

RECENT RESULTS ON THE MORPHOLOGY AND DEVELOPMENT OF CORAL POLYPS¹

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INTRODUCTION

Students of the cœlenterates have long been aware of the insufficiency of our knowledge of the morphology and development of the animals which produce the calcareous skeletons popularly known as corals. The skeletons themselves are thoroughly known, even to their microscopic detail, but of the polyps which formed them, and which covered them while alive, we know comparatively little.

It is not difficult to assign a reason for this. It has been the privilege of few naturalists to make a prolonged stay within tropical regions, which are the home of by far the greater number of living corals, especially of the larger massive forms which make up coral reefs; yet it is only by direct study on the spot that many of their characteristics can be determined, their development followed, or suitable material procured for later anatomical and histological investigation. Beyond the observation of their living external characters, the polyps must be narcotized and preserved under proper conditions, and slow decalcification carried out to remove the hard calcareous skeleton so as to obtain the soft tissues in their natural relationships for microscopic examination.

A residence for the last few years within the West Indies, in the region of coral reefs, has afforded me the opportunity of investigating the morphology and development of a certain number of coral polyps. In all about thirty species have been fully examined, both in their living condition and anatomically, and the development of several forms has been followed for longer or shorter periods. Only the principal results can be here outlined.²

¹A lecture delivered at the Marine Biological Laboratory, Woods Hole, Massachusetts.

²Fuller details will be found in volume VII, 7th memoir, of the *Memoirs of the National Academy of Sciences*, and in a series of four shorter papers in the *Annals and Magazine of Natural History* from May, 1902, to February, 1903.

BORING ALGÆ

One incidental result of the decalcification of so many freshly preserved corals has been the revelation that the madreporarian skeleton is almost universally infested with minute, filamentous, boring algæ. Every fragment decalcified, with the exception of pieces from near the growing apex of branching colonies, has yielded material of a fluffy texture within the spaces previously occupied by the corallum. Particles representing the organic matrix of the skeleton are mingled in the fluffy mass, but by far the greater part consists of microscopic algal filaments, which are usually green in color but occasionally red. Further, on cleaning away by maceration the animal tissues of freshly collected corals, the skeleton is frequently found to be green or pink in color, either as a whole or in part; and closer examination proves this to be due to the presence upon the surface and within the calcareous substance itself of closely ramifying filaments of green or red algæ. Not only the West Indian corals have been found thus infested with boring plants, but fragments from many Pacific species and even fossil corals of Paleozoic times have disclosed the same.

Of the green algæ two forms only have been found: one in which the filaments are provided with transverse walls, and another with continuous tubes, belonging to the group of the Siphonæ. Both are extremely variable as regards the size, form, and extent of branching of the filaments, and are often closely intermingled in the same fragment of coral. Only one species of red alga has been found, and this is represented by simple, closely intermingled filaments. The non-septate green species frequently bears club-shaped or spheroidal enlargements which contain spores, but no reproductive bodies have been found on the others. No fungi have been observed, so that probably the saproleginous *Achlya penetrans* of other writers is really an alga; old preserved material does not show the chlorophyll granules, although so obvious in fresh coralla.

Much significance has been attached in recent years to the presence of boring algæ and fungi in calcareous organisms other than corals, especially in shells of mollusks, both living and dead. Moreover, the corroding activity of these Thallophytes has been shown to play a very important role in the ultimate disintegration of dead calcareous matter, reducing the carbonate of lime once more to the soluble state. In this respect they are to be compared with the putrefactive bacteria in their action on dead organic matter generally. The physical and chemical processes involved in the entry of delicate plant filaments within the dense calcareous structures are not fully

understood, but the possibility of the ultimate destruction of an infested skeleton by this means is beyond doubt.

While the corroding algal filaments are thus general within the living superficial areas of the corallum, they are even more prevalent in the dead older parts, being particularly plentiful in so-called "rotten coral." Here they are associated with other superficial or boring organisms, such as boring mollusks, echiurids, sponges, and other agents of coral disintegration. The algæ continue their corroding activity even on the separate particles of dead coral after fragmentation, for fresh coral sand when dissolved in acids yields filaments in a living condition.

The universal occurrence of coral-boring algæ, possibly resulting in the ultimate disintegration and corrosion of the infested blocks, has manifestly some bearing upon the much discussed subject of the origin of the various forms of coral reefs, with which are associated the names of Darwin, Dana, Murray, Agassiz, and others. To account for the formation of many of the barrier reefs and atolls of coral seas it is necessary to assume a constant disintegration or removal of the older coral growth as the outer living edge of the reef continues its progress outward. In this destructive work the ever-present corroding activity of boring algæ is undoubtedly to be accorded an importance along with the more obvious coral-boring organisms, supplemented by actual solution in sea-water.

COLORATION

Almost all writers on coral reefs have emphasized the brightness and variety of hues exhibited by the living polyps. Different tints of brown, green, yellow, and blue are intermingled in never-ending variety, and even the same species may present much diversity in passing from one locality to another. Yet the color of living corals is in part incidental, that is, independent of the true nature of the polyps. Over West Indian coral areas the different shades of yellow or brown predominate, and these are found to be due mainly to the presence of zooxanthellæ or yellow algal cells within the endoderm of the polypal tissues. These are symbiotic unicellular plants, bearing yellow chromoplasts, and as a rule are distributed throughout the inner layer of the polypal wall, giving a light-yellow tinge to the colony where sparse, and a dark-brown effect where crowded. The two closely allied genera, *Astrangia* and *Phyllangia*, are the only forms in which zooxanthellæ have not been found, and the living tissues of these are characterized by an appearance of extreme

delicacy and transparency, well exemplified by the *Astrangia danae* of the eastern coast of the United States. Where colonies of other species are found growing in the absence of much light, the polyps are colorless, and zooxanthellæ are sparse or wanting.

Other more brilliant colors of corals are produced in various ways. Most are ectodermal, due either to fine, granular pigment matter within the layer, or to some superficial deposit. Distinct pigment cells may also occur, either in one or both layers of the body wall; at other times large pigment granules are more or less uniformly distributed, rendering the tissues dense and opaque. Experiments are much needed to determine the part which the zooxanthellæ and other coloring agents play in the physiology of the polyps, and also as to their adaptive significance.

THE POLYP WALLS

The external walls of coral polyps, represented by the column and disk, are constituted of the usual three cœlenterate layers: an outer ectoderm, an inner endoderm, and a middle mesogloea. The polypal walls are usually thin and delicate, when compared with the majority of polyps of the closely allied actinians, the difference being dependent on the degree of development of the middle layer or mesogloea. The ectodermal and endodermal epithelia are found to vary comparatively little in height throughout the Anthozoa, so that any diversity in thickness of the polypal wall as a whole is determined by that of the mesogloea. Support for the polyp is afforded by the skeleton in corals, hence there is no necessity for any special development of the middle layer, such as gives a certain degree of firmness to many actinians. In general the mesogloea of coral polyps is a mere separating lamella; where, as in the mesenteries, it may attain considerable thickness, it is usually a clear homogeneous substance, though in some species connective tissue cells occur sparsely.

Both the ectoderm and endoderm are richly provided with unicellular gland cells, which give out copious supplies of mucus when the polyps are irritated. An ectodermal muscle layer, the fibers either longitudinally or radially arranged, has been found only on the tentacles and disk, while the endodermal circular musculature of the column is usually only feebly developed. In some of the larger species the latter constitutes a diffuse endodermal sphincter, but never becomes so concentrated as to form a circumscribed or mesogloæal sphincter such as occurs in many actinians (bunodactids, sagartids).

On complete retraction of the polyp the upper part of the column

generally folds over the tentacles and greater part of the disk, due to the action of the circular musculature; but in some few cases the disk and tentacles remain wholly exposed, even when the greater part of the polyps is withdrawn within the skeleton. The term edge-zone, or *Randplatte*, so frequently employed in coral literature, refers to the lower, pericalicular portion of the column wall, the thecal wall having divided the polyp vertically into intra-calicular and extra-calicular parts, each containing portions of the mesenteries and gastro-cœlomic cavity.

Coral polyps in general remain retracted or partly retracted during the day, and expand to their full degree only at night time or when placed in the shade (negatively phototropic).

TENTACLES

The tentacles of coral polyps are arranged mostly in alternating, hexamerous cycles, the inner larger than the outer, as in the majority of hexactinians. Usually the cycles are close together around the margin of the disk, but in *Fungia*, *Siderastraea*, *Agaricia*, and one or two other genera the individual tentacles are widely separated and spread over nearly the whole of the disk. One tentacle arises from each mesenterial chamber, and thus corresponds in position with the septa below; in *Agaricia* and some other genera the outermost cycle of exotentacles is wanting, and no instance of the stichodactylinous arrangement (*i. e.*, in radial rows, several tentacles from each chamber) has been found. Perhaps the majority bear a knob of stinging cells at the apex, and smaller batteries along the stem. All are simple in form, except in *Siderastraea*, where the entocœlic members are bifurcated about midway along their length. Frequently the tentacles undergo invagination within the polypal cavity, even when the polyps are fully expanded; and occasionally on fullest expansion they temporarily disappear as outgrowths, becoming part of the discal expansion.

In fissiparous genera the hexamerous plan of the tentacles is altogether lost, and in extreme cases (*Macandrina*, *Pectinia*) the organs are merely dicyclic, having an inner entocœlic and an outer exocœlic series.

Frequently in adult gemmiferous polyps the last entocœlic and the exocœlic cycles are hexamerously incomplete, that is, growth ceases before the completion of the last entocœlic cycle commenced; otherwise the cycles follow the normal hexamerous plan with the formula, 6, 6, 12, 24, etc.

STOMODÆUM OR ŒSOPHAGUS

The stomodæum of all coral polyps fully investigated is found to be without siphonoglyphs or gonidal grooves, a structure characteristic of most actinians and aleyonarian polyps. Though the œsophagus is oval or slit-like in section, the extremities show no histological differences from the sides. In many species the stomodæal walls all round are deeply ridged and grooved, in a manner unlike anything which occurs in ordinary actinians; the ridges correspond with the insertion of the mesenteries, and where strongly developed are histologically different from the grooves.

MESENTERIES AND MESENTERIAL FILAMENTS

The mesenteries, like the tentacles, conform to the hexactinian cyclic plan—6, 6, 12, 24, etc., either throughout or during only the early stages of growth. Two great groups of corals, however, are recognizable, according as the asexual growth of the colonies takes place by budding or by fission. In the former the bud polyps are, to all intents and purposes, new polyps, having the mesenteries throughout arranged in hexamerous alternating cycles, with two pairs of directives, exactly as in polyps reared directly from larvæ. Though in the adult polyp the last cycle of mesenteries commenced may not reach the number of pairs necessary to complete the hexactinian plan, yet so far as the additions are made they follow the normal sequence. Where fissiparity is established, however, the cyclic arrangement is irregular, the early hexamerism is altogether lost, and no new pairs of directives arise. Whenever, as is the case in some polyps, directives and cyclic hexamerism are wanting, it may with good reason be assumed that the polyps are products of fission, not of gemmation (p. 102).

The mesenteries are restricted to the upper half or two-thirds of the polyp, being resorbed in the lower region as the polyp grows upward. Histologically the retractor and oblique muscles are always feebly developed, parieto-basilar muscles seem to be absent, and no evidence of mesenterial stomata is forthcoming.

Mesenterial filaments occur on nearly all the mesenteries, both complete and incomplete, though sometimes they are merely incipient on the youngest cycles. In all the species examined the filaments are simple, not trilobed as in most actinians. In the latter group two lateral lobes are developed, in addition to the median lobe, and these bear the ciliated bands, which are specially concerned in the circulation phenomena of the polyp. In both groups, however, the histology

of the terminal lobe is the same, but in certain corals it undergoes a remarkable modification, constituting what must be regarded as a special glandular organ. For a limited part of its course the filament becomes greatly enlarged, and all the cells, with the exception of the supporting cells, are charged with a finely granular secretion, yellowish in color. Sometimes the glandular differentiation may extend so as to include part of the mesenterial epithelium adjacent to the filament.

In the lower part of their course the mesenteries and filaments may become greatly convoluted, and, when much disturbed, the living polyps have the peculiar power of extruding the filament along with the part of the mesentery to which it is affixed; they can, however, be again indrawn as the polyps recover. Sometimes the filaments are forced out in such quantities as to give a ragged appearance to the surface of a colony. The extrusions take place through the oral aperture or any part of the column wall or disk; in the latter case minute pores are made in the polypal wall, but after the mesenteries and filaments are indrawn the punctures are healed, and the wall then affords no indication of their former presence.

The phenomenon of extrusion of the filaments is in some ways comparable with the emission of acontia through cinclidal pores which takes place in certain anemones (sagartids); but here the acontia are sent out as threads distinct from the mesenteries, and the cinclides are permanent apertures, whereas, in corals, a part of the mesentery accompanies the filament, and the openings are temporary and may be produced at any part of the polypal wall.

SKELETOGENIC TISSUES

All the researches on the development of corals, as well as on their adult relationships, serve to demonstrate that the entire coral skeleton is an ectoplasmic product of the basal disk, that is, it is formed altogether external to the polyp itself. On decalcification the polyps remain as perfect organisms, their walls intact throughout, intricate infoldings of the lower part representing the spaces formerly occupied by the skeleton. All the radial (costæ, septa) and tangential (theca) elements of the corallites correspond with so many infoldings of the basal part of the polyp, which have been produced *pari passu* with the deposition of calcareous matter.

Considering the colony as a whole, the polyps themselves are altogether superficial, however thick may be the coral stock. The soft tissues extend only a few millimeters within the skeletal mass, or in

large polyps a centimeter or so, being cut off from the skeleton below by transverse dissepiments.

The three cœlenterate layers lining the skeleton, and by which the skeleton is produced, have each undergone certain modifications compared with their character in the column and oral disk. In most instances the endoderm becomes greatly thickened and vacuolated in passing from the upper to the lower regions of the polyp, so that proximally it greatly reduces the polypal cavity, the mesenteries being also wanting in this region.

The mesogloea, as elsewhere throughout the polyp, is a thin homogeneous lamella, but in certain areas it is produced into conical or wedge-shaped processes, striated toward their extremity, and coming into direct contact with the skeleton. These have recently been shown by Bourne to take their origin from modified ectodermal cells, which he terms *desmocytes*, and the desmoidal processes are considered to serve as a means of attachment of the polyp to the corallum. They are best developed along the line of union of the mesenteries with the skeletotrophic tissues, and where skeletal formation is not in progress.

The basal ectoderm is the true skeletogenic epithelium, and varies greatly in character according as it overlies a region of active skeletal formation, or an older region where growth is stationary. At the apex of branches, and the edge of growing septa, the layer is broad and highly protoplasmic, while the individual cells, termed calicoblasts, have either distinct walls or are fused into a common mass or cenocyte. In the non-growing areas the skeletogenic layer is usually extremely narrow, being scarcely recognizable in sections of decalcified material. The calicoblasts are usually in an active state in the deepest or most proximal part of the polyp, as it is here that the calcareous dissepiments are continually being formed as the polyp grows upward.

In very carefully decalcified material, from rapidly growing regions, a homogeneous skeletal matrix or ground substance remains in the space formerly occupied by the skeleton. It resembles the mesogloea in its behavior toward reagents, though with the form and detailed microscopic appearance of the skeletal fibers. It is thus manifest that the calcareous skeleton, though formed externally to the polyp, is laid down within a colloidal matrix produced by the skeletogenic tissues. After decalcification of the older parts of the skeleton there is little evidence of this organic matrix except immediately next the calicoblast layer. Here the matrix is usually

represented by a thin homogeneous layer, which has been regarded as a skeletal membrane, coming between the actual polypal tissues and the corallum.

The *synapticula*, which are solid calcareous bars, uniting adjacent septa across an interseptal loculus, are found actually to perforate the skeletotrophic tissues lining the two walls of the loculus, and also any mesentery which may be included within the loculus. Recently they have been described as originating from independent continuous upgrowths of the basal disk, but the anatomy of the polyps gives no support for this conception.

ASEXUAL REPRODUCTION

Vegetative or asexual increase assumes a great importance in the growth of corals, resulting in the production of colonies or stocks, often of large size and complexity of form. Yet, however diverse in form the colonies may become, their origin can be reduced to two sharply-defined processes, namely, *budding* and *fission*. Many varieties of both types of increase have been studied, and reveal that the resulting colonies are characterized by morphological differences of much significance.

Budding or gemmation may take place from almost any part of the polypal wall, and in every case the buds are found to reproduce all the characteristics of the larval polyp. The mesenteries, tentacles, and septa display a cyclic hexamerism, and two pairs of directives occur. Also in the course of their development the organs in buds pass through practically the same stages as in polyps reared directly from larvæ. Hence it follows that coral polyps arising by gemmation are to be regarded as new and distinct individuals, just as much as polyps originating by sexual means.

It is otherwise where a colony increases by fissiparity. The process has been traced in *Manicina areolata* (Linn.) and *Favia fragum* (Esper) from the larva, through the simple polyp, until fission is fully established, leading to a complex polyp. The diagrammatic figures 14 and 15, with their explanation, fully illustrate the stages in *Manicina*. While yet simple, the polyp presents all the characters of an ordinary cyclic hexamerous species, including the presence of two pairs of directives. The first act of fission divides the stomodæum into practically equal parts, each with half the original number of complete mesenteries attached to it, and including, of course, only one pair of directives. The number of mesenteries increases with the growth of the fission polyp, and the hitherto incomplete pairs become

complete by reaching as far as the stomodæum. It is found, however, that in the later stages the mesenterial increase rarely proceeds equally all round the polyp. Fission of one or both of the two stomodæa may now take place, perhaps with a variable number of mesenteries attached to each moiety; the same process is continued, the incomplete mesenteries in turn become complete, and new pairs are developed, but additional directives are never formed. In every case the fission plane is within two entocoelæ.

Examination of parts of the polypal system of mature fissiparous corals, such as species of *Isophyllia*, *Mæandrina*, and *Favia*, fully confirms the results from the early fission stages of other forms. The mesenteries, septa, and tentacles are not disposed in ordinary cycles, no hexamerism or other regular arrangement is determinable, and directive mesenteries are absent. The important conclusion is thus reached that a fissiparous coral, however large, morphologically represents but one complex individual polyp, having many oral apertures and the mesenteries in separate stomodæal systems; on the other hand, a gemmiferous colony is constituted of numerous distinct individuals, practically all alike.

A third, somewhat intermediate form of non-sexual increase sometimes occurs. On most gemmiferous colonies certain polyps are found which are much larger than the others, growing to as much as double the usual size, and among them are various stages leading to division into two daughter polyps. They suggest that the polyps are undergoing ordinary fission, for which reason it has been assumed that both gemmation and fission may occur on one and the same colony. An anatomical examination of many such enlarged polyps reveals, however, that they are not instances of true fission as above established. The resulting moieties are found to be really new individual polyps, having two pairs of directives and cyclic hexamerism, just as in polyps arising in the ordinary way as buds or from larvæ. This is clearly shown in figure 16, representing a section through an enlarged polyp of *Cladocora arbuscula* in process of fission. In the living condition the whole polyp was surrounded by a single column wall, and provided with a single tentacular system and a bioral disk. Manifestly fission is taking place across the median plane, and, when completed, each half will represent a distinct hexamerous *Cladocora* polyp, comparable with others arising as ordinary buds.

The growth of these enlarged polyps has been followed step by step on several different species of *Madrepora*, *Porites*, *Solenastræa*, and *Oculina*. It is found that new pairs of mesenteries are added to an ordinary polyp without increasing the number of cycles, and that in

the end, when a double series of mesenteries has appeared, including two pairs of directives, the stomodæum divides, and half the mesenteries are apportioned to each. The process has been termed *fissiparous gemmation*. Instances of it occur on most gemmiferous colonies, but hitherto its significance, as contrasted with ordinary fission and gemmation, has not been understood.

SEXUAL REPRODUCTION

Coral polyps in general seem to be hermaphrodite, both ova and spermata occurring on the same or separate mesenteries. Whenever

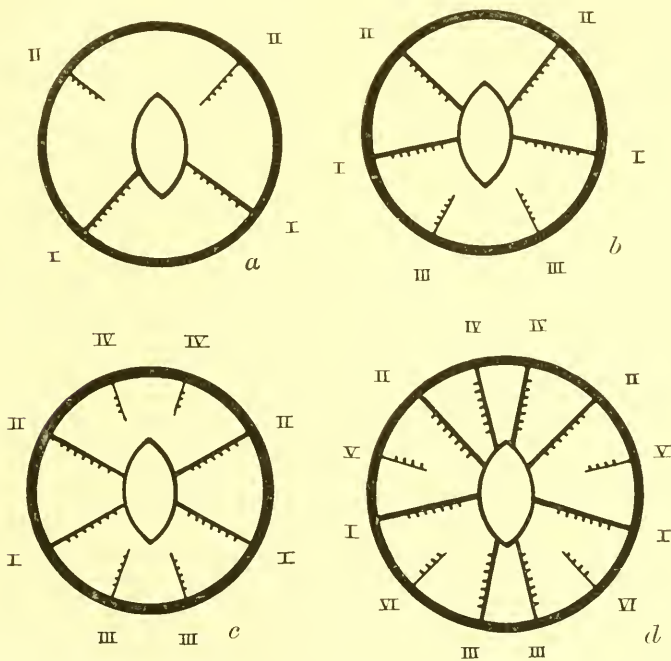


FIG. 10.—Four diagrammatic figures showing the order of appearance of the six primary pairs of mesenteries. In *a* only two pairs of mesenteries are present, of which one pair (I) is united with the stomodæum, while the other (II) is free; in *b* the second pair of mesenteries has become complete, and a third pair (III) has appeared on the ventral border; in *c* another pair (IV) is found within the dorsal chamber; in *d* the first four pairs of mesenteries to arise have all become complete, and the fifth and sixth pairs (v, vi) have appeared, but remain incomplete for a long period, the secondary mesenteries appearing in the meantime (cf. figure 11). The actual stages given are taken from *Manicina areolata*, but a like sequence is presented by other species whose development has been followed.

reproductive cells of only one kind are present, these are found to be ova, though one or two observers have described spermata only. However when the ova are developed in greatest number they are found to be accompanied by spermata, so there is good reason to suppose that, as a rule, coral polyps are protogynous.

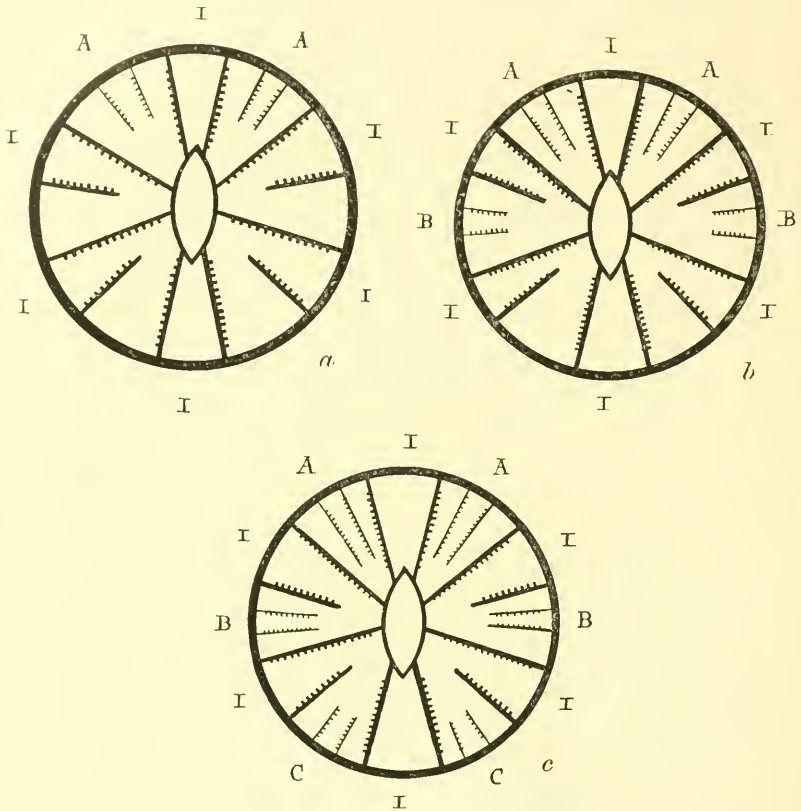


FIG. 11.—Three diagrammatic figures illustrating the manner of appearance of the six pairs of mesenteries (A-C) constituting the second cycle. The mesenteries arise in unilateral pairs within corresponding exocoelomic chambers on each side of the polyp. At first (a) a pair appears within the dorso-lateral exocoelomic chamber on each side; shortly after (b) a similar pair arises within each middle exocoelomic chamber; then (c) a pair within each ventro-lateral exocoelomic chamber. For a long time the pairs retain a difference in size, corresponding with their order of appearance. The sequence is that followed in the development of larval polyps of *Siderastrea radians*.

In some few cases the extrusion of free ova and spermata has been observed, but it may be questioned whether such instances are

not fortuitous in character, for in the same species free swimming larvæ have been found within the polypal cavity. Hence there is little doubt that all corals are viviparous. It is somewhat remarkable that though ripe polyps, and others charged with larvæ, have been abundantly met, none of the intermediate developmental stages be-

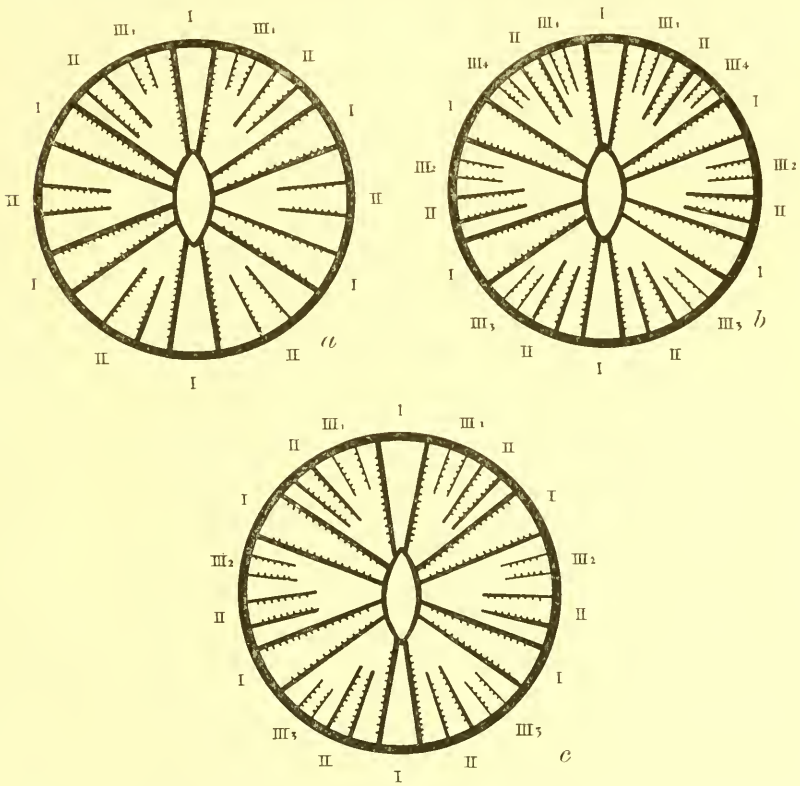


FIG. 12.—Three stages in the development of the twelve pairs of third-cycle mesenteries. All the six pairs of primary mesenteries are now complete, and the second-cycle pairs are all equal, but free from the stomodæum. In *a* a pair of third-cycle mesenteries (III) has appeared on each side, within the exocoelæ next the dorsal directives; in *b* a corresponding pair occurs within the dorsal of the two exocoelæ of all the six systems, the order being from the dorsal to the ventral aspect; in *c* another series of six pairs is commencing, situated within the ventral of the two exocoelæ in each system. Here, again, the growth in the dorsal region is in advance of that in the ventral.

tween the egg and larva has been encountered within the polyp. The only account of the segmentation and formation of the germ layers available is that given by H. V. Wilson¹ for *Manicina areolata*.

¹ *Journal of Morphology*, vol. II, 1889.

tremity, and the layer generally undergoes certain other modifications. The whole structure suggests a larval sense-organ for the forward, aboral pole, a similar organ occurring in the free-swimming larvæ of most of the higher groups of animals. It altogether disappears when fixation takes place by this extremity, thus having only a larval significance.

On first extrusion the oral aperture of the larva is usually indeterminate, the stomodæum is non-functional, and the interior is more or less filled with highly vacuolated tissue. Soon after liberation, however, the middle part of the latter becomes disorganized, and extrusions of yolk, zooxanthellæ, and cell débris take place through

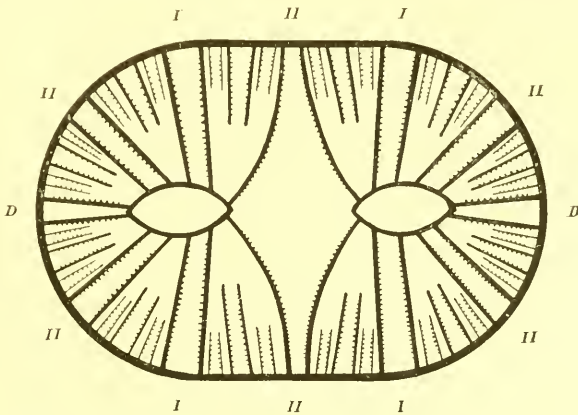


FIG. 14.—Diagrammatic figure illustrating the first stage of fission in a polyp of *Manicina*. Compared with the stage represented in figure 13, the six pairs of secondary mesenteries (II) have become complete, and an additional cycle of twenty-four pairs, constituting the fourth order or third cycle, has appeared. The stomodæum has become divided into halves, each having six pairs of mesenteries attached to it. The plane of division is entocœlic, and the pairs of directives (D) are situated at the opposite extremities.

the oral aperture, the larva becoming at the same time thinner walled and more transparent. The larvæ usually settle within from one to three days after being set free, but the free-swimming stage may continue for several weeks, though little or no development takes place in the meantime.

POST LARVAL DEVELOPMENT

Either before or shortly after extrusion of the larva, the six primary pairs of mesenteries (protocnemes), constituting the first cycle, make their appearance. The organs arise in bilateral pairs, in a

regular and well-defined order, which is uniform for all the species yet studied. The first two or three pairs arise around the oral extremity of the larva, while the others first appear at varying distances down the wall. The protoctenic sequence is represented by the Roman numerals in figure 10, and agrees with that established for the greater number of actinians. The first four pairs very early unite with the stomodæum, but the fifth and sixth pairs remain free or incomplete for a lengthened period, suggesting a different phylogenetic significance from the others.

The six pairs of second cycle mesenteries (metacnemes) arise after fixation, but in a manner altogether different from that followed by the first cycle. They appear on the polypal wall in unilateral pairs or couples within the six primary exocœles, and in a succession which

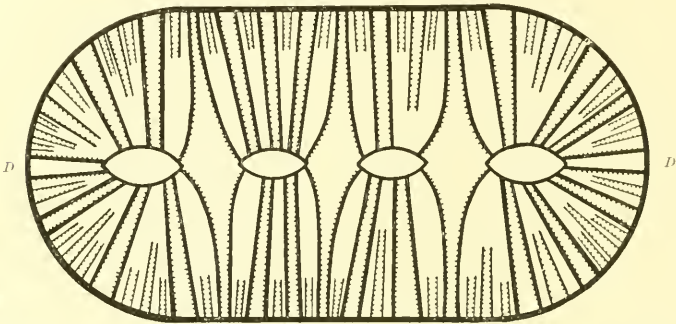


FIG. 15.—Arrangement of the mesenteries in a polyp of *Manicina* with four oral apertures and four stomodæal systems. The cyclic hexamerous plan is departed from, and only the two primary pairs of directives (D) are present.

is from the dorsal to the ventral side of the polyp, not the whole cycle at a time. For a long time, as shown in figure 11, the six pairs present a difference in size, corresponding with their dorso-ventral or antero-posterior order of appearance.

The twelve pairs of third-cycle mesenteries are found to develop in a succession which is altogether unexpected. They follow the same dorso-ventral order as the second cycle pairs, but in two series. A primary series of six pairs—one pair within each sextant—appears within the exocœle on the dorsal aspect of each of the second cycle mesenteries, one pair following upon another, and then another series of six pairs arises on the ventral aspect of the second cycle mesenteries in the same order (figure 12). In the later stages of growth the regularity of the mesenterial succession is not always

maintained; one region may be somewhat in advance of, or may lag behind, its normal development.

The sequence thus outlined in the briefest manner is sufficient to show that the development of the mesenteries in coral polyps is bilateral, and takes place in stages from one extremity to the other. The radial symmetry, characteristic of the adult polyp, is thus derived from primitively bilateral organs, which appear in an antero-posterior succession. Moreover, each cycle represents a separate period of growth, as compared with the successive growth in one direction of ordinary segmented animals.

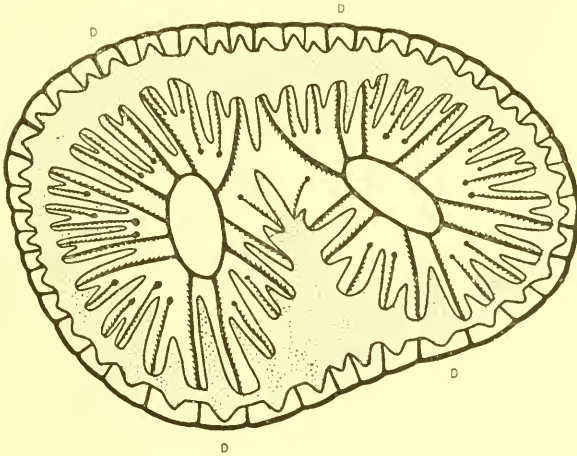


FIG 16.—Transverse section through the stomodeal region of a bial polyp of *Cladocora arbuscula*, showing the character and arrangement of the mesenteries in a late stage of fissiparous gemmation. The plane of separation is entocœlic, and each polyp exhibits nearly perfect cyclic hexamerism, with two pairs of directives (D). The figure should be compared with figures 14 and 15 representing true fission in corals.

The first two cycles of tentacles (prototentacles) generally arise a cycle at a time, either simultaneously or one following the other. The later tentacles are developed in an order in correlation with that of the mesenteries, sometimes entocœlic and exocœlic members appearing together. In the process of growth the exocœlic members are always relegated to the outermost cycles, in a manner first established by Lacaze-Duthiers for actinians; only the entocœlic tentacles are of any ordinal value. *Siderastrea radians* (Pallas) is exceptional in that the exocœlic tentacles appear in advance of the entocœlic.

The skeleton never appears until after fixation of the larva. It makes its first appearance in the form of minute plates or granules, as an ectoplastic product of the ectodermal cells (calicoblasts) of the base. A flat, circular, basal plate is formed by the union of these, and may be produced upward at the edge as the epitheca, while from its inner or polypal surface the septa begin to appear as vertical upgrowths formed within invaginations of the basal disk of the polyp. The skeletal cup first formed is known as the prototheca.

Like the tentacles, the first two cycles of septa (protosepta) may appear simultaneously, or the cycle of six entosepta may arise in advance of the cycle of six exosepta. The order of appearance of the later cycles is not yet thoroughly understood, the relative sizes in the mature corallum by no means indicating the actual order of development. As in the case of the mesenteries, the radial plan of the mature or less definite dorso-ventral or antero-posterior succession. Furthermore, as in the case of the tentacles, the exosepta remain exosepta throughout the course of their development, always constituting the outermost cycle. The entosepta beyond the primary six follow the same succession of growth as the mesenteries, so that the order assigned the secondary and tertiary mesenteries in figure 13 will also hold for the septa.

EXTINCT CORALS

Studies on the septal development of the extinct Paleozoic corals, known as the Rugosa or Tetracoralla, reveal that in these early forms the primary septal plan was hexamerous, like that of modern forms, but the later septal development is altogether different from anything found in recent corals. The metasepta appear in successive bilateral pairs, within only four of the six primary interseptal chambers, and the corallite retains a bilateral symmetry throughout its developmental stages, though afterward it may attain radial symmetry. Only two cycles of septa are ever present, a larger and a smaller (dicyclic), though some members of the primary cycle may differ in size from the remainder. The larger septa are entosepta and the smaller exosepta; only the former have any definite ordinal significance, the exosepta appearing at different times in different species.

On account of the manner of appearance and arrangement of the septa the Rugosa must be clearly separated from modern hexamerous, polycyclic Madreporaria; of all the living zoantharians they are most septa is derived from structures which appear bilaterally, in a more closely related to the zoanthids among the actiniarians.

SUMMARY

The studies thus briefly outlined enable the relationships of madreporarian coral polyps to be determined with much precision. With the exception of the characteristics dependent on the presence of a skeleton, they present no feature which separates them from ordinary hexamerous actinians. The development and arrangement of the mesenteries and the tentacles, in both the protocnemic and metacnemic stages, are the same in both groups. In the absence of siphonoglyphs from the stomodæum, and of lateral ciliated bands from the mesenterial filaments, coral polyps differ from the great majority of anemones, but some of the lower actinians are without siphonoglyphs and have but simple filaments. Modern Actiniaria (excluding the Ceriantheæ and Zoantheæ) and Madreporaria constitute a single group, one section of which forms a skeleton while this is absent in the other. On the other hand the Paleozoic rugose corals diverge from modern corals after the formation of the six primary septa, their septa are then added in the same sequence as are the mesenteries in the Zoantheæ; further, the single ventral siphonoglyph of the zoanthids was probably present in the rugose polyp, being now represented in the skeleton by the fossula. The Rugosa and Zoantheæ undoubtedly constitute a common group of skeleton-forming and skeletonless polyps, just as do the modern Madreporaria and ordinary hexamerous Actiniaria.

Modern Madreporaria may be defined as follows :

Madreporaria

Anthozoa of which the polyps are either simple or colonial. The basal ectoderm gives rise to a continuous external calcareous skeleton, usually consisting of basal, peripheral, and radial elements. Colonial polyps are in communication at the proximal termination of the column, and sometimes by basal canals ramifying through the skeleton. Tentacles in alternating cycles, often with a knobbed or swollen apex. Stomodæum smooth or ridged, without gonidial grooves or siphonoglyphs. The mesenteries include a primary cycle of six pairs, appearing successively in bilateral pairs, two pairs of which are directives, and usually a second series which arise antero-posteriorly as isocnemic exocelic pairs all round, becoming arranged in cycles. Mesenterial filaments simple, without lateral ciliated bands. Lower region of gastro-cœlomic cavity subdivided by septal invaginations, alternating with the mesenteries, sometimes perforated by skeletal growths. Reproduction sexual and asexual; asexual reproduction frequent, by gemmation and fissiparity.