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## XIV.—The morphology of the Madreporaria.—II. Increase of mesenteries in Madrepora beyond the protocnemic stage

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called *labyrinthica*, then the name *must* be *riparia*, because it occurs earlier on the page than *labyrinthica*.

If this conclusion be contrary to the International Rules, they must be very strange rules.

As to whether, when the type has been lost, the two names are to be regarded as denoting the same species or not, is entirely a matter for mutual discussion between arachnologists, who, if possible, would come to some definite conclusion on the point.

XIV.—*The Morphology of the Madreporaria*.—II. *Increase of Mesenteries in Madrepora beyond the Protocnemic Stage.*

By J. E. DUERDEN, Ph.D., A.R.C.Sc. (Lond.), Bruce Fellow, Johns Hopkins University\*.

IN the 'Johns Hopkins University Circulars' (1900), I refer briefly to the discovery that in the genus *Porites* the mesenteries beyond the primary six pairs (protocnemes) are added in bilateral pairs, within the entocœle of either the dorsal or ventral pair of directives. This method of mesenterial increase is shown to differ from that characteristic of recent corals generally. The results are also briefly contrasted with the method of mesenterial increase occurring in the three great divisions of the Actiniaria—Hexactiniæ, Zoantheæ, and Ceriantheæ. The close resemblance of the polyps of *Madrepora*† to those of *Porites*, with regard to the number and arrangement of the tentacles and mesenteries, suggested that perhaps a similar mode of mesenterial addition might be followed in that genus also, and the present investigation was undertaken to determine this.

In West-Indian waters at least three well-known types of

\* From the 'Johns Hopkins University Circulars,' vol. xxi. No. 157, pp. 59-66 (April, 1902). For Part I. see 'Annals' for May 1902, p. 381.

† Since the paper was written I have received Mr. T. Wayland Vaughan's reports, "Some Fossil Corals from the Elevated Reefs of Curaçao, Arube, and Bonaire," and "The Stony Corals of the Porto Rican Waters," 1901. Following Brook (1893), Vaughan points out that none of the species at present called *Madrepora* were included within this genus by Linnaeus in 1758, and that therefore the name cannot be retained for the forms embraced by Dana, Milne-Edwards and Haime, and later authors. Vaughan suggests its replacement by *Isopora*, a term first employed by Studer in 1878 in a subgeneric sense. More recently Prof. A. E. Verrill (1901) has come to the conclusion that the *Acropora* of Oken (1815) has much better claims for adoption in place of *Madrepora*.

*Madrepora* colonies are recognized—*M. palmata*, *M. cervicornis*, and *M. prolifera*. The late George Brook (1893) regarded all these as but *formæ* or varieties of one species; Gregory (1895, 1900) at first accepted Brook's suggestion, but, following upon a visit to the West Indies, reverted to the Lamarckian arrangement of the specific distinctness of the three; Vaughan (1901) follows Brook in considering them as only varieties of one species; Verrill (1901) agrees with Brook and Vaughan. So far as my own observations upon the living polyps extend, and upon their anatomy and histology, there are no differences of importance among the three types of growth, and a discussion of their specific recognition or otherwise becomes restricted to the peculiarities of form assumed by the skeleton.

The radial polyps of all the West-Indian *Madrepore* are characterized by the presence of only twelve tentacles, six entocœlic and six exocœlic, forming a single cycle, and usually varying in size in such a manner as to suggest larval relationships. On almost any colony, whether of the arborescent or palmate type of growth, polyps are occasionally met with which are slightly larger than the others and bear tentacles beyond the usual twelve, any even number from sixteen to twenty-four being represented. As the number of tentacles on any polyp is an indication of the number of internal mesenteries, it was to the polyps possessing more than twelve tentacles that attention was directed.

To procure these for microscopic examination involved considerable labour and care. The polyps of *Madrepora* are so small that the tentacles can only be counted with the assistance of a lens, and then only when in an expanded condition. Among a hundred polyps perhaps only one would display more than twelve tentacles, and on some colonies, especially those living near the surface, no such examples whatever would be found. By carefully chipping around the desired individual it could be isolated on a fragment of the colony of suitable size for study. The polyps were killed in corrosive-acetic or in formol, afterwards transferred to alcohol, then slowly decalcified with hydrochloric acid, and stained and sectionized.

The radial polyps and corallites of *Madrepora* are, as a rule, oval in section, the axial-abaxial diameter being the longer (fig. 1). The polyps with from sixteen to twenty or more tentacles were still more elongated, but with the longer diameter at right angles to the axial-abaxial plane (fig. 7), the tentacles still forming a single uninterrupted cycle all the way round. Two oral apertures were present on the disk of

upwards of thirty enlarged examples found; in only one or two doubtful instances was but one mouth remaining. Evidently therefore the increase of tentacles and mesenteries early results in oral fission, if the two, indeed, do not proceed *pari passu*. The plane of fission coincides with the median or axial-abaxial plane, and in some rare instances the two

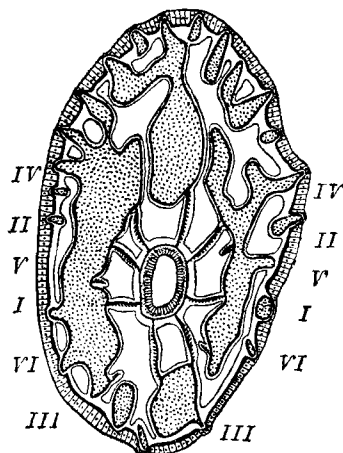


FIG. 1.

Transverse section through the stomodæal region of a projecting radial polyp of *Madrepora*. In relation to the axis of the branch the lower aspect of the section is axial and the upper is abaxial. The two mesenteries, *IV*, *IV*, forming a bilateral pair, are the dorsal directives, and mesenteries *III*, *III* are the ventral directives. Mesenteries *II*, *V* and *I*, *VI* on each side constitute two anisocnemic unilateral pairs. The polypal cavity is in communication with the superficial canals by means of several radiating canals. The outer polypal wall (coenosarc) is supported upon twenty-four costal ridges.

In this and all the figures the three coelenterate layers are represented as follows:—The *ectoderm* by the conventional columnar epithelium; the *mesoglaea* by a thick black line; and the *endoderm* as a clear layer. Owing to its narrowness the calicoblastic ectoderm is unrepresented, the skeletotrophic mesoglaea appearing to cover the corallium directly. The skeleton or corallum is indicated by the dotted areas.

polypal halves appeared to be in process of separation by the ingrowth of the middle tentacles and septa. Increase in the number of polyps in any colony of *Madrepora* by means of fission must, however, be very insignificant compared with the usual increase by coenosarc gemmation.

The early stage at which oral fission is accomplished in

the larger polyps of *Madrepora* is in marked contrast with the same phenomenon in *Porites*\*, for in numerous examples of the latter with tentacles and mesenteries in excess of twelve, often from twenty to twenty-four, I have only come upon one or two instances in which two oral apertures were displayed on a single disk. The problem of mesenterial increase in polyps of *Madrepora* is therefore more complex than in *Porites*, for from the beginning the new mesenteries in *Madrepora* are associated with two stomodæal tubes instead of only one.

A transverse section of an ordinary radial polyp of *Madrepora* through the stomodæal region is represented in fig. 1. Attention will be directed only to the mesenteries. Twelve of these are present, arranged in six bilateral pairs, of which two pairs, *III*, *IV*, situated at opposite extremities, are directives, and two pairs, *V*, *VI*, are incomplete—that is, are not attached to the stomodæum. The retractor muscles are sufficiently well developed on mesogloæal platings to admit of the paired arrangement of the mesenteries being established. In the figures the mesenteries are numbered I to VI, in accordance with the order in which the pairs are usually found to appear in the course of embryonic and larval development of both corals and anemones. Throughout their course the fifth and sixth mesenterial pairs never become inserted on the stomodæum, but disappear shortly below the lower termination of the stomodæum, and never bear mesenterial filaments. In Actinological literature the remaining eight complete mesenteries are known as the Edwardsian mesenteries; and the polyps of *Madrepora*, like those of *Porites*, are said to retain in the adult condition the Edwardsia-stage of mesenterial development, a stage passed through in the growth of most *Madreporaria* and *Actiniaria*.

Nearly all *Madreporarian* polyps pass beyond the stage with only twelve mesenteries, usually by the addition of alternating isocnemic pairs within the six primary exocoelæ, which in the end constitute one or more distinct cycles.

\* In the course of my former investigations on the order of mesenterial increase in *Porites* (1900) no evidence was presented that the additions in the end resulted in polypal fission. From an examination of material collected later it appears that when six new pairs of mesenteries have been formed the enlarged polyp, now possessing twenty-four mesenteries, may undergo division into equal halves, at any rate so far as concerns the oral aperture, stomodæum, and mesenteries. The mesenteries in each daughter polyp are arranged exactly as in ordinary polyps arising as buds. The introduction of fission, however, in no way modifies the morphological significance of the pinnate order in which the increase of mesenteries takes place.

While this is taking place the fifth and sixth primary pairs as a rule become complete. As already mentioned, *Porites* among corals is characterized by the mesenteries beyond the protocnemic stage being added in bilateral pairs, disposed pinnately within either the dorsal or ventral entocœles. Further, the incomplete fifth and sixth pairs never become united with the stomodæum. Figs. 2 and 3, with their explanations, will make these differences clear.

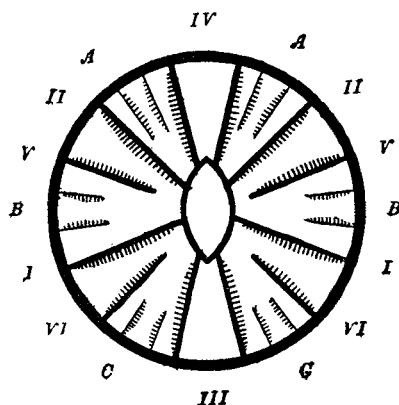


FIG. 2.

Diagram representing the order of appearance of the second cycle of mesenteries in most modern corals. The primary mesenteries, I-VI, are in the same condition as in the adult polyps of *Madrepora*, except that the fifth and sixth pairs are nearly united with the stomodæum. Within each of the six primary exocœles a new pair of mesenteries, A-C, has appeared, the sequence being represented by the comparative sizes of the mesenteries from the dorso-lateral to the ventro-lateral exocœles. Later all the primary mesenteries become inserted on the stomodæum and the second cycle pairs are equal. Afterwards the third cycle mesenteries arise successively in unilateral pairs within the exocœles between the pairs of the first and second cycles, first on one aspect of the second cycle mesenteries and then on the other aspect, and afterwards become equal in size. Thus several possible regions of growth occur within each primary exocœle, each capable of giving rise to an isocnemic mesenterial pair.

Over a score of the large polyps of *Madrepora* were sectionized transversely. All possessed more than twelve mesenteries, and two stomodæal tubes, divided all the way, were already present; but as regards the mesenterial increase, practically only three different stages are represented, in each of which twenty-four mesenteries already occur at one phase

or another of their establishment. The three conditions are represented in figs. 4-6, from camera lucida drawings of actual sections.

The earliest stage obtained is that represented in fig. 4. Twelve complete mesenteries are present and eight incomplete members, all attached to the inner boundary-wall of the polyp. From the disposition of the musculature and the relation of the complete to the incomplete members there is no difficulty in ascertaining which are the primary twelve

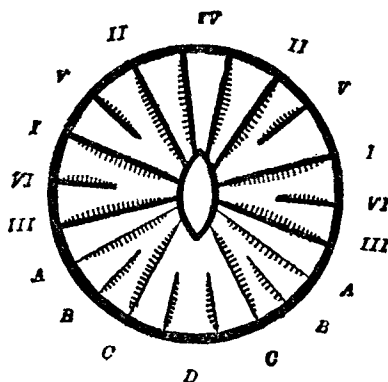


FIG. 3.

Diagrammatic arrangement of the mesenteries in a polyp of *Porites*, showing the manner of increase of the mesenteries beyond the six primary pairs. These latter are indicated by the thicker radial lines, and numbered I-VI. Four new bilateral pairs, A-D, have been successively added at one region within the entocoele of the ventral directives, III, III, the latter having become pushed far apart (cp. fig. 6). In some polyps of *Porites* the new mesenteries are added within the dorsal directive entocoele instead of the ventral.

mesenteries. They are indicated by the same numerals as in the simple polyp. Ventrally they have become widely separated from the dorso-ventral plane which passes through the entocoele of both pairs of directives, but in a symmetrical manner, so that six are on one side and the corresponding six on the other. As yet additional mesenteries are found only on the ventral (axial) side of the polyp, situated within the directive entocoele (III, III). They consist of two bilateral pairs of complete mesenteries and two incomplete pairs (A-D), the lettering not necessarily possessing any significance as to the order in which the mesenteries appeared. Each member of the new outermost complete pair (A) forms with the

primary complete directive mesentery adjacent to it (*III*) a new pair of directives, the musculature being on the faces of the mesenteries turned away from one another; the next incomplete and adjacent complete new mesenteries on each side form a unilateral anisocnemic pair (*B*, *C*), in which the musculature is on the faces turned toward each other, as in pairs *I* and *VI* of the simple polyp. The two members of the middle bilateral pair (*D*, *D*) of incomplete new mesenteries have as yet no corresponding complete mesenteries wherewith to constitute a unilateral pair. The primary dorsal (abaxial) directives (*IV*, *IV*) are somewhat widely separated, but no new mesenteries are intercalated between them.

With the exception of the presence of two stomodæal tubes instead of only one, the disposition of the new mesenteries so far exactly resembles the stage in the mesenterial increase in *Porites* represented in fig. 3.

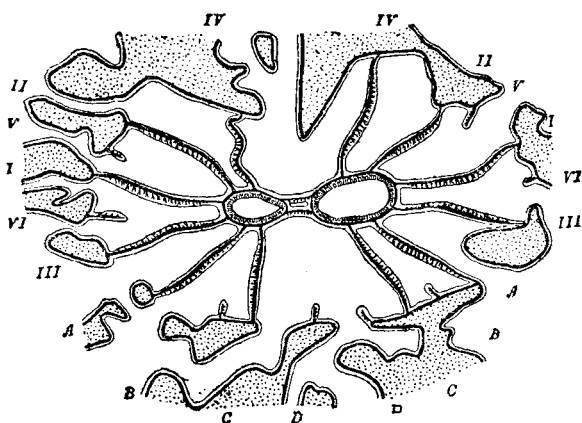


FIG. 4.

Transverse section through the stomodæal region of an enlarged polyp, wholly retracted within the corallum. The stomodæum is divided into two tubes, which are connected by two mesentery-like strands. Four pairs of new mesenteries, *A-D*, are present in addition to the six pairs in simple polyps.

Special importance attaches to the two mesentery-like strands which connect the two stomodæal tubes. Sometimes they are short, as in the section represented, or they may be much longer, the stomodæa then being widely apart. For a long time their significance was difficult to understand, and it was only from a study of the early stages in ordinary budding



in *Madrepora* that a satisfactory solution of their presence was reached. Full consideration of them will be deferred until later. In the meantime it will be noticed that eight mesenterial insertions—four primary and four new—are associated with each stomodæum, which is the number characteristic of an ordinary adult polyp; also that four incomplete mesenteries belong to each polypal half. Thus, regarding each of the mesentery-like strands as representing two mesenteries, the full complement of twelve mesenteries is associated with each stomodæum, as if the latter were separate polyps.

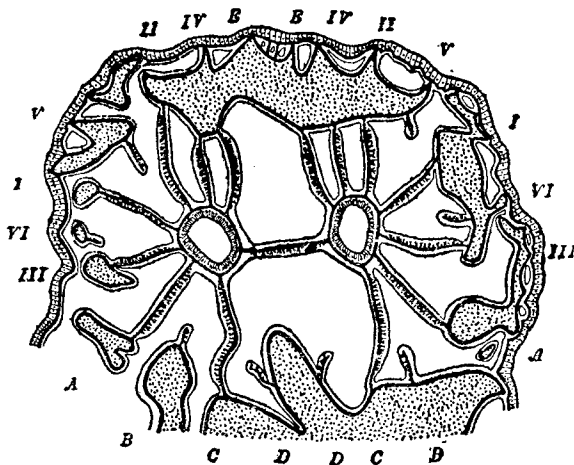


FIG. 5.

Transverse section through the stomodæal region of another enlarged polyp, with the dorsal and lateral areas free. Only a single mesenterial strand connects the stomodæal tubes. New mesenteries, *A-D*, have been added within the ventral entocœle, and one pair, *E, E*, within the dorsal entocœle.

Fig. 5 displays a further stage in the mesenterial development. There are now seven complete mesenteries extending from each stomodæum to the body-wall, and only a single connecting strand. Evidently the two additional complete mesenteries (*E, E*) represent the dorsal member of the two connecting mesenteries in the previous figure. They now form a new bilateral pair situated at the upper aspect of the polyp—that is, within the entocœle of the dorsal directives (*IV, IV*), and the musculature is so disposed that the mesentery to the left constitutes a pair of directives with the primary directive mesentery on that side, and likewise with the two

on the right side (*IV, E*). New mesenteries thus occur at the two axial extremities of the polyp, within both the dorsal and the ventral entocoelae, and each stomodæum has associated with it a dorsal and a ventral pair of directives, as in ordinary adult polyps.

Fig. 6 represents the final stage. Eight mesenteries now stretch from each stomodæum to the body-wall, and the two tubes are wholly disconnected. The two additional mesenteries (*F, F*) are disposed within the entocœle of the dorsal pair of mesenteries (*E, E*) shown to be added in the previous figure, and the retractor muscle is arranged on the faces turned

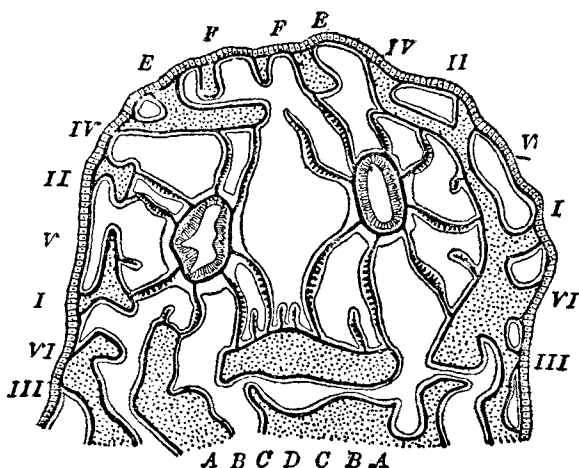


FIG. 6.

Transverse section through a third polyp in which the two stomodæal tubes are altogether distinct from one another. Four pairs of mesenteries, *A-D*, have been added within the ventral entocœle, and two pairs, *E, F*, within the dorsal entocœle.

towards each other, so that each mesentery will form an isocnemic pair with the corresponding incomplete mesentery (*D*) on the ventral aspect, a pair comparable with the mesenteries *II* and *V* of the simple polyp. The mesenterial system associated with each stomodæum is now constituted exactly as if each represented a distinct polyp (cp. fig. 1).

The three sections from separate polyps clearly demonstrate that in *Madrepora* new mesenteries beyond the protoconemes are added in bilateral pairs within the primary entocœle of the dorsal directives and also of the ventral directives,

For the disposition of the musculature and the relation of the complete and incomplete members leave no doubt that the mesenteries numbered *I* to *VI* on each side are really the protocnemes of the original polyp, and therefore the four bilateral pairs (*A-D*)—two complete and two incomplete—on the ventral aspect are new pairs which have been added within the entocœle of the primary ventral directives, now pushed widely apart; and similarly with the two bilateral pairs (*E, F*) on the dorsal aspect within the primary entocœle of the dorsal directives.

The accompaniment of fission of the stomodæal tube, involving a separation of the mesenteries attached to it into two series, has really no bearing upon the manner of mesenterial succession, which alone is sought to be established. I have already carried out investigations on mesenterial development and stomodæal fission in the West-Indian corals, *Manicina areolata* (Linn.), *Favia fragum* (Esper), and *Mæandrina labyrinthica* (Ell. & Sol.), &c.; but from the beginning the metacnemes in these are added in unilateral exocœlic pairs, as already described for the majority of actinians and corals (fig. 3), and the introduction of fission in no way modifies this method. Fission commences in young polyps of *M. areolata* and *F. fragum* after the third or fourth mesenterial cycle has become established. No new pairs of directives arise in the fission polyps, and the plane of division is not through the directive entocœles as in *Madrepora*, but is usually at right angles to the directive plane.

During the growth of the second cycle of mesenteries in most corals and actinians the fifth and sixth developmental pairs of protocnemes become complete, but this never happens in the enlarged polyps of *Madrepora* nor of *Porites*; the new pairs are also anisocnemic with the exception of those constituting directives.

The sequence represented in the three figures is that characteristic of all the polyps examined, but variations in the number of the mesenteries which may be relegated to either the dorsal or ventral extremity have been met with. Fig. 7 represents a section through a polyp in which three additional pairs (*C-E*)—two complete and one incomplete—are already added dorsally, and only two pairs (*A, B*)—one complete and one incomplete—ventrally. In all the examples previously considered no more than two new pairs are placed dorsally, the remaining four being ventral. The connecting pair in fig. 7, whether in the end attached dorsally or ventrally, will separate the two members of a bilateral pair of incomplete mesenteries. From the arrangement of the musculature, and

the relationships of the complete and incomplete mesenteries, it is clear that each polyp will, upon separation along the axial plane, possess twelve mesenteries with the paired arrangement exactly as in the adult.

Another polyp exhibited thirteen complete mesenteries with several alternating incomplete members, associated with one stomodæum, while on the other stomodæum were inserted the normal eight. Several large ova were developed in the single connecting mesentery of one polyp, while they were absent from the remaining mesenteries.

We may now return to a consideration of the median mesenterial strands connecting the two stomodæal invaginations. In some polyps two of these are found to extend as vertical partitions throughout the length of each stomodæum, and at the uppermost extremity of the polyp they pass along the narrow central portion of the disk intervening between

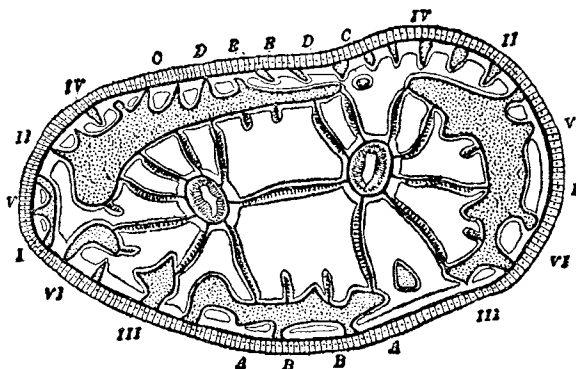


FIG. 7.

Transverse section through a large polyp projecting all the way round from the general surface of the colony. Only two mesenterial pairs, *A, B*, occur within the ventral entocœle, while three pairs, *C-E*, have been added within the dorsal entocœle.

the two oral apertures. Sometimes only one may be present, extending the whole way; in others the partition has disappeared above, but is complete below; while again, as in fig. 6, both partitions may be wholly absent, each presumably represented by the two distinct pairs of mesenteries (*E, E*; *F, F*) which stretch from the stomodæum to the dorsal region of the body-wall.

That each connecting strand actually becomes divided into

two mesenteries, and that these effect a union with the vertical body-wall, is clearly shown in the series of partly diagrammatic transverse sections (fig. 8, *A-D*), taken at different

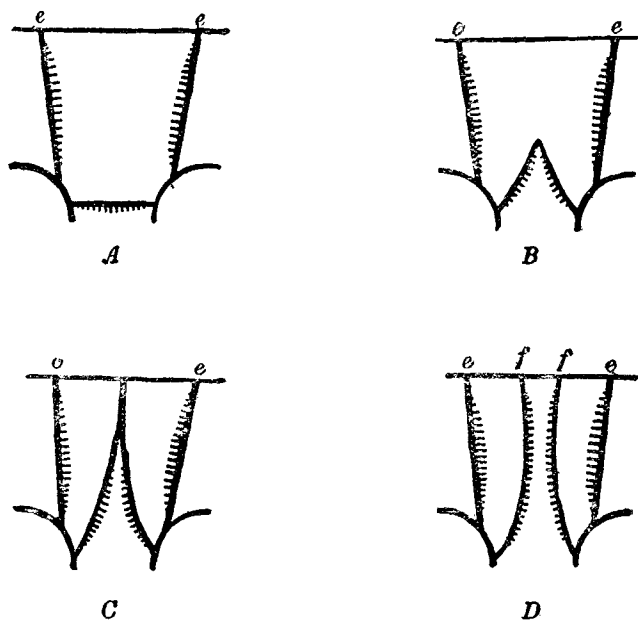


FIG. 8.

Diagrammatic figures taken at different levels from a single polyp to illustrate the manner in which a single mesenterial strand joining two stomodæal tubes becomes inserted on the polypal wall as a pair of distinct mesenteries: *A* is towards the inner termination of the stomodæum, *D* is from the upper extremity of the polyp, and *B* and *C* from intermediate sections.

levels from a single polyp. Fig. *A* is from a section through the lower stomodæal region, where only a single straight mesentery joins the two stomodæal tubes. The dorsal connecting mesentery is already divided, and presumably is represented by the two mesenteries, *e, e* (cp. fig. 5). In fig. *B*, taken from a section a little higher, the connecting mesentery is directed in an angular manner toward the dorsal part of the body-wall, and in the next it is actually inserted on the wall; while in the last figure (*D*), from a section near the upper extremity of the polyp, the two halves are altogether apart and appear as two distinct mesenteries, *f, f*.

The musculature is strongly developed throughout, whether the mesentery be simple or divided.

From the series of sections it appears that the two connecting mesenteries, which originally pass straight across the portion of the disk intervening between the two oral apertures, first begin to extend from their middle towards the periphery of the disk, and when that is reached each half becomes distinct. The separation then proceeds down the polypal wall, until ultimately the partition is divided throughout, and two mesenteries, each connected with its own stomodæum from the beginning, are now fully established, and in all respects resemble the older complete mesenteries.

The new incomplete mesenteries have a much simpler origin. They are never connected with the stomodæum, but in serial transverse sections can be seen to arise somewhere towards the upper extremity of the polypal wall, and to extend vertically as well as radiately for but a short distance. In no case do they pass downwards as far as the incomplete members of the primary series. In one or two instances I have failed to discover them. The incomplete mesenteries never bear filaments, but the complete mesenteries are all filamentiferous for some distance below the inner termination of the stomodæum. The connecting mesenteries, while still unattached to the column wall, also bear filaments at their free edge.

A knowledge of the early stages of gemmation in ordinary polyps of *Madrepora* assists towards an understanding of the peculiar relationships of the mesenteries during the process of fission. Figs. 9-13 represent a series of sections through a very young polyp from near the apex of a branch of *M. proliferæ*. The stage is so early that no tentacles have yet appeared. The bud is formed wholly from the superficial covering of the colony over one of the ordinary peripheral canals, and structurally is entirely unconnected with the older polyps, though in communication with them by means of the canal system. The sections are vertical and are taken from only one side of the polyp, but an exactly similar series is found to occur on the other half.

Fig. 9 is from a section passing through the oral aperture, which has just been formed. The stomodæal walls appear as simple intunnings of the superficial wall of the colony. The section is in the directive plane passing through the two directive entocœles, so that no trace of the mesenteries is included. The two slight elevations of the outer wall are probably the first indications of the axial entocœlic tentacles. The endodermal epithelium of the bud, including that forming



FIG. 9.

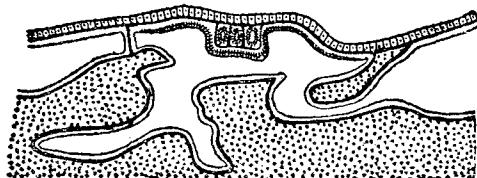


FIG. 10.

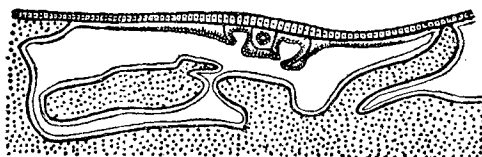


FIG. 11.

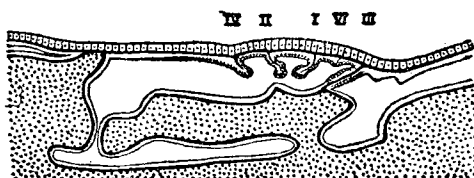


FIG. 12.

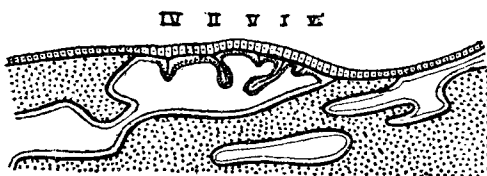


FIG. 13.

Figs. 9-13.—Series of sections illustrating the early stages in the formation of a bud polyp of *Madrepora*.

both the inner and outer lining of the stomodæum, differs altogether from that elsewhere lining the canals and gastric cavity of the polyps; the cells are columnar, strongly ciliated, non-vacuolated, and stain deeply.

Fig. 10 is from a section a little to one side of the oral aperture, and reveals four mesenteries extending vertically from the outer wall as far as the inturned stomodæal wall. In fig. 11 the two outermost mesenteries have become free at their lower extremity, but the two inner still retain their connexion with the infolded margin of the stomodæum. In the next figure all the primary mesenteries are free from the stomodæum, but the one to the right is connected with the inner wall of the peripheral canal. To the left of the mesentery the rudiment of an additional mesentery has now appeared. In the succeeding figure (fig. 13) the mesentery at the extreme right has disappeared and a rudiment of a second new mesentery occurs. Thus all the six mesenteries—four complete and two incomplete—of one side of an adult polyp of *Madrepora* are accounted for.

The important facts in the present connexion which the series of sections serve to demonstrate are as follows:—1. In the formation of a bud of *Madrepora* the six pairs of mesenteries characteristic of the adult polyps are all present at a very early stage, perhaps appearing simultaneously. 2. The four complete pairs arise at or near the angle between the disk and stomodæal wall, and extend all the way down the latter, and also radiate along the outer wall. 3. The two incomplete pairs arise on the body-wall (not yet differentiated into actual disk and column) some distance from the oral aperture, and from the beginning are wholly free from the stomodæum and extend only a short distance.

The above results from the bud-polyps may now be compared with the conditions occurring in the fission polyps of *Madrepora*. That no succession in the appearance of the new six pairs of mesenteries has been met with in the numerous fission polyps examined is evidently due to the circumstance that, as in the bud, all the six pairs appear at a very early stage, if not simultaneously. The presence of mesenterial strands connecting the two stomodæal tubes may be brought about by the close association of the complete mesenteries with each stomodæum at the time of separation of the latter. Obviously from the insertion of the mesenteries at about equal distances all round the stomodæal wall only two adjacent members will be directly opposite each other, and, arising from the same proliferating band of tissue, may grow as single lamellæ down the opposite aspect of each stomodæal



wall, and thus for a time remain as partitions uniting the two stomodæal tubes. It is only later, when each single partition begins to extend radiately across the disk and passes down the body-wall, that each strand becomes two distinct mesenteries and the mesenterial system for each polyp is normally established. The early appearance of the incomplete mesenteries and their perfect freedom from the stomodæum in the fission polyps are features likewise reproduced in the young bud polyps.

It has already been mentioned that the number of tentacles on the larger polyps may vary from sixteen to twenty-four, indicating that the passage from the twelve-tentacle stage to the stage with twenty-four is not abrupt. That such a succession should characterize the appearance of the tentacles, though not of the mesenteries, can be easily understood. In the development of corals and anemones it is found that, as a rule, the number of tentacles corresponds with the number of mesenterial chambers, the appearance of new tentacles following very closely upon the formation of additional mesenterial chambers. In the earliest stage of mesenterial addition in *Madrepora* (fig. 4) only eighteen mesenterial chambers are fully established, neglecting the two axial chambers where additions are taking place; thus there would be only as many tentacles. Fig. 5 possesses two additional peripheral mesenteries, hence two additional mesenterial chambers and tentacles. When all the mesenteries are connected peripherally twenty-four mesenterial chambers will be present, affording the possibility of twenty-four tentacular outgrowths.

The enquiry may now be made as to how far the metacnemic sequence characteristic of *Porites* and *Madrepora* conforms with what is already known of the mesenterial development of the *Zoantharia* generally. The development and anatomy of most modern corals reveal that the metacnemes are added as unilateral isocnemic pairs within the six primary exocœlic chambers, as in fig. 2, and the septa follow a corresponding succession. One, two, four, &c., unilateral pairs may arise successively within each primary system, and in the end become arranged in one, two, three or more cycles. The first cycle of metacnemes consists of six equal pairs, the second of twelve, the third of twenty-four, and so on. The metacnemes, unlike the protocnemes, exhibit perfect radial symmetry when the members of each cycle are fully developed; the presence of two pairs of directives imparts a bilateral character to the six pairs of primary mesenteries. Departures from the hexamerous plan are not infrequent in corals, but apparently no form has been described which

introduces a different fundamental type of metacnemic succession. The absence of directives and the irregular mesenteric systems described in certain colonial corals—*Lophophyllia*, *Mussa*, *Euphyllia*, &c.—are probably in all cases due to asexual methods of reproduction, and do not indicate the true characteristics such as would be revealed by polyps developed directly from larvæ.

Similarly with modern Actinians, exclusive of Zoanthids and Cerianthids. Their metacnemic sequence conforms most closely with that of modern corals. In many the metacnemes, even of the first cycle, are incompletely established (*Edwardsia*, *Gonactinia*, *Oractis*, *Peachia*), but so far as they go they indicate no new type of development. Dr. O. Carlgren (1897) has lately described an Actinian, *Endocœlactis*, the adult characteristics of which seem to show that the second and third cycles of mesenteries have been added in unilateral pairs within the primary entocœles, the directive entocœles excepted. The discovery is full of suggestiveness in connexion with the entocœlic succession followed in *Porites* and *Madrepora*. Carlgren, however, is inclined to regard the arrangement as merely an exception to the general plan of Hexactinian development, and places the genus under the subtribe Actininæ.

The entocœlic growth of mesenteries and septa is also different from anything which has yet been definitely established among fossil corals, including the Rugosa of Palæozoic times. It must be acknowledged that our acquaintance with the septal succession of extinct corals is very incomplete; a study of numerous types by means of serial sections will be necessary before an adequate knowledge of their method of growth is available. Thanks to the labours of R. Ludwig (1862, 1865) and A. Kunth (1869), we are more or less familiar with the septal plan of a large number of Rugose corals, in so far as this can be determined from the ridges and grooves exhibited on the outer surface of the coralla. According to Ludwig the primary plan in the Rugosa is hexamerous, whereas Kunth assumes a tetrameral condition both for the primary and secondary stages. Both writers find the metasepta to be added successively at four regions, in a manner which finds its expression in what is now known as Kunth's law.

Some of Ludwig's descriptions and figures (pl. xxvii. figs. 2) indicate that new septa were added within all the six primary chambers, while some few septal pairs appear to have been added axially, *i. e.* within an entocœle, as in

*Madrepora* and *Porites*. The definite establishment of this is a matter of the highest importance.

Recently (1902), I have been able to confirm the observation of Pourtales (1871) as to the primary hexamerous character of the Rugose coral *Lophophyllum proliferum* (McChesney), and by means of serial sections have definitely established the metaseptal sequence. The structure of Palæozoic corals so nearly conforms with that of recent forms as to warrant the assumption that the relationships of the polyp to the corallum were the same as those now thoroughly understood. The metaseptal arrangement in *Lophophyllum* is such as to indicate that the mesenterial additions took place successively at one region only within four of the six primary exocoelic chambers; two of the chambers are the middle exocoèles and the other two are the exocoèles on each side of one of the axial (directive) pairs of primary mesenteries; no additions were made in the two remaining primary exocoèles. So far as the septal arrangement in *Lophophyllum* can be taken as representative of the Rugosa generally, the order is shown to be most closely related to the living Zoanthæ. In this group of mainly tropical and colonial Actinians the metacnemes are added in succession at one region within the primary exocoèle on each side of the ventral pair of directives, whereas in the Rugosa they were added in two middle primary exocoèles in addition.

With their entocoelic metacnemes, therefore, *Porites* and *Madrepora* cannot yet be brought into conformity with either the extinct Rugose corals or the living Zoanthid polyps, seeing that these are characterized by exocoelic additions. In one feature, however, they all agree. The metacnemes in the Zoanthæ and in *Porites* and *Madrepora* arise successively, a bilateral pair more or less simultaneously on opposite sides of the polyp. In the end they are arranged on each side of the polyp so as to constitute unilateral pairs consisting of a complete and an incomplete moiety (anisocnemic), whereas in ordinary Hexactinians the metacnemic unilateral pairs are constituted of equal moieties which appear together (isocnemic).

The Cerianthids present in their mesenterial growth a method which most nearly approaches that under consideration, though differing in several important details. While Actinian writers such as Boveri and McMurich hold that the first four pairs of mesenteries to arise represent the four Edwardsian mesenteries, van Beneden (1897) considers that no such relationship can be maintained, and the results of

Carlgren (1897) upon the arrangement of the musculature would seem to indicate the same, as only one pair of directives are represented. The most important characteristic of the Ceriantheæ in the present connexion is that the later mesenteries are always developed within the axial entocœle on the asulcar aspect of the polyp, and that the organs in the adult remain as bilateral pairs. Carlgren has shown that the feeble retractor muscles in each mesentery are always on the face turned away from the directives—that is, the mesenteries do not constitute unilateral pairs in which the faces bearing the retractor muscles are *vis-a-vis*, as in all other Actinians and corals.

The numerous researches of the late H. de Lacaze-Duthiers and those of G. von Koch have demonstrated that the proto-septal stage of many modern corals is hexamerous; I have also established the same for several West-Indian species, and a like plan would seem also to have been characteristic of the extinct Rugosa. It is with the appearance of the metasepta that fundamental divergences are introduced. These seem to afford hope that they may serve as a means for arranging the Madreporaria on a more strictly morphological basis than is at present possible. At least three fundamental types are now known:—*a*, the cyclical, characteristic of most modern corals; *b*, the bilateral exocœlic, in *Lophophyllum* and probably other Rugosa; *c*, the bilateral entocœlic, now demonstrated for *Porites* and *Madrepora*.

The essential results may be now summarized:—

1. In most of the polyps of the genus *Madrepora* only the six bilateral pairs of primary mesenteries are developed, of which four pairs are complete and two incomplete. On any colony a few enlarged polyps may possess a greater number of mesenteries. The new mesenteries beyond the primary six pairs are added in complete or incomplete bilateral pairs at only the two axial extremities, the entocœle of the dorsal and ventral directives. The cyclic disposition is never assumed; the directives form isocnemic pairs, but the other pairs are all anisocnemic.

2. The pinnate method of mesenterial increase is distinct from that characteristic of most recent corals; in these the metacnemes are added in isocnemic pairs all round the periphery of the polyp, within the six primary exocœles, and in the end constitute one or more distinct alternating cycles.

3. The method of mesenterial increase beyond the proto-cnemic stage occurring in *Madrepora* is also characteristic of the genus *Porites*, except that in any one polyp of *Porites* the

new mesenteries are disposed at either the one or the other extremity, not at both.

4. Six new bilateral pairs of mesenteries appear practically simultaneously in *Madrepora*, but only later do they all extend down the polypal wall. In *Porites* the new pairs follow one another in a regular succession.

5. In *Madrepora* the mesenterial increase is early associated with fission of the stomodæum and in the end probably with complete polypal fission, in which half the mesenteries of each fission polyp are derived from the primary twelve of the original polyp and the other half are new formations. The resulting paired arrangement of the mesenteries, including the presence of two pairs of directives, is exactly as in primary polyps. Fission of the stomodæum appears very late in *Porites*, not until after the full establishment of six new pairs of mesenteries.

(References in No. 155, Jan. 1902; see 'Annals' for May 1902.)

## XV.—A Revision of the Fishes of the Family Stromateidæ.

By C. TATE REGAN, B.A.

SINCE the revision of this family by Gill \* in 1884, when he considerably enlarged its limits as understood by Günther †, no additions have been made to our knowledge of its affinities. The character which has always been taken as diagnostic of this family is the presence of teeth in the œsophagus, and Günther grouped the fishes which possessed this character into two genera, *Stromateus* and *Centrolophus*; to these Gill added the genus *Schedophilus*, placed by Günther in the Coryphænidæ, the genus *Palinurichthys* (*Pammelas*, Gthr.), placed by Günther in the Carangidæ, and the species *Psenes anomalus* (*Trachynotus anomalus*, Schleg.). Gill subdivided the family thus constituted as follows:—

### Subfamily CENTROLOPHINÆ,

with complex elongate gill-rakers extending backwards from the epibranchials of the last gill-arch, 11 abdominal and 14 caudal vertebrae, protractile premaxillaries, and normal persistent ventral fins.

Genus 1. *Centrolophus*; body elongate, dorsal spines slender.

2. *Schedophilus*; body ovate, dorsal with 4 short stout spines.

3. *Lirus*; body ovate, dorsal with 6 to 8 short stout spines.

\* Gill, Proc. Am. Phil. Soc. xxi. p. 664 (1884).

† Günther, 'Study of Fishes,' p. 452 (1880).