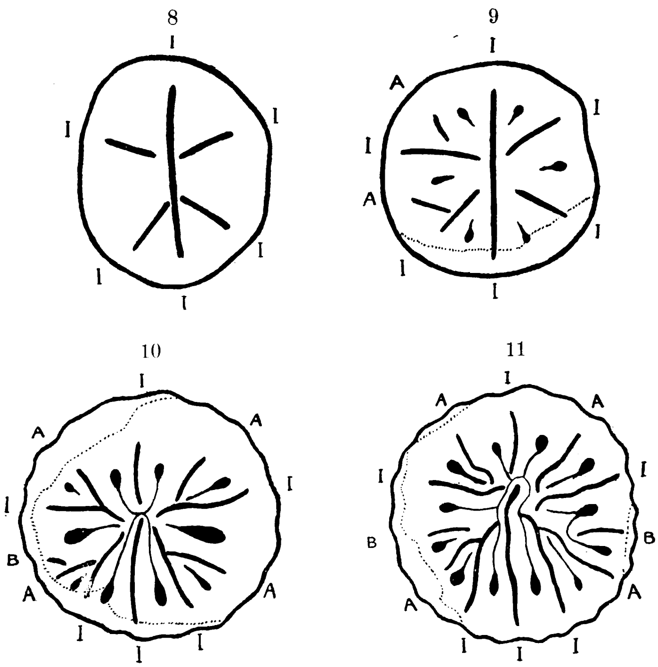


FIGURE 7. Section towards the upper region of a fourth individual. After Duerden.

ation, or both, have operated to produce an apparent anomaly in Lophophyllum in these respects.

The arrangement and order of appearance of the septa in the Zaphrentoid coral, as generally accepted, is illustrated in figure 15; (*h*) is the "cardinal" septum; (*g*) the "counter" septum; (*s*) the "alar" septa. The radiating lines indicate septal margins as they appear on the surface of the corallum when viewed from below. By the figure it will be seen that in the cardinal quadrant the septa first to appear take a position next the alar septa. In the counter quadrants the first to



FIGURES 8, 9, 10 and 11. Figures 1, 2, 3 and 4 of Duerden, inverted.

appear take a position next the counter septum. Let us carefully examine Duerden's figures to see if in any way they may reveal traces of a tetrameral arrangement of the septa according to the law apparent in the development of the septa in the Zaphrentoid coral as above explained.

By referring to figure 9, which it will be remembered is Duerden's diagram (figure 2) inverted, we observe the appearance of two secondary septa, each marked A, apparently as a unilateral pair. I have already remarked that this appearance as a unilateral pair may be explained on the principle of unequal growth. Since we are concerned only with their relation to the septa, marked in the figure by the Roman numeral

I, this unilateral order of appearance is of no significance, particularly as later figures almost conclusively show that it is simply a matter of unequal growth. It will be observed in figure 9 that the septum marked (A) bears a relation to the septum marked I in the lower left hand quadrant very similar to the relation which septum number 2 in the counter quad-

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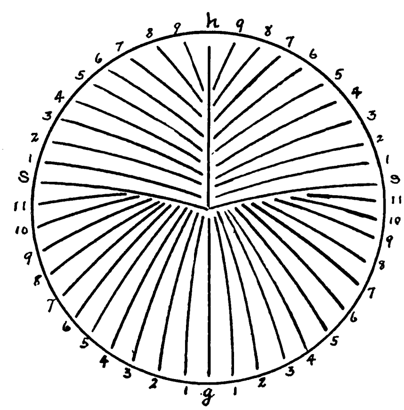

FIGURE 15. Plan of the septa in a Zaphrentoid coral.

rant of figure 15 bears to septum number 1. Likewise the septum marked (A) in the upper left hand quadrant of figure 9 holds a relation with reference to the adjacent primary septum similar to that which number 1 in the left hand cardinal quadrant of figure 15 bears to the adjacent transverse septum. It will be remembered, also, that in the above explanation of Duerden's figure 1, the comparative thinness of the upper pair of septa marked I was pointed out and that this was considered to be suggestive.

In figure 10 (figure 3 of Duerden, inverted) we observe a further increase in the number of secondary septa. Here the comparative thinness of the lower pair of septa marked I is again noticeable. In the upper quadrants are two secondary septa marked (A), each lying adjacent to the upper lateral "primary" septum on the side in which it appears. In the lower quadrants are two new septa marked (A) and in the left the beginning of a third, marked (B), which bears the relation to (A) that the latter holds with respect to the adjacent septum marked I. In this figure we also notice the division of the median septum into an upper and lower portion, the upper part of which, in Duerden's figures, is marked the "cardinal," the lower the "counter"; i. e., in Duerden's diagram 3, the upper (the lower here) is called the "cardinal," and the lower (the upper in figure 10) is called the "counter." Figures 4 and 11 mark an increase in the number of secondary septa, and a noticeable increase in the length of the "cardinal" septum, and a shortening of the "counter" septum. In figure 11 it will be observed how similar the general arrangement of the septa is to that given in figure 15. The lower portion of the median corresponds to (*g*) in figure 15, the upper to (*h*). In the upper quadrants the secondary septa (A) in their relations to the upper pair marked I, follow the plan exhibited in the cardinal quadrants of figure 15. In the lower quadrants the secondary septa marked (A) and (B), as also do the "primary" septa (Duerden) marked I, have an arrangement that strongly suggests the condition in the counter quadrant of figure 15. Figures 5 and 12 show this arrangement even better, and bear a striking similarity to figure 15. There is now evident a striking bilateral arrangement of the septa, which according to Duerden and Pourtalès proceeds from an unsymmetrical development of the secondary septa in only four of six primary interspaces—proceeding as they do on the assumption that there are six primary septa.

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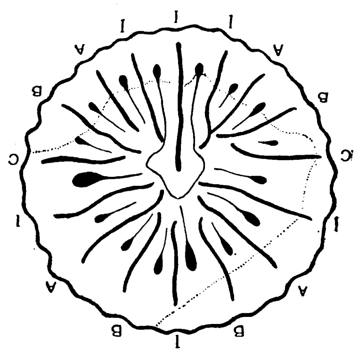

FIGURE 12. Figure 5 inverted.

An examination of figures 13 and 14 shows the position of the fossula in Lophophyllum to be in the same position as in the Zaphrentoid coral. To designate the cardinal septum always as the primary septum on the convex side of the corallum (after Nicholson) introduces some difficulty in making comparisons. The cardinal septum is to be regarded as that which, with the secondary septa in the same quadrant, exhibits a pinnate arrangement. That this may occur on the concave or convex side of the corallum is well known. According to Jakowlew the one fossula which can be determined is always developed on the cardinal septum.* Both the pinnate arrangement of the septa, which marks the position of the cardinal septum, and the fossula are by this author regarded as the product of the mode of growth of the corallum. However thatmay be, we have examples of the fossula and the cardinal

* "Ueber die Morphologie und Morphogenie der Rugosa," Verhandlungen der Russisch-Kaiserlichen Mineralogischen Gesellschaft zu St. Petersburg. Bd. XLI, Lief 2, 1904.

septum occurring on the concave side. Since we find not only the fossula, but also the pinnate arrangement of the septa, occupying the position of the lower portion of the median septum in Duerden's figures, this portion must be the cardinal, which in this specimen is on the concave side; and the upper portion is the counter instead of the cardinal, as Duerden has designated it. That this interpretation is correct is clearly shown by the figures. We have now simply to invert the diagrams to get a well organized Zaphrentoid type, in so far as the adult arrangement of septa and fossula are concerned.

It remains yet to consider the two upper "primary" septa of Duerden's figures in more careful detail. Certain studies

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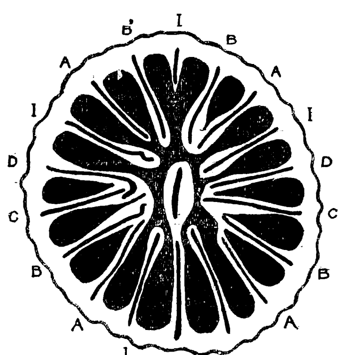

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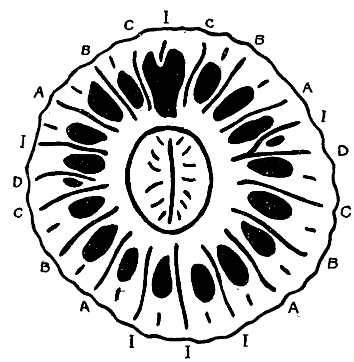

FIGURES 13 and 14. Figures 6 and 7 inverted.

which I have made on *Streptelasma profundum* from the Black River limestone seem to indicate most strongly a tetrameral plan of growth in the primary septa of the Rugosa; to use a borrowed phrase, "in so far as this type may be taken as representative." These studies will be given in greater detail presently. Their significance here, however, is to indicate that the tetrameral arrangement is not a secondary development on a hexameral basis, but on the contrary, that the hexameral arrangement in the tip of Lophophyllum is really only apparent and that *L. proliferum* from the beginning exhibits a quadripartite plan of the septa. To one who examines Duerden's figures the hexameral plan at first sight seems to be the only way of interpreting this very early condition. And I am well aware that by some it is likely to continue as the only interpretation.

Jakowlew came to the important conclusion that the primary spaces in which the secondary septa did not develop appeared adjacent to the counter septum without regard to whether the latter appeared on the convex or concave side of the polyp.* In so far as Jakowlew's careful comparative studies are conclusive this would again indicate that what Duerden has designated as the cardinal septum is really the counter septum, as I, by comparison with a typical Zaphrentoid arrangement above, have pointed out to be the case.

By an examination of the diagram of the adult we are further impressed with the fact that the so-called primary spaces in which secondary septa do not develop are at the time of maturity not to be distinguished in any respect from the spaces which separate the secondary septa in the same quadrants. We note also that the lateral septa marked I in the upper quadrants of Duerden's figures have a position and an order of appearance which, if they were to be regarded as secondary septa, would correspond to the septa marked by the Arabic numeral 1 in the counter quadrants of figure 15, which illustrates the usually accepted order of appearance in the Zaphrentoid coral. We are furthermore impressed by the fact that the later sections of the corallum (figures 7 and 14) show the appearance of the tertiary septa, in the two *Kammern* next the "cardinal" (Duerden) at the top of figure 7, having precisely the same relations to adjacent septa as do the tertiary septa in all *secondäre Kammern*. The tertiary septa may have no sequence value, but the fact that they appear at all in the "primary" interspaces next the "cardinal" septum is suggestive that these spaces do not differ essentially from the secondary interspaces.

I am aware that in support of the interpretation which I shall presently present as an explanation of the presence of this pair of so-called primary septa next the "cardinal" septum, I have no absolute proof. I have called the reader's attention to the striking resemblance which Duerden's diagrams have to the usually accepted arrangement and order of appearance of the septa in the Zaphrentoid coral when the diagrams are inverted and their structural features interpreted in the terms of Zaphrentis. In Streptelasma (figure 16) it will be seen that the tertiary septa are present also in all interspaces. As to any sequence in their order of appearance, it was not possible to determine in the specimen, as their lower ends were very thin, and the extent to which they went down into the calyx could not be traced. The lines representing the tertiary septa in figure 16 do not indicate their indistinctness at their lower ends.

With regard to the "ultimate fate of the two bilateral pairs of primary septa" Duerden expresses himself as follows:

* Ueber die Morphologie und Morphogenie der Rugosa," Seite 412.

"One pair forms the 'alar' or lateral septa of the paleontologist, while the two moities of the remaining pair, recognized by Ludwig and Pourtalès, but not accepted by Kunth, are disposed one on each side of the axial septum on the convex side of the calice."

By the several figures reproduced here, e. g., figure 5 or figure 12, we observe how accurately this statement disposes of the septa, so far as their position is concerned, according to the Zaphrentoid plan. We see the "two moities" occupying exactly the position which the first two secondary septa to appear in the counter quadrant should occupy and we see them appearing before those of the cardinal quadrant as the greater number of septa in the counter quadrant of the adult

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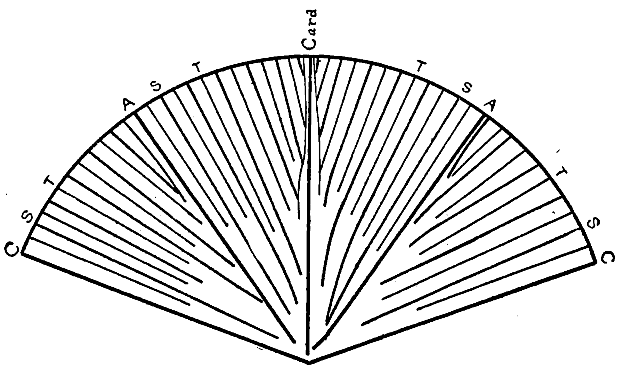

FIGURE 16.—*Streptelasma profundum.* Diagrammatic drawing somewhat enlarged.

would indicate to be the natural and logical order. The fact that the counter quadrant has the greater number of secondary septa supports the idea of acceleration in this quadrant. It is also to be noted that the number in the upper quadrant of Duerden's figures exceeds that in the lower quadrant by more than one, if we include the so-called "primary" septa.

How are we to account for this close resemblance of *L. proliferum* to a typical Zaphrentoid? Are we to regard these "primary" septa, which "are disposed one on each side of the axial septum on the convex side of the calice," as primary or secondary? If primary, what evidence is there that they are primary? If secondary, what evidence can be brought forward in support of their secondary nature, or what explanation can be offered of their appearance so early in the life history of the individual? The strongest evidence of their primary nature, of course, is their presence in the extreme tip of the corallum. There they are, and if they do not show by their presence a primary hexameral arrangement some very strong evidence must be brought forward to show why they do not.

I am aware of the difficulty of explaining away their very apparent primary character, especially as any perfect series of fossil forms is not at hand to give us the absolute proof that *L. proliferum* may be at the extreme end of an accelerated series in which the pair of "primary" septa under discussion appear at progressively earlier and earlier stages in the life history of the individual until at last in *L. proliferum* we have them established so early that they simulate the nature of primary septa. In my criticism of Duerden's paper I wish to accord the author the credit due his careful investigations and to acknowledge his wide acquaintance with the Anthozoa. I would be understood in offering any other interpretation of his figures than that which he gives as being conservative, and far from committing myself as to having settled the matter. At the same time I believe that such an acceleration, difficult as it might be to account for, is far from being impossible, if it is not quite probable. In the absence of definite proof we have to rely upon analogy to a large extent, and call to our service in interpreting the structures in *L. proliferum* the knowledge furnished by studies upon other forms.

The idea of acceleration is by no means a new one. The principle undoubtedly has been an all important factor in bringing about those mutations which are the true species in certain evolutional series. In fact, it seems to be in many cases the only means of interpreting certain aberrant individuals which are so often grouped together in a heterogeneous way. We may be unable to explain why certain structures appear earlier in the life of certain individuals than they did in ancestral forms; but it is undoubtedly to be explained in many cases as a reaction towards its environment on the part of the individual, the response being a new anatomical structure, or a different plan of development because of a new importance of old structures, such as the assumption of a greater physiological importance of certain ones. On this wise it would not be difficult to imagine that for some reason or other, obscure as that may be, the mesenteries next the "cardinal" septum in Duerden's figures are really secondary septa called into being so early as to appear to be primary septa. The striking resemblance of Duerden's figures, if I may again call attention to this fact, to the usually accepted Zaphrentoid type of arrangement and the fact that the so-called primary septa follow the well recognized law of Kunth, are offered in support of this interpretation; the possibility of acceleration makes the inference logical.*

If these two septa were called into being at a relatively early period, that is, before they normally would appear in a non-accelerated type, it is easy to conceive how, once established, this acceleration, as the name implies, would cause these septa to appear at an earlier and earlier stage until in a later geological type they would appear in the early nepionic stages so fully developed as to present the character of primary septa. Their true nature then, in the absence of a series showing this progressive acceleration, could be explained by noting the subsequent development of secondary septa that were not accelerated, and, in this connection, noting the final

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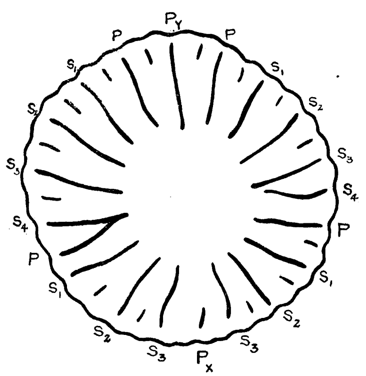

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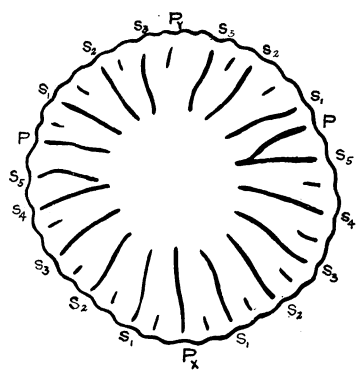

FIGURES 17 and 18. A portion, in each case of figures 7 and 14, with new lettering.

position of the septa that were accelerated, as I have done. Duerden's figures, to my mind, lend themselves in every respect to this interpretation.

At the risk of repetition I have at this place introduced a portion, in each case, of figures 7 and 14 with new lettering, which may serve to recapitulate and make a little clearer the foregoing discussion.

Figure 17 shows in a diagrammatic way the value of the septa as interpreted by Duerden in figure 7. (P_y), "cardinal septum" (Duerden); (P_x) "counter septum" (Duerden); (P)

* The suggestion of Boveri that the anomalous number of the septa of the first cycle in *Tealia crassicornis* may be explained as due to the precocious development of four septa belonging to the second cycle, is a recognition of the fact that acceleration in development may operate to conceal a primitive condition. Boveri's suggestion is supported by his own observations on the peculiar mesenterial arrangement in an undetermined larval form. (This suggestion was not seen until this article was written.)

other "primary septa," (Duerden); (S) secondary septa. The subscripts indicate the order of appearance.

Figure 18 is a portion of figure 14 and is figure 17 inverted. The lettering in this case indicates the author's interpretation of the value of the septa. (P_y) "cardinal septum" (author); (P_x) "counter septum" (author); (P) "alar septa" (author); (S) secondary septa. The subscripts indicate the order of appearance. Note that the cardinal and counter septum are reversed and that the number of primary septa are reduced by two.

Duerden, from his wide acquaintance with modern corals, makes the statement that no living coral presents such a mesenterial (septal) sequence as *L. proliferum*, yet it bears the closest resemblance to what is found to be characteristic of Zoanthoid polyps, except that the mesenterial increase takes place in only two exocoelic chambers in these forms, while, as Duerden would have it, in *L. proliferum* it is carried on in four such chambers. Of whatever value the fact may be, it yet remains that no modern coral has precisely the same septal sequence as is described for *L. proliferum*, which suggests that here we have merely a specialized type of the Zaphrentoid coral. Starting with the hypothesis that the primary septal plan of *L. proliferum* is hexameral, we have yet to investigate other corals, selected with the purpose of getting a primitive species as well as one which is favorable for study, to find out how far they lend support to the hexameral primary septal plan or tend to disprove it.

The difficulty involved in getting sections of coral tips that really show anything one way or the other is appreciated only after one has made the attempt. The tips either break at an inopportune moment, or after sectioning show nothing conclusive. Turning from sections which revealed little or nothing, I was more fortunate in securing some specimens of *Streptelasma profundum* from the Black River limestone. The specimens were silicified and had been removed from their matrix by acid. Though small, they showed the well-preserved septa on the inside of the corallum. These specimens were carefully examined. Two were found which revealed the arrangement of the septa at the base of the calyx on the inside of the coral so satisfactorily that they were set aside for detailed study. During the attempt to sketch the relations of the septa in one of these specimens the corallum was unfortunately broken into several pieces so that it was impossible to make a satisfactory drawing. A drawing of the other is given in figure 16, which in all essentials is like the one which was broken.

The corallum of *Streptelasma profundum* in figure 16 is represented as split on the counter septum and rolled out; the point toward which the heaviest lines converge is the apex; the curved line is the circumference of the calyx; (C) is the counter septum; (S), the secondary septa; (T), the tertiary septa; (Card), the cardinal septum. The corallum was so small and fragile that it was impracticable to attempt drawing to an exact scale, as the measurements could not be made in the corallum without the risk of breaking it. Care was exercised not to exaggerate the relations of the septa, so that in the drawing, though necessarily more or less diagrammatic, one sees a very close approximation to the actual appearance. In this figure it is obviously impossible to represent anything but lengths. In doing this I have tried to be true to facts. At the base of the corallum (and in describing the corallum from now on it must be remembered that we are looking down into the vase of the corallum) the septa are not so deep (by depth I mean extension from the wall inward) as a little way up, as though they had undergone resorption or ceased to grow. In modern corals a resorption of the mesenteries takes place at the base, as the animal grows upward.* It is not unlikely that this is the explanation of the tapering off that was observable in all the septa which extended deepest into the calyx. Of the four primary septa represented in the drawing, the counter extended farthest down, the cardinal next, and the alar septa next. The bending represented in the alar septum on the right is meant to represent the slight deflection of the inner edge of the septum upward, as though the mesentery has been crowded by the counter septum at the base. Attention is directed to the fact that only four septa appear in the early stage of the corallum. The alar septum on the left is appreciably longer than the secondary septum adjacent to the counter represented in the left hand portion of the figure by S. The latter showed greater depth near the base than the corresponding one on the right, as though it had been resorbed to a less extent, or as though it had grown faster. The second secondary septum in the left hand counter quadrant exhibits a condition of unequal growth. The order of development of the secondary septa is plainly seen to correspond exactly to that in the Zaphrentoid coral in figure 15. With respect to the tertiary septa, although examined with the aid of a powerful binocular in artificial light, it was impossible in all cases to tell to what length they extended down into the coral. In the cardinal quadrants near the main septum they merged with a ridge

*"Morphology of Coral Polyps," J. E. Duerden, Smithsonian Miscellaneous Collection, Quart. Issue, vol. ii, No. 1, 1904, p. 98.

represented by the curved line, which ridge was small and of about the same size as the tertiary septa.

As was stated above, the specimen was examined by the aid of a binocular in electric light. No doubt was left in my mind that the four septa indicated by the heaviest lines in the figure extended farthest down into the base of the calyx. Not content, however, with my observations, I submitted the specimen to two others, whose results tallied with mine. The results, therefore, seemed to indicate that *Streptelasma profundum* showed a primary tetrameral arrangement and that the further addition of the secondary septa proceeded in accordance with the law that the Zaphrentoid type has been shown to illustrate.

In the criticism offered above of Duerden's figures I have, I think, offered another possible interpretation of the occurrence of one of the pairs of so-called primary septa in the tip of *Lophophyllum proliferum*. Whether this interpretation is accepted or not, I think it is by no means established that the hexameral arrangement is a primitive one. In the first place, as I have pointed out above, *L. proliferum* is in some respects, notably because of its occurrence in Carbonic time, not a suitable specimen upon which to establish a primitive arrangement of the septa. *S. profundum* from the Ordovicic was selected for study mainly because of its early geological occurrence. The fact that it shows a primary tetrameral arrangement suggests that such was the primitive condition. To my mind it suggests this because it is a comparatively old type and, because, so far as the septal sequence is concerned, it shows absence of acceleration.

It is evident, I think, that the primitive condition of these septa in the Rugosa is not yet settled. The tetrameral arrangement, if primary, will so long as this is made the basis of classification, place those corals which possess it in a group by themselves. No modern corals exhibit the peculiar septal plan as revealed in *Streptelasma profundum;* nor, in fact, as revealed in *Lophophyllum proliferum.* The fact that Lophophyllum is quite distinct from anything that is modern perhaps gives some support to the view that it is merely an accelerated type of a Zaphrentoid coral, occurring as it does among an extinct group.

Whether the hexameral plan is derived from a tetrameral one is still an unsolved mystery. Developmental studies among modern forms may yet throw some light on this question.

From the wide prevalence of the tetrameral arrangement among the extinct Rugosa it is probable that it is something inherent rather than acquired by mode of growth, especially as it is characteristic not only of bent forms but also of simple, straight cones. At all events, one may take exception to the statement that "studies on the septal development of extinct Paleozoic corals reveal that in these early forms the primary septal plan was hexameral like that of modern forms."

Further studies upon well-preserved specimens of early Rugosa are much to be desired.

Postscript.

Since writing this article I have received and carefully read an excellent paper by Dr. Duerden on "The Fossula in Rugose Corals." In this article I find a full recognition of the principle of retardation in development. The author shows beyond question that the alar fossulae and the cardinal groups of shortened fused septa in Hadrophyllum are developmental stages when compared with the ephebic condition of a form like Streptelasma. Since retardation in development means the retention in the adult stage of characters which belong to earlier stages, nepionic or neanic, Hadrophyllum must be a retarded type when compared with a form like Streptelasma, which passes through a Hadrophyllum stage. Both forms are probably to be regarded as derived from a protostreptelasmic stock.

The author of the paper makes the point that,

"Whenever alar fossulæ are present they represent an incompletion in the establishment of the newer septa of the alar region as compared with species in which no alar fossulæ are represented; they have only a developmental significance and would not correspond with any structural peculiarity of the fully developed polyp."*

This is the point which I have insisted upon with reference to the pair of so-called "primary septa" in *L. proliferum;* namely, that they do not have the structural importance which Duerden gives to them, but that they have a developmental significance only.

Duerden further remarks:

"As would naturally be expected from such an explanation even individuals of the same species may vary much with regard to the presence or absence of alar fossulæ." †

This is evidently true. The only exception one might take to such a statement is the propriety of calling the variations

* "The Morphology of the Madreporaria, VI, The Fossula in Rugose Corals," p. 33.

† Ibid., p. 33.

members of the same species. For example, Hadrophyllums in which no alar fossulæ were present in the adult stage would be accelerated types and properly should be made a distinct genus.

Literature.

Manual of Paleontology, Nicholson and Lydekker, Vol. I.

Treatise on Zoology, edited by E. Ray Lankaster, Part II, Porifera and Cœlenterata.

"Relationships of the Rugosa (Tetracorolla) to the Living Zoäntheæ," J. E. Duerden, Johns Hopkins University Circular, January 1902.

"Report on the Actinians of Porto Rico," J. E. Duerden, U. S. Fish Commission for 1900, Vol. III.

"Morphology of Coral Polyps," J. E. Duerden, Smithsonian Misc. Collections, Vol. XLVII, Quart. Issue, Vol. II, No. 1, 1904.

"Hamilton Group of Thedford, Ontario," Hervey W. Shimer and Amadeus W. Grabau. Bull. Geol. Soc. Amer., Vol. XIII, pp. 149–186.

"Ueber die Morphologie und Morphogenie der Rugosa," von N. Jakowlew. Verhandlungen der Russisch-Kaiserlichen Mineralogischen Geselschaft," Bd. XLI, Lief 2, 1904.

Text-Book of Paleontology, Zittel.

"Deep Sea Corals," L. F. de Pourtalès. Illust. Catalog Mus. Comp. Zool., Harvard College, IV.

"Actinozœn und Bryozœn aus dem Carbonkalkstein im Government Perm," R. Ludwig, Palæontographica X.

"Korallen aus Paläolithischen Formationen," R. Ludwig, Palæontographica XIV, 1865–66.

"Beiträge zur Kenntniss fossiler Korallen," A. Kunth, Zeit. der Deutsch. Geol. Geselsch., xxi, 1869; xxii, 1870.

"The Morphology of the Madreporaria, VI; The Fossula in Rugose Corals," J. E. Duerden. Biol. Bull., Vol. IX, No. I, June, 1905.