VIII. *Colony-Formation in Astrœid Corals.*

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[PLATES 24–28.]

PREFACE.

Colony-formation in the Madreporaria was generally described as taking place by two principal methods, viz., budding and fission. This statement was based on the study of the hard parts, which were examined without reference to the polyps that formed them. Classification largely followed the supposed lines of colony-formation. Fission of a corallite was said to involve the longitudinal division of the stomodæum of the polyp it enclosed, and might be equal or unequal. Budding could form colonies in almost every conceivable way, bud-corallites arising from almost every part of the older corallites and from the intervening peritheca. DANA, MILNE EDWARDS and HAIME, DUNCAN, VON KOCH, ORTMANN and others evolved a complicated terminology, but all modes of budding might be summed up under two heads—(1) intra-calicinal budding, *i.e.*, budding within the calyx (this will include the supposed fission of corallites), (2) extra-calicinal budding, *i.e.*, budding outside the calyx.

The object of this paper is to show how colonies arise by asexual methods. It is based on the study of the polyps, increase of which must precede any increase of corallites in the skeleton. Indeed, it is now clear that no reliable data on colony-formation can be obtained from a study of coralla only, since (1) the limits of polyps do not necessarily coincide with corallite boundaries, (2) the earlier stages in polyp-formation are not adequately reproduced in the skeleton, (3) the septal arrangement is not a sure guide to the antecedent changes in the disposition and relationships of mesenteries, and (4) in the hard parts, new corallites, of which the polyps arose outside the tentacular rings of older polyps, may simulate intra-calicinal formations, whilst those, of which the new polyps were formed within the tentacular boundaries, may appear to be extra-calicinal. Stages in the budding of the polyps of Astræid colonies are herein described for the first time.

DUERDEN (9) studied polyp morphology in West Indian corals and drew a sharp morphological distinction between the various modes of budding and fission. His

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view was that polyps formed by budding were new individuals which passed through all the stages of those developed directly from the egg and finally possessed bilateral and hexameral symmetries.* In fission, the stomodæum of a polyp was supposed to be divided along its entire length into two stomodæa. By the division of the column-wall between the two stomodæa and by the completion of a tentacular ring around each mouth-opening, two distinct " unioral " polyps would be formed; by continued fission of the stomodæa, without corresponding division of the column-wall, a " multioral " meandering polyp, surrounded by a tentacular fringe, would result. It was maintained that fission invariably deprived the polyps of directive couples and hexameral symmetry.†

Later, DUERDEN (12) introduced a third process intermediate between budding and fission, which he termed " fissiparous gemmation," to explain the occasional presence of " bioral " (or distomodæal) polyps in certain gemmiferous species, viz., *Acropora (Madrepora) muricata* (LINN.), *Cladocora arbuscula* (LES.), and *Oculina diffusa* LAM. In each such polyp there were typically up to twenty-four mesenteries arranged in such a manner that, on separation, each half of the polyp would have two directive couples and hexameral symmetry. A prior stage was said to be represented in the enlarged " unioral " (or monostomodæal) polyps of *Porites astræoides* LAM., *Stephanocœnia intersepta* (ESP.), and *Solenastrea hyades* (DANA), in which the single stomodæum of each polyp was supposed to divide when twenty-four mesenteries were formed.

DUERDEN interpreted " fissiparous gemmation " as " the components of the bud-polyp separating from the parent body "; " the division of the stomodæum had not the same significance as in true fissiparity," but was " rather a separation of two distinct stomodæa, one belonging to the parent and one to the bud " (p. 153); and added further that the phenomenon might be regarded as " stomodæal budding " (9, p. 497). No stages in the actual division of stomodæa in the Madreporaria were described by DUERDEN or by any other worker.

In the allied group of Actinians, bioral polyps had been observed by JOHNSTON, THORELL, GOSSE, FOOT, G. Y. and A. F. DIXON, who regarded them as monstrosities or as the result of coalescence of individuals. TORREY (30) described such examples of *Metridium fimbriatum*, but did not find a single instance of full severance of the " dividing polyps," though he had kept a number of them under observation for nine months (p. 351). PARKER (28), who studied similar specimens of *Metridium marginatum*, concluded that " direct evidence of actual fission is wanting " (p. 48), but suggested that longitudinal fission was the asexual method of reproduction in that species;

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* Actual observation on the sequence of primary mesenteries in buds is still wanting.

† DUERDEN described " budding " in *Madrepora muricata* LINN., *Porites astræoides* LAM., *Astrangia solitaria* LES., *Phyllangia americana* ED. and H., *Cladocora arbuscula* (LES.), *Orbicella annularis* (ELL. and SOL.), *Solenastrea hyades* (DANA), *Oculina diffusa* LAM., *Siderastrea siderea* (ELL. and SOL.), and " fission " in *Favia fragum* (ESP.), *Dichocœnia stokesi* ED. and H., *Isophyllia dipsacea* DANA, *Manicina areolata* (LINN.), *Colpophyllia gyrosa* (ELL. and SOL.), and *Mœandrina labyrinthica* (ELL. and SOL.).

he did not, however, exclude the possibility of his "natural pairs"—which he regarded as the final products of fission—having been formed by the settling near each other of larvæ, nor of his "monoglyphic" forms having changed to the "diglyphic" bilateral condition by subsequent development of a second directive couple.

In a former paper (22, p. 34), I had tentatively employed the term "gemmation" to denote extra-tentacular budding or the development of fresh polyps from the edge-zone and cœnosarc, and "fissiparity" to signify the formation of new polyps in the oral-disc areas of older ones, *i.e.*, as synonymous with intra-tentacular budding. Since there is no evidence of stomodæal fission in the Madreporaria, and since, so far as can be seen from a study of the Astræidæ, such a process does not exist, the term bud is here used for new polyps, whether formed outside or inside the tentacular rings of older ones.

The descriptions in the text have been reduced as much as possible, the text-figures and plates being essentially portions of the text. A correct idea of the internal anatomy of polyps and of the mesenterial relationships of adjacent polyps can be gained only by studying entire series of sections. The text-figures have been constructed from camera lucida tracings of transverse sections of polyps and buds. These may have been drawn at different levels, but each figure belongs to a single series of sections.

In 1915, I spent six months in America in examining coral collections and types in the United States National Museum, Washington, Museum of Comparative Zoology of Harvard University, Peabody Museum of Yale University, the American Museum of Natural History, New York, and in studying living corals at the Carnegie Biological Station, Tortugas, and at the Bermuda Biological Station. Dr. T. WAYLAND VAUGHAN kindly invited me to a cruise on the yacht "Anton Dohrn" along the Florida reef coast from Key West to Miami, but owing to adverse weather conditions we could not proceed beyond Key Vaca. I had the pleasure of discussing, with him and with Prof. A. E. VERRILL, problems relating to the Madreporaria, and with Prof. G. H. PARKER his work on Actinians. For help received in various ways, during my stay in America, my thanks are due to the following gentlemen:—Dr. T. WAYLAND VAUGHAN, Dr. PAUL BARTSCH, Profs. A. E. VERRILL, CHARLES SCHUCHERT and W. R. COE, Profs. E. L. MARK and G. H. PARKER, Dr. SAMUEL HENSHAW, Dr. THOMAS BARBOUR and Dr. H. B. BIGELOW, Mr. CH. W. JOHNSON, Dr. A. G. MAYOR, Dr. W. J. CROZIER, Dr. F. A. LUCAS and Dr. R. W. MINER.

I am indebted to the Royal Society, the Managers of the Francis Maitland Balfour Fund and to the Governing Body of Emmanuel College for grants in aid of the above visits, and of my subsequent research at Cambridge. I have also to thank Mr. W. BROCKETT, of the Cambridge Zoological Laboratory, for assistance in making sections of polyps.

INTRODUCTION.

The paper is based primarily on many series of sections of well-preserved polyps of eleven species, from the following sources:—*Favia hululensis* GARD., *Favia abdita*

(ELL. and SOL.), *Goniastrea retiformis* (LAM.), *Cœloria dædalea* (ELL. and SOL.), *Leptoria gracilis* DANA, and *Echinopora lamellosa* ESP., from Prof. STANLEY GARDINER'S Maldivian Collection; *Hydnophora microcona* (LAM.), collected by him from Wakaya, Fiji; *Favia favus* (FORSK.), from the Red Sea, sent by Mr. CYRIL CROSSLAND; *Favia fragum* (ESP.), *Colpophyllia gyrosa* (ELL. and SOL.) and *Orbicella annularis* (ELL. and SOL.) from the West Indian region, received by Prof. GARDINER from Dr. WAYLAND VAUGHAN; lastly, a distomodæal polyp of *Goniastrea retiformis* was from a colony, from Ceylon, sent by Dr. JOSEPH PEARSON.

New corallites were described as arising by the fission of existing corallites in *Favia favus*, *Favia hululensis*, *Favia abdita*, *Favia fragum*, *Goniastrea retiformis*, *Cœloria dædalea*, *Leptoria gracilis*, *Colpophyllia gyrosa* and *Hydnophora microcona*; less frequently by budding within older corallites (viz., by intra-tentacular budding) in the species of *Favia*; and by budding outside older corallites (viz., by extra-tentacular budding) in *Orbicella annularis* and *Echinopora lamellosa*. There is, however, no such phenomenon as the formation of fresh stomodæa by fission, and consequently the above species of *Favia*, *Goniastrea*, *Cœloria*, *Leptoria*, *Colpophyllia* and *Hydnophora* are further examples of intra-tentacular budding.

Cœloria dædalea, *Leptoria gracilis*, *Colpophyllia gyrosa* and *Hydnophora microcona* are examples of colonies, the polyps of which rest on valleys in the corallum and possess more than two stomodæa. *Orbicella annularis* and *Echinopora lamellosa* have their soft parts made up of distinct polyps, each polyp having but a single stomodæum. *Favia* and *Goniastrea* have not more than two or three stomodæa within the same oral-disc, and hence, in this respect, occupy an intermediate position between the above two groups. They give the clue to the mode of formation of new intra-tentacular stomodæa and to the peculiar disposition of mesenteries associated with two or more stomodæa within a circle of tentacles, the further developments of which result in meandering and frequently branching polyps, often of great size.

Of the exact mode of formation of the new stomodæa nothing was known, nor has the formation of the stomodæum been described in larval polyps of the Madreporaria except in *Flabellum rubrum* ED. and H. Here, GARDINER described an attached post-larval stage widely open at its free end, without tentacles and stomodæum, and suggested that "the only logical method of conceiving the formation of the stomodæum of the adult to take place is to suppose that the external body-wall grows inwards, catching up the edges of the mesenteries in its progress. It finally reaches the mesenterial filaments, which, by fusion together, assisted by the downgrowth of the body-wall, form the stomodæum" (17, p. 151).

In the Astræid colonies I have studied, new stomodæa appear to be formed in two ways, viz., (1) by invagination of the oral-disc (intra-tentacular budding), and of the edge-zone or cœnosarc (extra-tentacular budding) into the cœlenteric cavity, subsidiary mesenteries meeting the new stomodæa as they are invaginated; the enterostomes are formed by rupture of the lower ends of the stomodæa; (2) by union of the marginal filaments of the broader subsidiary mesenteries, the mouth-openings of the new stomodæa appearing subsequently as small splits in the oral-disc, edge-zone or cœnosarc.*

I. INTRA-TENTACULAR BUDDING.

This type is characteristic of *Favia*, *Goniastrea* and the meandroid genera. Its principal features are (1) the presence of two, or more than two, stomodæa within the same tentacular ring, (2) the presence of one or two couples of mesenteries between every two neighbouring stomodæa. One of the mesenteries of each couple is either attached, or directed, to the original stomodæum of the polyp, whilst the other becomes related to the second or new stomodæum. Such couples are termed *interstomodæal* couples. Such a couple is *completely principal* when the two mesenteries are attached to their respective stomodæa, *incompletely principal* when only one of the mesenteries is attached to a stomodæum, or *subsidiary* when neither is attached, the inner margin of each mesentery being free and usually bearing a filament.

Intra-tentacular budding is of five kinds :—

(1) Two or three stomodæa within a common tentacular ring.
  (*a*) Two inter-stomodæal couples of mesenteries between every two neighbouring stomodæa.
    (i) *Distomodæal condition*, in which two stomodæa are present, *e.g.*, *Favia favus*, *F. hululensis*, *F. fragum*, *Goniastrea retiformis*.
    (ii) *Tristomodæal condition*, in which three stomodæa are present, in a single row or at the angles of an imaginary triangle, *e.g.*, *Favia fragum*.
  (*b*) One inter-stomodæal couple of mesenteries between every two neighbouring stomodæa.
    (iii) *Triple stomodæal condition*, in which three stomodæa are disposed at the angles of an imaginary triangle, *e.g.*, *Goniastrea retiformis*.
(2) More than three stomodæa within a common tentacular boundary, *i.e.*, polystomodæal condition.
    (iv) *Intra-mural* (*Linear*) *polystomodæal condition*, in which stomodæa are arranged in a single linear row along the middle of each polyp. The polystomodæal polyps often branch, are discontinuous or continuous throughout the colony, *e.g.*, *Cœloria dædalea* (discontinuous polystomodæal polyps), *Leptoria gracilis*, *Colpophyllia gyrosa* (continuous polystomodæal polyps).
    (v) *Circum-mural polystomodæal condition*, in which stomodæa are arranged around discontinuous collines or monticules. The monticular rings of a colony are usually connected with one another and constitute a single polystomodæal polyp continuous throughout the colony, *e.g.*, *Hydnophora microcona*.

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* This method would account for the presence of more stomodæa, in transverse sections of some polystomodæal polyps, than mouth-openings in the oral-disc.

Intra-tentacular budding takes place in polyps of *Favia* and *Goniastrea*, which may have been formed at first by extra-tentacular budding, resulting in distomodæal, tristomodæal, and triple stomodæal conditions. These, however, are temporary conditions leading to the monostomodæal condition by the formation of distinct tentacular rings around the mouth-openings and by the division of the column-walls of the polyps—in the skeleton, calcareous partitions are formed across the corallites. The polystomodæal condition is permanent in the meandroid genera, and is due to a continuation of intra-tentacular budding without subsequent separation of the daughter polyps.

(i) *Distomodæal Condition.*

(Figs. 1 A–C, 2–8 A–C ; Plate 24, figs. 1 *a* and *b*–5 *a* and *b* ; Plate 25, figs. 11 *a* and *b* ; Plate 26, fig. 3.)

(1) *Formation.*—Part of a monostomodæal polyp grows in the form of a diverticulum. The oral-disc, with the surrounding tentacular ring, is elongated in the direction of the diverticulum. As the outgrowth increases in size, additional subsidiary couples of mesenteries arise in it, tentacles appear over the new inter-mesenteric chambers, and the tentacular ring becomes greatly elongated. Sooner or later a new stomodæum is formed in the diverticulum, which thus becomes an intra-tentacular bud. If any principal mesenteries of the mother-polyp are included in the diverticulum, they are vertically broken before the new stomodæum is formed, their free margins secondarily developing filaments.

The two couples of mesenteries between the two stomodæa become the interstomodæal couples, which may grow into completely principal or incompletely principal couples, or

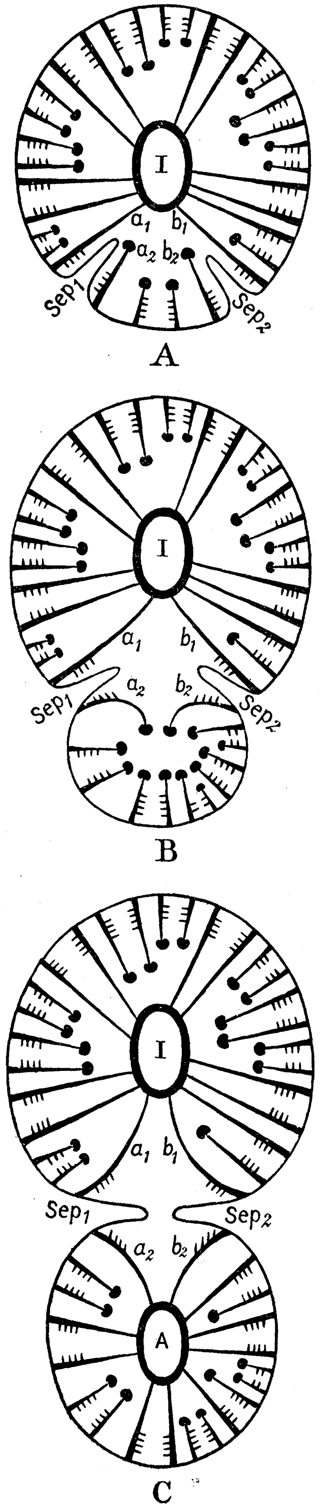

FIG. 1, A–C.—*Formation of distomodæal condition.*—a_1 a_2, b_1 b_2, two interstomodæal couples of mesenteries between mother-polyp and intra-tentacular bud. *Sep*$_1$, *Sep*$_2$, two interstomodæal septa ; other septa not shown. I, A, stomodæa of mother-polyp and bud. fig. A. Monostomodæal condition ; mother-polyp. fig. B. Later stage. Mother-polyp showing an intra-tentacular diverticulum (the commencement of a bud). fig. C. Distomodæal condition, a_2 and b_2 meeting stomodæum A. By the growth of the bud and by the consequent alteration in position of the interstomodæal couples *Sep*$_1$ and *Sep*$_2$ have become opposed to each other.

remain subsidiary. Both mother-polyp and bud have, at this stage, a common tentacular ring, oral-disc, column-wall and cœlenteric cavity, *i.e.*, the original mono-

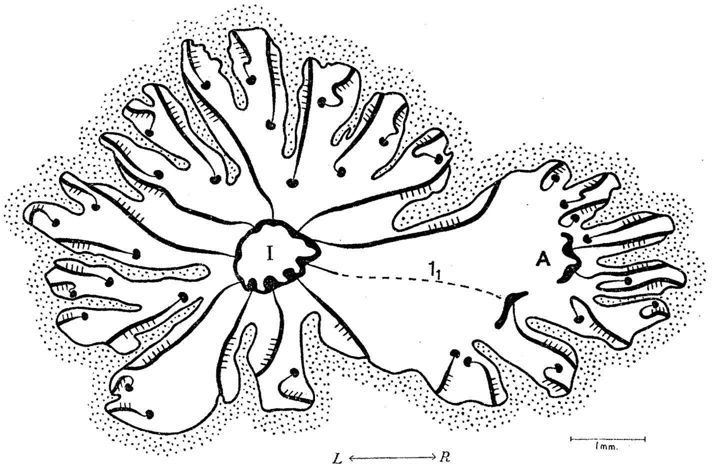

FIG. 2.—*Favia favus* (FORSK.).—Transverse section through stomodæal region of a monostomodæal polyp from a colony. I, stomodæum of polyp. On one side of stomodæum I, a new stomodæum (A), has commenced to be formed. Principal mesentery 1_1 has been vertically split to take part in the formation of the bud (the dotted line shows its original connection with stomodæum I). Interstomodæal couples of mesenteries cannot be determined, since such possible couples between stomodæa I and A are subsidiary, and their component mesenteries have not been directed towards the stomodæa. Oral and basal views of same are shown in Plate 24, figs. 2 *a* and *b*. (220 *b* IV.)

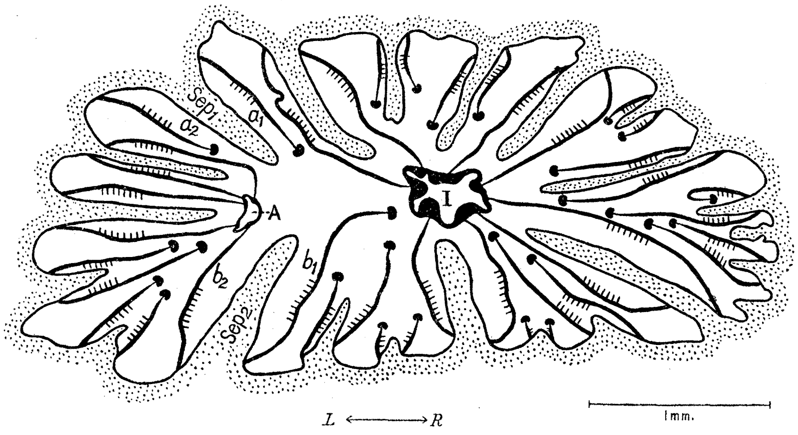

FIG. 3.—*Goniastrea retiformis* (LAM.).—Transverse section through stomodæal region of a distomodæal polyp, from a colony. I and A, stomodæa of mother-polyp and bud. a_1 a_2, b_1 b_2, interstomodæal couples of mesenteries. Sep_1, Sep_2, interstomodæal septa. Stomodæum A, which has just been formed, is short, narrow and very slightly thickened at attachments of mesenteries. (105 *b* IV.)

stomodæal polyp has assumed the distomodæal condition. The two interstomodæal septa, *i.e.*, those under the entocœles of the inter-mesenteric couples, have become broader than all other septa.

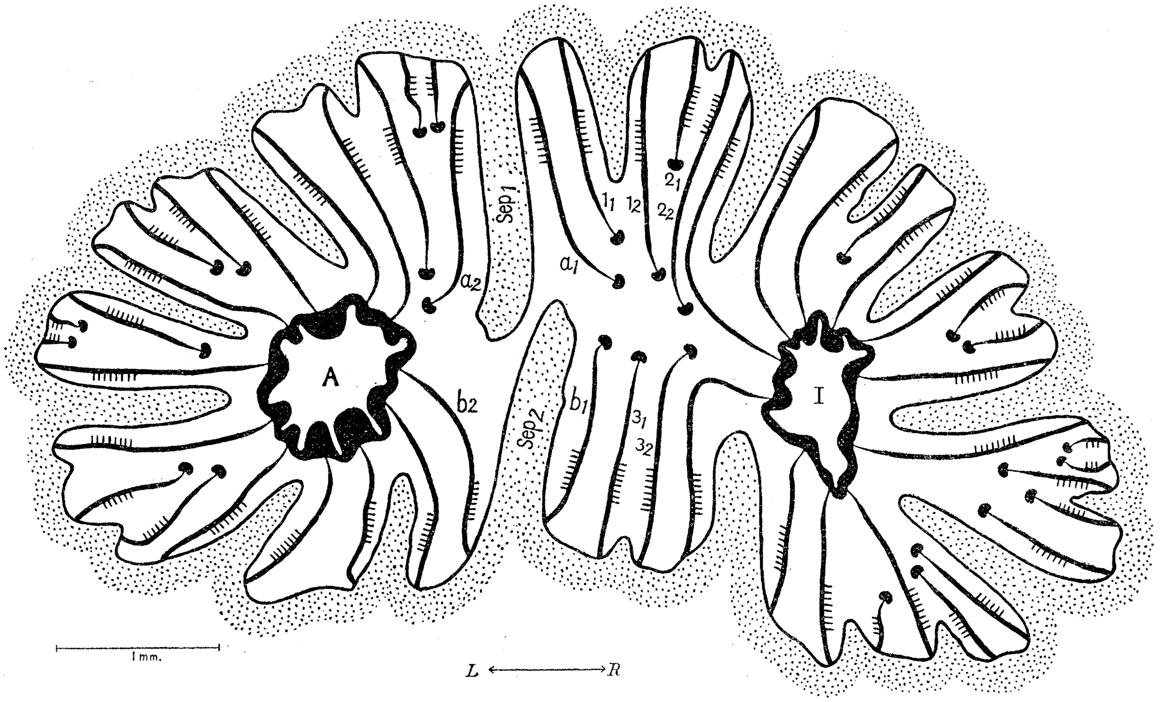

Fig. 4.—*Favia hululensis*, Gard.—Transverse section through stomodæal region of a distomodæal polyp, from a colony. I and A, stomodæa of mother-polyp and intra-tentacular bud. a_1 a_2, b_1 b_2 will probably become the interstomodæal couples of mesenteries between stomodæa I and A. *Sep*$_1$, *Sep*$_2$, interstomodæal septa. (106 *a* V.)

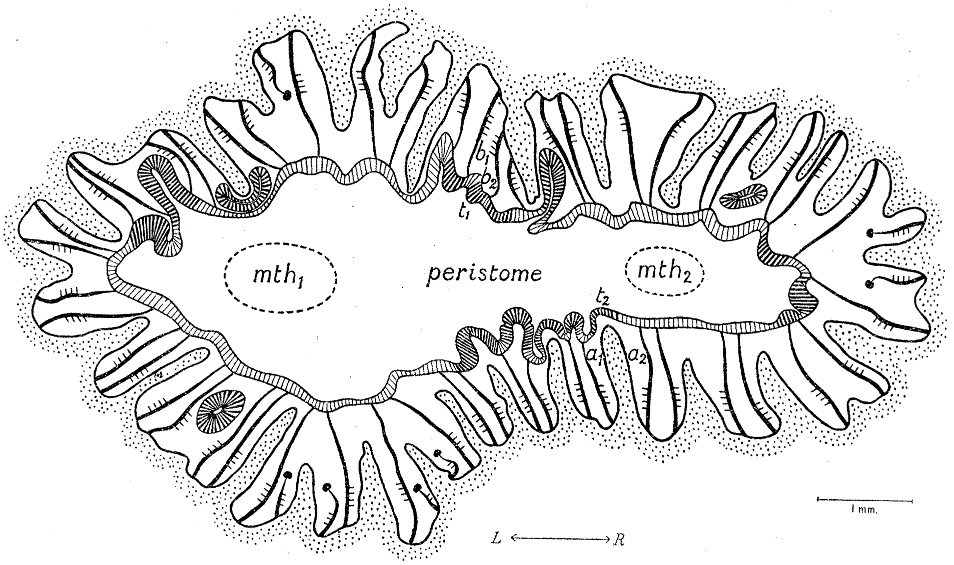

Fig. 5.—*Favia favus* (Forsk.).—Transverse section through tentacular region of a distomodæal polyp, from a colony. The tentacles included in the section are represented by thickly striped regions, the oral-disc by thinly striped regions. The mouth-openings of mother-polyp and bud (*mth*$_1$ and *mth*$_2$) are shown by dotted lines. Interstomodæal couples of mesenteries (a_1 a_2, b_1 b_2) are completely principal. The positions of the interstomodæal tentacles (t_1 and t_2) suggest that, on separation of bud from mother-polyp, t_1 will be placed over the future couple a_1 b_1 of the mother-polyp and t_2 over the couple a_2 b_2 of the bud. (203 *f* I.)

Further growth consists in the formation of additional couples of mesenteries and of tentacles over the new inter-mesenteric chambers, in the increase in size of the new stomodæum and in the attachment of more mesenteries to the stomodæum. The number of principal couples, normal to the monostomodæal condition of a species, is

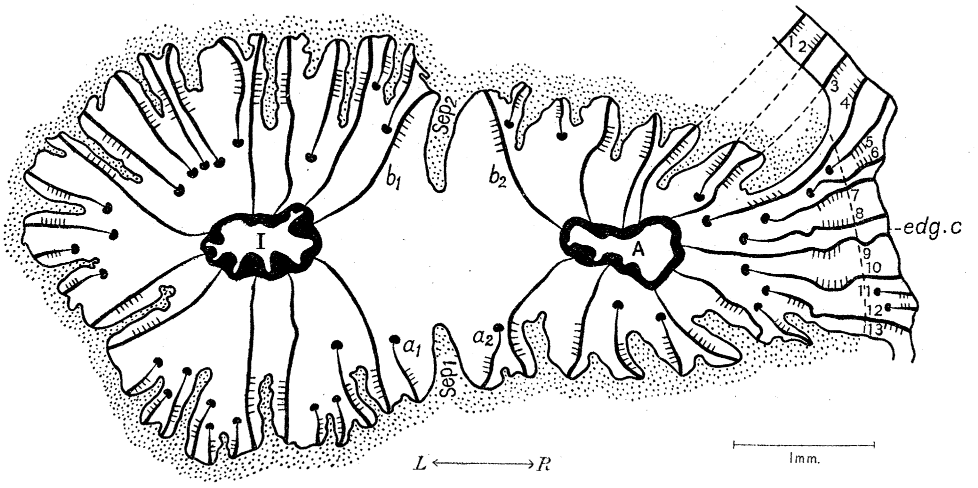

FIG. 6.—*Favia fragum* (ESP.).—Transverse section through stomodæal region of a distomodæal polyp, from the edge of a colony. I and A, stomodæa of mother-polyp and intra-tentacular bud. a_1 a_2 and b_1 b_2, interstomodæal couples of mesenteries. *Sep*$_1$, *Sep*$_2$, interstomodæal septa. Mesenteries 1–10 and 13 are continuous between bud and edge of colony (*edg.c.*); 11 and 12 form the newest couple and are still confined to the edge-zone. Dotted line represents boundary between bud and edge of colony. Oral and basal views of same are shown in Plate 25, figs. 1, *a* and *b*. (500 *f* I.)

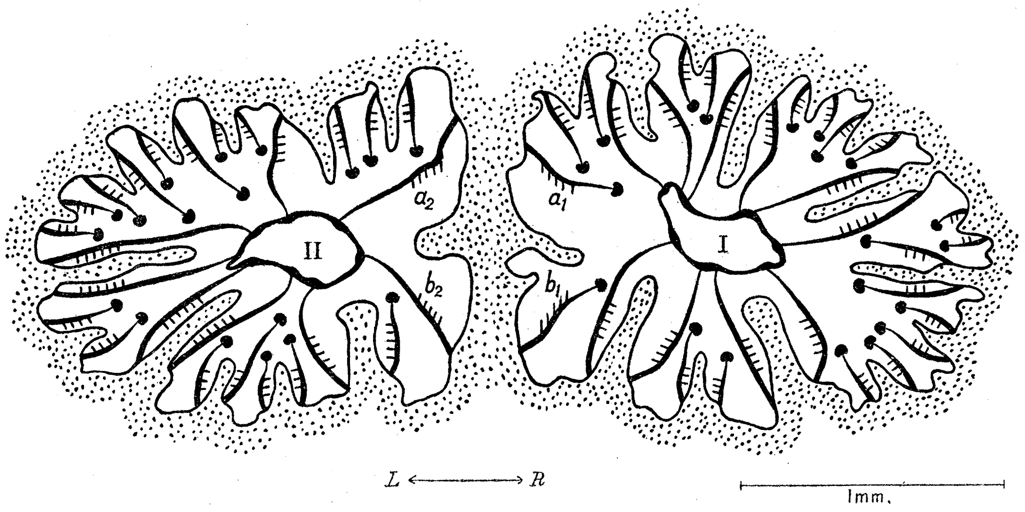

FIG. 7.—*Goniastrea retiformis* (LAM.).—Transverse section through stomodæal region of a distomodæal polyp which has just been separated into two monostomodæal polyps by the division of the column-wall and the formation of two distinct tentacular rings. I and II, stomodæa. The mesenteries of the original interstomodæal couples are being re-grouped to form two ordinary couples, viz., a_1 b_1 and a_2 b_2. Although separation has taken place, a_1 and b_1 are still subsidiary; these may grow and meet stomodæum I or remain permanently subsidiary. From a colony from Ceylon. (305 *k* I.)

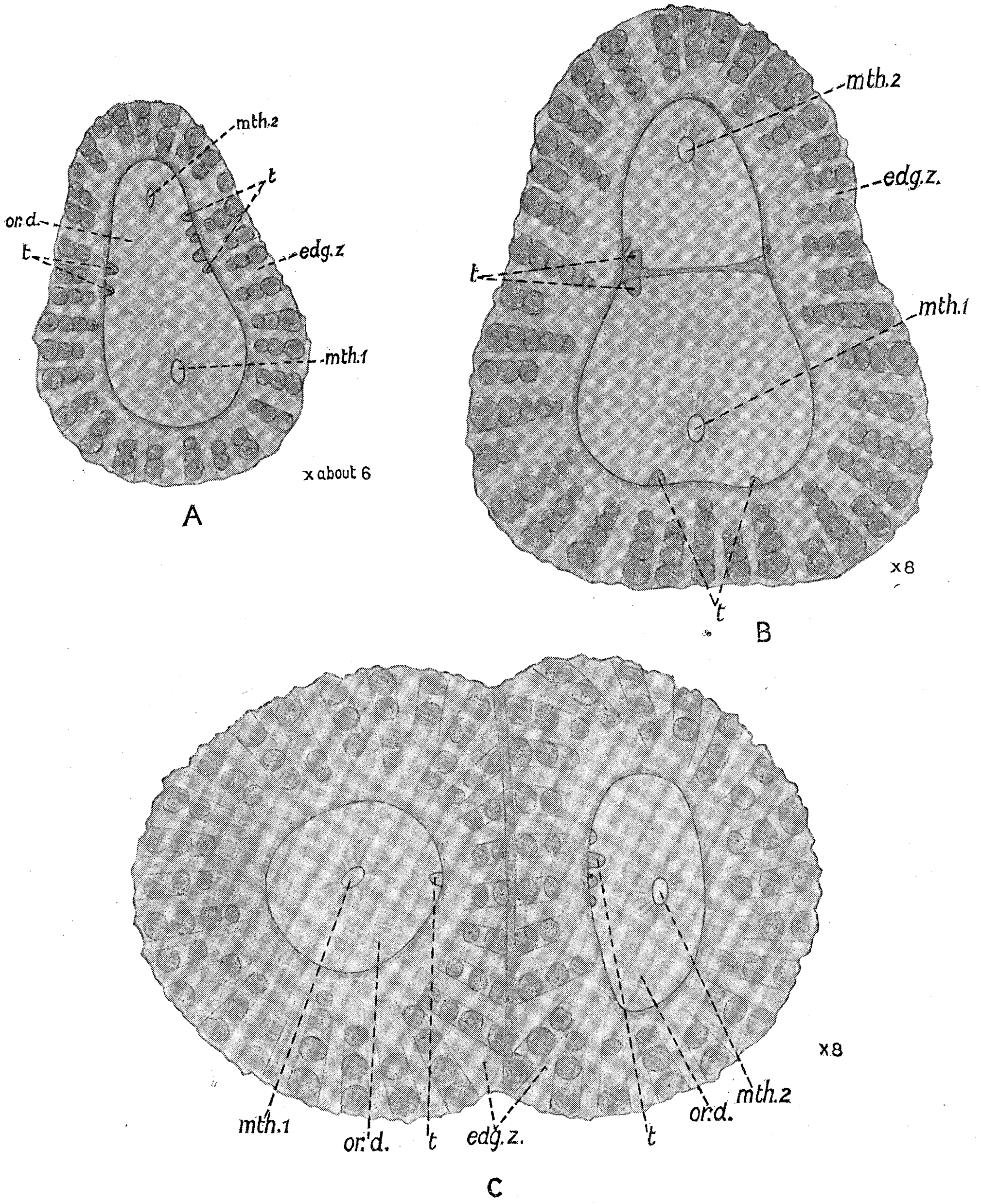

Fig. 8. A–C.—Distomodæal polyps from a colony of *Favia favus* (Forsk.), at different stages of growth. Edge-zone is raised by toothed costæ into radiating ridges with conical projections; mth_1, mth_2, mouth-openings of mother-polyp and bud; *t*, tentacles; *or.d.*, oral-disc; *edg.z.*, edge-zone. A. The mouth-openings are wide apart and surrounded by a common tentacular ring. (Fig. 5 is a transverse section through tentacular region of this polyp.) × 8. B. A thin ridge has appeared across oral-disc. × 10. C. Two oral-discs have been formed, for mother-polyp and bud, by division of the original common oral-disc. The two oral-discs, which are surrounded by distinct tentacular rings, have been elongated along different planes. × 10.

usually reached in the bud while it is small and connected to the mother-polyp, but subsidiary couples are added until its full size is reached. The limits of a bud are fixed when the mesenteries of the two interstomodæal couples have joined their respective stomodæa. The sagittal plane of the bud, *i.e.*, the plane along which it is compressed, may or may not correspond with that of the mother-polyp.

(2) *Separation of Bud.*—The parts of the column-wall over the interstomodæal septa grow inwards and fuse across the distomodæal polyp, thus dividing it into two distinct polyps. This is accompanied by further growth of the interstomodæal septa, which finally fuse to form a dividing wall between the bud and parent corallites. The single tentacular ring is divided into two smaller rings (hence giving rise to separate oral-discs) for the mother-polyp and bud. The bud is now separated from the mother-polyp, except towards the surface, viz., in the edge-zone, where the connection is permanently retained.

The two mesenteries of the interstomodæal couples in the mother-polyp approximate towards each other, with the result that they assume the condition of an ordinary couple. The same recoupling takes place in the bud. Subsequently, septa are formed below the entocœles of the two new couples. Of the two tentacles over the interstomodæal couples, one remains with the mother-polyp and the other goes to the bud.

Distomodæal polyps are formed in colonies of most Astræid species which do not possess bilateral and hexameral symmetries (*i.e.*, have no directive couples), and occasionally in those possessing these symmetries. The polyps become either monostomodæal or polystomodæal and lie on the corallum in separate corallites or in meandering valleys. DUERDEN states that, in symmetrical forms, the bilateral and hexameral symmetries are retained in both parent and bud polyps (12).

(3) *Temporary Forms of the Distomodæal Condition.*—These are of importance as affecting the growth of colonies. Division may take place at any one of the following four stages :—

(I). Unequal distomodæal condition :—

- (*a*) Mother-polyp as large, and with as many couples of mesenteries, as normal monostomodæal polyp ; bud smaller and with fewer couples (fig. 5).
- (*b*) Mother-polyp not so large, and with not so many couples of mesenteries, as normal monostomodæal polyp ; bud smaller and with fewer couples.

(II). Sub-equal or equal distomodæal condition :—

- (*c*) Mother-polyp as large, and with as many couples of mesenteries, as normal monostomodæal polyp ; bud sub-equal or equal to mother-polyp (fig. 6).
- (*d*) Mother-polyp not so large, and with not so many couples of mesenteries, as normal monostomodæal polyp ; bud sub-equal or equal to mother-polyp (figs. 2 and 3).

(*b*) and (*d*) are examples of premature intra-tentacular budding ; in (*c*) and (*d*) the sub-equal or equal distomodæal condition is the result of the growth of a previous unequal condition.

(ii) *Tristomodæal Condition.*

(Figs. 9 A–C, 10 ; Plate 24, figs. 16 *a* and *b*, 17 *a* and *b*.)

The method of formation of the tristomodæal condition is similar to that of the distomodæal condition. Two diverticula, instead of one, grow out from a monostomodæal polyp, in each of which a new stomodæum is formed. Each of the two buds is related to the mother-polyp by two interstomodæal couples, but there are no such couples between the two buds.

When the parts of the column-wall over the two interstomodæal septa between the mother-polyp and one of the buds fuse, the tristomodæal polyp is divided into a distomodæal and a monostomodæal polyp, this being the separated bud. When the soft parts over the four interstomodæal septa fuse in pairs, the tristomodæal polyp is divided into three monostomodæal polyps, these being the original mother-polyp and the two buds.

In both cases the edge-zone connects the products of division.

There are two forms of the tristomodæal condition :—

(*a*) *Linear*, when the two buds are formed at opposite ends, usually in the sagittal plane, of the mother-polyp ; the three stomodæa being arranged in a single row.

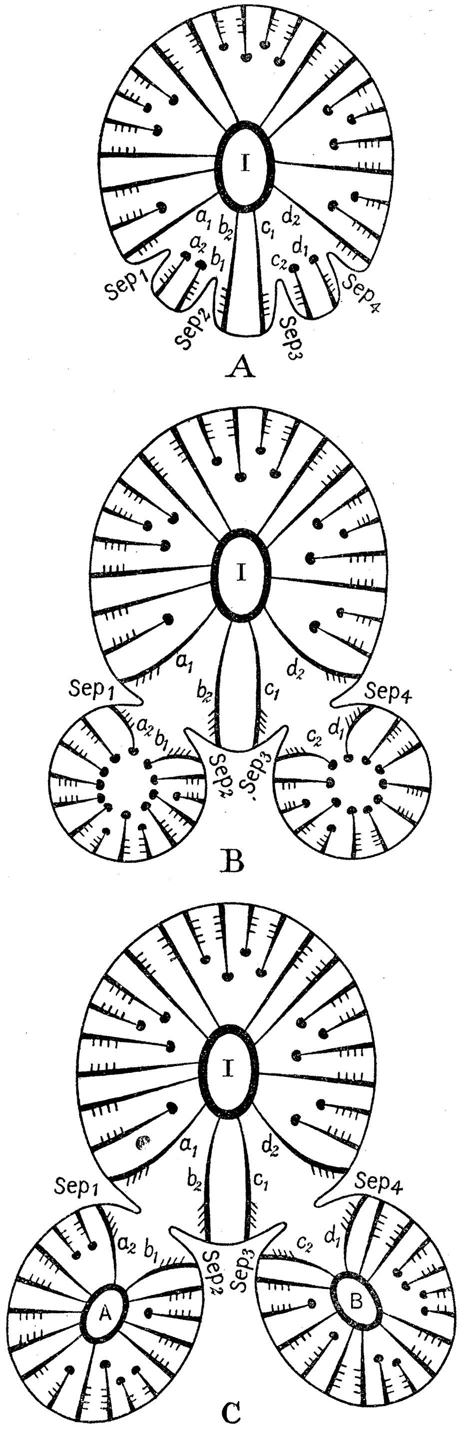

Fig. 9.—*Formation of tristomodæal condition* (triangular variety).—a_1 a_2, b_1 b_2, c_1 c_2, d_1 d_2, four interstomodæal couples of mesenteries between mother-polyp and the pair of intra-tentacular buds. Sep_{1-4}, four interstomodæal septa ; other septa not shown. I, A and B, stomodæa of mother-polyp and buds. fig. A. Mother-polyp. fig. B. Mother-polyp showing a pair of intra-tentacular diverticula (commencing buds) separated from each other by b_2 and c_1. fig. C. Tristomodæal condition. a_2 and b_1 meeting stomodæum A, c_2 and d_1 meeting stomodæum B. Sep_1 and Sep_2, Sep_3 and Sep_4 will join across to form walls of new corallites under buds. On separation of buds, mesenteries of interstomodæal couples will be re-grouped to form four ordinary couples, viz., a_1 b_2, a_2 b_1, c_1 d_2 and c_2 d_1.

(*b*) *Triangular*, when the two buds arise from neighbouring entocœles of the mother-polyp ; the three stomodæa lie at the corners of an imaginary triangle.

The linear tristomodæal condition is present in colonies of *Favia fragum*, *Goniastrea retiformis* and of many meandroid species. I have found the triangular variety only in *Favia fragum*, at the edges of colonies, but, not improbably, it occurs in *Goniastrea retiformis* and in some of the meandroid species.

Temporary Forms of the Tristomodœal Condition.

(I.) Unequal tristomodæal condition :—

1. One part large, two parts equal and small :—
   (*a*) Mother-polyp as large as normal monostomodæal polyp ; buds sub-equal or equal but smaller than mother-polyp.

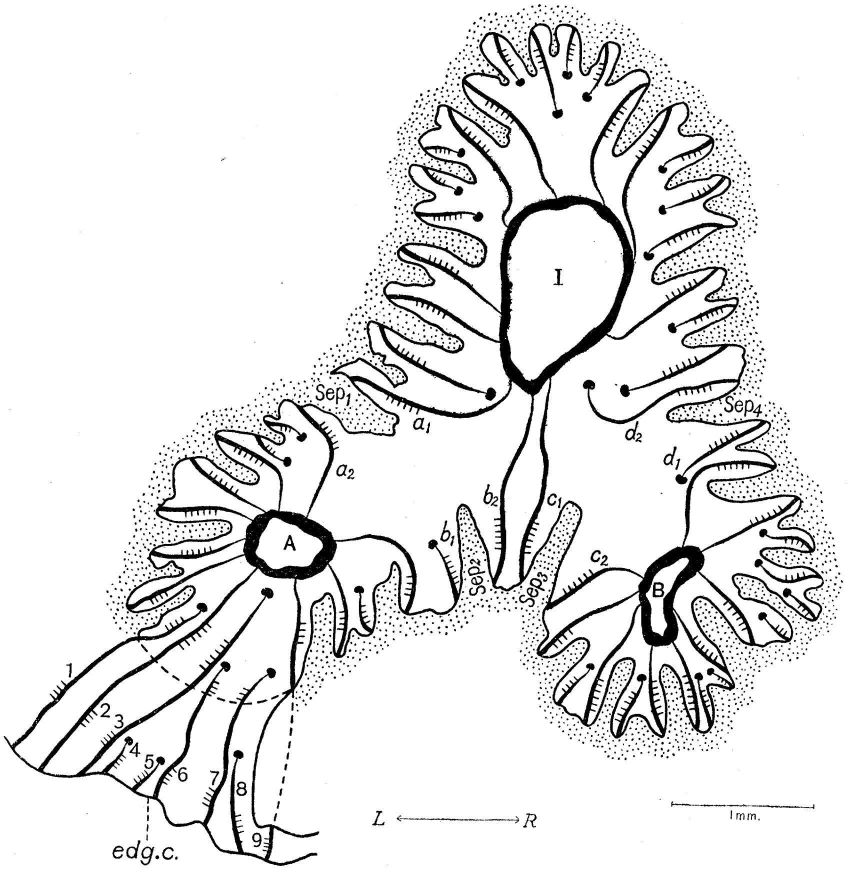

Fig. 10.—*Favia fragum* (Esp.).—Transverse section through stomodæal region of a tristomodæal polyp (triangular variety), from the edge of a colony. I, A and B, stomodæa of mother-polyp and the pair of buds. $a_1 a_2$, $b_1 b_2$, $c_1 c_2$, $d_1 d_2$, interstomodæal couples of mesenteries. *Sep* $_{1-4}$, interstomodæal septa. Mesenteries 1–3, 6, 7 and 9 are continuous between one of the buds and edge of colony (*edg.c.*) ; a similar continuity exists between mesenteries of the other bud and edge of colony, although it is not shown in the figure. Oral and basal views of same are shown in Plate 24, figs. 16 *a* and *b*. (500*f* II.)

(*b*) Mother-polyp not so large as normal monostomodæal polyp ; buds sub-equal or equal but smaller than mother-polyp.

2. Two parts equal and large, one part small :—

(*c*) One bud sub-equal or equal to mother-polyp, both as large as normal monostomodæal polyp ; second bud smaller than the two former.

(*d*) One bud sub-equal or equal to mother-polyp, both not so large as normal monostomodæal polyp ; second bud smaller than the two former.

3. Three parts unequal :—

(*e*) Mother-polyp as large as normal monostomodæal polyp ; buds unequal and smaller than mother-polyp.

(*f*) Mother-polyp not so large as normal monostomodæal polyp ; buds unequal and smaller than mother-polyp.

(II.) Sub-equal or equal tristomodæal condition :—

(*g*) Mother-polyp as large as normal monostomodæal polyp ; buds sub-equal or equal and as large as mother-polyp.

(*h*) Mother-polyp not so large as normal monostomodæal polyp ; buds sub-equal or equal and as large as mother-polyp.

(*b*), (*d*), (*f*), and (*h*) are examples of premature intra-tentacular budding.

(iii) *Triple Stomodæal Condition.*

(Figs. 11 A–C, 12.)

A double-diverticulum grows out from a monostomodæal polyp, the tentacular ring following the direction of growth. Additional subsidiary couples appear in each half of the diverticulum, and tentacles arise over the new inter-mesenteric chambers. Two new stomodæa are formed, either simultaneously or not, in the two halves of the diverticulum ; the latter thus becomes a double-bud. The two couples of mesenteries between the mother-polyp and double-bud and the couple between the two halves of the bud become the three interstomodæal couples, which may be completely or incompletely principal, or remain subsidiary.

The mother-polyp and double-bud have at this stage—this is the triple stomodæal condition—a common tentacular ring, oral-disc, column-wall and cœlenteric cavity, the three mouth-openings lying in the common oral-disc.

The three interstomodæal couples are distinguishable only when the two new stomodæa have been formed and the mesenteries of these couples have joined, or have been directed towards, their respective stomodæa. When the two interstomodæal couples between the first stomodæum and the two new stomodæa have become completely principal, the double-bud is clearly marked out from the mother-polyp ; when the interstomodæal couple between the two new stomodæa has grown to be completely principal, the two halves of the double-bud become distinct.

The triple stomodæal condition is identical with the triangular tristomodæal condition in external appearance. The differences are internal :—In the triple stomodæal condition there is only one interstomodæal couple between every two stomodæa ; in the tristomodæal condition, although an interstomodæal couple is not present between the two new stomodæa, there are two such couples between the first stomodæum and each of the two new stomodæa.

So far I have found the triple stomodæal condition only in *Goniastrea retiformis.** In this species, in which the permanent condition is monostomodæal, the regions of the column-wall over the three interstomodæal septa of the triple stomodæal condition broaden and fuse to give three monostomodæal polyps, the connection between the three products of division being retained in the edge-zone. The common tentacular ring is divided into separate tentacular rings for the three polyps.

In the meanwhile, a re-coupling of the mesenteries of the three interstomodæal couples is effected. Every two such mesenteries in the mother-polyp and in each half of the double-bud are approximated towards each other to form an ordinary couple. Of the three entocœlic tentacles involved, one goes to each polyp.

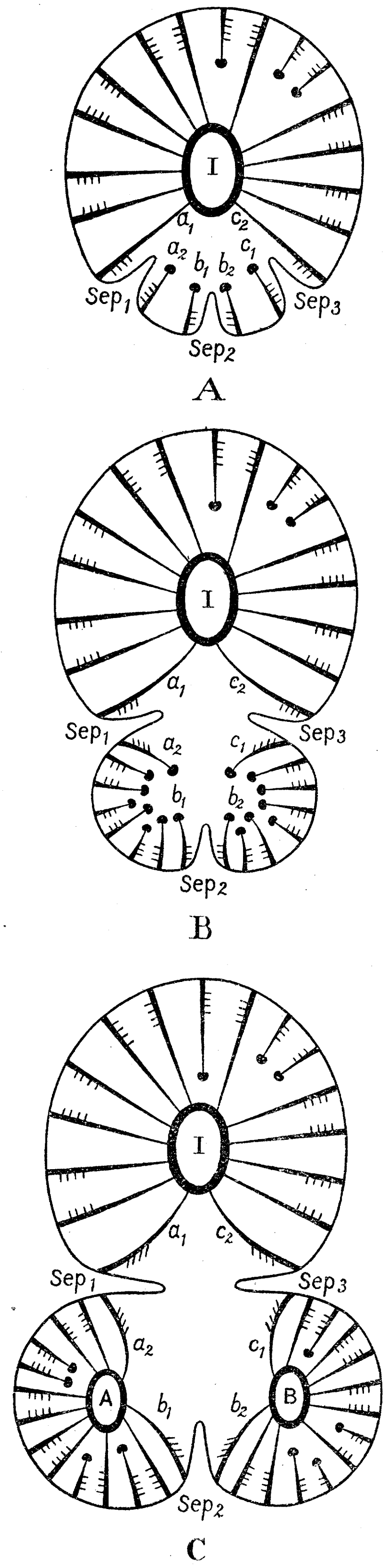

FIG. 11, A–C.—*Formation of triple stomodæal condition.*—a_1 a_2, b_1 b_2, c_1 c_2, three interstomodæal couples of mesenteries between mother-polyp and double-bud. *Sep* $_{1-3}$, three interstomodæal septa ; other septa not shown. I, A and B, stomodæa of mother-polyp and double-bud. fig. A. Mother-polyp. fig. B. Mother-polyp showing double-diverticulum (commencing double-bud). fig. C. Triple stomodæal condition. a_2 and b_1 meeting stomodæum A ; b_2 and c_1 meeting stomodæum B. *Sep* $_{1-3}$ will join across to form walls of new corallites under bud. On separation of the halves of bud from mother-polyp and from each other, mesenteries of the interstomodæal couples will be re-grouped to form three ordinary couples, viz., $a_1\,c_2$, $a_2\,b_1$, $b_2\,c_1$.

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* Polystomodæal conditions of four or more stomodæa, with only one interstomodæal couple between every two neighbouring stomodæa, have not been found in any of the species I have studied.

If the soft parts over only two of the interstomodæal septa meet, the triple stomodæal condition will be divided into a distomodæal and a monostomodæal polyp. In this case, the mesenteries of only two of the interstomodæal couples will be re-grouped, *i.e.*, the two mesenteries in the monostomodæal polyp will form an ordinary couple, whilst those in the distomodæal polyp will be re-arranged into a second interstomodæal couple. Of the two tentacles over the interstomodæal couples, one now belongs to the monostomodæal polyp and the other to the distomodæal polyp.

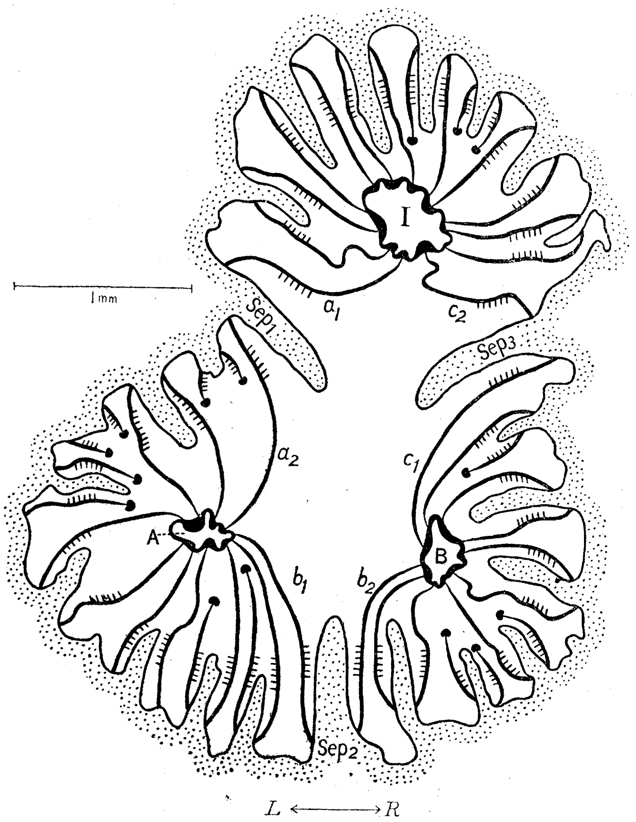

FIG. 12.—*Goniastrea retiformis* (LAM.).—Transverse section through stomodæal region of triple stomodæal polyp, from a colony. I, A and B, stomodæa of mother-polyp and double-bud. $a_1 a_2$, $b_1 b_2$, $c_1 c_2$, interstomodæal couples of mesenteries. *Sep* $_{1-3}$, interstomodæal septa. (105 *b* V.)

The temporary forms of the triple stomodæal condition are as many as, and similar to, those of the triangular tristomodæal condition on p. 325. By the premature or late separation of one-half of the double-bud or of the mother-polyp, the following distomodæal forms will ensue :—

a, *b*, *c*, &c., to the left refer to temporary forms on p. 325, those on the right to forms on p. 323. M = mother-polyp ; P = normal monostomodæal polyp ; $\frac{\text{DB}}{2}$ = one-half of double-bud ; $<$ = smaller than ; — = separate.

Temporary triple stomodæal forms.	Resulting monostomodæal polyps.		Resulting distomodæal forms.
$\{a$ —	$\mathrm{M}\,(=\mathrm{P})\}$	$= \left\{\text{two sub-equal or equal } \frac{\mathrm{DB}}{2}\text{, each} < \mathrm{P}\ (\&\ \mathrm{M})\right\}$	$= d^*$
$\{a$ —	$\frac{\mathrm{DB}}{2}\,(<\mathrm{P})\}$	$= \left\{\mathrm{M}\ (=\mathrm{P}) + \text{remaining } \frac{\mathrm{DB}}{2} < \mathrm{P}\ (\&\ \mathrm{M}\right\}$	$= a$
$\{b$ —	$\mathrm{M}\,(<\mathrm{P})\}$	$= \left\{\text{two sub-equal or equal } \frac{\mathrm{DB}}{2}\text{, each} < \mathrm{P}\ (\&\ \mathrm{M})\right\}$	$= d^*$
$\{b$ —	$\frac{\mathrm{DB}}{2}\,(<\mathrm{P})\}$	$= \left\{\mathrm{M}\ (<\mathrm{P}) + \text{remaining } \frac{\mathrm{DB}}{2} < \mathrm{M}\ (\&\ \mathrm{P})\right\}$	$= b$
$\{c$ —	$\mathrm{M}\,(=\mathrm{P})\}$	$= \left\{\text{one } \frac{\mathrm{DB}}{2}[=\mathrm{P}\ (\&\ \mathrm{M})] + \text{remaining } \frac{\mathrm{DB}}{2} < \mathrm{P}\ (\&\ \mathrm{M})\right\}$	$= a^*$
$\{c$ —	$\text{large } \frac{\mathrm{DB}}{2}\,(=\mathrm{P})\}$	$= \left\{\mathrm{M}\ (=\mathrm{P}) + \text{small } \frac{\mathrm{DB}}{2} < \mathrm{M}\ (\&\ \mathrm{P})\right\}$	$= a$
$\{c$ —	$\text{small } \frac{\mathrm{DB}}{2}\,(<\mathrm{P})\}$	$= \left\{\mathrm{M}\ (=\mathrm{P}) + \text{large } \frac{\mathrm{DB}}{2} = \mathrm{M}\ (\&\ \mathrm{P})\right\}$	$= c$
$\{d$ —	$\mathrm{M}\,(<\mathrm{P})\}$	$= \left\{\text{one } \frac{\mathrm{DB}}{2}[<\mathrm{P}\ (\&\ \mathrm{M})] + \text{remaining } \frac{\mathrm{DB}}{2} < \mathrm{P}\ (\&\ \mathrm{M})\right\}$	$= b^*$
$\{d$ —	$\text{large } \frac{\mathrm{DB}}{2}\,(<\mathrm{P})\}$	$= \left\{\mathrm{M}\ (<\mathrm{P}) + \text{small } \frac{\mathrm{DB}}{2} < \mathrm{M}\ (\&\ \mathrm{P})\right\}$	$= b$
$\{d$ —	$\text{small } \frac{\mathrm{DB}}{2}\,(<\mathrm{P})\}$	$= \left\{\mathrm{M}\ (<\mathrm{P}) + \text{large } \frac{\mathrm{DB}}{2} = \mathrm{M}\ (<\mathrm{P})\right\}$	$= d$
$\{e$ —	$\mathrm{M}\,(=\mathrm{P})\}$	$= \left\{\text{two unequal } \frac{\mathrm{DB}}{2}\text{, each} < \mathrm{M}\ (\&\ \mathrm{P})\right\}$	$= b^*$
$\{e$ —	$\frac{\mathrm{DB}}{2}\,(<\mathrm{P})\}$	$= \left\{\mathrm{M}\ (=\mathrm{P}) + \text{remaining } \frac{\mathrm{DB}}{2} < \mathrm{M}\ (\&\ \mathrm{P})\right\}$	$= a$
$\{f$ —	$\mathrm{M}\,(<\mathrm{P})\}$	$= \left\{\text{two unequal } \frac{\mathrm{DB}}{2}\text{, each} < \mathrm{M}\ (\&\ \mathrm{P})\right\}$	$= b^*$
$\{f$ —	$\frac{\mathrm{DB}}{2}\,(<\mathrm{P})\}$	$= \left\{\mathrm{M} < \mathrm{P}\text{, } + \text{remaining } \frac{\mathrm{DB}}{2} < \mathrm{M}\ (\&\ \mathrm{P})\right\}$	$= b$
$\{g$ —	$\mathrm{M}\,(=\mathrm{P})\}$	$= \left\{\text{two sub-equal or equal } \frac{\mathrm{DB}}{2}\text{, each} = \mathrm{P}\ (\&\ \mathrm{M})\right\}$	$= c^*$
$\{g$ —	$\frac{\mathrm{DB}}{2}\,(=\mathrm{P})\}$	$= \left\{\mathrm{M}\ (=\mathrm{P}) + \text{remaining } \frac{\mathrm{DB}}{2} = \mathrm{M}\ (\&\ \mathrm{P})\right\}$	$= c$
$\{h$ —	$\mathrm{M}\,(<\mathrm{P})\}$	$= \left\{\text{two sub-equal or equal } \frac{\mathrm{DB}}{2} \text{ each} = \mathrm{M}\ (<\mathrm{P})\right\}$	$= d^*$
$\{h$ —	$\frac{\mathrm{DB}}{2}\,(<\mathrm{P})\}$	$= \left\{\mathrm{M}\ (<\mathrm{P}) + \text{remaining } \frac{\mathrm{DB}}{2} = \mathrm{M}\ (<\mathrm{P})\right\}$	$= d$

The two parts of the resulting distomodæal forms marked (*) have had a common origin and therefore bear no relation of mother-polyp and bud, although they simulate such a condition. In colonies of *Goniastrea retiformis* it is impossible to distinguish between these two types of distomodæal conditions.

(iv) *Intra-Mural* (*Linear*) *Polystomodæal Condition.*

(Figs. 13–15 ; Plate 25, figs. 5 *a* and *b*, 10 *a* and *b* ; Plate 26, figs. 1, 2, 4–8.)

The polyps of this condition lie in long or short valleys. Each such polyp has an elongated column-wall, the tentacles standing over the intermesenteric chambers ; its stomodæa are arranged in a linear row, at more or less regular intervals, along the middle of its single long oral-disc.

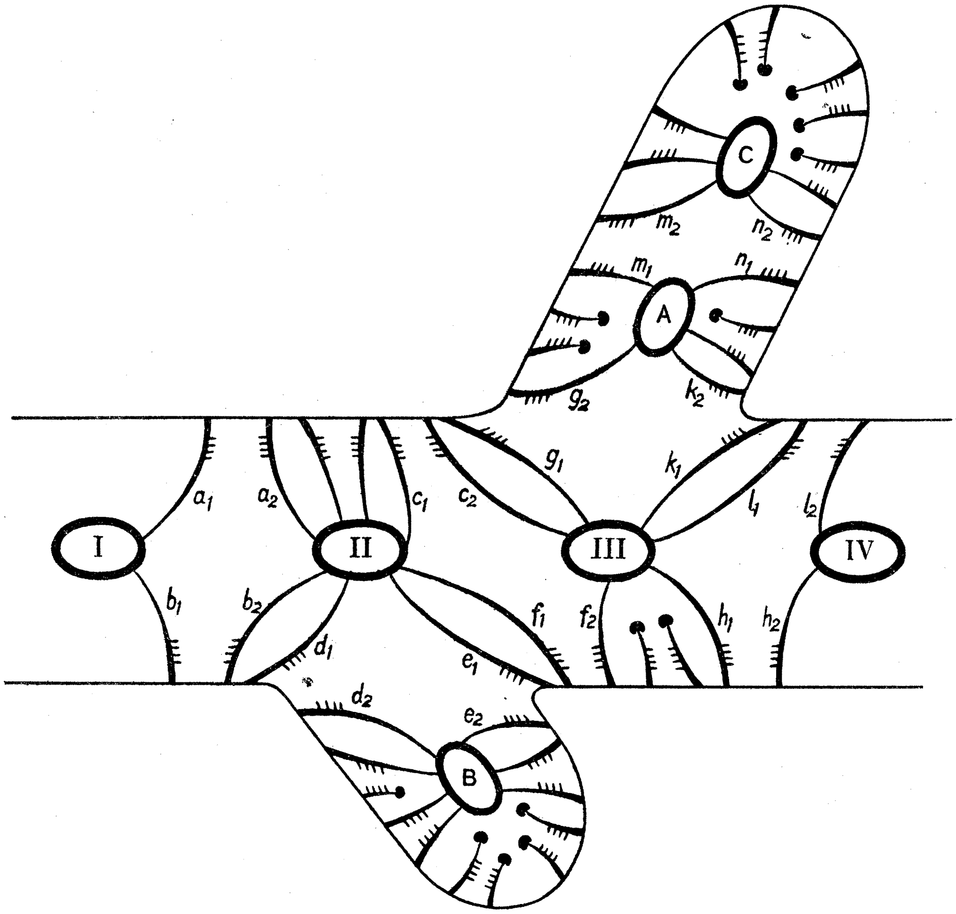

FIG. 13.—*Formation of intra-mural polystomodæal branches.*—Lateral branching on distomodæal mode. I–IV, stomodæa in main region of polyp. A and B, stomodæa in lateral intra-tentacular buds. C, subsequently formed stomodæum in upper branch. $a_1\,a_2$—$n_1\,n_2$, interstomodæal couples of mesenteries. $d_1\,d_2$, $e_1\,e_2$, $g_1\,g_2$, $k_1\,k_2$, interstomodæal couples between main region of polyp and branches. Septa not shown.

Polystomodæai polyps are of two forms :—

(I.) *Discontinuous*, when the stomodæa of a colony are in separate polystomodæal polyps. Such colonies may be grouped under two heads :—

1. Neighbouring polyps connected by edge-zone. The walls of adjacent valleys are

usually fused to form collines, over which the edge-zones are continuous, *e.g.*, *Cœloria dædale* (ELL. and SOL.).

2. Neighbouring polyps tending to lose continuity of edge-zone. This tendency to discontinuity is due to the valleys having free and high walls, *e.g.*, *Mussa*.

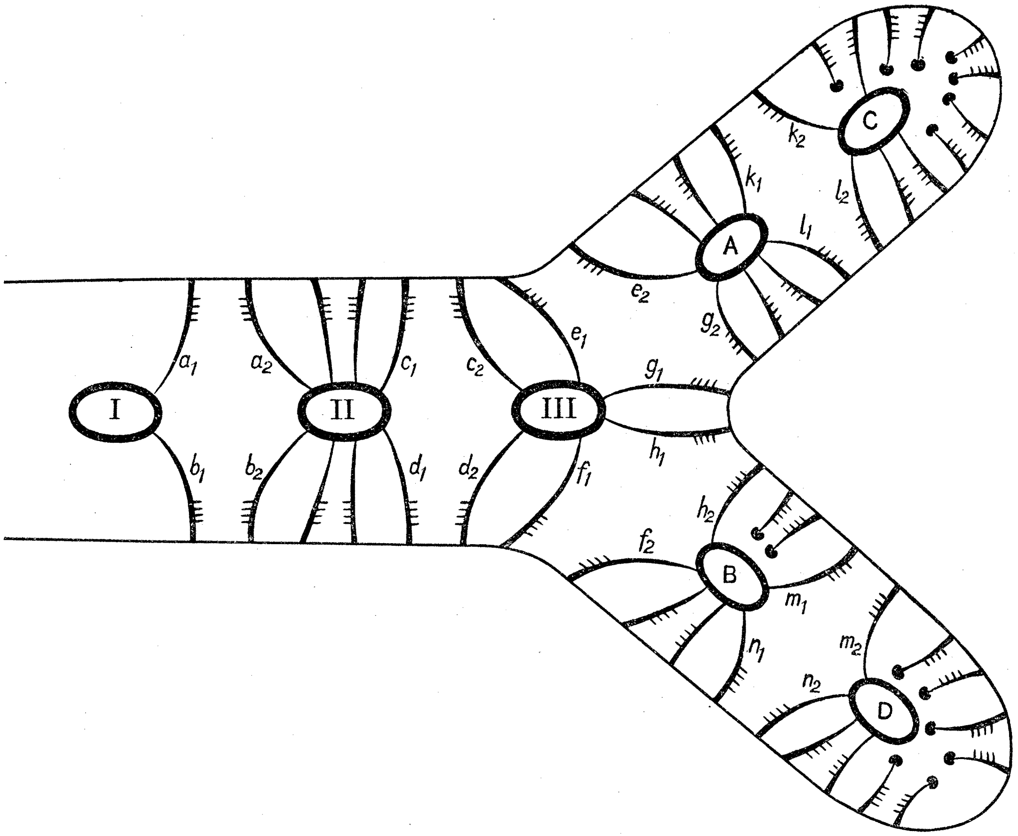

FIG. 14.—*Formation of intra-mural polystomodæal branches.*—Dichotomy on triangular tristomodæal mode. I–III, stomodæa in main region of polyp. A and B, stomodæa in terminal pair of intra-tentacular buds. C and D, subsequently formed stomodæa in branches. a_1 a_2—n_1 n_2, interstomodæal couples of mesenteries. e_1 e_2, f_1 f_2, g_1 g_2, h_1 h_2, interstomodæal couples between main region of polyp and branches. Septa not shown.

(II.) *Continuous*, when the stomodæa are in a single meandering polystomodæal polyp, *i.e.*, when a single polystomodæal polyp constitutes the entire soft parts of a so-called "colony," *e.g.*, *Manicina areolata* (LINN.).

Discontinuous polystomodæal polyps may or may not be branching; continuous polystomodæal polyps form branching systems.*

The stomodæa in unbranching, and those in linear regions of branching, polystomodæal polyps are correlated on the distomodæal plan, *i.e.*, between every two adjacent

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* In a new species of *Flabellum* (*F. multiflore*, GARD.), GARDINER found from one to eight stomodæa arranged in a row along the centre of the oral-disc; no branching had yet taken place (18, p. 953).

stomodæa there are two interstomodæal couples which are usually completely principal, but may less frequently be incompletely principal or subsidiary. Such unbranching polyps or linear parts of branching polyps are the result of repeated intra-tentacular budding on the distomodæal mode. The parts of the column-wall over the two interstomodæal septa, between every two stomodæa, remain separate or fuse incompletely, *i.e.*, for a short distance from the base of the polyp. Interstomodæal septa are usually broader than any other septa. When the soft parts over a pair or more of such septa fuse along the entire height of the column-wall, the polystomodæal polyp becomes divided into two or more shorter polyps. In colonies of meandroid species monostomodæal polyps are occasionally present, formed by the separation of a monostomodæal area from a polystomodæal polyp.

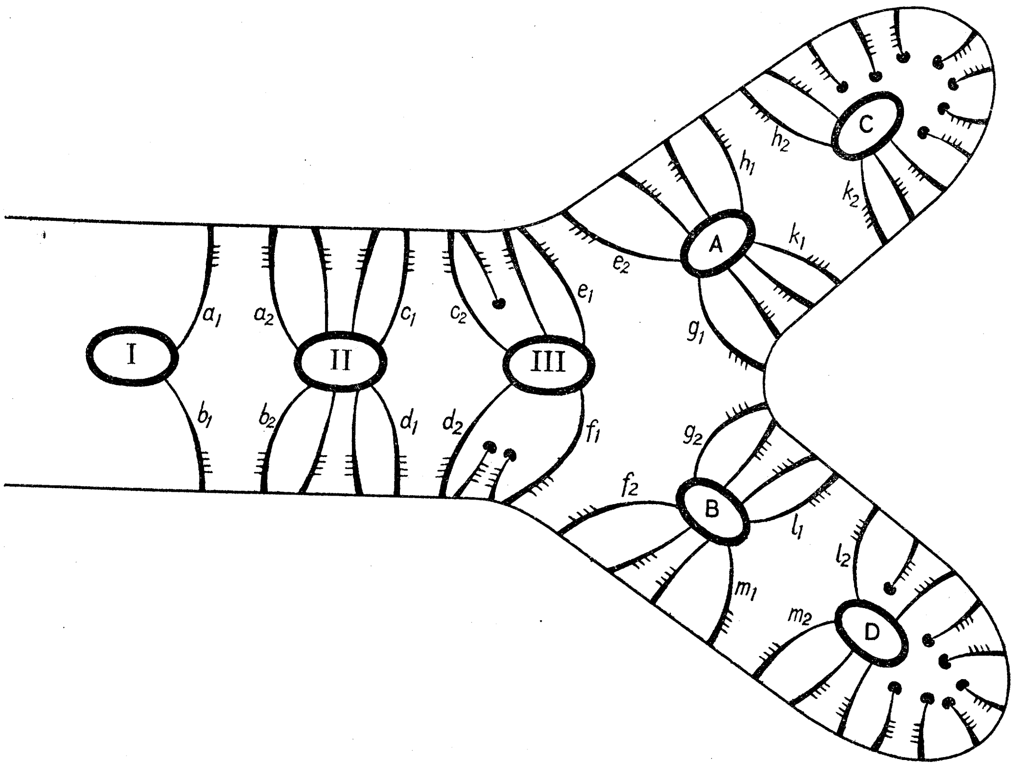

FIG. 15.—*Formation of intra-mural polystomodœal branches.*—Dichotomy on triple stomodæal mode. I–III, stomodæa in main region of polyp. A and B, stomodæa in terminal double-bud. C and D, subsequently formed stomodæa in double-branch. a_1 a_2—m_1 m_2, interstomodæal couples of mesenteries. e_1 e_2, $f_1 f_2$, g_1 g_2, interstomodæal couples between main region of polyp and double-branch. Septa not shown.

Branching of polystomodæal polyps is of three modes :—

(I.) *Lateral Branching.*

1. *Distomodœal mode,* when budding takes place on one or both sides of a polystomodæal polyp, the bud or buds arising on the distomodæal plan, *i.e.*, the stomodæum

of every lateral bud is joined to the adjacent stomodæum of the linear region of the polyp by two interstomodæal couples of mesenteries.

(II.) *Dichotomous Branching or Terminal Forking.*

2. *Triangular tristomodæal mode,* when a pair of intra-tentacular buds are formed at one of the ends of a polystomodæal polyp. The stomodæum of each bud becomes related independently with the terminal stomodæum of the linear region of the polyp by two interstomodæal couples, but the two stomodæa of the buds are not similarly connected. When the arms have grown to unequal lengths, such a forked polyp may simulate the condition of a polystomodæal polyp with a lateral branch.

3. *Triple stomodæal mode,* when a double-bud is formed at one of the ends of a polystomodæal polyp. The stomodæum of each half of the double-bud is joined to the terminal stomodæum of the linear region of the polyp by a single interstomodæal couple; the two stomodæa of the double-bud are also connected by an interstomodæal couple.

Meandering polyps may be formed by repetition of one of these modes of branching, or by combination of two or all the three modes. The invariable presence of two or more subsidiary couples at the ends of the polyps (contrasted with their general absence at the sides) in *Cœloria dædalea, Leptoria gracilis* and *Colpophyllia gyrosa* suggest that the longitudinal growth of such polyps is mainly confined to their extremities.

(v) *Circum-Mural Polystomodæal Condition.*

(Figs. 16–18.)

This condition may be derived from intra-mural polystomodæal condition when the column-walls, and consequently the collines, are not developed at intervals; such discontinuity is occasionally present in colonies characterised by the intra-mural polystomodæal condition, *e.g., Leptoria gracilis.*

In *Hydnophora microcona* the discontinuous column-walls are very short, the skeletal collines below them being usually conical and hence termed "monticules." Hence, the circum-mural condition is in the form of connected rings of stomodæa, a ring being present in the soft parts around each monticular projection; such rings may therefore be termed "monticular rings." Between every monticular projection and its surrounding stomodæa is a tentacular boundary consisting of an exocœlic cycle, which is adjacent to the monticule, and an entocœlic one. The stomodæa of a monticular ring are disposed in single file, at more or less regular intervals, around the middle of its oral-disc. Two interstomodæal couples of mesenteries are present, which usually become completely principal, between every two stomodæa of the same ring. The monticular rings of a colony form a continuous polystomodæal system.

In effect, the entire surface of the "colony" consists of a single oral-disc with a vast number of stomodæa. At more or less equal intervals over the whole are projecting "islets," viz., incomplete bits of column-wall surrounded by tentacles, including similarly incomplete bits of collines, the monticules. The arrangement is such that the stomodæa appear as rings around these monticular projections, though this, of course, is only a secondary feature.

Since the monticular rings are contiguous, some stomodæa are common to two or more rings ; in other words, the tentacles round the monticular projections belong to several stomodæa. Such stomodæa serve as connecting links of their neighbouring rings ; consequently there is a secondary *stellate* grouping of stomodæa, each common stomodæum being the centre of a stellate group of three to six stomodæa. Thus, in fig. 18, stomodæa III, B, IV, D, IX, C, VII, form a ring round monticular projection 2 ; stomodæum VII serves to connect the rings around monticular projections 1, 2, 3 and 4 ; it is also the centre of a secondary stellate grouping of stomodæa III, N, XI and C.

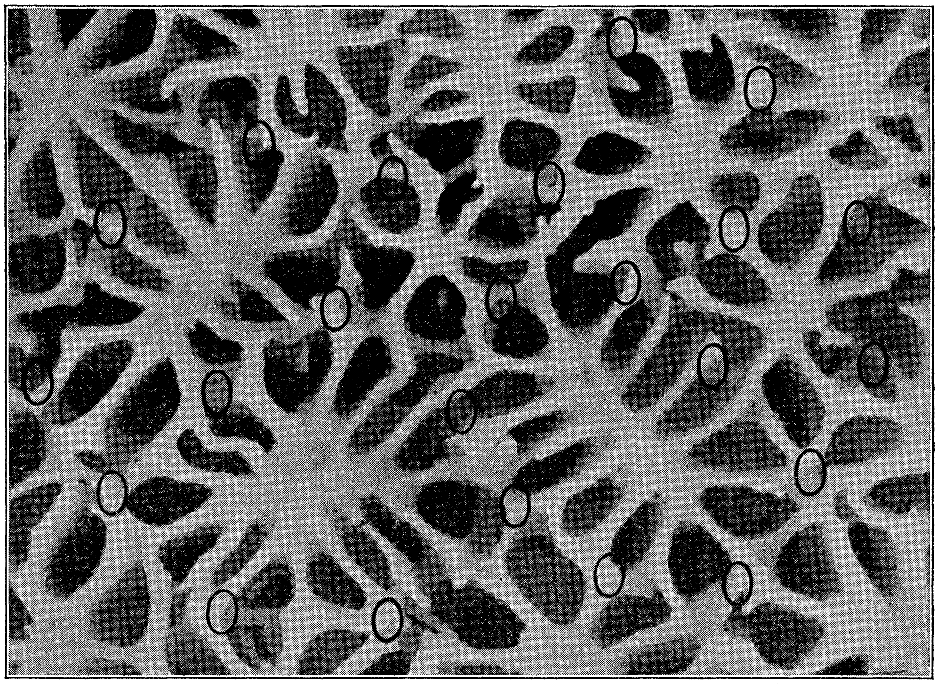

FIG. 16.—*Hydnophora microcona* (LAM.).—Photograph of corallum of a colony greatly magnified, showing monticular projections from which the septa appear to radiate. The positions of the stomodæa in the polyp over same are represented as black ovals.

Formation of Monticular Rings of Stomodæa in Colonies of Hydnophora microcona.—Outside or inside an existing monticular ring one or two new stomodæa are formed which, with two stomodæa or one stomodæum of the ring, constitute a triple stomodæal condition. The column-wall attachments of the mesenteries of the three interstomodæal couples are external to the three stomodæa which they connect. As growth proceeds, the three stomodæa are pushed farther apart so that the mesenteries of the three interstomodæal couples are approximated towards the centre of the triangle formed by these stomodæa, and the two such mesenteries in each part are re-grouped to form an ordinary couple. In the meantime, a monticular projection arises in the centre of the triangular area formed by the three stomodæa. The original triple stomodæal condition has now become an incipient monticular ring, the three re-grouped couples of mesenteries lying as the radii of the ring. New stomodæa are also formed, between these three stomodæa, on the distomodæal mode; consequently, the extent of the new monticular rings is increased. But the regularity shown in the diagram is seldom followed, there being any number, up to nine or ten stomodæa. The mesenteries are so disposed that, at the final stage, there are two interstomodæal couples between every two adjacent stomodæa of the new ring.

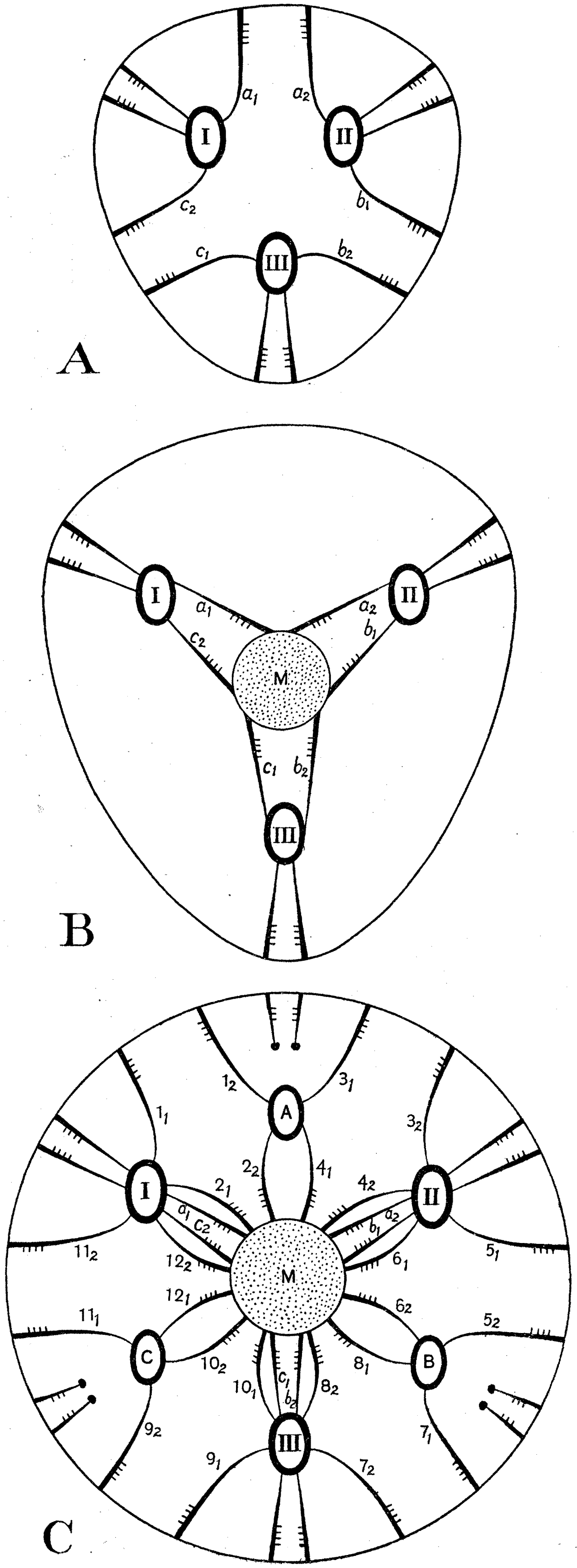

FIG. 17.—*Formation of circum-mural poly-stomodœal condition in Hydnophora microcona* (LAM.).—Septa are not shown. fig. A. Triple stomodæal condition. I–III, stomodæa. a_1 a_2, b_1 b_2, c_1 c_2, inter-stomodæal couples of mesenteries, directed away from stomodæa. fig. B. Incipient monticular ring of stomodæa. a_1 c_2, a_2 b_1, c_1 b_2, re-grouping to form three ordinary couples. fig. C. Monticular ring of stomodæa, *i.e.*, circum-mural poly-stomodæal condition. A, B and C, new stomodæa formed between I–III. 1_1 1_2—12_1 12_2, interstomodæal couples of mesenteries; odd numbers towards periphery of ring, even numbers towards monticule. a_1 c_2, a_2 b_1, c_1 b_2, have become ordinary couples.

[In these *diagrams* no attempt is made to show the relative sizes of the different stages of growth; thus stage in fig. B here is much less magnified than that in fig. A, etc.]

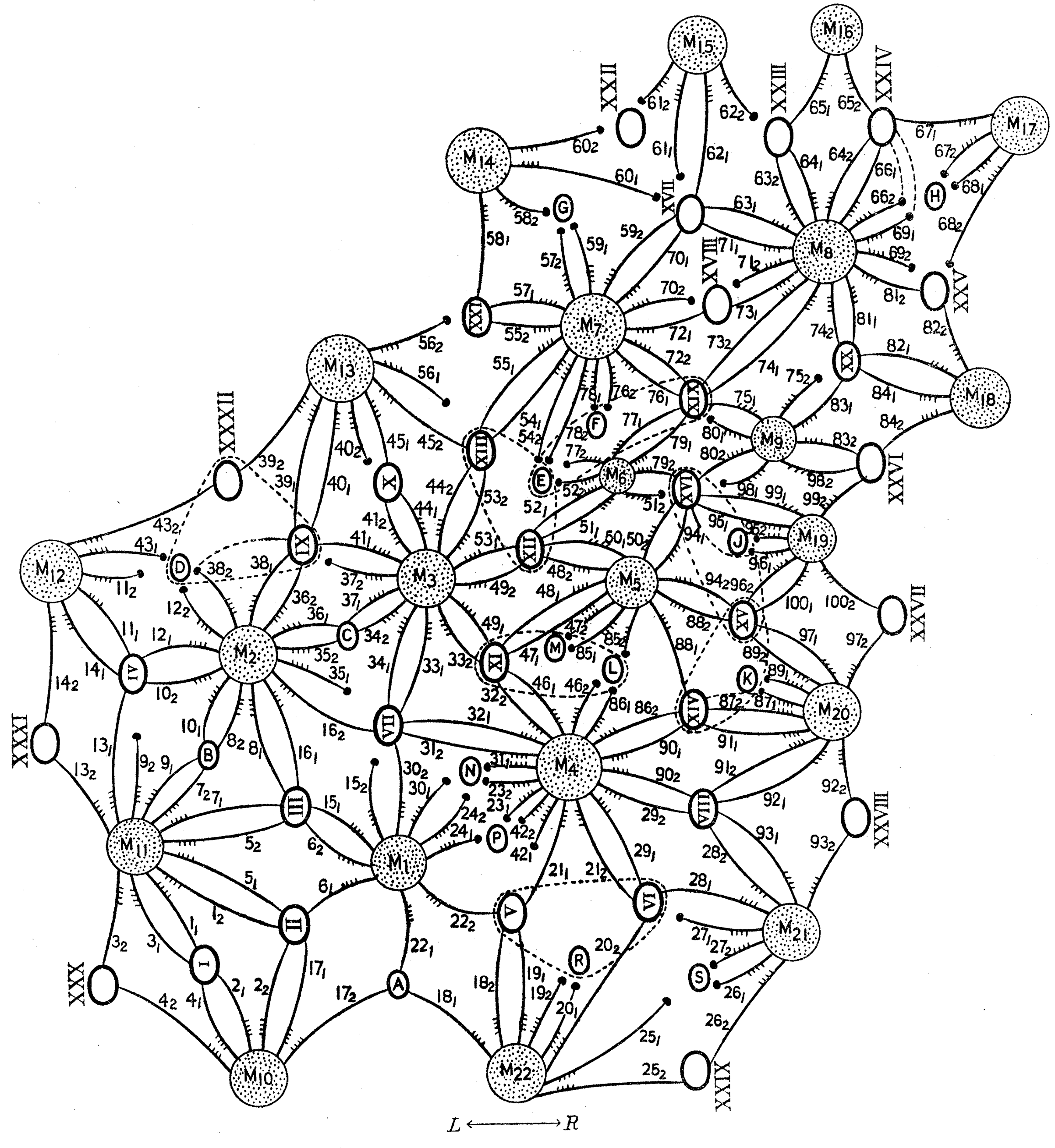

FIG. 18.—*Hydnophora microcona* (LAM.).—Correlation of stomodæa in a part of a colony. I—XXXII, fully formed stomodæa. A–C, stomodæa newly formed. D–S, mark the positions where new stomodæa would soon be formed. 1_1 1_2—100_1 100_2, interstomodæal couples of mesenteries. Other mesenteries not figures. M_{1-22}, monticules. Dotted lines indicating triple stomodæal conditions, in the centre of each a new monticule will arise. Septa not shown. [This *diagram* has been constructed from sections marked 110 *e* IV.]

Growth of colonies of *Hydnophora microcona* is by the formation of new monticular rings. Consequently, stomodæa and mesenteries are constantly re-arranged. The only interstomodæal couples that can be recognised are the latest to be formed. Among the mesenteries that constitute ordinary couples are many which originally formed interstomodæal couples. The arrangement of mesenteries becomes more complex, since new monticular rings are interpolated among, and are connected with, older rings, at least one stomodæum being common to two neighbouring rings. The whole process becomes inconceivably complex in *Hydnophora,* for every colony increases laterally while at the same time it becomes domed over the surface. This, of course, occurs in all colonial Astræidæ, but in some species of *Hydnophora* special parts of the surface form secondary domes which themselves may become elongated and give rise to branches. When a stomodæum is formed between two older stomodæa of a monticular ring, it becomes connected to the older stomodæum on each side by two newly formed interstomodæal couples of mesenteries ; such connection is usually effected at an early stage of the formation of the new stomodæum.

The arrangements of mesenteries and stomodæa of this condition were studied from serial sections of a piece containing thirty-two fully formed (I–XXXII) and sixteen incipient (A–S) stomodæa, from a colony of *Hydnophora microcona.* Stomodæa I–XXI, XXIII–XXVI, and A–S are disposed in nine complete rings round monticular projections 1–9 and seven triple stomodæal conditions. Eight of the new stomodæa, viz., D, E, F, J, K, L, M and R, take part in forming triple stomodæal conditions. A, B, C, G, H, N, P, and S lie in old monticular rings. The rings around monticular projections 10 to 22, being at the periphery of the sections, are only partly included. The stomodæa also comprise thirty-six stellate groups, or groups radiating from central stomodæa (I–XX and A–S). The numbers of three-stomodæa, four-stomodæa, five-stomodæa and six-stomodæa groups are respectively sixteen, seven, ten, and three. All the mesenteries of stomodæa I–XXI, XXIII–XXVI and XXXII are seen, but only some of the mesenteries of XXII and XXVII–XXXI are included in the piece. Interstomodæal couples, which are incompletely principal, are 9_1 9_2, 11_1 11_2, 12_1 12_2, 15_1 15_2, 19_1 19_2, 20_1 20_2, 25_1 25_2, 26_1 26_2, 30_1 30_2, 31_1 31_2, 35_1 35_2, 37_1 37_2, 38_1 38_2, 40_1 40_2, 43_1 43_2, 46_1 46_2, 47_1 47_2, 51_1 51_2, 52_1 52_2, 54_1 54_2, 57_1 57_2, 58_1 58_2, 59_1 59_2, 62_1 62_2, 66_1 66_2, 67_1 67_2, 70_1 70_2, 71_1 71_2, 75_1 75_2, 76_1 76_2, 77_1 77_2, 80_1 80_2, 86_1 86_2, 87_1 87_2, 89_1 89_2, 95_1 95_2, 96_1 96_2, 98_1 98_2. Subsidiary interstomodæal couples are 23_1 23_2, 24_1 24_2, 27_1 27_2, 42_1 42_2, 56_1 56_2, 60_1 60_2, 61_1 61_2, 68_1 68_2, 69_1 69_2, 78_1 78_2, 85_1 85_2. The remaining interstomodæal couples are completely principal.

In this piece there is evidence of the vertical breaking of some principal mesenteries in order to be united to new stomodæa ; the original stomodæal attachments of such mesenteries are visible in some of the upper sections. This process explains how the number of principal mesenteries meeting a stomodæum does not increase above a certain maximum. Stomodæum X represents a later stage of stomodæal formation than A, B or C ; its narrowness in the original sections and its attachment to only three mesenteries indicate its recent origin. It is conceivable that mesentery 52_2 (see stomodæa E, XII and XIII) may be so approximated towards 53_2 as to form an interstomodæal couple with it while retaining its original coupling with 52_1. The result of such a change will be a modified form of triple stomodæal condition with one interstomodæal couple between stomodæa XIII and XII, viz., 53_1 and 53_2, and one such couple between XII and E, viz., 52_1 and 52_2, but two interstomodæal couples between XIII and E, viz., 54_1 and 54_2, 53_2 and 52_2. The fewness of principal couples of mesenteries that are not interstomodæal (all the six mesenteries around stomodæum III take part in six interstomodæal couples) is due to the arrangement of stomodæa to form monticular rings, many of the stomodæa forming connecting links between two or more neighbouring rings, *i.e.*, serving as centres of stellate groups of stomodæa.

II. Extra-Tentacular Budding.

(Figs. 19–22 ; Plate 24, figs. 18 *a* and *b*–20 *a* and *b* ; Plate 25, figs. 1 *a* and *b*–4 *a* and *b*, 6 *a* and *b*–9 ; 11 *a* and *b*–14 *a* and *b*.)

By this method colony formation in *Cyphastrea, Echinopora, Leptastrea, Galaxea, Diploastrea* and *Orbicella annularis* (Ell. and Sol.) is effected ; it is also found in certain species of *Favia, e.g., F. abdita* (Ell. and Sol.), and in the peripheral growth of most colonies of *Favia* and *Goniastrea.* Its principal features are (1) the presence of only one stomodæum within a tentacular ring and (2) the absence of interstomodæal couples of mesenteries between stomodæa of neighbouring polyps.

(i) *In Biradial Genera* (i.e., *Genera with Bilateral and Hexameral Symmetries*).

In the coralla of these genera, viz., *Cyphastrea, Echinopora, Leptastrea, Galaxea,* and *Diploastrea,* the thecæ are usually separated by perithecal intervals of varying width ; they are covered by wide cœnosarcal regions between the polyp centres, and in these regions budding takes place.

Fig. 19 shows the relations between the mesenteries of three polyps and one bud, taken from the edge of a colony of *Orbicella annularis* (Ell. and Sol.). Mesenteries 1 and 2, which form an ordinary couple in polyp III, constitute a directive couple in the bud ; 15 and 16, forming a directive couple in polyp II, belong to two different couples in polyp I. Mesenteries 7, 16, 17 and 18 are principal in two polyps ; 1, 2, 3, 5 and 15 are principal in one polyp and subsidiary in another ; 4 is subsidiary in two polyps. The pleats of mesenteries 1, 2, 5, 8, 12 and 16 are reversed in one of the polyps. The only two mesenteries which retain the same coupling in two polyps are 17 and 18. Mesenteries 22 and 23, which lie in the entocœle between 3 and 4 (in the cœnosarc), are continued into polyps III and II respectively ; 8–12 and 19–21 are continued to the edge of colony. The stomodæal ectoderm of the bud is still thin.

In another bud (from the same colony), containing five primary and four secondary couples of mesenteries, only one directive (primary) couple is found ; the latter is formed by the continuation of a principal and of a subsidiary mesentery of two adjacent couples of a neighbouring polyp.

Mesenteries of other biradial genera exhibiting the same relationships, more particularly those of *Echinopora lamellosa* (Esp.), were also examined.

(ii) *In Genera without Biradial Symmetry.*

In these genera, *e.g.*, *Favia* and *Goniastrea*, in which colony-formation is mainly by intra-tentacular budding, extra-tentacular budding occurs at the growing edges of colonies, *i.e.*, in these genera *intercalary growth*, which is the principal mode of increase in size of colonies, is by intra-tentacular budding, *peripheral growth* by extra-tentacular budding. It is important to note that, in these two genera, neither bilateral (*i.e.*, two directive couples) nor hexameral symmetry is present at any stage in the development of extra-tentacular buds.

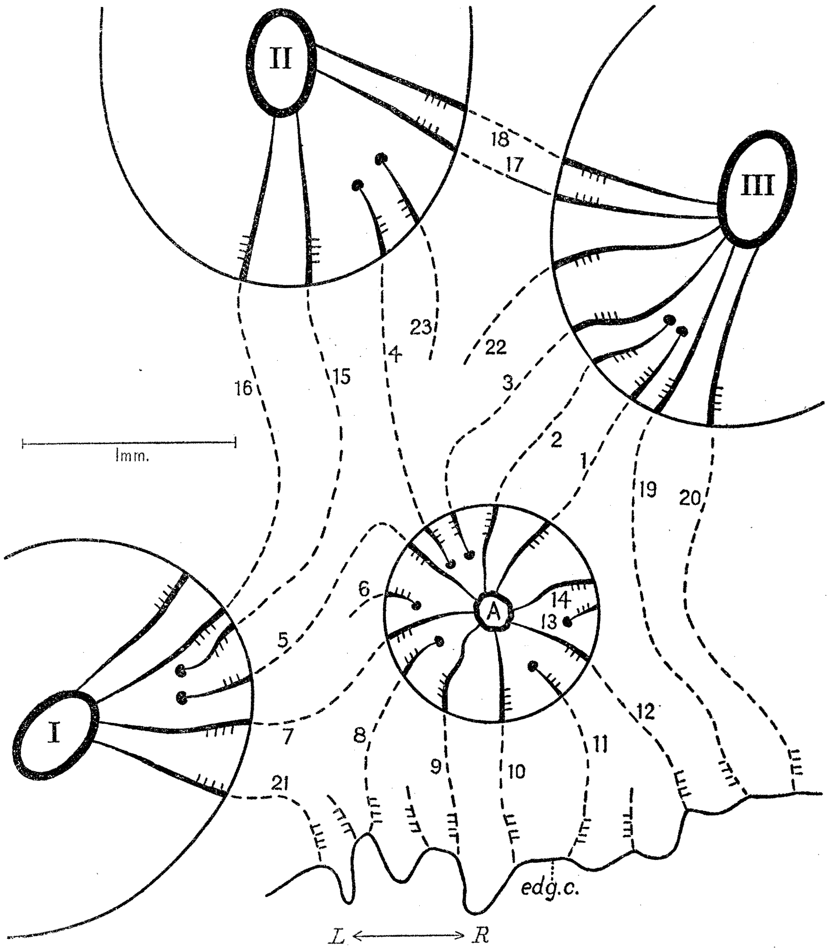

FIG. 19.—*Orbicella annularis* (ELL. and SOL.).—Transverse section through stomodæal region of an extra-tentacular bud and parts of three adjacent monostomodæal polyps from the edge of a colony. I–III, stomodæa of polyps. A, stomodæum of bud. *Edg.c.*, edge of colony. Broken lines showing continuations of some mesenteries through edge-zones and cœnosarc. (500 *g* I.)

In all the colonies of *Favia abdita* (ELL. and SOL.) that were examined, colony-formation is entirely by extra-tentacular budding. Fig. 20 was constructed from transverse sections of a piece containing a large polyp and two unequal buds, from a colony of this species. The oral-disc area of each bud is formed in the edge-zone of the large polyp, and has a slit-like mouth opening in the centre ; a tentacular ring has begun to be formed around the oral-disc of each bud. As some of the mesenteries of the large polyp are continued into the buds which are as yet small, the column-walls of polyp and buds are continuous ; as growth proceeds they become discontinuous.*

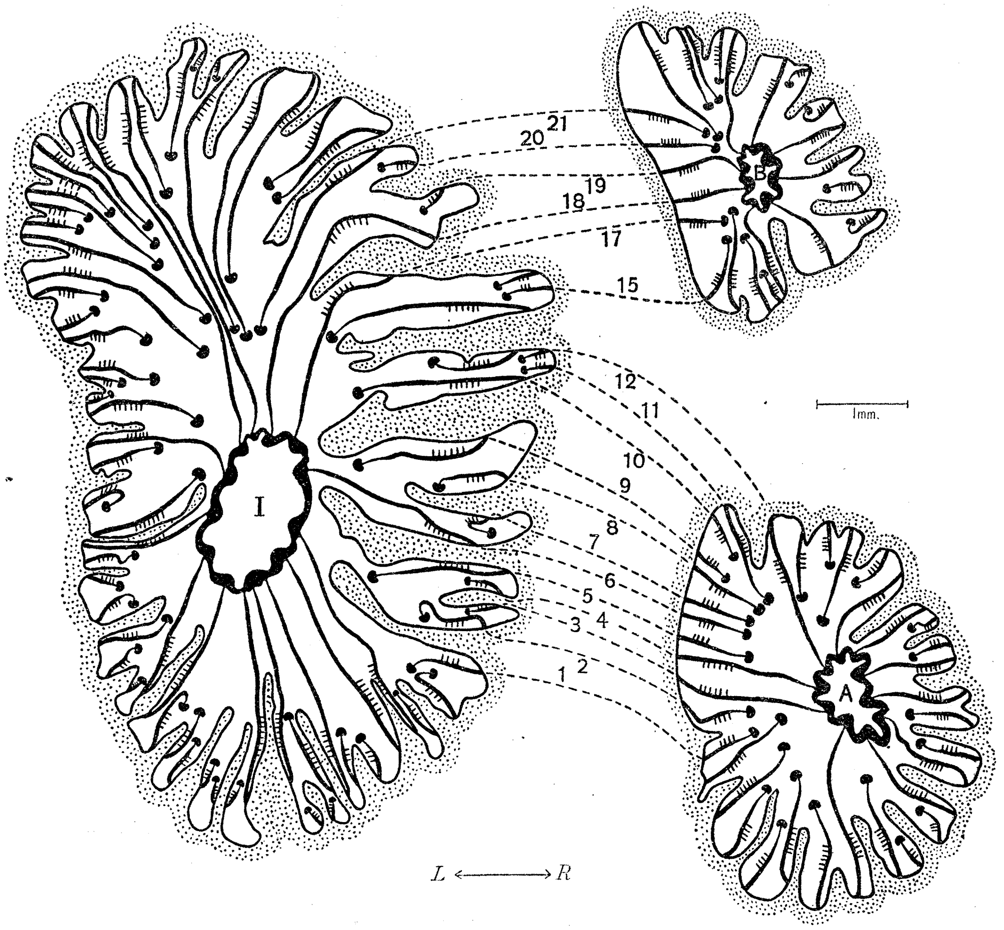

Fig. 20.—*Favia abdita* (Ell. and Sol.).—Transverse section through stomodæal region of a full-grown monostomodæal polyp and two extra-tentacular buds, from a colony. I, stomodæum of polyp. A and B, stomodæa of buds. Broken lines showing continuations of some mesenteries through edge-zones and cœnosarc. Oral and basal views of same are shown in Plate 25, figs. 2 *a* and *b*. (103 *p* III.)

Mesenteries 1–12 are continuous between polyp and bud (A) ; similarly 15–21 (with the exception of 16) are continuous between polyp and bud (B). Since 16 does not extend into bud (B) the pleats of 17 are reversed in position so that 17 may form a couple with 15 ; consequently the pleats of 18–21 are also reversed. Thus the couplings of mesenteries 15–21 are different in bud (B) from those in the polyp. Mesentery 18 is principal in two adjacent polyps ; 3, 4, 6, 12, 17, 19 are principal in one polyp and

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* The task of tracing mesenteries of the buds to the polyp was particularly difficult, as the former were at a higher level than the latter ; further, bud A was somewhat higher in position than bud B.

subsidiary in another; 1, 2, 5–11, 15, 20, 21 are subsidiary in two polyps. Mesenteries 15, 17–21 belong to different couples in polyp and bud. The numerical ratios of principal to subsidiary mesenteries in the polyp and two buds of fig. 20 are roughly 1 : 5, 1 : 3, 1 : 2. The sagittal planes of the three stomodæa do not correspond with one another.

Owing to the depth and irregular contour of the corallites, to the oblique position of the buds on the inner surface of corallite-walls and to the fact that adjacent corallite-walls meet at angles without flat perithecal intervals, the appearance in the skeleton of *Favia abdita* is that of intra-tentacular budding, though the real relationships, as sketched above, are clear in the soft parts. In spirit specimens, the oral-discs are shrunk down into the corallites, and the edge-zone lines the greater part of the inner surface of corallite-walls; consequently the small extra-tentacular buds are seen within the calices, placed in oblique positions over the corallite-walls. In all the colonies examined, even the smallest mouth-openings are extra-tentacular.

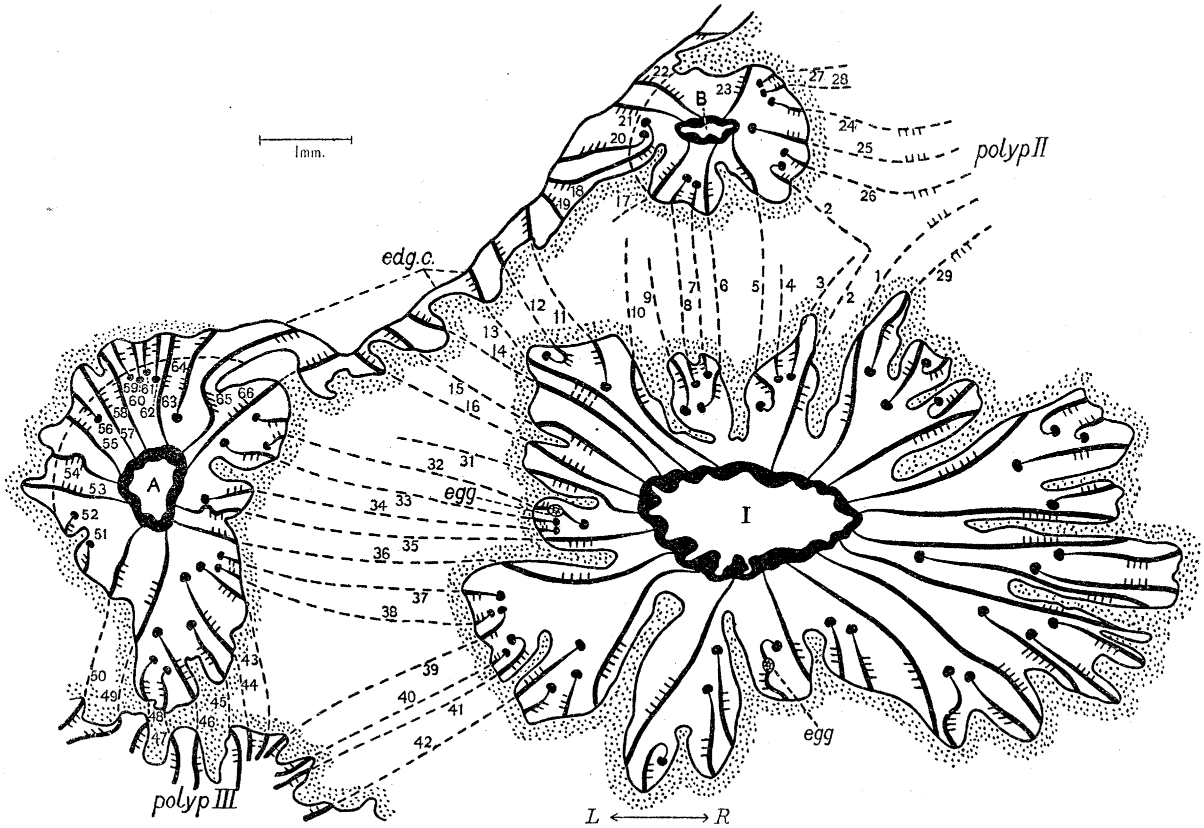

FIG. 21.—*Favia favus* (FORSK.).—Transverse section through stomodæal region of a full-grown monostomodæal polyp and two extra-tentacular buds, from the edge of a colony. I, stomodæum of polyp. A and B, stomodæa of buds. *Edg.c.*, edge of colony. Broken lines showing continuations of some mesenteries through edge-zones and cœnosarc. Oral and basal views of same are shown in Plate 24, figs. 18 *a* and *b*. (203 *h* II.)

In *Favia favus* (Forsk.) colony-formation is mainly by intra-tentacular budding, but extra-tentacular budding takes place at the edge; fig. 21 shows the arrangement of mesenteries of a large monostomodæal polyp and two much smaller extra-tentacular buds from the growing edge of a colony of this species (Plate 24, figs. 18 *a* and *b*), the buds being at the extreme edge of the colony. The buds and polyp are connected only by the edge-zone, their column-walls being separate from one another. The polyp is full-sized, having thirteen principal and eighteen subsidiary couples of mesenteries. The larger bud (A) has a small mouth-opening in the centre of a distinctly marked oral-disc surrounded by an imperfect tentacular ring consisting of a few tentacles; it has seven principal and nine subsidiary couples of mesenteries. In bud (B) the mouth-opening is hardly recognisable; the oral-disc is marked out, but no tentacles have yet appeared; it has four principal and four subsidiary couples of mesenteries. There are no directive couples in the buds, though the latter were undoubtedly formed by extra-tentacular budding. Mesenteries 32–38 are continuous between polyp and bud (A); 2, 5–8 between polyp and bud (B); 11–16 between polyp and edge of colony; 53–66 between bud (A) and edge of colony; 18, 20–22 between bud (B) and edge of colony. Mesenteries 35 and 36 are principal in two polyps; 2, 5, 6 are principal in one polyp and subsidiary in another; 7, 8, 32, 33, 34, 37, 38 are subsidiary in two polyps; 1, 2, 26 belong to different couples in adjacent polyps. The numerical ratios of principal to subsidiary mesenteries in the polyp and the two buds are about 2 : 5, 2 : 3, 1 : 1. Polyps 11 and 111 are not included in the sections, but mesenteries 1, 24, 25, 26, 29 are continued into polyp 11, and 39–50 into polyp 111.

The mesenteries of two small extra-tentacular buds, on the edge of a colony of *Favia fragum* (Esp.), have also been traced (Plate 25, figs. 1 *a* and *b*); they show the same relationships. Each of the two buds, though much smaller than either part of the distomodæal polyp, has as many principal couples, viz., six, and four subsidiary couples.

An earlier stage of growth was found on the edge of a colony of *Favia hululensis* (Plate 24, figs. 20 *a* and *b*). This diverticulum shows the probable method of formation of mesenteries in extra-tentacular buds. Neither mouth-opening nor tentacles are yet formed, but it is in every other respect a polyp. In its upper half, *i.e.*, just below where the mouth would open (fig. 22 A), mesenteries 2+9, 10+13, 14+15, 16+19, 20+23, 24+1 are bent towards the centre of the cœlenteric cavity in such a manner that their adjacent halves form couples, viz., 9 and 10, 13 and 14, 15 and 16, 19 and 20, 23 and 24, 1 and 2. 2+9 and 10+13 are continuous between the diverticulum and polyp 1; 14+15, 16+19, 20+23, 24+1 begin from one part of the edge of the colony and terminate at a different part; in their loops lie the couples 3 and 4, 5 and 6, 7 and 8, 11 and 12, 17 and 18, 21 and 22. In the lower half of the diverticulum (fig. 22 B) these bent mesenteries have been vertically divided in the middle, and mesenterial filaments have been developed along the free margins of the twelve halves. Presumably this vertical division began from the base of the diverticulum and was being continued up to the oral-disc. As a result of such division, twelve mesenteries constituting six ordinary couples will be

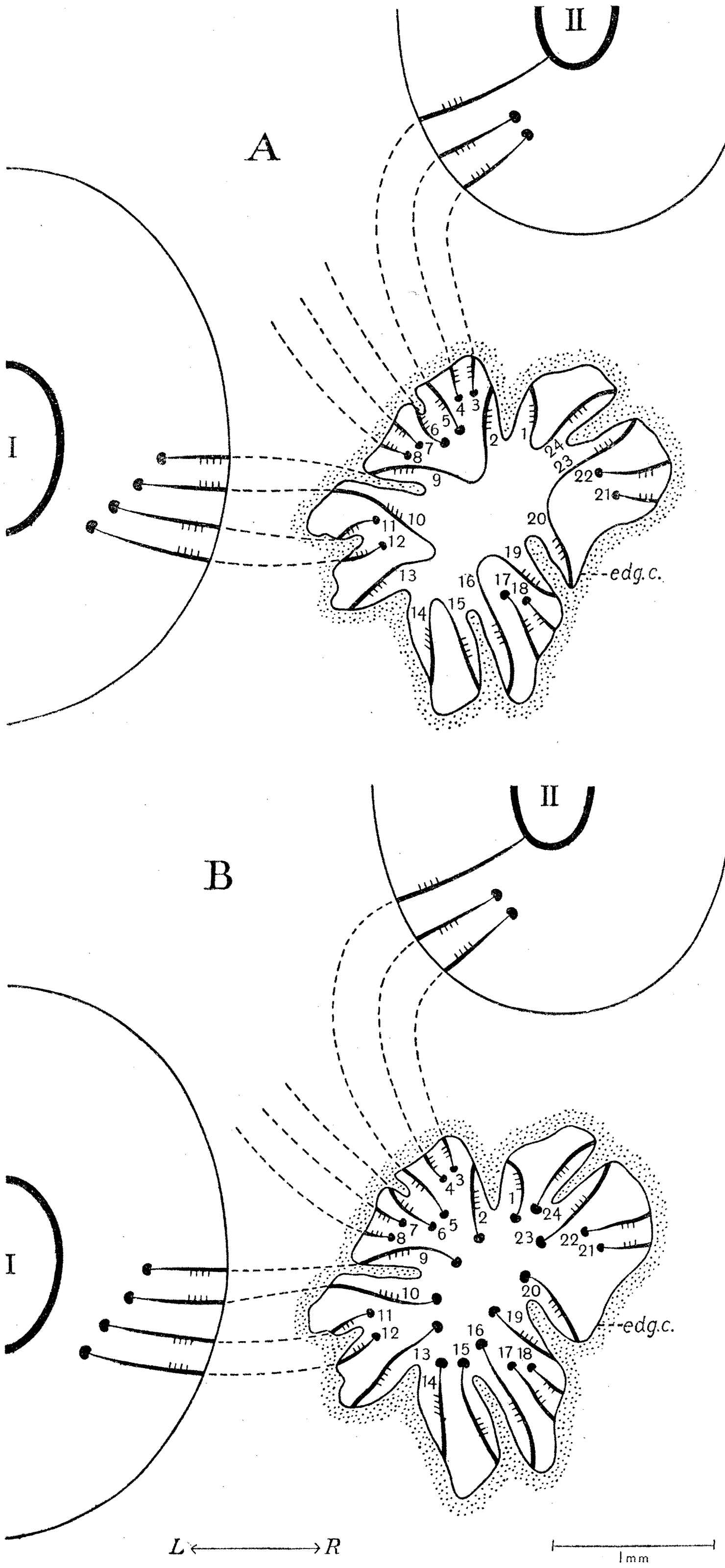

FIG. 22.—*Favia hululensis*, GARD.—Transverse sections through an extra-tentacular diverticulum and parts of two adjacent monostomodæal polyps, from the edge of a colony. I and II, stomodæa of polyps. Broken lines showing continuations of some mesenteries through edge-zones and cœnosarc. The outer periphery of diverticulum between mesenteries 2 and 13 is part of edge of colony (*edg.c.*). Oral and basal views of same are shown in Plate 24, figs. 20 *a* and *b*. fig. A. Transverse section through upper half of diverticulum. fig. B. Transverse section through lower half of diverticulum. (106 *a* VI.)

formed. Since these six couples and their entocœlic septa were broader than the remaining couples and septa of the diverticulum, the six couples would probably become principal when the stomodæum was formed. Mesenteries 3–5 are continuous between the diverticulum and polyp 11 ; 6–8 between the diverticulum and the intervening edge-zone ; 11 and 12 between the diverticulum and polyp 1 ; 17, 18, 21, 22 between the diverticulum and the edge of the colony. There is no sign of formation of directive couples in the diverticulum.

A method of formation, similar to that in *Favia hululensis*, would also explain the arrangement of mesenteries in extra-tentacular buds of biradial genera.

In the meagre account which FOWLER (14) has given of budding in *Madrepora aspera*, DANA, he remarks that the stomodæum is " invaginated to a considerable depth into the future polyp cavity before it is perforated for communication between the cœlenteron and the exterior, and also apparently before any mesenteries are formed " (p. 13). On the contrary, in the extra-tentacular diverticulum of *Favia hululensis*, most of the principal mesenteries are formed before the stomodæum opens, and in all the extra-tentacular buds I have examined most of the principal couples have already appeared.

GARDINER (16) describes extra-tentacular budding in *Cœnopsammia* as follows :— " Budding takes place from the blind ends of the cœnosarcal canals at the basal margin of the single polyp or colony. A number of the cœnosarcal canals fuse together and a mouth breaks through. The inter-mesenterial spaces of the daughter polyp on the inner side, *i.e.*, towards the parent polyp, are each formed directly from a single cœnosarcal canal, while those at the sides are formed by the branching of these canals. The mesenteries are formed from the dividing walls of the cœnosarcal canals, *i.e.*, from the extrathecal portions of the mesenteries of the parent polyp. The young corallite appears to be very rapidly formed, and has from the first a diameter of 2·5 mm." (p. 364). He added further that, in the various colonies examined, he found only " one bud without a corallite," and that he traced the connections of two buds, each about 3 mm. in diameter, with the parent polyp. From this, it would appear that the method of formation of extra-tentacular buds in *Cœnopsammia* was somewhat similar to the one I have described above in reference to *Favia hululensis ;* in buds of *Cœnopsammia* stomodæa were formed first, and their mouth-openings appeared subsequently as splits in the oral-disc. GARDINER does not, however, mention the growth of mesenteries from the edge of the colony into buds, which may, and does, take place in Astræid corals, and thus helps the spreading of colonies.

III. SUMMARY OF BUDDING.

Extra-tentacular and intra-tentacular budding are the two methods of polyp-formation, and consequently of colony-formation, in the Astræidæ. Fission in the sense of the vertical division of the stomodæum does not occur in the family.

Extra-tentacular budding is characteristic of *Cyphastrea, Echinopora, Leptastrea, Galaxea, Diploastrea, Orbicella annularis* (ELL. and SOL.), and *Favia abdita* (ELL. and SOL.), the polyps of which remain monostomodæal at every stage of development and do not possess interstomodæal couples of mesenteries. Intra-tentacular budding occurs in *Favia*, *Goniastrea* and the meandroid genera, viz., *Cœloria*, *Leptoria*, *Colpophyllia*, *Hydnophora*, etc. In *Favia* and *Goniastrea* intra-tentacular budding results in distomodæal, tristomodæal and triple stomodæal conditions, which finally break up into monostomodæal polyps. In the meandroid genera the permanent condition of polyps is polystomodæal, monostomodæal polyps being rare or absent. In all these genera interstomodæal couples are present.

The distomodæal condition may be reached (1) by intra-tentacular budding in monostomodæal polyps which were formed by the same method, (2) by intra-tentacular budding in monostomodæal polyps formed by the extra-tentacular method, but which were without directive couples, (3) by intra-tentacular budding in monostomodæal polyps containing directive couples, (4) from the triple stomodæal condition by the separation of the mother-polyp or of one of the halves of the double-bud.

In colonies of biradial genera, intra-tentacular budding occasionally takes place, resulting in distomodæal polyps. In *Favia* and *Goniastrea* extra-tentacular budding occurs in the periphery of colonies. The intra-mural polystomodæal polyps, in the colonies of meandroid genera, is the result of repeated intra-tentacular budding; such polyps are capable of lateral and dichotomous branching, the former on the distomodæal mode, the latter on the tristomodæal and triple stomodæal modes. The circum-mural polystomodæal condition of *Hydnophora microcona*, *i.e.*, the arrangement of stomodæa in the form of connected monticular rings, is the result of modifications of triple stomodæal conditions.

IV. General Considerations.

(i) *Mesenteries*.

The following points with regard to mesenteries in the colonial Astræidæ are established, irrespectively of the methods of colony-formation. Mesenteries are continuous in the cœnosarc between neighbouring polyps and extend to the edges of colonies, such extensions of mesenteries being feebly or not at all pleated. In polyps, new couples arise only in exocœles, but in the cœnosarc may be formed in entocœles. A mesentery continuous between two polyps may be principal in both polyps, principal in one polyp and subsidiary in the other, or subsidiary in both polyps, its pleats being sometimes reversed in one of the polyps. Mesenteries common to two polyps may retain the same coupling or be differently coupled; those of directive couples retain the same disposition in both polyps or are differently coupled in one polyp, with or without reversal of pleats. In buds the normal number of principal couples is reached when they are small, whilst subsidiary couples are added until the adult condition is reached.

The presence of well-developed filaments on the margins of mesenteries of an extra-tentacular diverticulum of *Favia hululensis* (fig. 22 B), before the formation of a stomodæum, is a significant fact bearing on the question of the origin of mesenterial filaments.

The filaments in question could only have been formed by the modification of the endoderm where the mesenteries have split. If the new stomodæum were to be formed by the union of these filaments, it would be different from that of a sexually developed polyp, since in the latter the inner layer of the stomodæum is said to be ectodermal in origin (32, p. 197). If it were to be formed by invagination of the oral-disc, assisted by coalescence of the filaments, the stomodæum would have a composite origin, being both ectodermal and endodermal. On the other hand, so close is the resemblance between the histology of the filaments and of the stomodæum that it is almost impossible to conceive that one of them originated from ectoderm and the other from endoderm. The matter clearly requires further investigation.

(ii) *Interstomodæal Couples of Mesenteries.*

Two interstomodæal couples of mesenteries are present between a mother-polyp and its intra-tentacular bud whether the latter be single, as in the distomodæal condition, or double, as in the triple stomodæal condition; but their formation may or may not synchronise with that of new stomodæa. The presence of such couples between every two contiguous stomodæa of di- or poly-stomodæal polyps is as striking a phenomenon as the presence or absence of the two directive couples of mesenteries.

The primary function of mesenteries in polyps was probably mechanical, to serve as buttresses to the stomodæa, *i.e.*, to support and keep them in position, hence the thickening of the mesoglæa of mesenteries. When there are two or more stomodæa in a polyp, viz., within the same tentacular boundary and suspended in the same cœlenteric cavity, interstomodæal couples of mesenteries are an effective method of supporting and keeping them apart at the required intervals. On the other hand, when the stomodœa are in separate polyps, viz., within separate tentacular rings and in separate cœlenteric cavities, interstomodæal couples are not necessary. In this connection, it may be repeated that, in the monostomodæal genera *Favia* and *Goniastrea*, no interstomodæal couples of mesenteries are found between the completely separated polyps, although such couples are always found in the distomodæal, tristomodæal and triple stomodæal conditions, before mother-polyps and buds are separated.

(iii) *Directive Couples of Mesenteries and their Value in Classification.*

Extra-tentacular budding is characteristic of genera having two directive couples of mesenteries in their polyps, whilst intra-tentacular budding is usual in genera having no directive couples. The presence or absence of directive couples is not due to the particular form of budding. It has already been seen that, in biradial genera, intra-tentacular budding occasionally occurs, and this is always accompanied by the formation, in the buds, of directive couples. On the other hand, in *Favia abdita* (ELL. and SOL.) in which extra-tentacular budding is the rule, directive couples are absent from every polyp;

nor are they developed in extra-tentacular buds formed at the periphery of colonies of *Favia* and *Goniastrea*.* The possibility of two directive couples of mesenteries between the two subsequently separating stomodæa in a distomodæal polyp of *Favia* or *Goniastrea* is at once obviated by the formation of two interstomodæal couples, the pleats of the mesenteries of such a couple facing each other. Judging from DUERDEN'S account (12), two directive couples are present in each half of the occasional bioral polyps of *Acropora* (*Madrepora*) *muricata* (LINN.), *Porites astrœoides*, LAM., *Cladocora arbuscula* (LES.), and *Oculina diffusa*, LAM. In *Echinopora*, *Orbicella*, etc., two directive couples are formed in every bud, whether extra or intra-tentacular, by re-grouping of mesenteries of different couples of adjacent polyps, with or without reversal of pleats, or as new structures.

FOWLER (15) noted the absence of directive couples of mesenteries in *Lophohelia prolifera;* BOURNE (2) suggested that such absence, which he discovered in *Mussa corymbosa* and *Euphyllia glabrescens*, might be a primitive condition or connected with fissiparity. DUERDEN (12) found three directive couples of mesenteries and up to eleven extra couples meeting the stomodæa in the occasional enlarged polyps of *Cladocora arbuscula* (LES.), *Stephanocœnia intersepta* (ESP.), *Solenastrea hyades* (DANA) *and Oculina diffusa*, LAM. In a similar polyp of *Orbicella annularis* (ELL. and SOL.), I have found three directive couples of mesenteries and five extra couples meeting the stomodæum and six new couples not meeting the stomodæum.

G. Y. and A. F. DIXON (6, 7 and 8), CALGREN (4), BLOCHMANN and HILGER (1), McMURRICH (26) and PARKER (27) have recorded similar examples of variation in the number of directive couples of mesenteries among Actinians. According to McMURRICH (26, p. 121), the absence of directive couples has no phylogenetic significance, but is essentially an individual peculiarity which may secondarily rise to the value of a specific or even a generic character. On the other hand, BOVERI (3) regards the absence (real or apparent) of two directive couples from *Gyractis* as of sufficient value to create the *Holactiniœ* for its reception; for the same reason KWIETNIEWSKI (21) established the *Thalassianthœ* for two species of *Thalassianthus*.

To conclude, directive couples of mesenteries are either present or absent in the different genera of the *Astrœidœ*, independent of whether budding is extra- or intra-tentacular, though the two methods of budding are, as has been seen, not mutually exclusive. If the chief value were given in classification to the types of budding, a species like *Favia abdita* would have to be dissociated from *Favia* and placed nearer genera like *Cyphastrea* and *Echinopora* in which growth is by extra-tentacular budding. As I have elsewhere pointed out (22, p. 35), the presence or absence of two directive couples of mesenteries has a constant morphological value in all genera and species. It hence possesses an importance in classification over and above any growth-phenomenon like budding.

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* Similarly, directive couples are absent from *Favia versipora* (LAM.) and *Favia wakayana* (GARD.), in which colony-formation appears to be entirely by extra-tentacular budding.

(iv) *Evolution of the Astræidæ.*

This study of Astræid corals leads to the conclusion that the two groups represented by *Cyphastrea, Echinopora, Leptastrea, Galaxea, Diploastrea* and *Orbicella annularis*, and by *Favia, Goniastrea, Cœloria, Leptoria, Colpophyllia, Manicina, Hydnophora*, etc., have been derived from solitary forms, along two different lines of descent, as shown below :—

Solitary polyp-ancestor, with two directive couples, and six, or some multiple of six, couples of mesenteries.

(1) Bilateral (two directive couples) and hexameral symmetries present in every polyp.

(2) Colony-formation primarily by extra-tentacular, secondarily by intra-tentacular, budding.

(3) Polyps monostomodæal.

Cyphastrea, Echinopora, Leptastrea, Galaxea, Diploastrea, Orbicella annularis.

(1) Bilateral (two directive couples) and hexameral symmetries absent from every polyp.

(2) Colony-formation primarily by intra-tentacular, secondarily by extra-tentacular, budding.

(3) Polyps ranging from mono- to polystomodæal.

Monostomodæal condition :
Favia and *Goniastrea.*
|
Intra-mural polystomodæal condition :
Cœloria, Leptoria, Colpophyllia, Manicina.
|
Circum-mural polystomodæal condition :
Hydnophora.

If the process of evolution has been as sketched above, the family Astræidæ has to be abolished, and two separate families should be constituted for its two widely divergent groups. At this stage I do not propose to suggest family names, for the same phenomenon may be found in other groups of Madreporaria, and the question will arise whether the loss of directive couples and hexameral symmetry is or is not the primary feature in the evolution of corals from Actinian-like ancestors.

The universal presence of a solitary hexameral stage in the development of both Actinians and Madreporarians indicates that they had a common origin. Up to the present, views on their further evolution have been mainly based on the sequences of their mesenterial succession, as shown in development; these views are most conflicting. In ontogeny, however, alteration and suppression of the stages of evolution are now known to be inevitable. I submit that the comparative study of the adult morphology should be the basis for classification; the same study is more likely to give a true account of the lines of evolution.

(v) *Individuality in Corals.*

Workers on colonial Madreporaria were inclined to regard unioral polyps as the individuals of a colony, and distinct corallites as representing such individuals in the corallum. This was in conformity with the general tendency among biologists to look upon organisms having repetition of organs of digestion as "colonies."

Such a colonial mode of growth is primarily associated with a sedentary habit of life for which size, coupled with many digestive spaces, seems all important; a repetition of digestive cavities would seem to be what is best suited to the physiological needs of sedentary organisms. Such a repetition implies increase of size, and this would be accompanied by increase or repetition of generative organs to ensure the wide distribution of the organisms. The only record of differentiation of polyps in the Madreporaria is that described by Fowler (14) in *Madrepora durvillei* (Ed. and H.), in which, associated with the normal biradial polyps, he found a second type characterised by six modified mesenteries.

Duerden's view (12, p. 141) that a "fissiparous" coral (whether composed of monostomodæal polyps or constituting a single meandering polystomodæal system) was an individual, was not based on the continuity of mesenteries and cœlenteric cavity, but on his derivation of such coral from a sexually produced biradial polyp, having two directive couples of mesenteries, by continued fission unaccompanied by formation of further directive couples. The polyps of a "gemmiferous" colony were to be regarded as individuals, since each of them was formed anew and passed through all the stages of sexually produced polyps, finally possessing two directive couples of mesenteries and hexameral symmetry (11, p. 391). This view is now untenable since, as seen in *Orbicella annularis* (Ell. and Sol.) and *Echinopora lamellosa* (Esp.), the mesenteries of older polyps take part in the formation of buds and the cœlentera are continuous throughout the colony. Moreover, extra-tentacular budding is not a criterion of individuality, since it takes place in "fissiparous" genera as well, nor is it the immediate cause of the formation of directive couples of mesenteries.

The formation of new stomodæa is a mode of growth peculiar to corals. Since the mesenteries and cœlenteric cavities of each "colony" are continuous, and since the polyps, irrespective of size or age, bear gonads during the reproductive period, the polyps are to be regarded as local aggregations of mesenteries and tentacles around the stomodæa of a continuously growing sedentary organism. In *Manicina areolata* (Linn.) and *Hydnophora microcona* (Lam.), in which a single polystomodæal polyp constitutes the entire "colony," the mesenteries are grouped around stomodæa, but these, as we have already seen, are connected to the monostomodæal Astræids by a series of other genera. The individuality of corals is further evidenced by the various forms of growth which they assume in conformity with environmental conditions, *i.e.*, thin and incrusting, massive, branching, etc., or, if secondarily detached, more or less rounded balls as in *Cyphastrea chalcidicum*, KLUNZ., and *Siderastrea radians*, PALLAS.

V. CLASSIFICATION OF THE ASTRÆIDÆ.

The foregoing account of colony-formation in the Astræidæ will probably be found to be of wide applicability in the Madreporaria, and perhaps in the Anthozoa. The formation of polyps by budding leads to a re-grouping of the Astræids, which I have investigated, as follows :—

I. Solitary forms with one stomodæum.

II. Colonial forms with more than one stomodæum.

- 1. Two directive couples present in each polyp ; monostomodæal condition only.
    - (i) Polyps remaining permanently connected by edge-zone and cœnosarc, *e.g.*, *Cyphastrea*, *Echinopora*, *Leptastrea*, *Galaxea*, *Diploastrea*, *Orbicella annularis* (ELL. and SOL.).
    - (ii) Polyps secondarily losing organic continuity, *e.g.*, *Cylicia*.*
- 2. Directive couples absent ; mono- to poly-stomodæal conditions.
    - (i) Polyps remaining permanently connected by edge-zone and cœnosarc.
        - (*a*) Monostomodæal condition permanent ; bi- or tri-stomodæal conditions temporary.
            - (a_1) Triple stomodæal condition absent, *e.g.*, *Favia*.
            - (a_2) Triple stomodæal condition present, *e.g.*, *Goniastrea*.
        - (*b*) Polystomodæal condition permanent.
            - (b_1) Stomodæa arranged in single rows along the middle of elongated polyps, *i.e.*, intra-mural polystomodæal condition, *e.g.*, *Cœloria*, *Leptoria*, *Colpophyllia*, *Manicina*.
            - (b_2) Stomodæa arranged around monticular projections to form connected monticular rings, *i.e.*, circum-mural polystomodæal condition, *e.g.*, *Hydnophora*.
    - (ii) Polyps remaining connected by edge-zone and cœnosarc, or secondarily losing organic continuity.
        - (*a*) Polystomodæal condition permanent ; mono-, di-, and tri-stomodæal conditions temporary, *e.g.*, *Mussa*.
        - (*b*) Mono-, di-, and tri-stomodæal conditions permanent ; polystomodæal condition, if present, temporary, *e.g.*, *Euphyllia*, *Eusmilia*.

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* The position of this genus in the Astræidæ is doubtful.

SUMMARY.

1. Colony-formation is by extra-tentacular or intra-tentacular budding only, fission of the stomodæum never occurring.

2. Extra-tentacular budding leads to colonies with separate monostomodæal polyps joined by the cœnosarc.

3. Intra-tentacular budding results in three or a triplet of stomodæa within a single tentacular ring, and may lead to colonies with separate polyps or to meandroid colonies.

4. Such intra-tentacular budding is always accompanied by the formation of inter-stomodæal couples of mesenteries, the function of which is regarded as mechanical, viz., to keep the stomodæa apart.

5. The polyps are everywhere connected by mesenteries and cœlenteric spaces; in budding every possible re-arrangement of mesenteries is found.

6. The presence or absence of directive couples of mesenteries is the important feature in classification and not budding, which varies in individual colonies and in different species of the same genus.

7. The ancestral form is supposed to have been a solitary polyp with two directive couples of mesenteries and hexameral symmetry, which by the retention or loss of these broke up into two lines of descent.

8. The genera of these two groups should now be placed in different families.

9. The coral colony must now be regarded as the individual, not the separate polyps. Colony-formation commenced either by extra-tentacular or intra-tentacular budding. The former remained fixed and was always followed by the separation of polyps, the latter further differentiated into various types of budding, which, with the separation or non-separation of the polyps, serve to distinguish genera.

EXPLANATION OF TERMINOLOGY.

1. *Calyx.*—The cavity enclosed in a corallite.

2. *Cœnosarc.*—The soft parts of a colony overlying the peritheca.

3. *Colline.*—The calcareous partition formed by the fusion of the walls of two adjacent valleys of a meandroid colony.

4. *Colony.*—The entire soft and hard parts of a Madreporarian coral containing more than one stomodæum.

5. *Corallite.*—The part of the corallum in which a monostomodæal polyp lies.

6. *Corallite-wall.*—The wall of a corallite inclusive of theca and any perithecal deposit.

7. *Corallum.*—The hard parts of a Madreporarian colony.

8. *Edge-zone.*—The soft parts of a colony covering the outer free surface of a corallite-wall; indistinguishable in some cases.

9. *Enterostome.*—The lower opening of the stomodæum into the cœlenteric cavity.

10. *Interstomodœal septum.*—A septum under the entocœle of an interstomodæal couple of mesenteries.

11. *Mesenteries :*

Couple of mesenteries.—Two adjacent mesenteries of a polyp with their pleats *vis-à-vis.* The pleats are reversed in position in a directive couple. The term *pair of mesenteries* has reference to developmental sequence.

In a *completely principal couple,* both the mesenteries meet the stomodæum ; in an *incompletely principal couple,* one of the mesenteries meets the stomodæum, the other does not ; in a *subsidiary couple,* neither of the mesenteries meets the stomodæum.

An *interstomodœal couple* lies between two adjacent stomodæa in a common tentacular ring, each mesentery being related to one of the stomodæa.

Principal and subsidiary mesenteries—used with reference to genera which have lost the bilateral and hexameral symmetries, hence also the cyclic arrangement. *Principal mesenteries* meet the stomodæum, *subsidiary mesenteries* do not. The terms primary, secondary, protocnemes, metacnemes are applicable to the developmental sequence of mesenteries.

12. *Mesoglœa.*—A descriptive term for the middle or supporting lamina of Cœlenterates.

13. *Monticule.*—Short discontinuous colline, usually conical in shape, as in *Hydnophora microcona.*

14. *Oral-disc.*—The circumoral part of the wall of a polyp bounded by the outermost cycle of tentacles.

15. *Peristome.*—The space overlying the oral-disc.

16. *Peritheca.*—That part of the corallum of colonial Madreporaria which subsequently is deposited outside.

17. *Polyp.*—Any division of the soft parts of a colony which has a distinct circumoral tentacular boundary ; used only for purposes of description. Polyps may contain one, two, three or many stomodæa, hence range from mono- to poly-stomodæal conditions.

Buds are new polyps formed outside or inside the tentacular rings of older polyps.

Mother-polyps are those polyps in which intra-tentacular buds are formed.

18. *Symmetry :*

Radial.—The repetition of similar parts (mesenteries and cœlenteric spaces) around the stomodæa.

Hexameral.—The presence of six, or some multiple of six, mesenteries around a stomodæum.

Bilateral.—Indicated by the compression of the stomodæum and the presence of a directive couple of mesenteries at each of its ends.

Biradial.—Bilateral symmetry combined with radial symmetry.

19. *Valley.*—Part of the corallum in which a polystomodæal polyp lies.

REFERENCES.

(1) Blochmann, F., and Hilger, C. "Ueber Gonactinia prolifera, Sars." 'Morph. Jahrb.,' vol. XIII, p. 385 (1888).

(2) Bourne, G. C. "The Anatomy of *Mussa* and *Euphyllia* and the Morphology of the Madreporarian Skeleton." 'Quart. Journ. Micr. Sci.,' vol. XXVIII, p. 21 (1888).

(3) Boveri, Th. von. "Das Genus *Gyractis*." 'Zool. Jahrb.,' vol. VII, p. 241 (1893).

(4) Calgren, Oskar. "Studien über Nordische Actinien." 'Kongl. Svenska Vetenskaps-Akademiens Handlingar, Stockholm,' vol. 25, No. 10 (1893).

(5) Dixon, F. "On the Arrangement of the Mesenteries in the Genus *Sagartia*, Gosse." 'Sci. Proc. Roy. Dublin Soc.,' N.S., vol. VI, p. 136 (1888).

(6) Dixon, G. Y. "Remarks on *Sagartia venusta* and *Sagartia nivea*." 'Sci. Proc. Roy. Dublin Soc.,' N.S., vol. VI, p. 111 (1888).

(7) Dixon, G. Y. and A. F. "Notes on *Bunodes thallia*, *Bunodes verrucosa* and *Tealia crassicornis*." 'Sci. Proc. Roy. Dublin Soc.,' N.S., vol. VI, p. 310 (1889).

(8) *Idem.* "Report on the Marine Invertebrate Fauna near Dublin." 'Proc. Roy. Irish Acad.,' 3rd ser., vol. II, p. 19 (1891).

(9) Duerden, J. E. "West Indian Madreporarian Polyps." 'Nat. Acad. Sci., U.S.A., vol. VIII, p. 403 (1902).

(10) *Idem.* "The Morphology of the Madreporaria." II.—"Increase of Mesenteries in Madreporaria beyond the Protocnemic Stage." 'Johns Hopkins University Circulars,' vol. XXI, No. 157, p. 59 (1902); and 'Ann. Mag. Nat. Hist.,' ser. 7, vol. X, p. 96 (1902).

(11) *Idem.* III. "The Significance of Budding and Fission." 'Ann. Mag. Nat. Hist.,' ser. 7, vol. X, p. 382 (1902).

(12) *Idem.* IV. "Fissiparous Gemmation." 'Ann. Mag. Nat. Hist.,' ser. 7, vol. XI, p. 141 (1903).

(13) Foot, F. J. "Notes on the Astræacea of the Coast of Clare." 'Proc. Nat. Hist. Soc., Dublin,' vol. III, p. 63. (1863).

(14) Fowler, G. H. "The Anatomy of the Madreporaria." II. "*Madrepora*," 'Quart. Journ. Micr. Sci.,' vol. XXVII, p. 1 (1887); and 'Stud. Owen's Coll.,' vol. II, p. 1 (1890).

(15) *Idem.* III. "*Turbinaria*, *Lophohelia*, *Seriatopora*, *Pocillopora*." 'Quart. Journ. Micr. Sci.,' vol. XXVIII, p. 1 (1888); and 'Stud. Owen's Coll.,' vol. II, p. 17, (1890).

(16) Gardiner, J. Stanley. "On the Anatomy of a supposed New Species of *Cœnopsammia* from Lifu." 'Willey Zool. Results,' Part IV, p. 357 (1899).

(17) Gardiner, J. Stanley. "South African Corals of the Genus *Flabellum*, with an account of their anatomy and development." 'Marine Invest., South Africa,' vol. II, p. 117 (1902).

(18) *Idem.* "Fauna Geogr. Maldives and Laccadives," pp. 953 and 954 (1904).

(19) GOSSE, P. H. 'Actinologia Britannica: A History of the British Sea Anemones and Corals,' London (1860).

(20) JOHNSTON, G. "A History of the British Zoophytes," 2nd ed., London (1847).

(21) KWIETNIEWSKI, C. R. "Actiniaria von Ternate." 'Abhandl. Senckenberg. Gesellsch.,' vol. XXIII (1897).

(22) MATTHAI, GEORGE. "A Revision of the Recent Colonial Astræidæ possessing Distinct Corallites." 'Trans. Linn. Soc., London,' 2nd ser., Zool., vol. XVII, p. 1 (1914).

(23) *Idem.* "On *Favia conferta*, Verrill, with Notes on other Atlantic Species of Favia." 'British Antarctic ("Terra Nova") Expedition, Nat. Hist. Report, Zool.,' vol. V, No. 2 (1919).

(24) McMURRICH, J. PLAYFAIR. "Contributions on the Morphology of the Actinozoa." II. "On the Development of the Hexactiniæ." 'Journ. Morph.,' vol. IV, p. 303 (1891).

(25) *Idem.* III. "The Phylogeny of the Actinozoa." 'Journ. Morph.,' vol. V, p. 125 (1891).

(26) *Idem.* IV. "On some Irregularities in the Number of the Directive Mesenteries in the Hexactiniæ." 'Zool. Bull.,' vol. I, No. 3, p. 115 (1897).

(27) PARKER, G. H. "The Mesenteries and Siphonoglyphs in *Metridium marginatum* Milne Edwards." 'Bull. Mus. Comp. Zool.,' vol. XXX, No. 5, p. 259 (1897).

(28) *Idem.* "Longitudinal Fission in *Metridium marginatum* Milne Edwards." 'Bull. Mus. Comp. Zool.,' vol. XXXV, No. 3, p. 43 (1899).

(29) THORELL, T. "Om den inre Byggnaden af Actinia plumosa Müll." 'Öfversigt af Kongl. Vetenskaps. Akademiens Förhandlingar, Stockholm,' Bd. 15, No. 1, p. 7 (1859).

(30) TORREY, HARRY BEAL. "Observations on Monogenesis in Metridium." 'Proc. California Acad. Sci.,' 3rd ser., Zool., vol. I, p. 345 (1898).

(31) TORREY, HARRY BEAL, and MERY, JANET RUTH. "Regeneration and non-sexual Reproduction in *Sagartia Davisi*." 'Univ. California Pub. Zool.,' vol. I, No. 6, p. 211 (1904).

(32) WILSON, HENRY V. "On the Development of *Manicina areolata*." 'Journ. Morph.,' vol. II, p. 191 (1889).

EXPLANATION OF PLATES.

a, oral view of polyp; *b*, basal view of same.

(Figured polyps were taken from decalcified colonies.)

PLATE 24.

FIGS. 1–17. Intra-tentacular budding. FIGS. 1–9. *Favia favus* (FORSK.). Red Sea. × 2.

FIGS. 1–3.—Monostomodæal polyps showing stages of development of intra-tentacular diverticula. Diverticula narrower than mother-polyps. (Text-fig. 2 is a transverse section through stomodæal region of fig. 2.)


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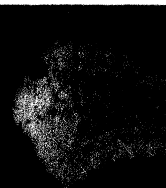
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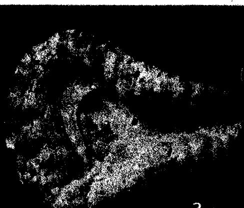
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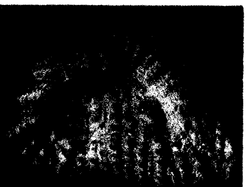
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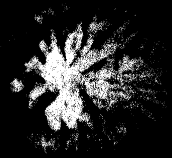
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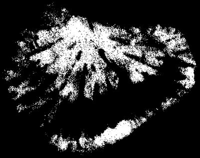
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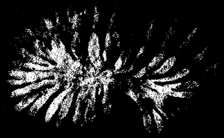
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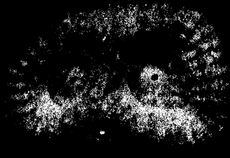
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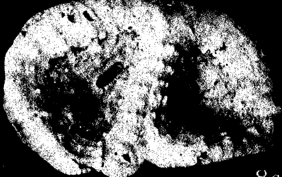
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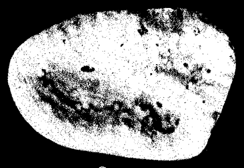
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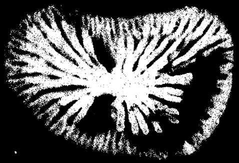
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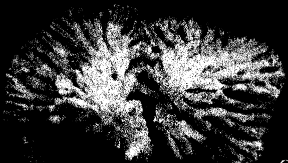
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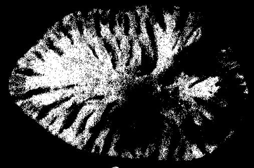
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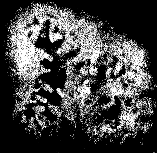
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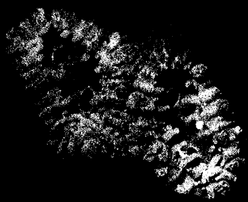
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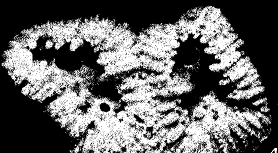
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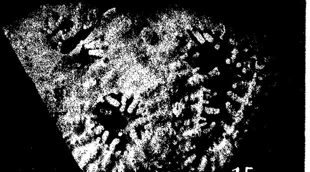
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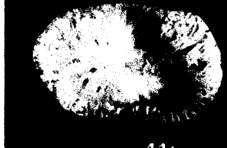
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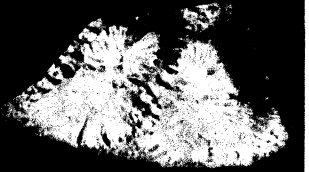
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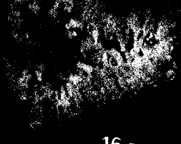
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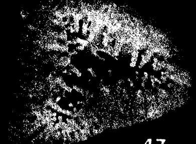
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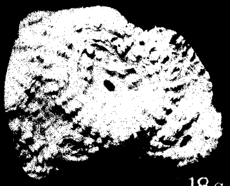
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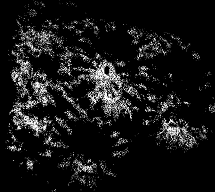
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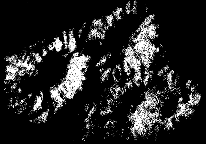
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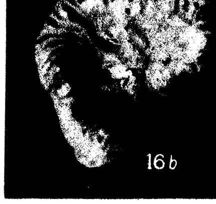
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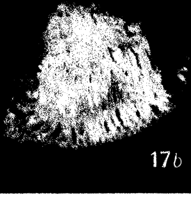
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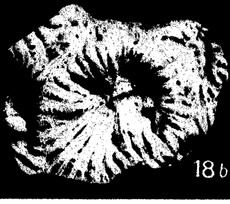
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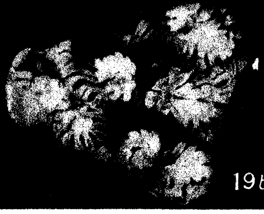
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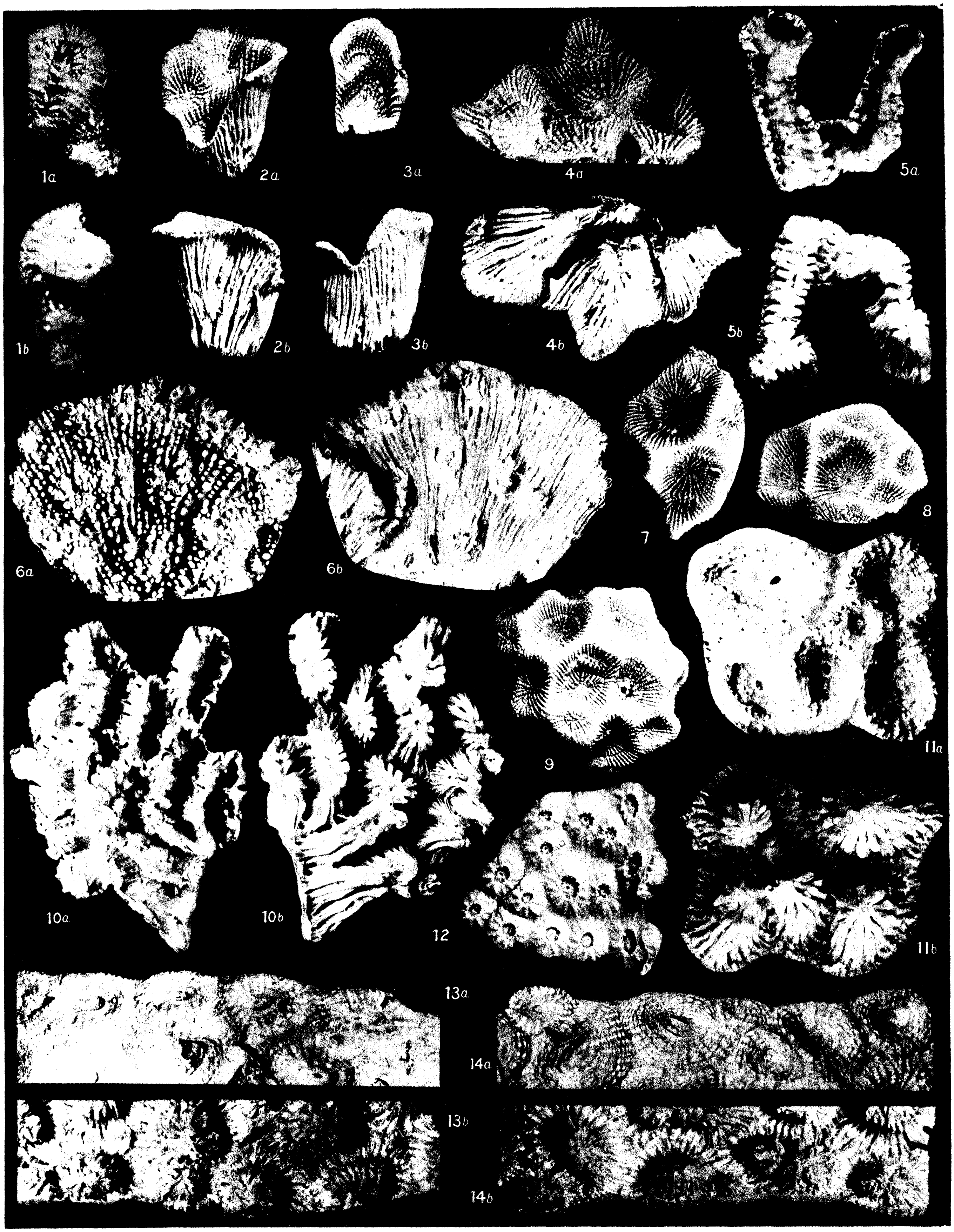
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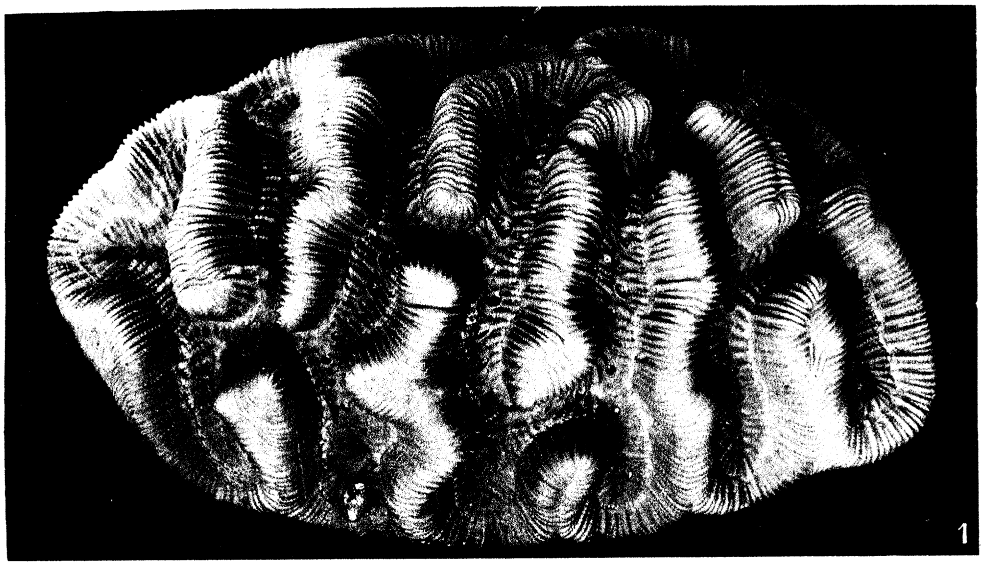
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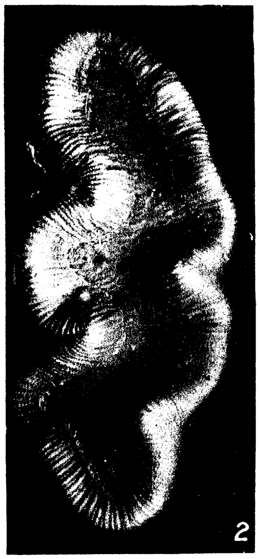
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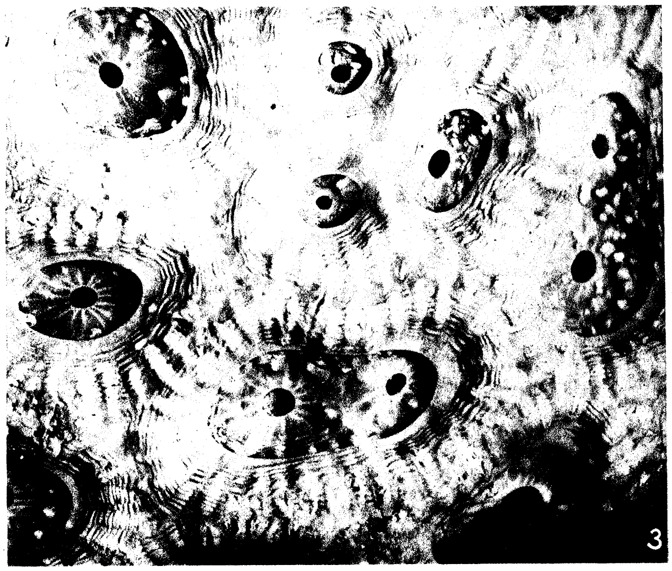
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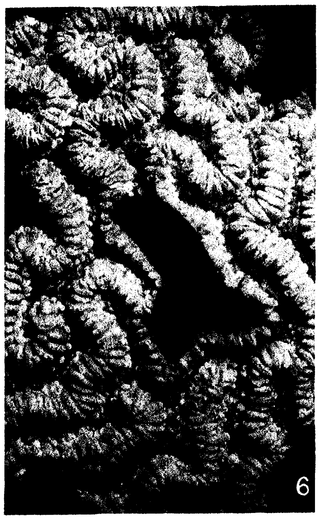
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FIGS. 4 and 5.—Distomodæal polyps, each with a single elongated tentacular ring. (Fig. 5 is from the edge of a colony.)

FIGS. 6 and 7.—Distomodæal polyps in which a distinct tentacular ring has been formed around each mouth-opening. Column-walls still continuous.

FIG. 8.—A mother-polyp and bud whose column-walls have been completely separated.

FIG. 9.—Large monostomodæal polyp to left (probably original mother-polyp) with distomodæal polyp to right; the tentacular ring separating the latter is clearly shown. The distomodæal polyp appears to come under II (*d*) on p. 323.

FIG. 10.—*Favia hululensis*, GARD.—A distomodæal polyp with two distinct tentacular rings but column-walls continuous; appears to come under II (*d*) on p. 323.

FIGS. 11–17.—*Favia fragum* (ESP.).—West Indian region. × 3.

FIG. 11.—A distomodæal polyp with a single elongated tentacular ring.

FIG. 12.—A distomodæal polyp with tentacular ring considerably constricted between the two mouth-openings. The left half of polyp is elongated, perhaps for future triangular tristomodæal condition.

FIG. 13.—Two distomodæal polyps, each with a single elongated oral-disc containing two mouth-openings. Column-walls of polyps quite separate.

FIG. 14.—A distomodæal and a monostomodæal polyp, the latter with an intra-tentacular diverticulum. Column-walls of polyps quite separate.

FIG. 15.—Two distomodæal polyps. Left polyp with two distinct tentacular rings, but column-wall not yet completely divided. Right polyp with a single elongated tentacular ring, presumably to assume later the triangular tristomodæal condition.

FIG. 16.—Triangular tristomodæal polyp, from edge of a colony. Three mouth-openings at the corners of the triangular oral-disc. Mouth-opening of mother-polyp to right; mouth-openings of pair of buds to left, at extreme edge of colony. Basal view (fig. 16 *b*) shows a single column-wall. (Text-fig. 10 is a transverse section through stomodæal region of this polyp.)

FIG. 17.—A triangular tristomodæal polyp with a common tentacular boundary.

FIGS. 18–20.—Extra-tentacular budding.

FIG. 18.—*Favia favus* (FORSK.).—A large monostomodæal polyp and two small extra-tentacular buds at the extreme edge of colony. (Text-fig. 21 is transverse section through stomodæal region of this piece.) × 2.

FIGS. 19 and 20.—*Favia hululensis*, GARD. × 2.

FIG. 19.—A row of extra-tentacular buds at extreme edge of colony to left.

FIG. 20.—Two extra-tentacular buds at lower margin (edge of colony). (The extra-tentacular diverticulum of text-figs. 22 *a* and *b* is seen at lower margin between the buds and monostomodæal polyp to left.)

PLATE 25.

FIG. 1.—*Favia fragum* (ESP.).—A piece containing a distomodæal polyp and two extra-tentacular buds, from the edge of a colony. (Text-fig. 6 is a transverse section through stomodæal region of this distomodæal polyp.) West Indian region. × 3.

FIGS. 2–4.—*Favia abdita* (ELL. and SOL.).—Pieces from a colony, showing extra-tentacular budding. Buds small and placed obliquely at a higher level than polyps. (Text-fig. 20 is a transverse section through stomodæal region of fig. 2.) Hulule, Maldives. × 2.

FIG. 5.—*Cœloria dœdalca* (ELL. and SOL.).—A piece from a colony, containing two short polystomodæal polyps. Hulule, Maldives. × 2.

FIG. 6.—*Echinopora lamellosa* (ESP.).—A piece from a colony, showing extra-tentacular budding. Small buds along upper margin (edge of colony). Column-walls of polyps (fig. 6 *b*) oblique in position. Hulule, Maldives. × 3.

FIGS. 7–9.—*Favia abdita* (ELL. and SOL.).—Oral views of undecalcified pieces from three colonies, showing extra-tentacular budding. Hulule, Maldives. × 2.

FIG. 10.—*Cœloria dædalea* (ELL. and SOL.).—A piece from a colony, containing monostomodæal to short discontinuous polystomodæal polyps, from same colony as fig. 5. Hulule, Maldives. × 2.

FIG. 11.—*Favia favus* (FORSK.).—A piece from a colony, containing monostomodæal and distomodæal polyps. The smallest polyp, with distinct column-wall, is probably an extra-tentacular bud. Red Sea. × 2.

FIG. 12.—*Orbicella annularis* (ELL. and SOL.).—A piece from a colony, showing extra-tentacular budding. West Indian region. × 3.

FIGS. 13 and 14.—*Favia favus* (FORSK.).—Two pieces from edge of a colony, showing extra-tentacular buds along free margins. Red Sea. × 2.

PLATE 26.

FIG. 1.—*Manicina areolata* (LINN.).—Oral view of a full-grown undecalcified colony, the soft parts forming a single meandering polystomodæal polyp. Many of the mouth-openings are in a distended condition. West Indian region. Nat. size.

FIG. 2.—*Manicina areolata* (LINN.).—Oral view of a young undecalcified colony. West Indian region. Nat. size.

FIG. 3.—*Favia favus* (FORSK.).—Oral view of part of an undecalcified colony. Note distomodæal and monostomodæal polyps. Red Sea. × 3.

FIG. 4.—*Colpophyllia gyrosa* (ELL. and SOL.).—Oral view of part of a decalcified colony. A single polystomodæal polyp with forked ends, to left of fig.; a single mouth-opening in each arm of the fork. A lateral bud on each side of polyp. West Indian region. × 3.

FIG. 5.—*Leptoria gracilis*, DANA.—Oral view of part of a colony, showing meandering polystomodæal condition with lateral branching and terminal forking. Hulule, Maldives. × 2.

FIG. 6.—*Leptoria gracilis*, DANA.—Oral view of part of a decalcified colony. Hulule, Maldives. × 2.

FIG. 7.—Basal view of above. × 2.

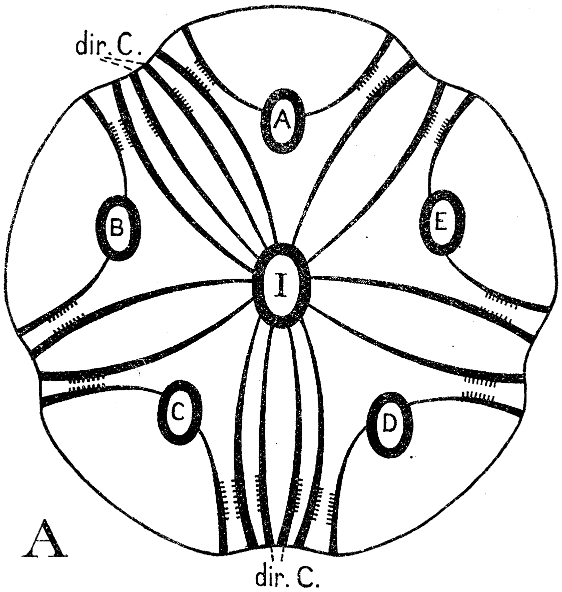
FIG. 8.—Basal view of fig. 4. Nat. size.

APPENDIX. (*Received August* 7, 1924.)

COLONY-FORMATION IN *Isophyllia, Symphyllia, Mussa, Manicina* AND *Merulina.*

Isophyllia (figs. 23A and B; Plate 27, figs. 1–14, 17).

During a stay at the Bermuda Biological station in the summer of 1915, I was able to collect many specimens of *Isophyllia*, ranging from the early attached mother-polyp, through an ascending series, to large colonies at the maximum size of growth. These were narcotised in the usual way in magnesium sulphate, and fixed by pouring 40 per cent. formaldehyde into sea water containing the narcotised colonies, and also by means of Flemming's fluid and corrosive acetic solution. A considerable number of attached stages and large entire colonies were dried for the study of the hard parts. Serial transverse sections of five of the early attached stages gave some indication of the mode of intra-tentacular budding characteristic of *Isophyllia*. A large number of live colonies were also kept under observation in the laboratory in aquaria of running



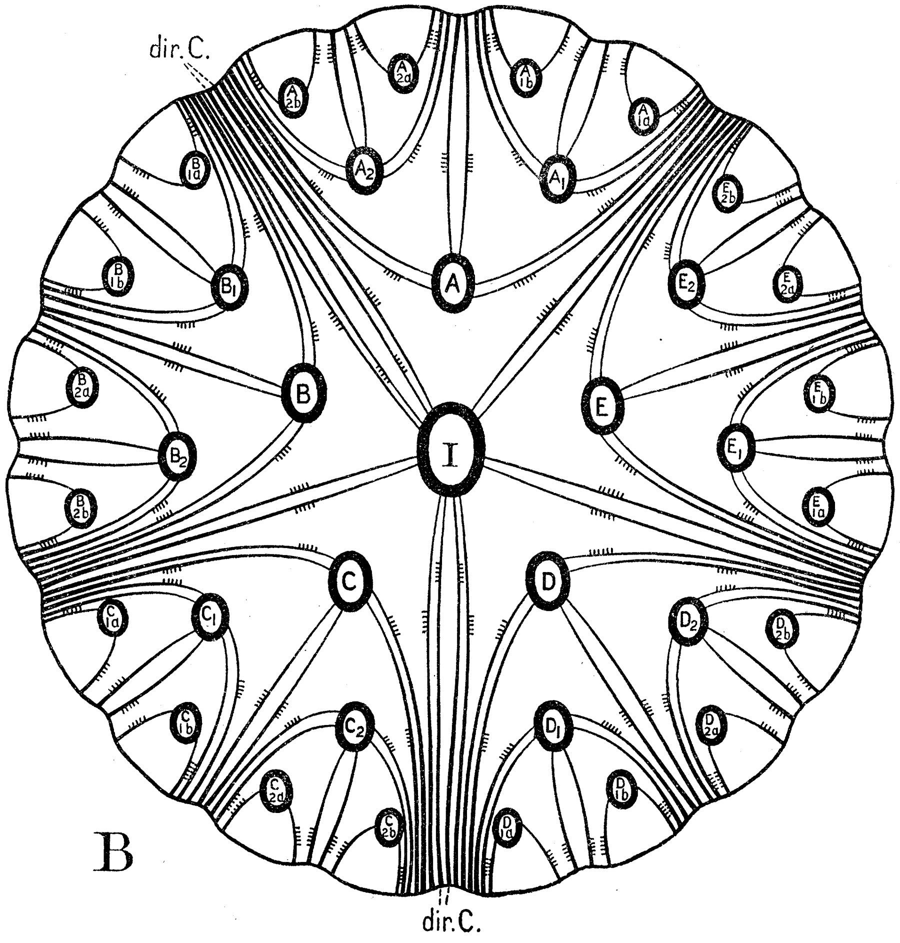


FIG. 23A.—*Isophyllia dipsacea* (DANA).—Diagrammatic representation of an early stage, showing a complete primary ring of five intra-tentacular buds around the mother-polyp. I, stomodæum of mother-polyp. A–E, stomodæa of primary buds. *dir.C.*, directive couple of mesenteries.

FIG. 23B.—*Isophyllia dipsacea* (DANA).—Later stage, showing secondary ring of 10 and tertiary ring of 20 intra-tentacular buds. I, A–E, as before. A_1, A_2,—E_1, E_2, stomodæa of secondary buds. A_1a,–A_1b, A_2a, A_2b—E_1a, E_1b, E_2a, E_2b, stomodæa of tertiary buds. *dir.C.*, directive couple of mesenteries.

sea water, *Isophyllia*, like *Manicina*, being greatly suited for study in the living condition.

Isophyllia is found in abundance around the group of islands constituting the Bermudas, attached to limestone rocks and other substrata. Two species have been recorded from this locality, viz., *I. dipsacea* (DANA) and *I. fragilis* (DANA), the former having heavier coralla and wider valleys than the latter. The species are subject to wide range of variation, contrasting in this respect with most other Atlantic Astræidæ north of Pernambuco. From their abundance and wide range of variation the Bermudian species of *Isophyllia*, unlike other coral species of the Atlantic region, appear to be in a flourishing condition.

Colony-formation in *I. dipsacea* and *I. fragilis* is by means of intra-tentacular budding around the stomodæum of the original mother-polyp, *i.e.*, by *circumoral intra-tentacular budding*.

The monostomodæal attached stage possesses two directive couples of mesenteries, and is hexameral in symmetry. In one such stage sectioned (700 *a* IV, length of oral-disc 4 mm., width 2·5 mm.)* occur two diverticula separated by an ordinary completely principal couple, each diverticulum possessing a continuous group of six subsidiary couples of mesenteries; between the remaining principal couples lie 1 to 3 subsidiary couples.

In a subsequent stage (700 *a* III, greatest length of oral-disc 13 mm., greatest width 7 mm.) there are three intra-tentacular buds, one on one side of the mother-polyp, the remaining two on the opposite side. Two directive couples of mesenteries are attached to the stomodæum of the mother-polyp.

The maximum number of intra-tentacular buds in the primary ring of a young colony of *Isophyllia dipsacea* (700 *a* V) is probably five. The stomodæa of the buds are related, on the distomodæal mode, to that of the mother-polyp, but are without any such relation among themselves. The two directive couples of mesenteries remain attached to the stomodæum of the mother-polyp.

Fig. 23A represents the stage with a complete primary ring of five buds around the mother-polyp, I being the stomodæum of the latter and A–E being the stomodæa of the former. Only the directive and interstomodæal couples are figured. Fig. 23B represents a colony containing, in addition to the primary ring of five buds, a secondary ring of ten and a tertiary ring of twenty buds. Each stomodæum of the primary ring is related, on the distomodæal mode, to two secondary stomodæa; each stomodæum of the secondary ring is similarly related to two stomodæa of the tertiary ring.

The formation of primary buds around the mother-polyp results in primary lobes;

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* The edge-zone of this polyp has fused with that of a distomodæal mother-polyp, but column-walls have remained separate; this condition is probably the result of the growth of two larvæ which settled side by side. I have obtained several other double colonies in the Bermudas. The youngest monostomodæal mother-polyp stage in the collection measured 3 mm. in width and 1·5 mm. in height, while a somewhat later stage of about the same height was 4 mm. in diameter.

similarly the appearance of secondary and tertiary buds give rise to lobes of the second and third order. Such rings of stomodæa and lobes are formed in succession outside the preceding ones, growth in *Isophyllia* being circumferential, not interstomodæal.

In *Isophyllia annectens* (VERRILL), colony-formation is by circumoral intra-tentacular budding as in *I. dipsacea*, but while, in the latter, this method results in colonies consisting, as a rule, of continuous polystomodæal polyps, in the former each colony finally becomes divided into discontinuous polystomodæal polyps, by the formation of complete transverse partitions. Such discontinuous polyps, not unusually, consist of a central stomodæum surrounded by three or more stomodæa. Mono-, di- or tri-stomodæal polyps, when present in these two species, are temporary stages in the formation of polystomodæal areas which simulate the intra-mural polystomodæal condition of genera such as *Cœloria*.

This is seen to be the case in a polyp consisting of a central stomodæum I and three additional stomodæa (II, III and IV) around it (240 *c* I, a piece from the edge of a colony from South Bight, Andros Island, Bahamas). There was some indication, on a surface view, that a distinct tentacular ring was being formed around stomodæum II, doubtless prior to separation from stomodæum I.

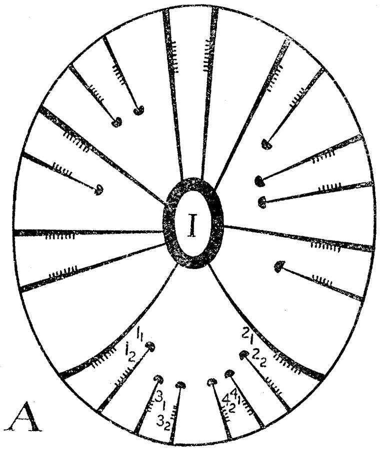
In *Mussa* (*Isophyllia*) *rigida* (DANA)—another Atlantic species—colonies are composed of mono-, bi- and tri-stomodæal polyps; polystomodæal condition is absent in full-grown colonies, although colony-formation appears to be by means of circum-oral intra-tentacular budding as is indicated by the presence of more than two intra-tentacular diverticula in some polyps (*e.g.*, 240 *b* I and III). But, of course, early attached stages are necessary for a final determination of the method of colony-formation in this species. My observations are based on three small colonies from South Bight, Andros Island, Bahamas, two of which have been decalcified. Three series of transverse sections of this species were studied. In a monostomodæal polyp from the middle of a colony (240 *b* II), two intra-tentacular diverticula containing respectively five and four subsidiary couples of mesenteries are clearly visible. In a distomodæal polyp (240 *b* III) from the edge of the same colony, stomodæum II has just begun to be invaginated (the mouth-opening was visible in the spirit specimen); the stomodæum itself is quite short, and to it three completely principal couples of mesenteries are attached; its inner lining (ectoderm) has not undergone sufficient modification to be clearly distinguishable, in transverse section, from the rest of the oral-disc ectoderm.

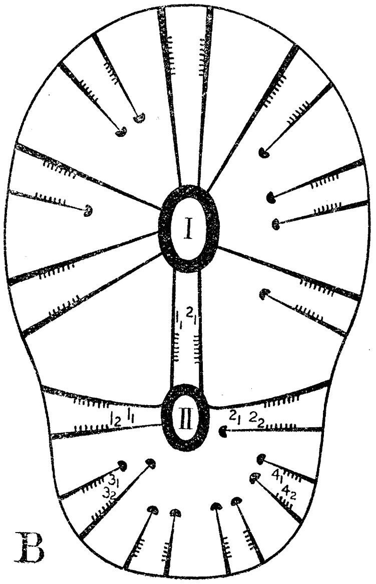
It is interesting to compare circum-oral budding, as seen in *Isophyllia dipsacea*, with circum-mural budding occurring in *Hydnophora microcona*:—(1) In both, rings of stomodæa are formed; (2) since these rings open into one another, each colony consists of a continuous polystomodæal polyp having a double row of tentacles and a continuous cœlenteric cavity; (3) the secondary stellate arrangement of stomodæa in *Hydnophora microcona* somewhat resembles the stage with the primary ring of stomodæa in *Isophyllia dipsacea*, since in both conditions a central stomodæum is surrounded by a ring of stomodæa. But there are important differences between the two conditions, viz., (1) in *Isophyllia dipsacea* budding is on the distomodæal mode, whilst in *H. microcona* budding is on the triple stomodæal mode; (2) the primary arrangement of buds is circum-oral in *Isophyllia*, circum-mural in *Hydnophora*; (3) in *Isophyllia* the rings of stomodæa have a somewhat concentric arrangement, whereas in *Hydnophora* the monticular rings (hence also the stellate groups) lie side by side; (4) in *Isophyllia* stomodæa of the primary ring are each related to the central stomodæum but not to one another, whereas in *H. microcona* the stomodæa of every monticular ring and stellate group are related to one another on the distomodæal mode; (5) in *I. dipsacea* the colline is continuous over the entire corallum, whilst in *H. microcona* discontinuous monticules are present.

In large colonies of *I. dipsacea*, the concentric arrangement of stomodæa is not so evident as in small colonies, since, in the former, the later buds are not regularly disposed into rings. Such colonies simulate the condition in *Manicina areolata*.

Symphyllia (figs. 24–26; Plate 28, fig. 14).

Colony-formation in *Symphyllia* is strikingly different from any of the other intra-tentacular modes that I have investigated. Two series of transverse sections have been examined; one of these (115 *a* I,, 23 mm. long and 22 mm. broad in alcohol) was a lateral lobe





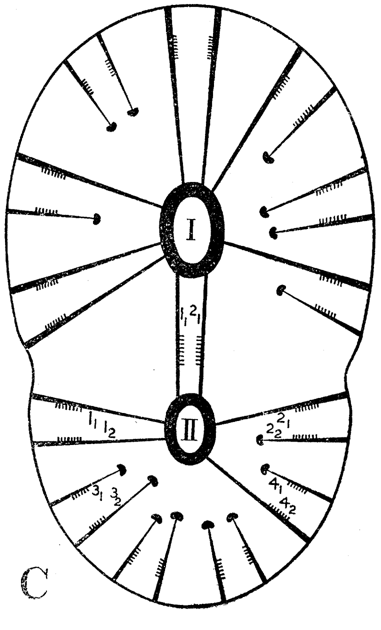


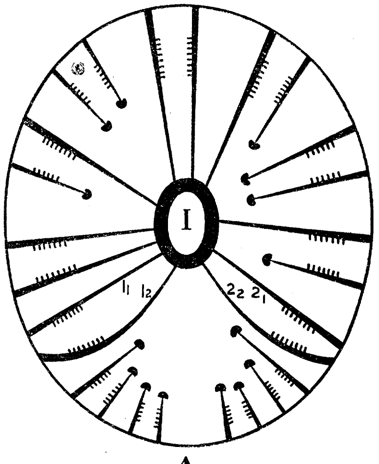
FIG. 24A.—*Symphyllia sinuosa* (QUOY and GAIM). Diagrammatic representation of a monostomodæal polyp, showing the formation of an intra-tentacular diverticulum between mesenteries 1_1 and 2_1. I, stomodæum of polyp.

FIG. 24B.—*Symphyllia sinusoa* (QUOY and GAIM). Diagrammatic representation of a stage showing the conversion of the intra-tentacular diverticulum into a bud, and the formation of mesenterial strands connecting the two stomodæa. I, stomodæum of polyp. II, stomodæum of intra-tentacular bud.

FIG. 24C.—*Symphyllia sinuosa* (QUOY and GAIM). Diagrammatic representation of a stage in which the inner halves of mesenteries 1_1 and 2_1 have become definite strands connecting stomodæa I and II.

which had begun to fork at its blind end, containing three stomodæa in a linear row, and a stomodæum in each arm of the fork. The colony, from which the piece was taken, was probably from the Maldives, well preserved, consisting of a continuous, though comparatively small, polystomodæal polyp. The second piece (115 *y* I, 22 mm. in diameter) was taken from a colony, from Rotuma, consisting of a median region and two pairs of lateral lobes.

The invariable presence of one or two mesenterial strands connecting neighbouring stomodæa is a highly significant fact which suggests that intra-tentacular budding in *Symphyllia* takes place in some such manner as is represented in the figs. 24A, B and C. Fig. 24A is a monostomodæal polyp in which an intra-tentacular diverticulum is being formed between mesenteries 1_1 and 2_1, stomodæum I being the stomodæum of the polyp. In fig. 24B stomodæum II has been formed in the diverticulum which has thus become a bud, and the two principal mesenteries 1_1 and 2_1 have been bent towards it in such a manner that they have joined stomodæum II at their bents; the subsidiary mesentery 1_2 has also met the new stomodæum. In fig. 24C the direct continuity



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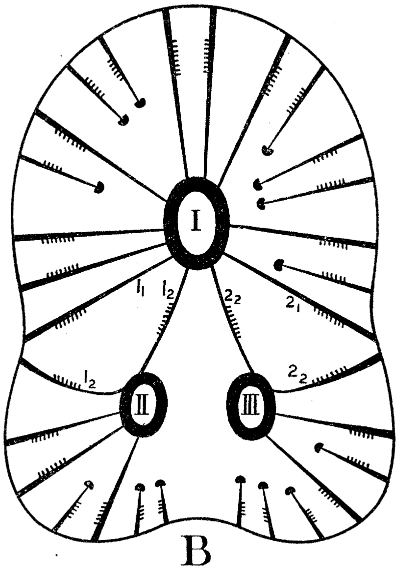

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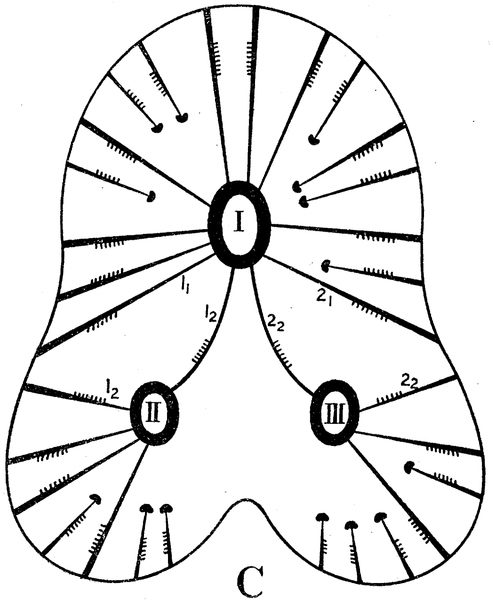

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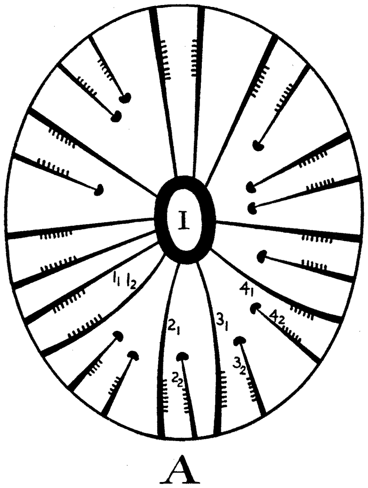
FIG. 25A.—*Symphyllia sinuosa* (QUOY and GAIM). Diagrammatic representation of a monostomodæal polyp, showing the formation of a double intra-tentacular diverticulum between mesenteries 1_2 and 2_2. I, stomodæum of polyp.

FIG. 25B.—*Symphyllia sinuosa* (QUOY and GAIM). Diagrammatic representation of a stage showing the conversion of the double intra-tentacular diverticulum into a pair of buds, and the formation of mesenterial strands connecting the stomodæa. I, stomodæum of polyp. II and III, stomodæa of buds.

FIG. 25C.—*Symphyllia sinuosa* (QUOY and GAIM). Diagrammatic representation of a stage in which the inner halves of mesenteries 1_2 and 2_2 have become definite strands connecting I with II and I with III.

between the two halves of the mesentery 1_1 and of 2_1 have been lost, so that, at this stage, the inner halves of 1_1 and 2_1 appear like two connecting strands between stomodæa I and II, with their pleats facing each other. Additional couples may appear between stomodæa I and II, one or two of which may subsequently become interstomodæal.

If mesenteries 1_2 and 2_2 have joined stomodæum I and are bent towards and fuse with the new stomodæum II, the inner halves of these two mesenteries would appear like a directive couple linking the two stomodæa. In the above two cases, if interstomodæal couples appear, they would be new formations. But if mesentery 2_2 joined stomodæum I, and stomodæum II caught up mesenteries 1_1 and 2_2 at their bents, the inner halves of these mesenteries, linking the two stomodæa, would not form a couple, since their pleats would face the same side. An interstomodæal couple would appear on the right side, *i.e.*, the side towards which the pleats of the connecting mesenterial strands are directed, formed by 2_1 attached to stomodæum I and the outer half of 2_2 joined to stomodæum II. Finally, if mesentery 1_2 had met stomo-



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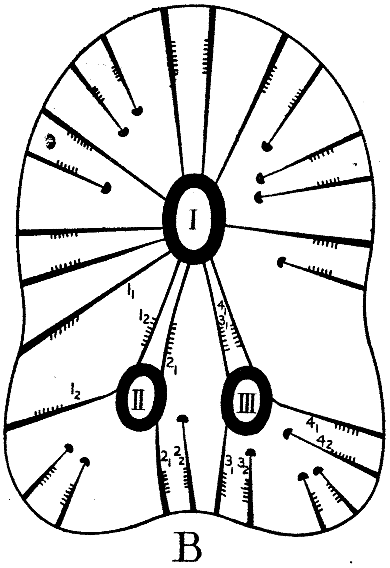

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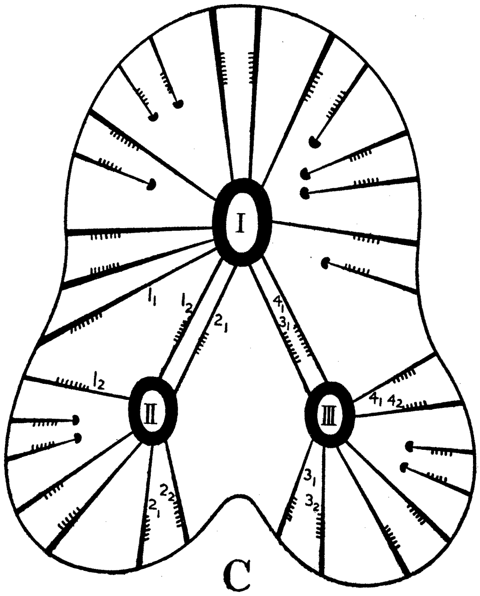

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FIG. 26A.—*Symphyllia sinuosa* (QUOY and GAIM). Diagrammatic representation of a monostomodæal polyp, showing the formation of two intra-tentacular diverticula, one between mesenteries 1_2 and 2_1 and the other between 3_1 and 4_1. I, stomodæum of polyp.

FIG. 26B.—*Symphyllia sinuosa* (QUOY and GAIM). Diagrammatic representation of a stage showing the conversion of the intra-tentacular diverticula into buds, and the formation of double mesenterial strands connecting stomodæa. I, stomodæum of polyp. II and III, stomodæa of buds.

FIG. 26C.—*Symphyllia sinuosa* (QUOY and GAIM). Diagrammatic representation of a stage in which the inner halves of mesenteries 1_2 and 2_1, 3_1 and 4_1 have become definite strands connecting I with II and I with III.

dæum I, and mesenteries 1_2 and 2_1 joined stomodæum II, an interstomodæal couple, viz., 1_1 attached to stomodæum I and the outer half of 1_2 meeting stomodæum II, would be formed on the left side towards which the pleats of the two linking mesenterial strands would also be directed.

It would be seen from the above suggestions that, in *Symphyllia*, the presence of mesenterial strands stretching between adjacent stomodæa is the primary condition, whilst interstomodæal couples may or may not be present. In other words, whilst in *Cœloria*, *Leptoria*, etc., adjacent stomodæa are *indirectly* connected by interstomodæal couples, in *Symphyllia* neighbouring stomodæa are *directly* connected by mesenterial strands. The latter condition may be termed *direct linkage* of stomodæa, and the former *indirect linkage* of stomodæa.

DUERDEN noted the presence of one or two mesenterial strands stretching between two stomodæa in *Porites* (10), but does not give an adequate explanation of their occurrence. In any case, the presence of such connecting mesenterial strands cannot be explained on the hypothesis of stomodæal fission, unless they are regarded as having appeared *de novo* subsequently to fission.

In terminal forking or dichotomous branching, as seen in *Symphyllia*, the terminal stomodæum is linked to the stomodæum of each bud by means of a mesenterial strand. The probable formation of these mesenterial strands is represented by figs. 25A–C. Fig. 25A shows a monostomodæal polyp (its stomodæum being marked I) in which a double intra-tentacular diverticulum is being formed between mesenteries 1_2 and 2_2; in fig. 25B, two new stomodæa (II and III) have been formed, mesenteries 1_2 and 2_2 having been arched towards II and III and met their respective stomodæa at their bents. In fig. 25C, the direct connection between the two halves of 1_2 and of 2_2 is lost, with the result that, at this stage, stomodæum I is linked with stomodæum II by a mesenterial strand which is the inner half of 1_2; similarly stomodæum I is linked with stomodæum III by a mesenterial strand, which is the inner half of 2_2; the outer halves of these mesenteries remain as principal mesenteries of stomodæa II and III respectively. There is no direct linkage between the stomodæa of buds II and III. In this case, the pleats of the connecting mesenterial strands between stomodæa I and II, and between I and III, are turned away from each other, as in a directive couple; stomodæa I and II are also indirectly connected by means of a completely principal interstomodæal couple, such a connection subsisting between I and III as well. It is not clear, from the sections, whether there was such indirect linkage between the stomodæa of buds II and III.

Another type of dichotomous branching is possible in *Symphyllia*, as illustrated by figs. 26A–C. Fig. 26A represents a monostomodæal polyp in which two intra-tentacular diverticula are being formed, one between 1_2 and 2_1 and the other between 3_1 and 4_1. In fig. 26B, a new stomodæum has been formed in each diverticulum, thus turning it into a bud. Mesenteries 1_2 and 2_1 have arched towards and met II, whilst 3_1 and 4_1 have similarly met III. In fig. 26C the continuity between the two halves of 1_2, 2_1, 3_1 and of 4_1 has been lost, so that the inner halves of mesenteries 1_2 and 2_1 form a directive couple of connecting strands between stomodæa I and II, and the inner halves of mesenteries 3_1 and 4_1 form an ordinary couple of linking strands between stomodæa I and III. It is conceivable that, in double linkage of stomodæa in a forked end, other mesenterial arrangements may occur, viz., both the double strands may form directive couples, or both ordinary couples, or they may not form couples at all. Stomodæa I and II are indirectly connected by means of an interstomodæal couple; a similar indirect connection may subsist between I and III, and perhaps between II and III.

In the second series of transverse sections (115 *y* I) the relations of some of the mesenteries at the cut end of the piece cannot be determined. Nine completely principal and two incompletely principal couples are clearly seen; in addition, four principal mesenteries are visible at the cut end, but their column-wall attachments have been lost; of the latter, one or two are, perhaps, linking mesenterial strands between this stomodæum and the next. Of over twenty-five subsidiary couples, there are two groups of nine and six couples, the former at one corner and the latter at the other corner of the blind end of the piece, perhaps forming two intra-tentacular diverticula.

Young colonies of *Symphyllia* are composed of continuous polystomodæal polyps; as colonies increase in size, transverse partitions appear here and there, forming discontinuous polystomodæal polyps, which remain sinuous. Colonies of *Symphyllia* attain to a much larger size than those of *Isophyllia*, and have thick, massive corolla.

Mussa (Plate 28, figs. 4–11, 13).

In *Mussa corymbosa*, budding results in branching colonies, as in *Euphyllia* and *Eusmilia*. The growth-form is arborescent, the connection between polyps on the branches being maintained by the extensive cœnosarcal regions, which, however, in course of growth, often lose their organic continuity. Short discontinuous polystomodæal condition is the permanent feature of this species. Mono-, di- and tri-stomodæal polyps, which are not infrequently present, are temporary stages; these, with further growth, lead to the polystomodæal condition. The presence of septal bridges between columellar centres would suggest that corresponding mesenterial strands directly link adjacent stomodæa. Budding is intra-mural in this genus, as in *Symphyllia*. In the latter the polystomodæal polyps are long and sinuous, though discontinuous, and the adjacent walls of valleys are completely fused, forming massive colonies, whilst in *M. corymbosa* the discontinuous polystomodæal polyps are short and the walls of valleys are free except where branching takes place.

Manicina (Plate 26, figs. 1 and 2; Plate 27, figs. 15, 16, 18, and 19; Plate 28, figs. 1–3).

Colony-formation is by intra-mural budding accompanied by lateral and dichotomous branching as in *Colpophyllia*, the soft parts of the colony usually consisting of a sinuous polystomodæal polyp.

Merulina (fig. 27).

In two species of *Merulina* which have been examined, viz., *M. ampliata* and *M. maldivensis*, colony-formation takes place by repeated lateral budding on the distomodæal mode and terminal forking (*i.e.*, on the tristomodæal and triple stomodæal modes), branching being invariably at an acute angle. Both species are restricted to the Indo-Pacific region; large colonies of *M. ampliata* were obtained from Ceylon, Maldives and Red Sea (?), representatives of which were also studied in Washington; only small pieces of *M. maldivensis* were dredged from Maldives. Colonies are characterised by a fan-wise mode of growth, being usually thin and spreading and more or less flat. When parts of colonies grow into upright columns, lateral branching of polyps takes place around the columns. Polyps are invariably linear, many of them extending from edge to edge over entire length of calicinal surface, but are not sinuous nor branching

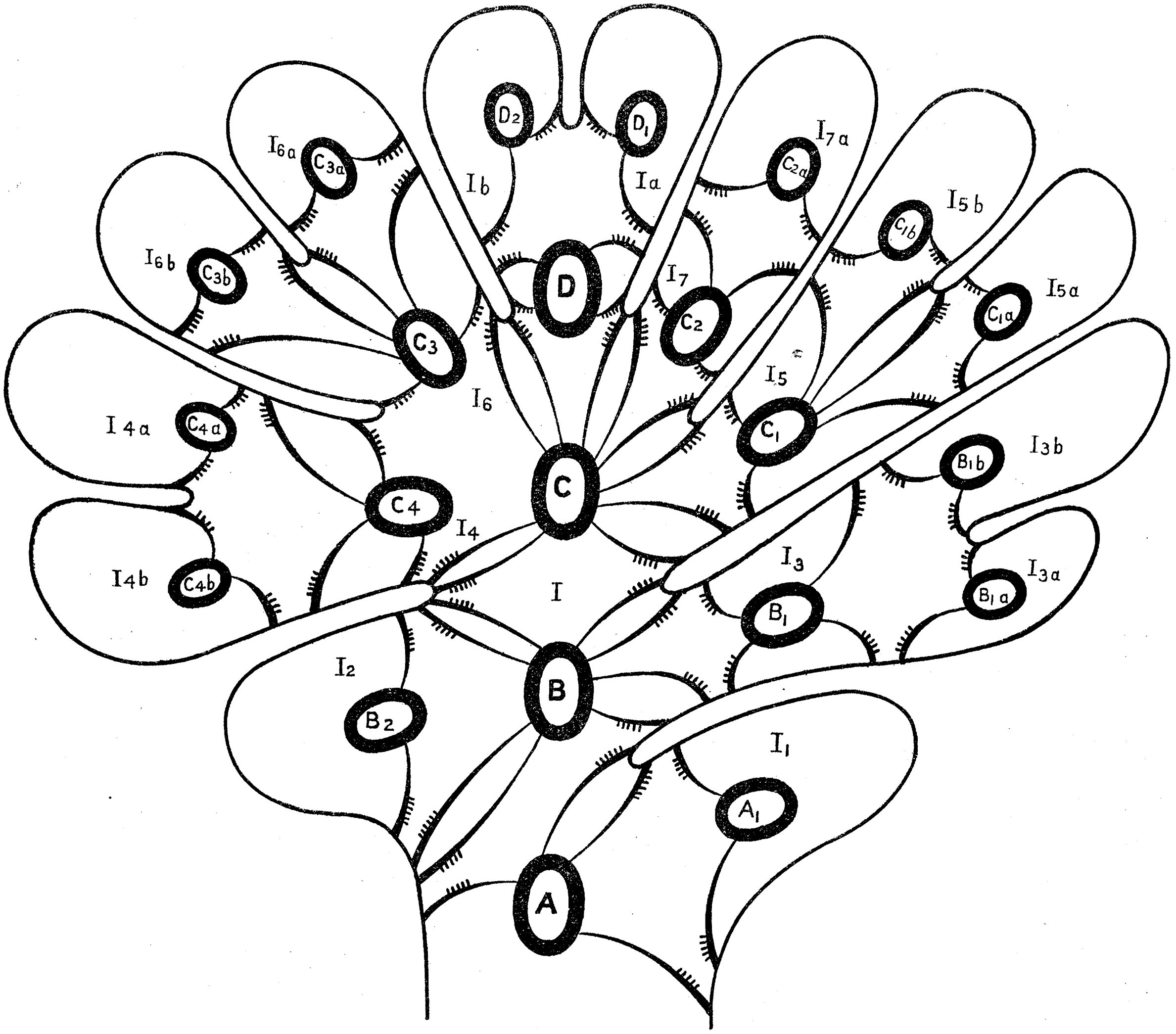


FIG. 27.—*Merulina ampliata* (ELL. and SOL.).—Diagrammatic representation of colony-formation.

in the transverse plane; they are somewhat oblique, with one side often higher than the other, and are restricted to the upper surface; owing to the oblique shape of polyps, principal mesenteries vary greatly in length.

Fig. 27 represents the method of colony-formation in *Merulina*. Stomodæa A, B, C, D form a linear series along the middle of a colony to which stomodæa A_1, B_1, C_1 and C_2 on the right and B_2 on the left are related on the distomodæal mode, whilst C_3 and C_4 and D_1 and D_2 are connected, respectively, to C and D, on the triple stomodæal mode. Stomodæa C_1a and C_1b, and C_3a and C_3b are related, on the tristomodæal mode, to C_1 and C_3; B_1a and B_1b, and C_4a and C_4b, on the triple stomodæal mode, to B_1 and C_4; C_2a, on the distomodæal mode, to C_2. The median valley is numbered I, the lateral branches on the right I_1, I_3, I_5 and I_7; I_2 being the only lateral branch on the left. I*a* and I*b*, I_4 and I_6, I_3a and I_3b, I_4a and I_4b, I_5a and I_5b, I_6a and I_6b, are formed by dichotomous branching. It would be noticed that, in all these cases, branching takes place at an acute angle and the colony spreads outwards fan-wise.

EXPLANATION OF PLATES.

PLATE 27.

(Views of polyps from decalcified colonies.)

FIGS. 1–14.—*Isophyllia dipsacea* (DANA). Bermudas.

FIGS. 1–5.—Monostomodæal mother-polyps at different stages of growth. × 3. Fig. 1 is of 700 *a* I and fig. 3 of 700 *a* II.

FIG. 6.—Distomodæal mother-polyp, showing the stage with two circumscribed oral-disc areas. × 2.

FIG. 7.—Tristomodæal mother-polyp. × 2.

FIG. 8.—Mother-polyp with four primary intra-tentacular lobes around central mouth. × 2.

FIG. 9.—Mother-polyp with four primary intra-tentacular lobes around central mouth; in each lobe a mouth-opening is visible. × 2.

FIG. 10.—Mother-polyp with five primary intra-tentacular lobes around central mouth. × 2.

FIG. 11.—Mother-polyp with five primary intra-tentacular lobes around central mouth; the primary lobe on the left has given rise to a secondary intra-tentacular lobe. × 2.

FIG. 12.—Distomodæal mother-polyp. 700 *a* IV. × 3.

FIG. 13.—Distomodæal mother-polyp in which a third mouth has begun to be formed. 700 *a* III. × 3.

FIG. 14.—Distomodæal mother-polyp, with three additional primary intra-tentacular lobes in which mouth-openings have not yet appeared. × 3.

FIGS. 15, 16 and 18.—*Manicina areolata* (LINN.). Tortugas, Caribbean Sea. Monostomodæal mother-polyps at different stages of growth. × 3.

FIG. 17.—*Isophyllia dipsacea* (DANA). Bermudas. Mother-polyp with five primary intra-tentacular lobes around central mouth; the primary lobe on the left has given rise to a secondary intra-tentacular lobe.

FIG. 19.—*Manicina areolata* (LINN.). Tortugas, Caribbean Sea. Distomodæal mother-polyp.

PLATE 28.

FIGS. 1–3.—*Manicina areolata* (LINN.). Tortugas. Decalcified mother-polyps. × 3.

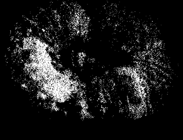
FIG. 1.—Distomodæal mother-polyp.

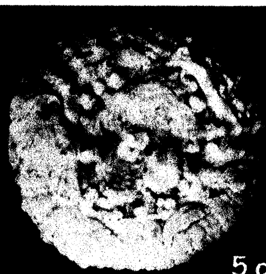
FIGS. 2 and 3.—Tristomodæal mother-polyp.


1a.


2a


3a


4a


5a


6a


1b

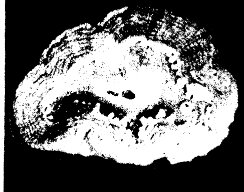

2b


3b


4b


5b


6b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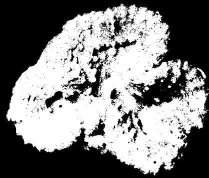
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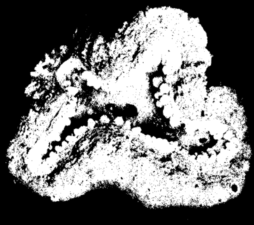
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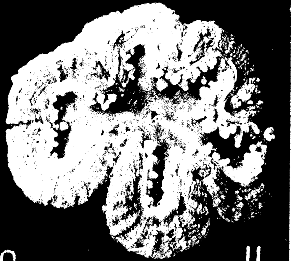
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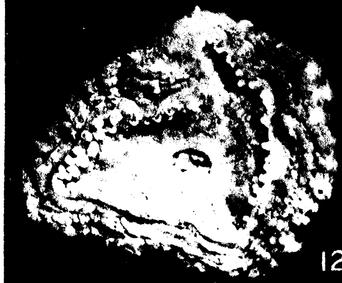
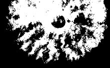

12a

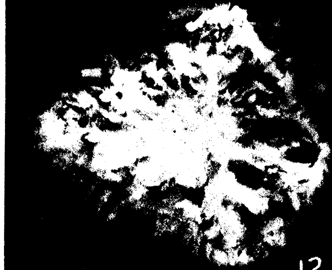

13a


14a


15a.

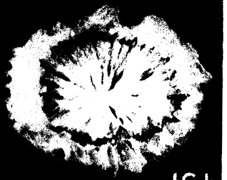

15b


16a


12b


13b


14b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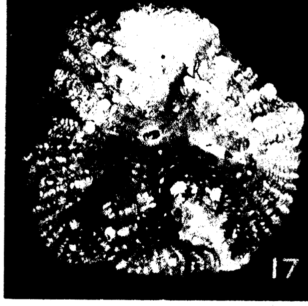
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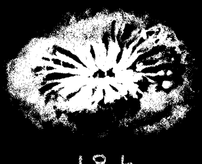
18a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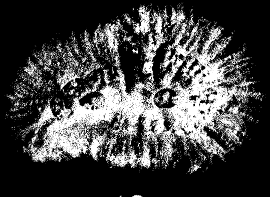
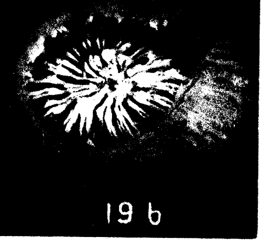
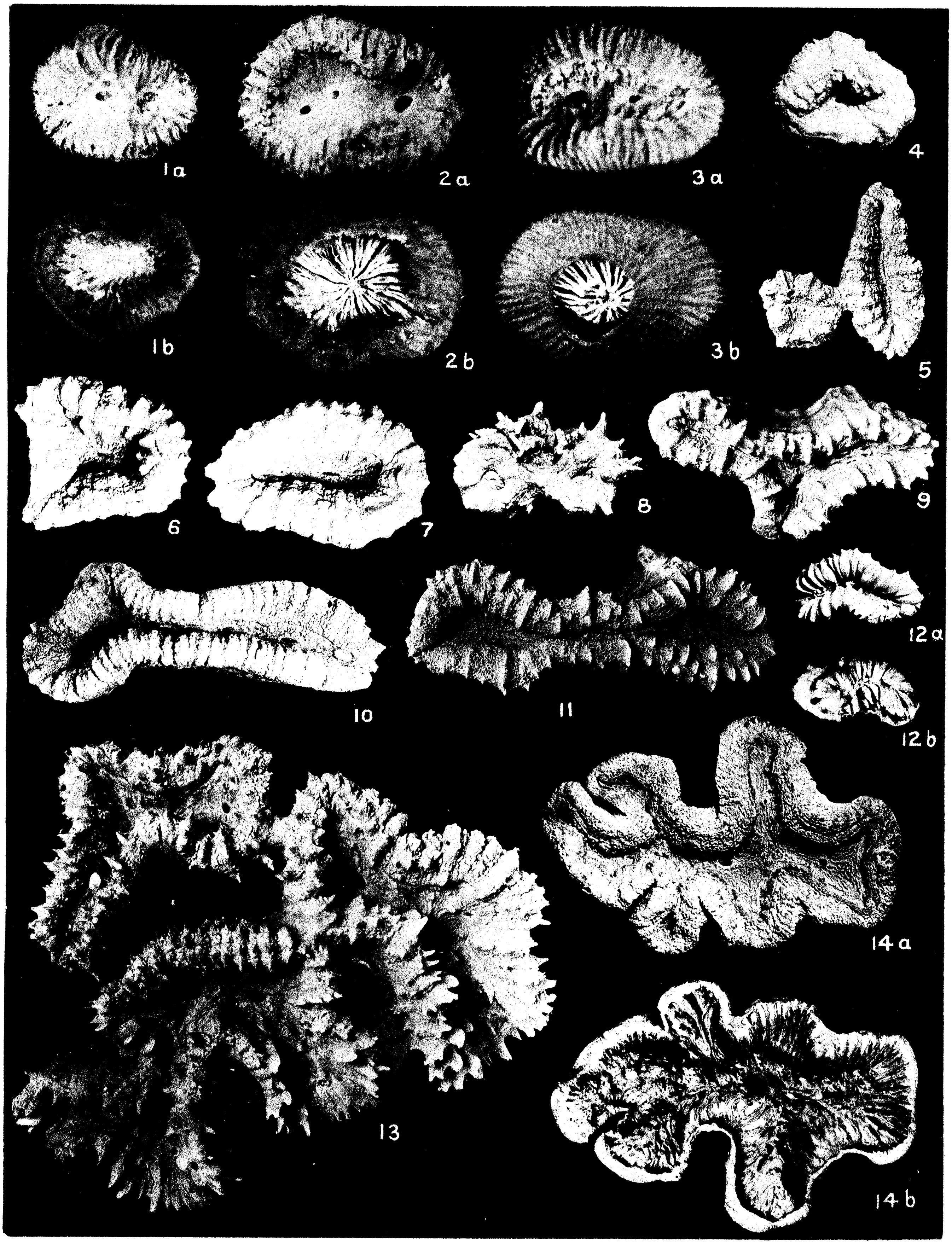

19a


19b


1a
2a
3a
4
1b
2b
3b
5
6
7
8
9
10
11
12a
12b
13
14a
14b

FIGS. 4–11.—*Mussa corymbosa* (FORSK.). Red Sea. Undecalcified polyps from colonies. Nat. size.

FIG. 4.—Monostomodæal polyp.

FIG. 5.—A tristomodæal and a monostomodæal polyp.

FIG. 6.—Monostomodæal polyp, with two intra-tentacular diverticula at one end.

FIG. 7.—Distomodæal polyp.

FIG. 8.—Distomodæal polyp which has undergone constriction into two monostomodæal polyps.

FIG. 9.—Tristomodæal polyp ; the left intra-tentacular bud is becoming constricted off.

FIG. 10.—Polyp with five mouth-openings in a linear row.

FIG. 11.—Polyp with six mouth-openings in a linear row.

FIG. 12.—*Eusmilia aspera* (DANA.). Tortugas, Caribbean Sea. Tristomodæal polyp from colony. Decalcified. Nat. size.

FIG. 13.—*Mussa corymbosa* (FORSK.). Red Sea. Part of colony with three polystomodæal polyps Undecalcified. Nat. size.

FIG. 14.—*Symphyllia sinuosa* (QUOY and GAIM). Rotuma. Entire colony consisting of one polystomodæal polyp. Decalcified. 115 *y*. Nat. size.

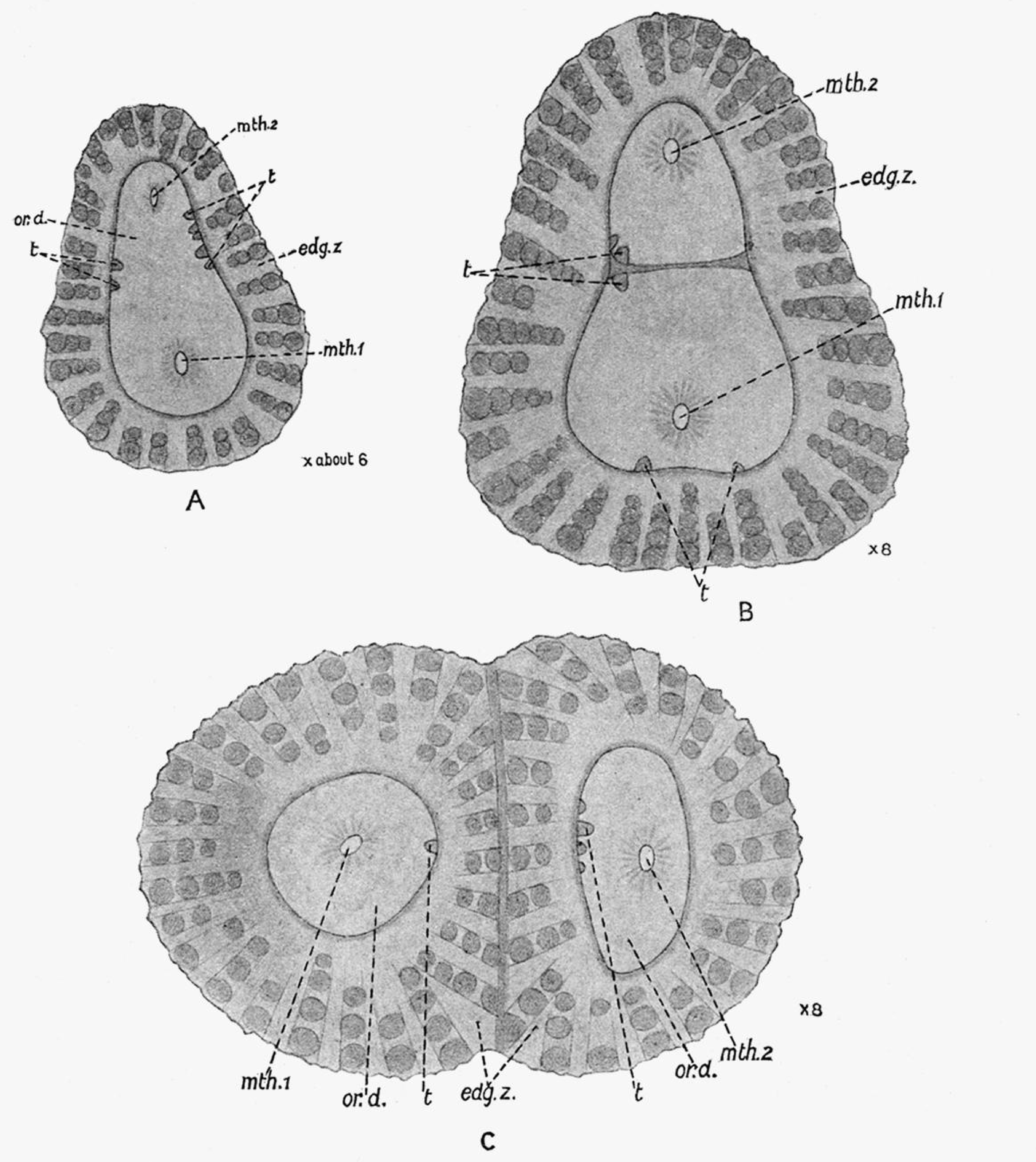


FIG. 8. A–C.—Distomodæal polyps from a colony of *Favia favus* (FORSK.), at different stages of growth. Edge-zone is raised by toothed costæ into radiating ridges with conical projections; mth_1, mth_2, mouth-openings of mother-polyp and bud; *t*, tentacles; *or.d.*, oral-disc; *edg.z.*, edge-zone. A. The mouth-openings are wide apart and surrounded by a common tentacular ring. (Fig. 5 is a transverse section through tentacular region of this polyp.) × 8. B. A thin ridge has appeared across oral-disc. × 10. C. Two oral-discs have been formed, for mother-polyp and bud, by division of the original common oral-disc. The two oral-discs, which are surrounded by distinct tentacular rings, have been elongated along different planes. × 10.

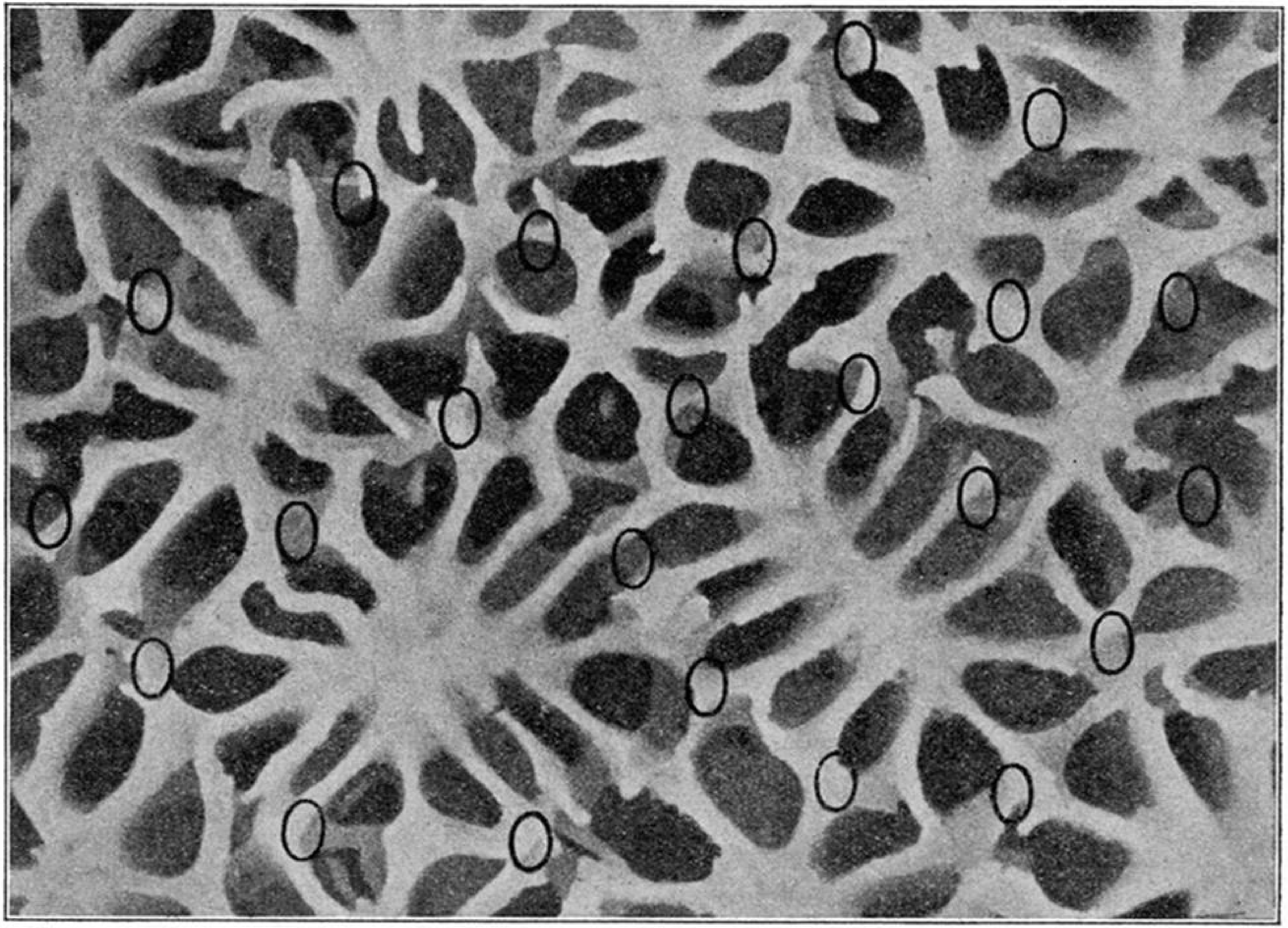


FIG. 16.—*Hydnophora microcona* (LAM.).—Photograph of corallum of a colony greatly magnified, showing monticular projections from which the septa appear to radiate. The positions of the stomodæa in the polyp over same are represented as black ovals.

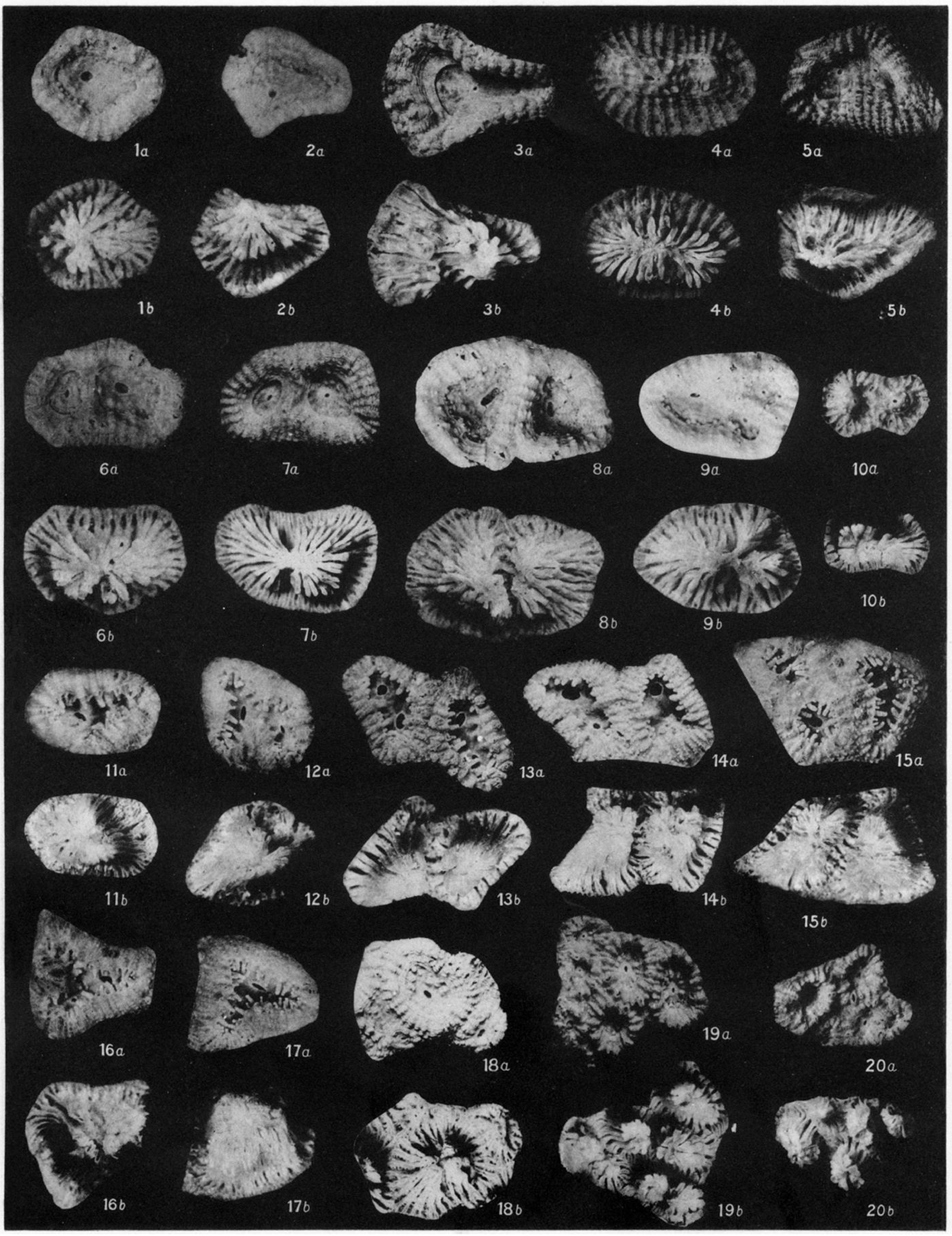


PLATE 24.

FIGS. 1–17. Intra-tentacular budding. FIGS. 1–9. *Favia favus* (FORSK.). Red Sea. × 2.

FIGS. 1–3.—Monostomodæal polyps showing stages of development of intra-tentacular diverticula. Diverticula narrower than mother-polyps. (Text-fig. 2 is a transverse section through stomodæal region of fig. 2.)

FIGS. 4 and 5.—Distomodæal polyps, each with a single elongated tentacular ring. (Fig. 5 is from the edge of a colony.)

FIGS. 6 and 7.—Distomodæal polyps in which a distinct tentacular ring has been formed around each mouth-opening. Column-walls still continuous.

FIG. 8.—A mother-polyp and bud whose column-walls have been completely separated.

FIG. 9.—Large monostomodæal polyp to left (probably original mother-polyp) with distomodæal polyp to right; the tentacular ring separating the latter is clearly shown. The distomodæal polyp appears to come under II (*d*) on p. 323.

FIG. 10.—*Favia hululensis*, GARD.—A distomodæal polyp with two distinct tentacular rings but column-walls continuous; appears to come under II (*d*) on p. 323.

FIGS. 11–17.—*Favia fragum* (ESP.).—West Indian region. × 3.

FIG. 11.—A distomodæal polyp with a single elongated tentacular ring.

FIG. 12.—A distomodæal polyp with tentacular ring considerably constricted between the two mouth-openings. The left half of polyp is elongated, perhaps for future triangular tristomodæal condition.

FIG. 13.—Two distomodæal polyps, each with a single elongated oral-disc containing two mouth-openings. Column-walls of polyps quite separate.

FIG. 14.—A distomodæal and a monostomodæal polyp, the latter with an intra-tentacular diverticulum. Column-walls of polyps quite separate.

FIG. 15.—Two distomodæal polyps. Left polyp with two distinct tentacular rings, but column-wall not yet completely divided. Right polyp with a single elongated tentacular ring, presumably to assume later the triangular tristomodæal condition.

FIG. 16.—Triangular tristomodæal polyp, from edge of a colony. Three mouth-openings at the corners of the triangular oral-disc. Mouth-opening of mother-polyp to right; mouth-openings of pair of buds to left, at extreme edge of colony. Basal view (fig. 16 *b*) shows a single column-wall. (Text-fig. 10 is a transverse section through stomodæal region of this polyp.)

FIG. 17.—A triangular tristomodæal polyp with a common tentacular boundary.

FIGS. 18–20.—Extra-tentacular budding.

FIG. 18.—*Favia favus* (FORSK.).—A large monostomodæal polyp and two small extra-tentacular buds at the extreme edge of colony. (Text-fig. 21 is transverse section through stomodæal region of this piece.) × 2.

FIGS. 19 and 20.—*Favia hululensis*, GARD. × 2.

FIG. 19.—A row of extra-tentacular buds at extreme edge of colony to left.

FIG. 20.—Two extra-tentacular buds at lower margin (edge of colony). (The extra-tentacular diverticulum of text-figs. 22 *a* and *b* is seen at lower margin between the buds and monostomodæal polyp to left.)

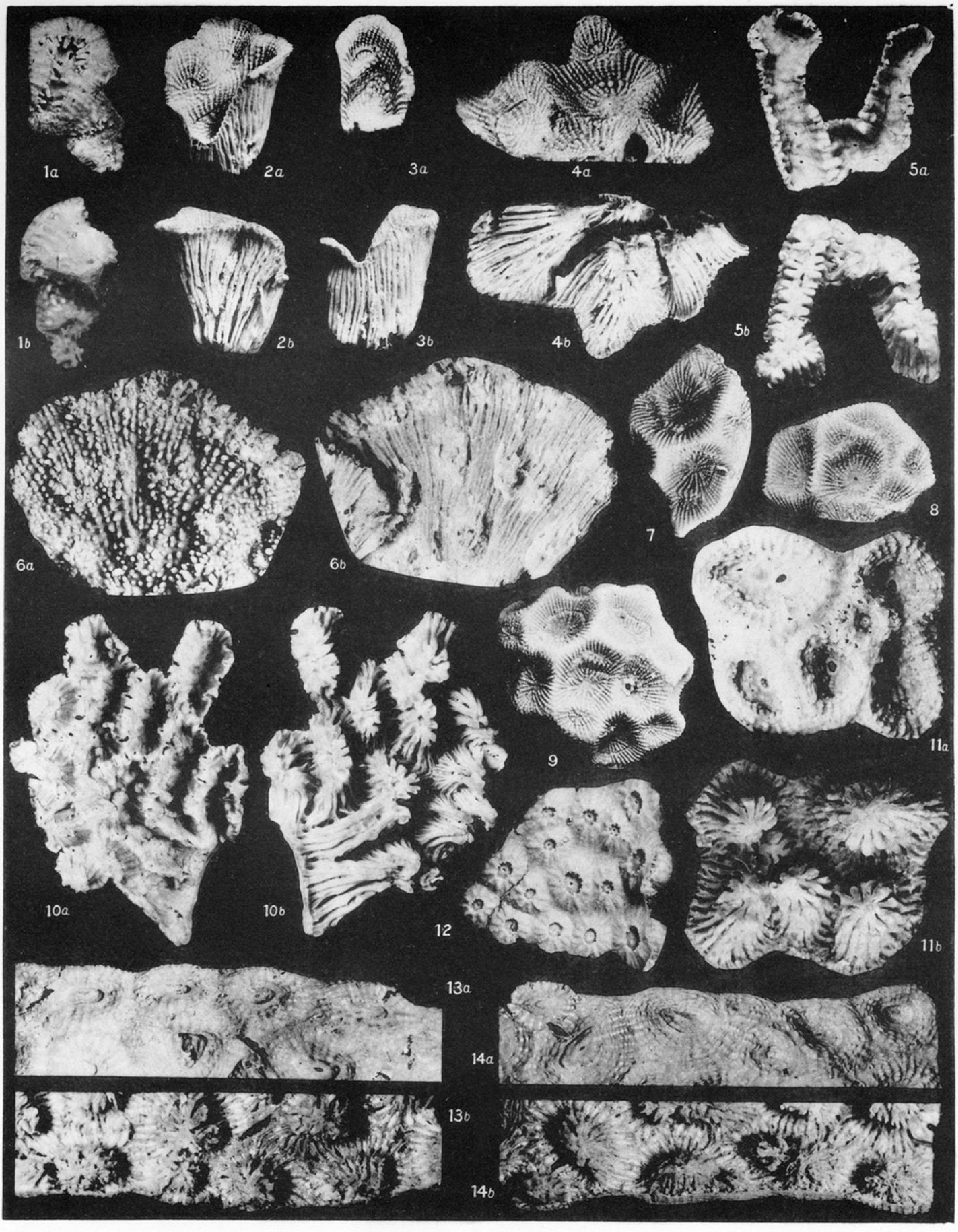


Plate 25.

Fig. 1.—*Favia fragum* (Esp.).—A piece containing a distomodæal polyp and two extra-tentacular buds, from the edge of a colony. (Text-fig. 6 is a transverse section through stomodæal region of this distomodæal polyp.) West Indian region. × 3.

Figs. 2–4.—*Favia abdita* (Ell. and Sol.).—Pieces from a colony, showing extra-tentacular budding. Buds small and placed obliquely at a higher level than polyps. (Text-fig. 20 is a transverse section through stomodæal region of fig. 2.) Hulule, Maldives. × 2.

Fig. 5.—*Cœloria dœdalca* (Ell. and Sol.).—A piece from a colony, containing two short polystomodæal polyps. Hulule, Maldives. × 2.

Fig. 6.—*Echinopora lamellosa* (Esp.).—A piece from a colony, showing extra-tentacular budding. Small buds along upper margin (edge of colony). Column-walls of polyps (fig. 6 *b*) oblique in position. Hulule, Maldives. × 3.

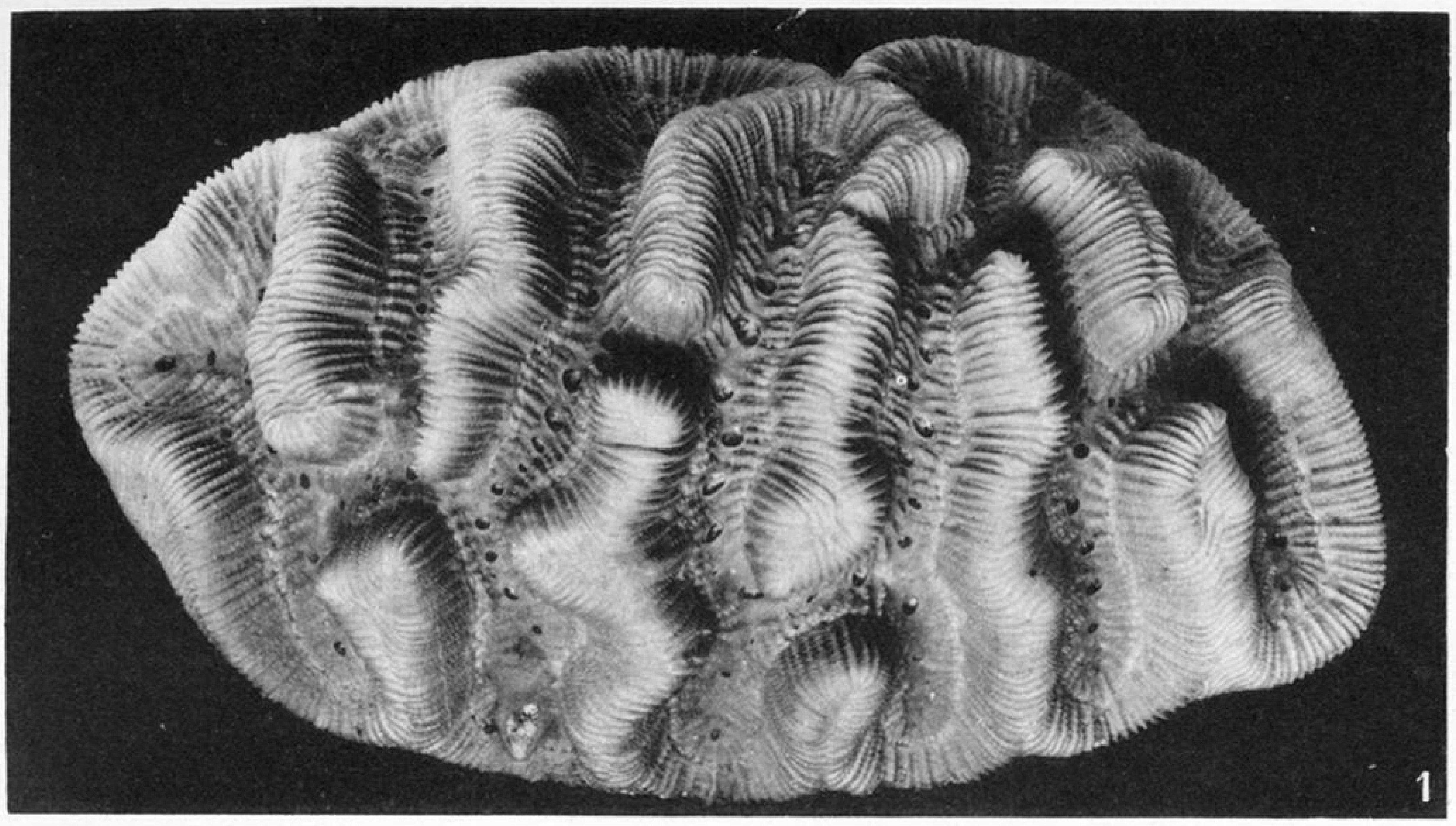
Figs. 7–9.—*Favia abdita* (Ell. and Sol.).—Oral views of undecalcified pieces from three colonies, showing extra-tentacular budding. Hulule, Maldives. × 2.

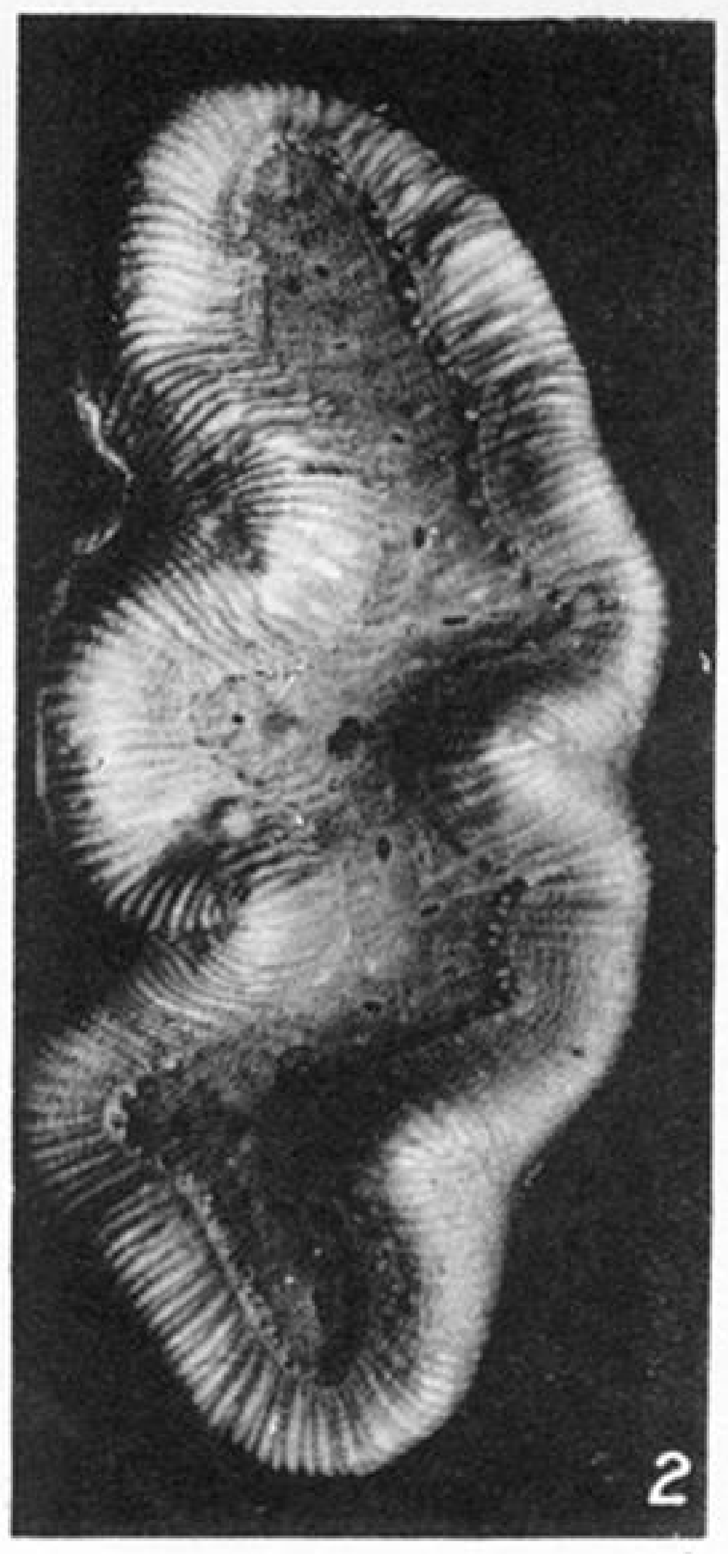
Fig. 10.—*Cœloria dœdalea* (Ell. and Sol.).—A piece from a colony, containing monostomodæal to short discontinuous polystomodæal polyps, from same colony as fig. 5. Hulule, Maldives. × 2.

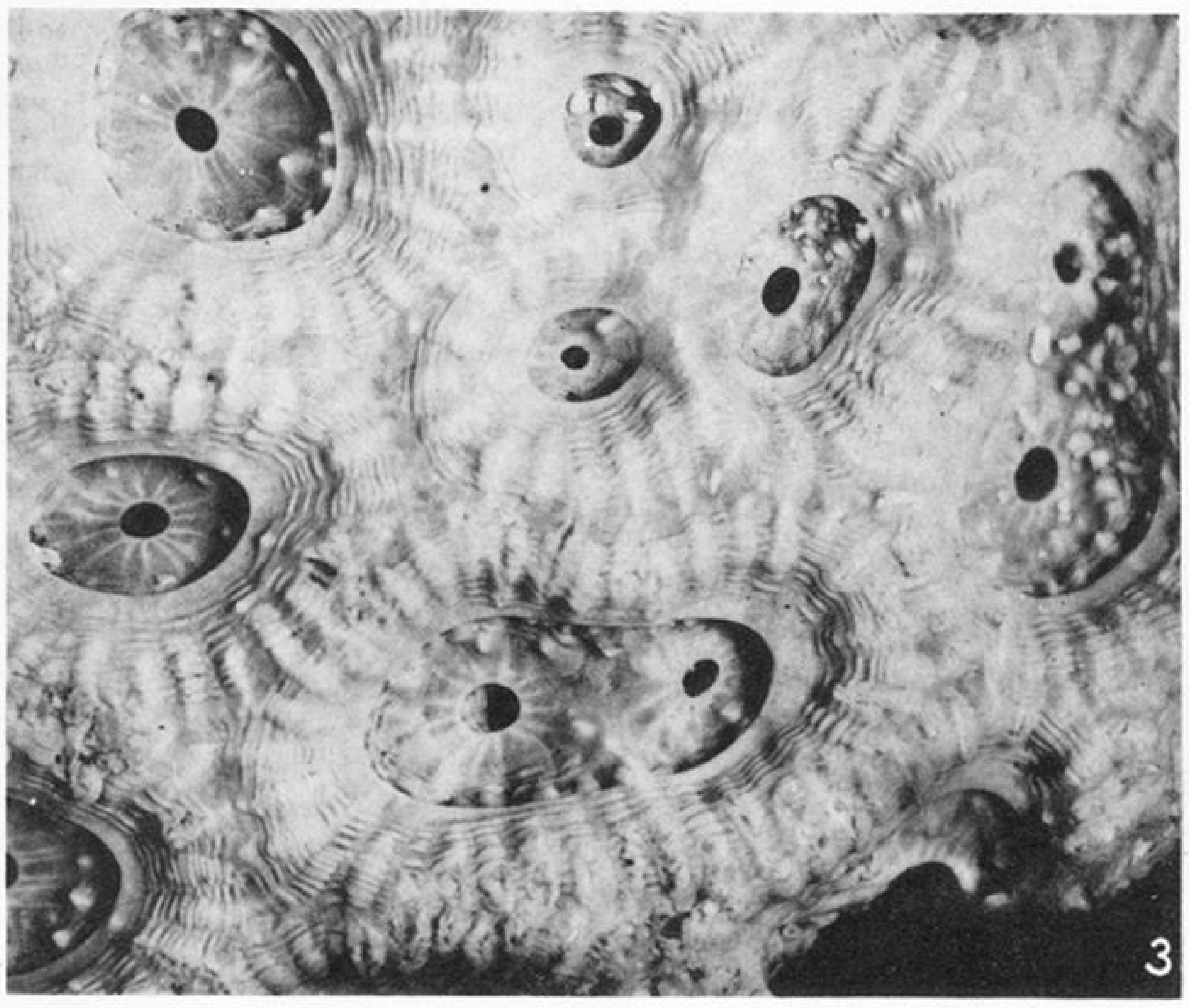
Fig. 11.—*Favia favus* (Forsk.).—A piece from a colony, containing monostomodæal and distomodæal polyps. The smallest polyp, with distinct column-wall, is probably an extra-tentacular bud. Red Sea. × 2.

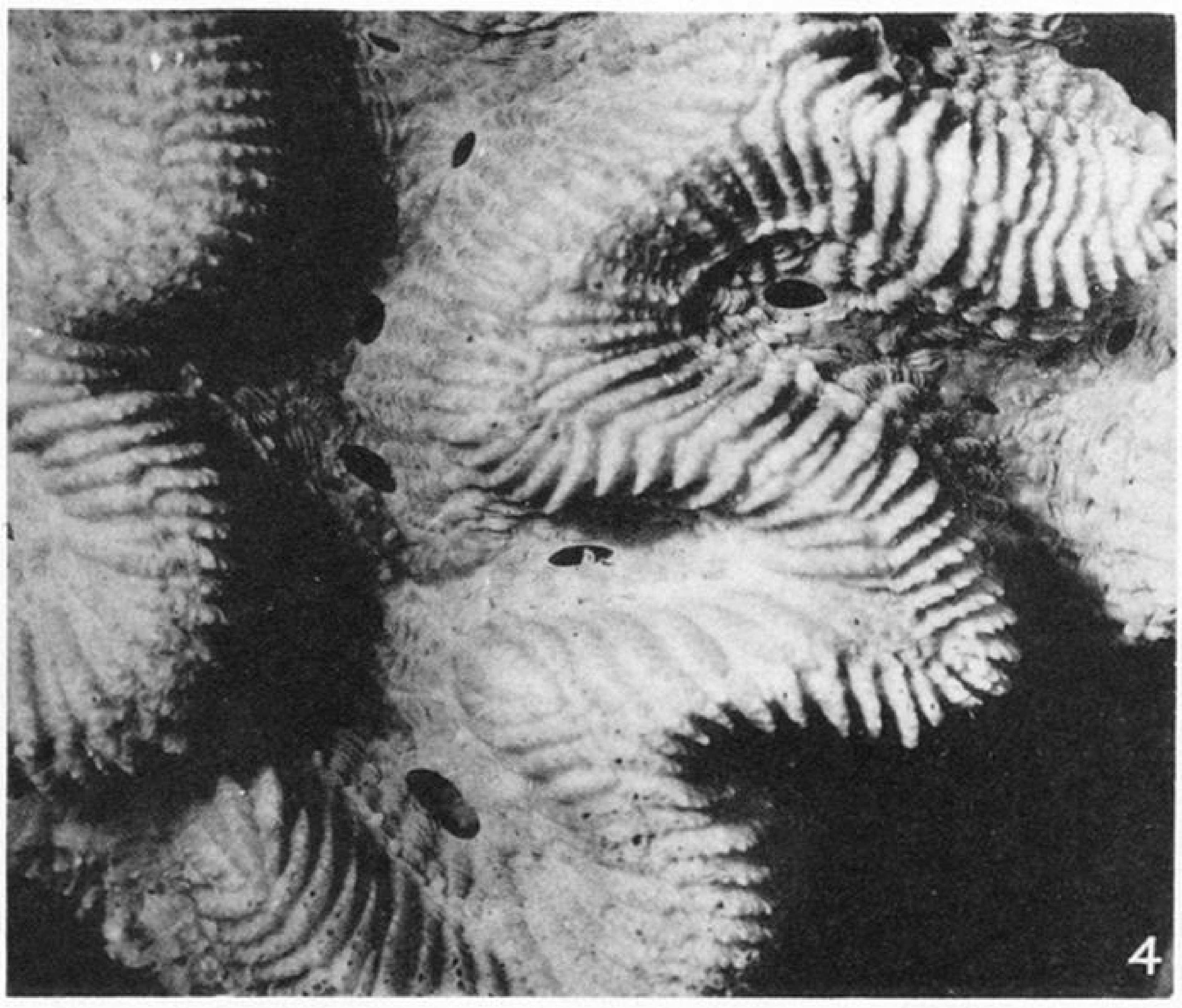
Fig. 12.—*Orbicella annularis* (Ell. and Sol.).—A piece from a colony, showing extra-tentacular budding. West Indian region. × 3.

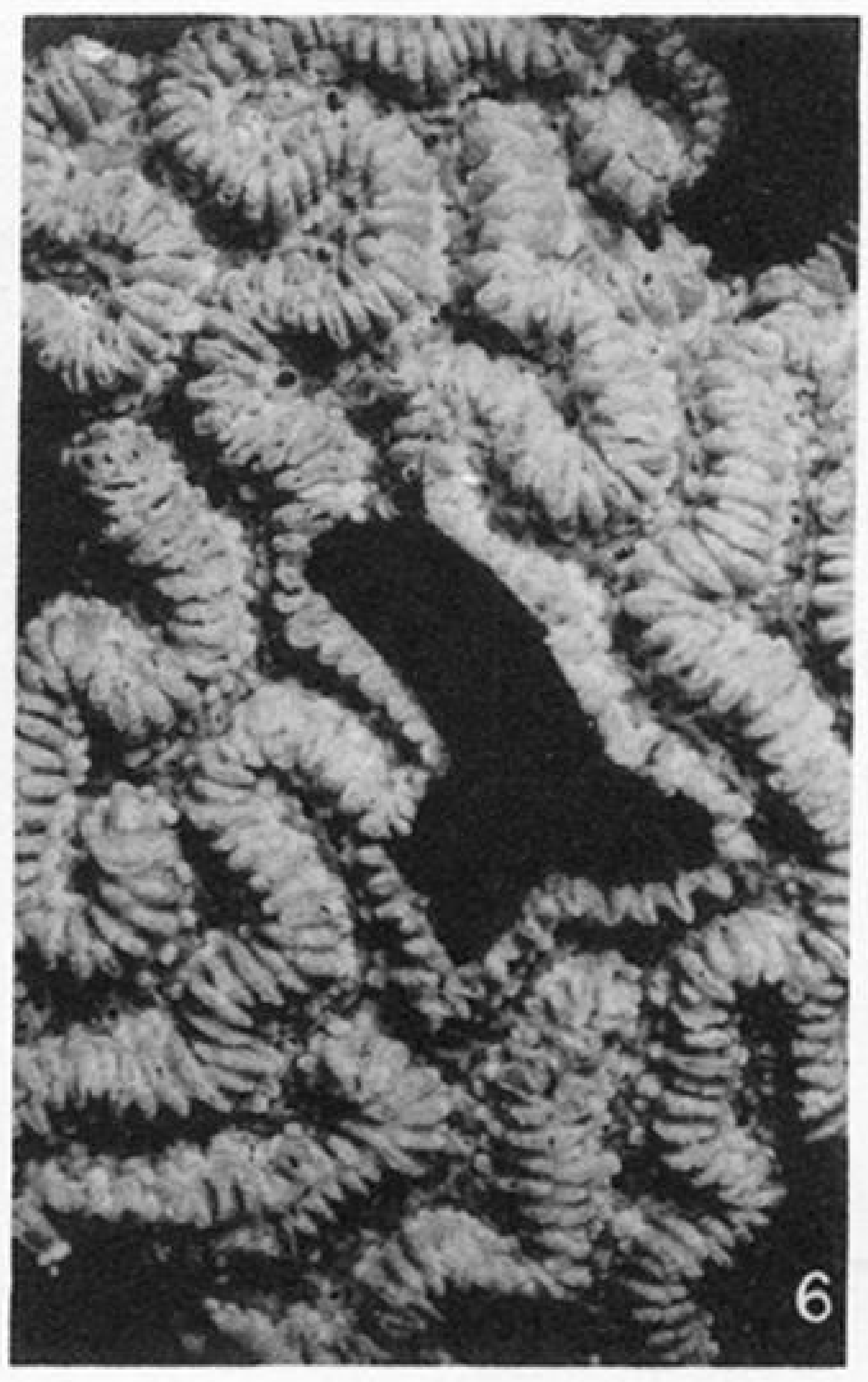
Figs. 13 and 14.—*Favia favus* (Forsk.).—Two pieces from edge of a colony, showing extra-tentacular buds along free margins. Red Sea. × 2.

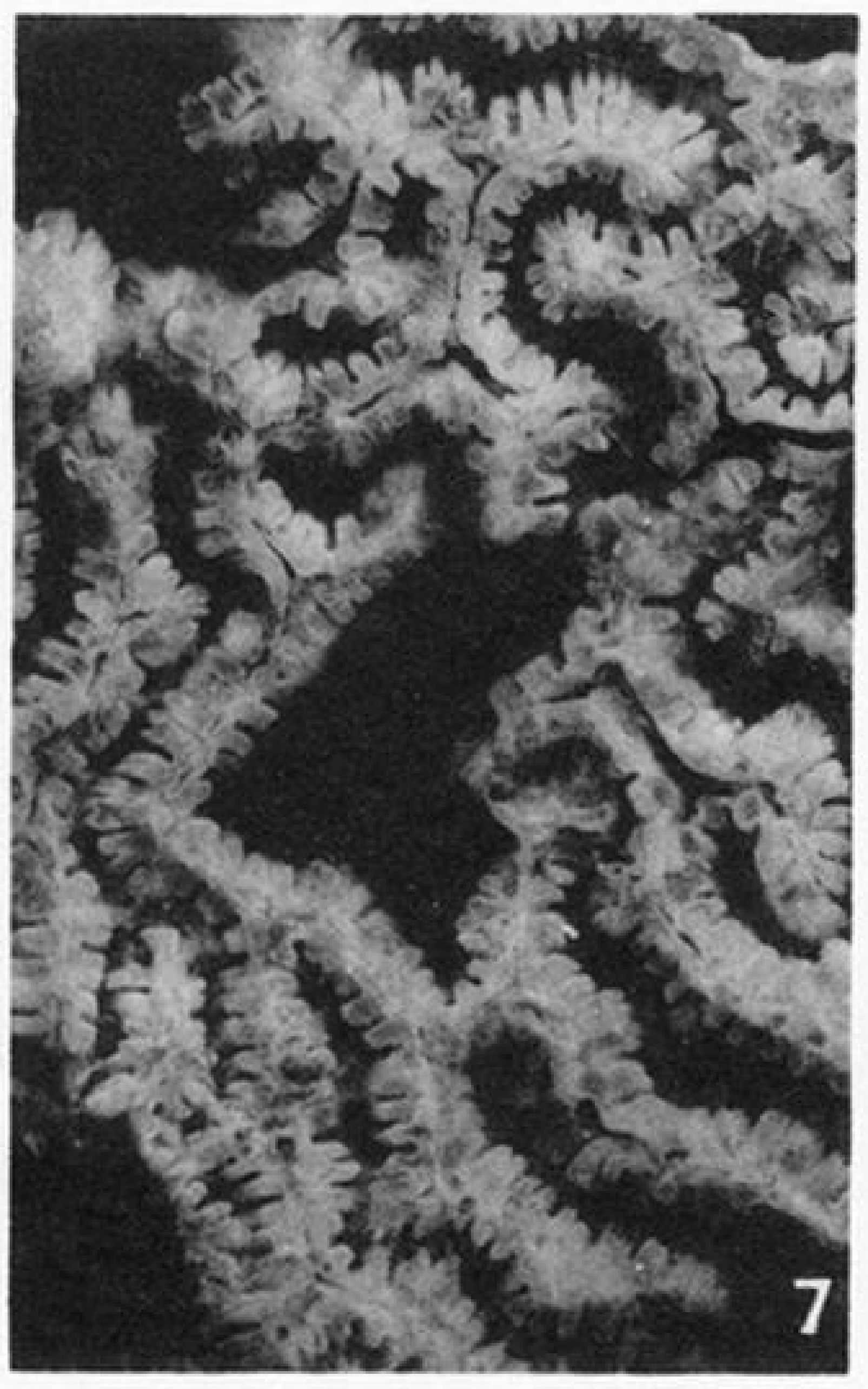












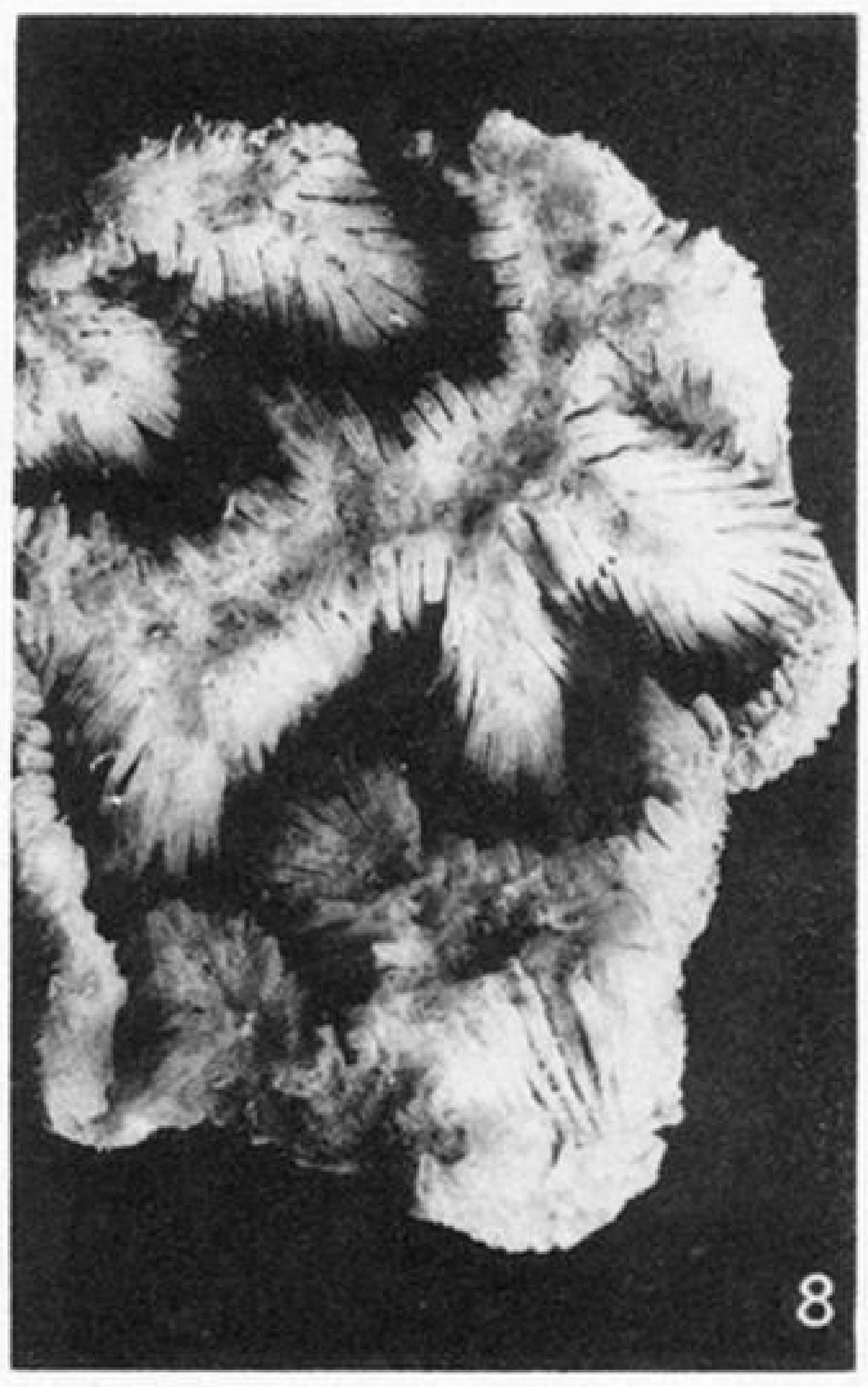


PLATE 26.

FIG. 1.—*Manicina areolata* (LINN.).—Oral view of a full-grown undecalcified colony, the soft parts forming a single meandering polystomodæal polyp. Many of the mouth-openings are in a distended condition. West Indian region. Nat. size.

FIG. 2.—*Manicina areolata* (LINN.).—Oral view of a young undecalcified colony. West Indian region. Nat. size.

FIG. 3.—*Favia favus* (FORSK.).—Oral view of part of an undecalcified colony. Note distomodæal and monostomodæal polyps. Red Sea. × 3.

FIG. 4.—*Colpophyllia gyrosa* (ELL. and SOL.).—Oral view of part of a decalcified colony. A single polystomodæal polyp with forked ends, to left of fig.; a single mouth-opening in each arm of the fork. A lateral bud on each side of polyp. West Indian region. × 3.

FIG. 5.—*Leptoria gracilis*, DANA.—Oral view of part of a colony, showing meandering polystomodæal condition with lateral branching and terminal forking. Hulule, Maldives. × 2.

FIG. 6.—*Leptoria gracilis*, DANA.—Oral view of part of a decalcified colony. Hulule, Maldives. × 2.

FIG. 7.—Basal view of above. × 2.

FIG. 8.—Basal view of fig. 4. Nat. size.

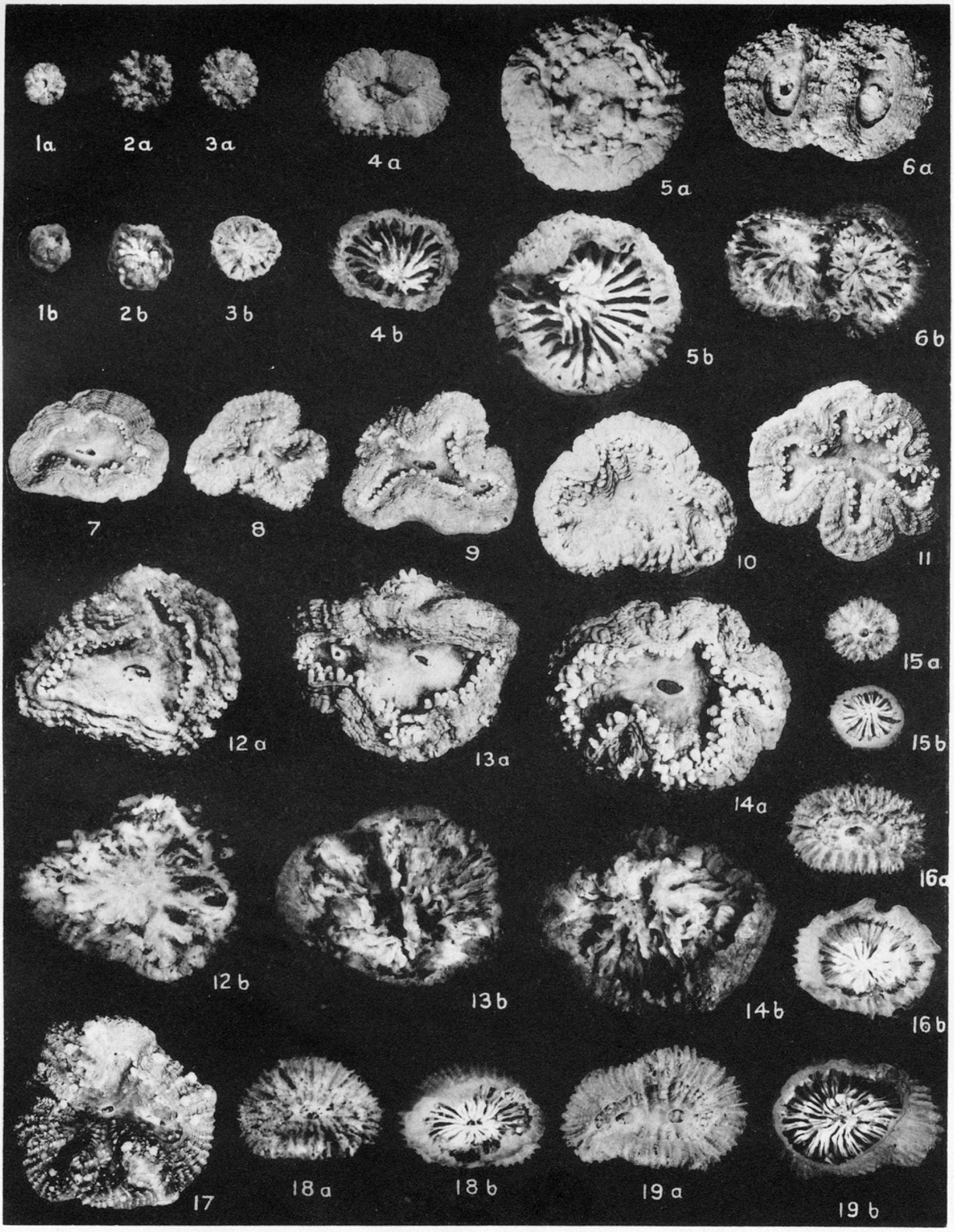


Plate 27.

(Views of polyps from decalcified colonies.)

Figs. 1–14.—*Isophyllia dipsacea* (Dana). Bermudas.

Figs. 1–5.—Monostomodæal mother-polyps at different stages of growth. × 3. Fig. 1 is of 700 *a* I and fig. 3 of 700 *a* II.

Fig. 6.—Distomodæal mother-polyp, showing the stage with two circumscribed oral-disc areas. × 2.

Fig. 7.—Tristomodæal mother-polyp. × 2.

Fig. 8.—Mother-polyp with four primary intra-tentacular lobes around central mouth. × 2.

Fig. 9.—Mother-polyp with four primary intra-tentacular lobes around central mouth; in each lobe a mouth-opening is visible. × 2.

Fig. 10.—Mother-polyp with five primary intra-tentacular lobes around central mouth. × 2.

Fig. 11.—Mother-polyp with five primary intra-tentacular lobes around central mouth; the primary lobe on the left has given rise to a secondary intra-tentacular lobe. × 2.

Fig. 12.—Distomodæal mother-polyp. 700 *a* IV. × 3.

Fig. 13.—Distomodæal mother-polyp in which a third mouth has begun to be formed. 700 *a* III. × 3.

Fig. 14.—Distomodæal mother-polyp, with three additional primary intra-tentacular lobes in which mouth-openings have not yet appeared. × 3.

Figs. 15, 16 and 18.—*Manicina areolata* (Linn.). Tortugas, Caribbean Sea. Monostomodæal mother-polyps at different stages of growth. × 3.

Fig. 17.—*Isophyllia dipsacea* (Dana). Bermudas. Mother-polyp with five primary intra-tentacular lobes around central mouth; the primary lobe on the left has given rise to a secondary intra-tentacular lobe.

Fig. 19.—*Manicina areolata* (Linn.). Tortugas, Caribbean Sea. Distomodæal mother-polyp.

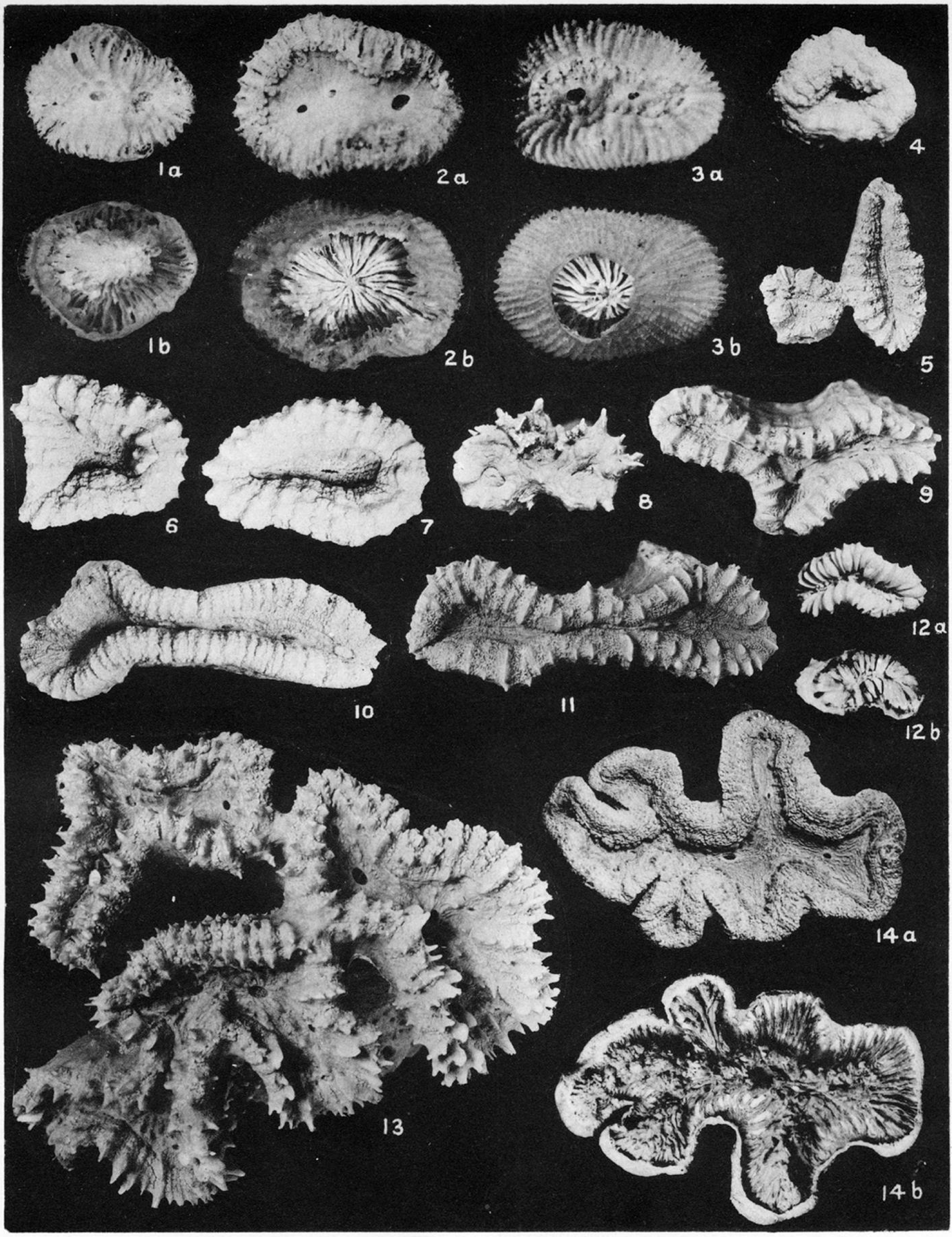


Plate 28.

Figs. 1–3.—*Manicina areolata* (Linn.). Tortugas. Decalcified mother-polyps. × 3.

Fig. 1.—Distomodæal mother-polyp.

Figs. 2 and 3.—Tristomodæal mother-polyp.

Figs. 4–11.—*Mussa corymbosa* (Forsk.). Red Sea. Undecalcified polyps from colonies. Nat. size.

Fig. 4.—Monostomodæal polyp.

Fig. 5.—A tristomodæal and a monostomodæal polyp.

Fig. 6.—Monostomodæal polyp, with two intra-tentacular diverticula at one end.

Fig. 7.—Distomodæal polyp.

Fig. 8.—Distomodæal polyp which has undergone constriction into two monostomodæal polyps.

Fig. 9.—Tristomodæal polyp ; the left intra-tentacular bud is becoming constricted off.

Fig. 10.—Polyp with five mouth-openings in a linear row.

Fig. 11.—Polyp with six mouth-openings in a linear row.

Fig. 12.—*Eusmilia aspera* (Dana.). Tortugas, Caribbean Sea. Tristomodæal polyp from colony. Decalcified. Nat. size.

Fig. 13.—*Mussa corymbosa* (Forsk.). Red Sea. Part of colony with three polystomodæal polyps Undecalcified. Nat. size.

Fig. 14.—*Symphyllia sinuosa* (Quoy and Gaim). Rotuma. Entire colony consisting of one polystomodæal polyp. Decalcified. 115 *y*. Nat. size.