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Colony Formation in Fungid Corals. I. Pavona, Echinophyllia, Leptoseris and Psammocora

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COLONY FORMATION IN FUNGID CORALS

I. *PAVONA*, *ECHINOPHYLLIA*, *LEPTOSERIS* AND *PSAMMOCORA*

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In recent Fungid corals colony formation is by intra-tentacular budding, extra-tentacular budding never occurring.

Intra-tentacular budding in *Pavona* is on the distomodaeal, triangular tristomodaeal and triple stomodaeal modes, with direct linkage, in *Echinophyllia* and *Leptoseris* is usually accompanied by mesenterial curvature and cleavage, in *Psammocora* is peripheral.

Intra-tentacular budding results in the cyclic polystomodaeal condition; the subsidiary polyp areas are originally arranged in concentric rows around the primary polyp area which, during growth, shifts from a central to an excentric position.

Cyclic polystomodaeal condition is primarily continuous, discontinuity being secondary.

Discontinuity of the cyclic polystomodaeal condition, when it occurs, is at first due to the appearance of concentric ridges, subsequently of radial ridges. When the two systems of ridges are equally well developed, their intersection results in short polystomodaeal, tri-, di-, or monostomodaeal polyps.

It has already been shown that colony formation in Astraeid corals takes place by budding, extra-tentacular and intra-tentacular, and descriptions of various modes of budding have been given in previous publications (Matthai 1919, p. 73; 1926, pp. 313–367; and 1928, pp. 2–3).

Stephenson (1931) described briefly the early stages in budding (extra-tentacular), and consequent colony formation, in *Pocillopora bulbosa* and *Porites haddoni*, as seen on surface view of larvae reared on the Great Barrier Reef, as well as the production of colonies by the fusion of planulae. This was supplemented by a short account by Manton (1932) of surface observations, made on the same reef, of formation of new polyps by extra-calicinal (extra-tentacular) budding in the adult live colony of *Pocillopora bulbosa*. In a subsquent report (Stephenson 1933, pp. 190–199) incorporated his observations on living colonies of the Astraeid genera *Favia* and *Lobophyllia*, extending over a period of about eight months in the former and about seven months in the latter, and concluded 'that the reproduction in both genera was the result of intra-tentacular budding (at least in the majority of polyps), that no fission was involved, and that the new mouths were formed *de novo* and not split off from the old ones' (p. 209). Hyman (1940, p. 607) and Vaughan & Wells (1943, pp. 10 and 42–47) gave summaries of previous work on extra-tentacular and intra-tentacular budding in Astraeid corals.

Asexual reproduction leading to colony formation in Fungid corals has not hitherto been studied on the same lines as in Astraeid corals. It is herein described for the first time.

In Fungid corals colony formation is now known to take place by budding in the oral disk region of the first polyp that has developed from an attached larva. The edge zone

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* The author died while the MS. of this paper was in the hands of the printer. The proofs have been seen through the press by R. B. Seymour Sewell, F.R.S.

does not take any part in this process which is, therefore, comparable to intra-tentacular budding in Astraeid corals. Consequently, directive couples of mesenteries and hexameral symmetry are absent from all subsidiary polyp areas of Fungid colonies.

Budding in colonial Fungid corals is cyclic, the buds being formed in concentric rows around the primary polyp area. The resulting colony is, therefore, characterized by the *cyclic polystomodaeal condition*. This condition is at first continuous throughout the colony, but may, subsequently, become discontinuous. The discontinuity is primarily due to the appearance of concentric ridges resulting in the formation of concentric rows of polystomodaeal polyps. When such ridges are not formed between adjacent rows, a cyclic polystomodaeal polyp may consist of more than one row of buds. This condition may also be brought about by secondary budding at the base of a concentric row. Secondary budding will further account for irregularly placed buds in a cyclic polystomodaeal polyp. Buds often arise on the wall of a cyclic polystomodaeal polyp, when they appear to be oblique in position. When lateral and dichotomous branching take place the cyclic polystomodaeal polyp becomes sinuous.

Discontinuity of the cyclic polystomodaeal condition is secondarily due to the formation of radial ridges across the concentric rows of buds, resulting in radial polystomodaeal polyps. It often happens that radial ridges are formed across already existing low concentric ridges. A radial polystomodaeal polyp may consist of one or more rows of buds. Secondary budding may take place at the base, and on the wall, of a radial polystomodaeal polyp as in the case of a cyclic polystomodaeal polyp. Lateral and dichotomous branching of a radial polyp do not usually lead to the sinuous condition.

When concentric and radial ridges are equally well developed, their intersection results in short polystomodaeal, tri-, di- or monostomodaeal polyps.

It will, therefore, be seen that the continuous cyclic polystomodaeal polyp comprising a colony is the primary condition in recent colonial Fungid corals, which secondarily leads to the discontinuous polystomodaeal condition of varying length and sinuosity, and finally to the monostomodaeal condition. On the other hand, in recent colonial Astraeid corals the reverse process has taken place, i.e. the monostomodaeal polyp is the primary condition which, in the group characterized by absence of directive couples of mesenteries, has, by intra-tentacular budding, secondarily given rise to the discontinuous polystomodaeal condition of varying length and sinuosity, and finally to the continuous polystomodaeal condition constituting an entire colony.

The cyclic polystomodaeal condition characteristic of recent colonial Fungid corals is essentially different from the circumoral polystomodaeal condition seen in the Astraeid genera *Isophyllia* and *Isophyllastrea* (Matthai 1926, pp. 356–360, figures 23 A and B, plate 27, figures 1 to 14 and 17; 1928, figures 27 to 31, 33 to 35; 1940, p. 190). In both the latter, as in other Astraeid genera, growth is radial; the primary feature is, therefore, the radial polystomodaeal condition, concentric ridges being absent. Each subsidiary stomodaeum in the first ring surrounding the primary central stomodaeum indicates the commencement of a radial lobe which repeatedly bifurcates as it grows towards the periphery. Radial ridges are formed between adjacent lobes and arms of lobes. Even if the final condition of the colony be a continuous polystomodaeal polyp, the radial lobes that pass towards the periphery are evident both in the soft and hard parts. As growth is more or less even, the primary polyp area continues to remain central in position. Discontinuity of the polystomodaeal polyp, when it occurs, is due to convergence and meeting of radial ridges or to transverse partitions secondarily appearing in the radial lobes. Each bud-stomodaeum is also indirectly linked with its corresponding mother-stomodaeum by two interstomodaeal couples of mesenteries, one such couple on each side. In the Astraeid genera *Lobophyllia*, *Symphyllia* and *Mycetophyllia*, which appear to be characterized by the circumoral polystomodaeal condition, growth is likewise radial and more or less even, the first polyp area retaining its original central position and concentric ridges are not formed, but one or more mesenterial strands are formed directly linking adjacent stomodaea (Matthai 1940, pp. 185–186).

In the recent colonial Fungidae, owing to greater distal growth, the primary polyp area, which was at first central, assumes an excentric position, and the concentric rows of subsidiary polyp areas become incomplete on the proximal side. The continuity of the cyclic polystomodaeal condition may be interrupted by the subsequent appearance of concentric ridges, and radial ridges, when formed, are secondary. Interstomodaeal couples of mesenteries, for indirect linkage of adjacent stomodaea, occur less frequently than in the Astraeidae, or are absent.

Vertical cleavage of mesenteries is a common phenomenon connected with intra-tentacular budding in the recent colonial Fungid genera so far studied, whether adjacent stomodaea are directly linked by mesenterial strands or not. In Astraeid genera mesenterial cleavage takes place less frequently, having been recorded in *Favia* (Matthai 1926, figure 2, pp. 342–344, figures 22 A and B), *Coeloria* (Matthai 1928, figure 1), *Maeandrina* (Matthai 1928, figure 9), *Merulina* (Matthai 1928, figure 15), *Hydnophora* (Matthai 1926, pp. 337–338, figure 18; 1928, figures 17 and 18), *Symphyllia* (Matthai 1926, pp. 360–364; 1928, figure 26) and *Mycetophyllia* (Matthai 1928, figure 32). In the last two genera, viz. *Symphyllia* and *Mycetophyllia* (probably also in *Lobophyllia*), mesenterial cleavage is the rule as it is associated with the formation of mesenterial strands, directly linking neighbouring stomodaea, by the bending of certain mesenteries and fusion at their bends with new stomodaea.

Pavona varians (Verrill)*

In living colonies of *Pavona varians* (Verrill), Yonge (1930, p. 41) observed 'frequent mouths surrounded by a very variable number of low tentacles'. In sections, tentacles of *P. varians* (Verrill) appear to be rudimentary, terminal batteries being small and subterminal ones hardly visible. Colony formation usually takes place by intra-tentacular budding in such a manner that the stomodaeum of the bud is usually linked directly with that of the mother-polyp by one or more mesenterial strands, aided less frequently by budding on the distomodaeal mode, as in certain Astraeid corals (Matthai 1926, pp. 318, 330).

The presence of one mesenterial strand effecting complete direct linkage between two stomodaea and its relation to a completely principal interstomodaeal couple indirectly linking the same two stomodaea on the right side are explained in figures 1 A to C. During the course of formation of an intra-tentacular bud a mesentery of a principal couple

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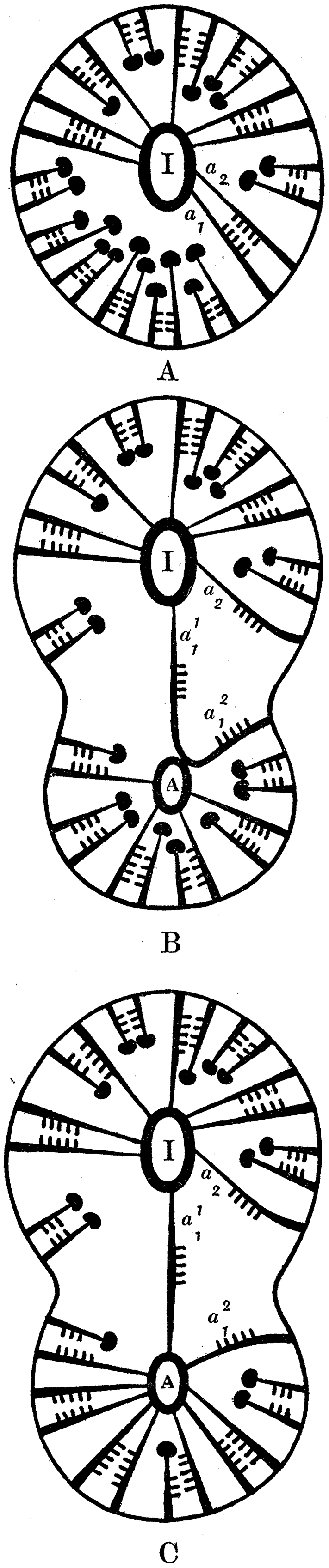
* The specific names employed in this paper are provisional.

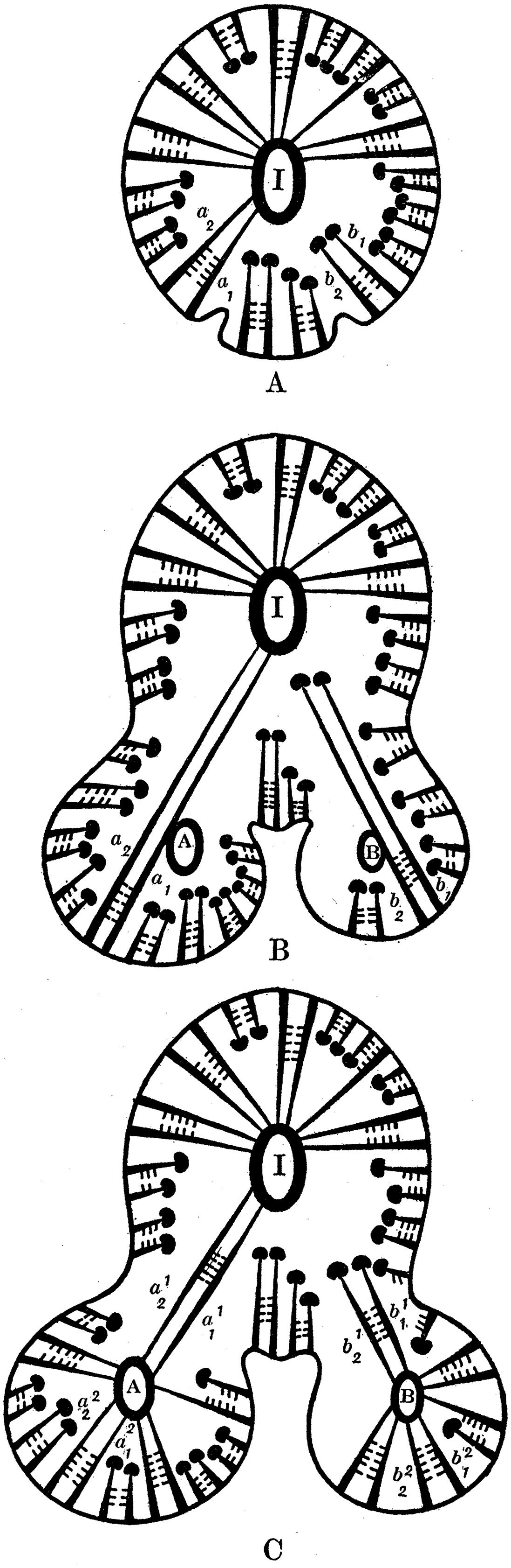


Figures 1, A to C. *Pavona varians* (Verrill). Intra-tentacular budding on the distomodaeal mode, with direct linkage. I, stomodaeum of mother-polyp. *A*, stomodaeum of intra-tentacular bud. $a_1 a_2$, one completely principal couple of mesenteries of mother-polyp adjacent to the intra-tentacular diverticulum. a_1^1, inner part of a_1 forming a principal mesenterial strand directly linking stomodaea I and *A*. a_1^2, outer part of a_1, forming a completely principal interstomodaeal couple on the right side with a_2. Figure 1A. Mother-polyp with incipient intra-tentacular diverticulum. Figure 1B, later stage, showing transformation of diverticulum into bud, and mesentery a_1 bending towards and meeting the new stomodaeum A. Figure 1C, final stage, viz. distomodaeal condition, with direct linkage, in which a_1 has been divided into a_1^1 and a_1^2.

adjacent to the bud is bent towards the new stomodaeum while it is being formed, the mesentery ultimately uniting, at its bend, with the new stomodaeum. As a result of this union the principal mesentery is divided at its bend into an inner part connected with the two stomodaea at opposite ends (i.e. complete direct linkage), and an outer part which becomes a principal mesentery of the bud and forms a completely principal interstomodaeal couple with the adjacent mesentery of the original completely principal couple. In this case, one of the couples on the left side, between the mother-polyp and bud, may subsequently form an interstomodaeal couple. This is comparable to intra-tentacular budding on the distomodaeal mode, but is distinguished from it by the presence of a mesenterial strand directly linking stomodaeum of mother-polyp with that of bud, and may therefore be regarded as *intra-tentacular budding on the distomodaeal mode with direct linkage*. Direct linkage of two stomodaea by means of a single mesenterial strand will be incomplete when the latter is attached to only one of the two stomodaea. In *P. varians* direct linkage of two stomodaea may also be effected by two mesenterial strands. Lateral branching takes place by intra-tentacular budding on the distomodaeal mode, usually with, sometimes without, direct linkage.

Intra-tentacular budding on the distomodaeal mode, with direct linkage, was recorded for the first time in *Symphyllia* (Matthai 1926, pp. 360–363, figures 4 A to C) in which one or two mesenterial strands stretch between neighbouring stomodaea. In this connexion all possible cases were discussed, viz. the two mesenterial strands forming an ordinary couple with the pleats of one strand facing those of the other, or a directive couple with the pleats directed away from each other, or the mesenterial strands not forming a couple at all, with their pleats turned to the right or to the left side (Matthai 1928, p. 228, figure 26). In *Mycetophyllia* neighbouring stomodaea were found to be linked by one, two or three mesenterial strands, i.e. by single, double or treble direct linkage (Matthai 1928), p. 251, figure 32); in the first two cases the formation of the mesenterial strand or stands was at an initial stage, comparable to the stage represented by figure 1B; in the last case, two of the strands formed an ordinary couple. It appears that in *Lobophyllia* direct linkage may be effected by four mesenterial strands forming two ordinary couples (Matthai 1928, figure 25).

Figures 2 A to C illustrate intra-tentacular budding on the triangular tristomodaeal mode with direct linkage of the stomodaeum of each bud and that of the mother-polyp by means of a couple of mesenterial strands as shown in dichotomous branching or terminal forking. Direct linkage may be completely, or incompletely, principal or subsidiary according as the couple is attached to the stomodaea of mother-polyp and bud, or only to one of the two stomodaea. It is conceivable that direct linkage may also be incompletely principal if one of the two mesenterial strands forming a couple is connected only to one stomodaeum, whilst the other is connected to both stomodaea. When a pair of intra-tentacular diverticula become a pair of buds, the stomodaeum of each bud unites with the mesenteries of a couple in such a manner that the latter become divided into inner parts forming a linkage couple and outer parts forming a principal couple of the bud. In this case, there are usually one or more couples of mesenteries between the two buds. Forking here is analogous to dichotomous branching on the triangular tristomodaeal mode that takes place in some Astraeid corals (Matthai 1926, pp. 324, 331 and 362) but



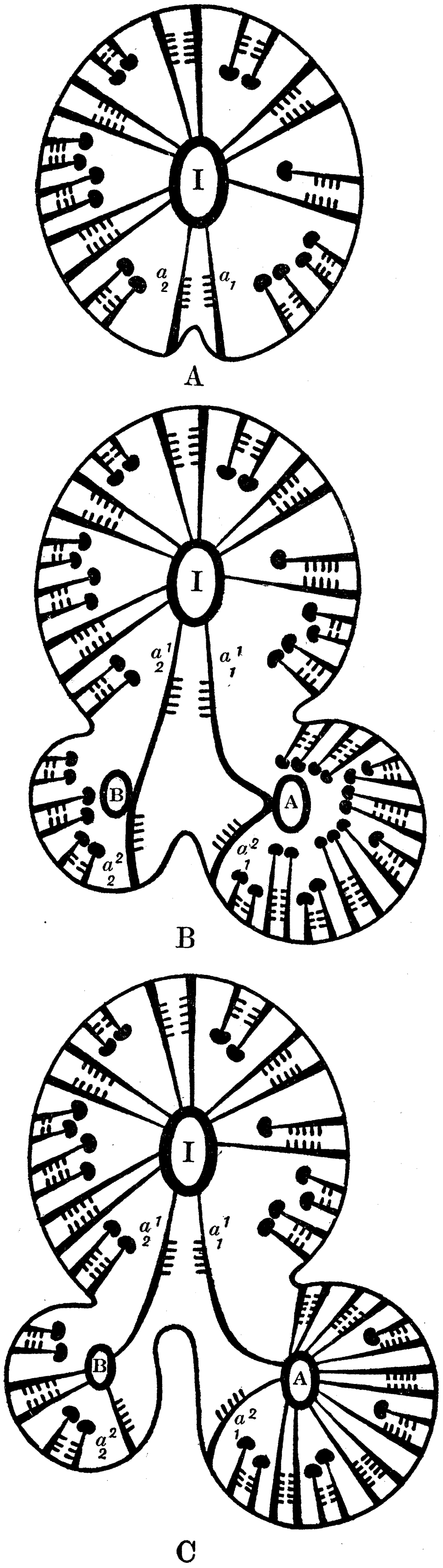
FIGURES 2, A to C. *Pavona varians* (Verrill). Intra-tentacular budding on the triangular tristomodaeal mode, with direct linkage. I, stomodaeum of mother-polyp. *A*, *B*, stomodaea of intra-tentacular buds. $a_1 a_2$, one completely principal couple of mesenteries of mother-polyp. $b_1 b_2$, one subsidiary couple of mesenteries of mother-polyp. a_1^1, a_2^1, inner parts of a_1 and a_2 forming a completely principal couple of mesenterial strands directly linking stomodaea I and *A*. a_1^2, a_2^2, outer parts of a_1 and a_2 forming a completely principal couple of left bud. b_1 1, b_2 1, inner parts of b_1 and b_2 forming a subsidiary couple of mesenterial strands directly linking stomodaea I and *B*. b_1^2, b_2^2, outer parts of b_1 and b_2 forming a completely principal couple of right bud. Figure 2A, mother-polyp. Figure 2B, later stage, showing formation of a pair of intra-tentacular buds. Figure 2C, final stage, viz. triangular tristomodaeal condition, with direct linkage, in which a_1 a_2 and b_1 b_2 have met stomodaea *A* and *B* respectively so as to be divided into a_1^1, a_2^1 and a_1^2, a_2^2, b_1^1, b_2^1 and b_1^2, b_2^2.

is different from it in the presence of mesenterial strands directly linking stomodaeum of mother-polyp with those of the two buds, hence may be considered as *intra-tentacular budding on the triangular tristomodaeal mode with direct linkage*. Interstomodaeal couples may be formed between the mother-polyp and bud.

Dichotomous branching or terminal forking on the triangular tristomodaeal mode, with double direct linkage, was previously considered in the case of *Symphyllia* (Matthai 1926, pp. 363–364, figures 26 A to C) in which one of the two double strands could form an ordinary couple and the other a directive couple, or both form directive or ordinary couples or not form couples at all. Interstomodaeal couples of mesenteries, or indirect linkage of stomodaea, might or might not be present.

Figures 3 A to C show intra-tentacular budding on the triple stomodaeal mode with direct linkage of the stomodaeum of each bud and that of the mother-polyp by means of a single mesenterial strand and indirect linkage of the stomodaea of the two buds by means of an interstomodaeal couple of mesenteries as shown in dichotomous branching or terminal forking. As a double intra-tentacular diverticulum becomes a double bud in the region of a completely principal couple of mesenteries, each mesentery of the couple is bent towards the stomodaeum of its side, and gets divided where it unites with the stomodaeum. Of the two parts of each mesentery, the inner becomes a principal mesenterial strand directly linking the stomodaeum of mother-polyp and the corresponding stomodaeum of the double bud. The outer parts of the mesenteries form a completely principal interstomodaeal couple between the stomodaea of the double bud. In this case, the pleats of the two linkage strands face each other as in an ordinary couple, and there are no ordinary couples of mesenteries between the two halves of the double bud nor an interstomodaeal couple between the mother-polyp and each half of the double bud. Forking here is comparable to dichotomous branching on the triple stomodaeal mode seen in certain Astraeid corals (Matthai 1926, pp. 327, 332, 361), but differs from it in the presence of mesenterial strands directly linking stomodaeum of mother-polyp with those of the double bud, and therefore may be looked upon as *intra-tentacular budding on the triple stomodaeal mode with direct linkage*.

Dichotomous branching or terminal forking on the triple stomodaeal mode, with single direct linkage, was described before in *Symphyllia* (Matthai 1926, p. 363, figures 25 A to C) in which the pleats of the two mesenterial strands are turned away from each other as in the case of a directive couple. Here an interstomodaeal couple of mesenteries between the two stomodaea of the buds, i.e. indirect linkage, is absent. This condition was seen in a sectioned piece (Matthai 1928, p. 228, figure 26). It is also possible that the mesenterial strands may not form a couple at all, their pleats facing the right or left side. In the piece examined, only two interstomodaeal couples were present, one of which being completely principal and indirectly linking the original stomodaeum A with the bud-stomodaeum E and the other being incompletely principal and indirectly linking the former with bud-stomodaeum D. There was no interstomodaeal couple, and therefore no indirect linkage, between the two bud stomodaea. On the other hand, in *Pavona*, the two bud stomodaea are indirectly linked by means of a completely principal interstomodaeal couple, there being no interstomodaeal couples, hence no indirect linkage, between the mother- and bud-stomodaea.



FIGURES 3, A to C. *Pavona varians* (Verrill). Intra-tentacular budding on the triple stomodaeal mode, with direct linkage. I, stomodaeum of mother-polyp. *A*, *B*, stomodaea of double intra-tentacular bud. $a_1 a_2$ one completely principal couple of mesenteries of mother-polyp. a_1^1, inner part of a_1 forming a principal mesenterial strand directly linking stomodaea I and *A*. a_2^1, inner part of a_2 forming a principal mesenterial strand directly linking stomodaea I and *B*. a_1^2 and a_2^2, outer parts of a_1 and a_2, forming a completely principal interstomodaeal couple between stomodaea *A* and *B*. Figure 3A, mother-polyp. Figure 3B, later stage, showing formation of a double intra-tentacular bud. Figure 3C, final stage, viz., triple stomodaeal condition, with direct linkage, in which a_1 and a_2 have met stomodaea *A* and *B* respectively, so as to be divided into a_1^1, a_1^2 and a_2^1, a_2^2.

From the above observations it appears that in *Pavona* and *Symphyllia*, and probably also in *Mycetophyllia* and *Lobophyllia*, the presence of one or more mesenterial strands stretching between adjacent stomodaea—the counterparts of the mesenterial strands in the corallum being the septal lamellae linking neighbouring columellar centres—is the primary condition, whilst interstomodaeal couples, and therefore indirect linkage, may or may not be present. Attention was previously directed to the relative importance of direct and indirect linkage in the case of *Symphyllia* (Matthai 1926, p. 363).

The bending of mesenteries towards, and fusion at their bends with new stomodaea and consequent vertical cleavage, as shown in figures 1 A to C, 2 A to C and 3 A to C are similar to what has taken place in an intra-tentacular bud of *Mycetophyllia* (Matthai 1928, mesenteries d_1, e_2 and f_2 in figure 32). All these cases are comparable to the bending and cleavage of mesenteries in an extra-tentacular diverticulum at the edge of a colony of *Favia hululensis* Gard. (Matthai 1926, pp. 342–344, figures 22 A and B, plate 24, figures 20 *a* and *b*).

In figure 4 the polystomodaeal polyp has undergone dichotomous branching, beyond III, on the triangular tristomodaeal mode, with direct linkage of the new stomodaea IV and V by 5_1 and 5_2 (a subsidiary couple of mesenterial strands) and 8_1 and 8_2 (a completely principal couple of mesenterial strands) respectively. The right branch of the primary fork contains only two polyp areas, viz. IV and IX formed on the distomodaeal mode with direct linkage by 15_1 and 15_2 (a completely principal couple of mesenterial strands), and has not yet undergone lateral or dichotomous branching. In the left branch, bud VI was formed by lateral branching on the distomodaeal mode, 12_1 and 12_2 being probably a subsidiary interstomodaeal couple between V and VI. Beyond V, in the left branch, dichotomous branching on the triple stomodaeal mode, with direct linkage, has taken place, the stomodaea VII and VIII of the two new buds being directly linked with V by mesenterial strands 13_2 and 13_1 respectively, and indirectly linked with each other by the completely principal interstomodaeal couple 14_1 and 14_2. From the arrangement of mesenteries in the intra-tentacular diverticulum (*intra-tent divert*) and in polyp area VII, it is unlikely that directly linking mesenterial strands will be formed between stomodaeum VII and the new stomodaeum that will appear in the diverticulum, i.e. the new bud will be formed on the usual distomodaeal mode as in Astraeid corals.

Mesenterial strand 1 directly linking stomodaea I and II becomes split in lower sections into two parts, and forms completely principal couples with 2_1 and 2_2 respectively; similarly, mesenterial strand 3 becomes split into two parts forming couples respectively with 4_1 and 4_2; 5_1+6_1 and 5_2+6_2 probably formed a subsidiary couple of polyp area III before the appearance of stomodaeum IV. Similarly, 8_1+9_1 and 8_2+9_2 constituted a completely principal couple of polyp area III before stomodaeum V was formed. Between IV and V are two subsidiary couples of mesenteries, viz. 10_1 and 10_2, 11_1 and 11_2. 13_1+14_1 and 13_2+14_2 probably constituted a completely principal couple of polyp area V before the formation of stomodaea VII and VIII in a pair of diverticula. 15_1 and 15_2 were probably continuous with 16_1 and 16_2, forming a completely principal couple of polyp area IV before stomodaeum IX made its appearance.

Bud VIII is the youngest in the piece sectioned. It has comparatively few mesenteries and its stomodaeum is newly formed, being short and narrow. The appearance in the sections suggests that the stomodaeum has been formed by invagination of the oral disk,

FIGURE 4. *Pavona varians* (Verrill). Transverse section through stomodaeal region of a piece from the edge of a colony from Tahiti, containing eight stomodaea and an intra-tentacular diverticulum. Only part of stomodaeum I is included in the piece sectioned. I–IX, stomodaea of polystomodaeal polyp; *intra-tent divert*, intra-tentacular diverticulum. The number and disposition of mesenterial strands and of interstomodaeal couples effecting direct and indirect linkage respectively are shown in this figure. Dotted areas represent parts of skeleton (P_1).

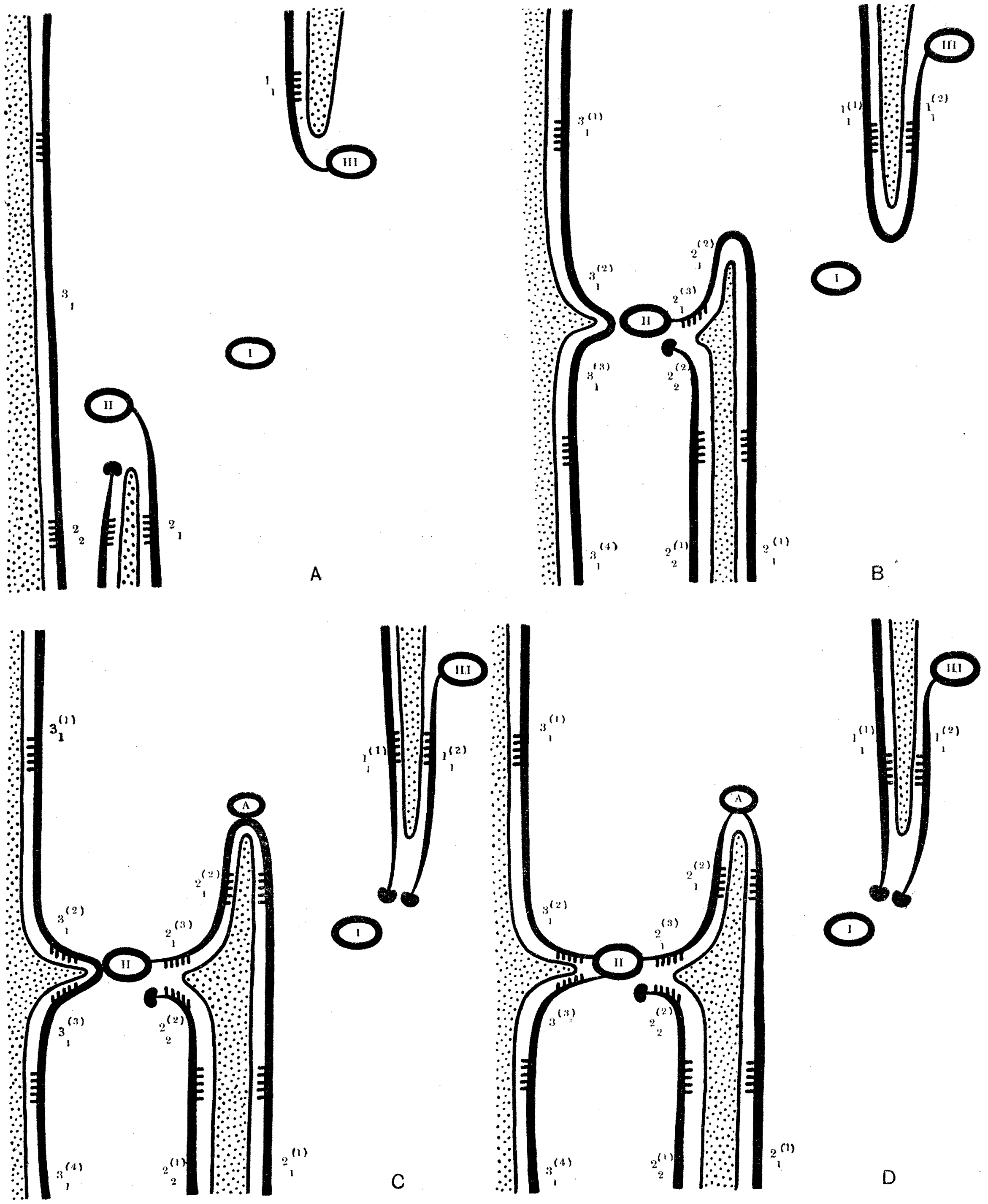
being distinguishable from the latter by the greater number of nuclei in its inner lining, but ridges have not yet been formed at the mesenterial attachments (cf. Matthai 1919, plate III, figure 3; 1923, figure 17; 1926, figure 3). In the intra-tentacular diverticulum (*intra-tent divert*) of VII, containing five couples of mesenteries, a stomodaeum has not yet been formed and filaments are poorly developed on the mesenteries. Polyp area VII, bud VIII and the intra-tentacular diverticulum form a linear series at the growing edge of the colony from which the sectioned piece was taken.

Echinophyllia aspera (Ellis & Solander)

The course of mesenteries is reflected in a general manner on that of the septo-costae (see Matthai 1920 in this connexion). But the latter do not indicate the mesenterial arrangement in couples nor the differentiation into principal and subsidiary mesenteries. Since septo-costae are upturned to a varying degree around columellar centres, mesenteries curve round them and get vertically divided at their bends.

Bud formation is shown in figures 5A to D. Figure 5A represents three polyp areas with their respective stomodaea I, II and III. 1_1 is one of the principal mesenteries of III; 2_1 and 2_2 form an incompletely principal couple of II. Mesentery 3_1 follows a straight course. Mesenteries around I are not shown in the diagram. In figure 5B, mesentery 1_1 has curved around the upgrowing end of its entocoelic septum, 1_1 (1) and 1_1 (2) being the two arms of the bent mesentery. As the entocoelic septum between 2_1 and 2_2 is growing upwards as well as inwards towards the columella, 2_1 has been doubly curved and has now three arms, viz. 2_1 (1), 2_1 (2) and 2_1 (3); by the ingrowth of septum, 2_2 has also been curved towards stomodaeum II, 2_2 (1) and 2_2 (2) being its two arms. 3_1 is curving over the ingrowth of its entocoelic septum towards the columella, 3_1 (1), 3_1 (2), 3_1 (3) and 3_1 (4) being its four arms. In figure 5C the two arms 1_1 (1) and 1_1 (2) have become separate mesenteries by vertical cleavage at the bend and are directed towards stomodaeum I, their split margins having developed filaments. Bud-stomodaeum *A* is being formed by invagination, and has caught 2_1 at its first bend between 2_1 (1) and 2_1 (2). By the continued ingrowth of its entocoelic septum, 3_1 has been pushed inwards to such an extent that it has met stomodaeum II at its curve between 3_1 (2) and 3_1 (3). In figure 5D, both 2_1 and 3_1 have been vertically divided by fusion at their bends with stomodaea *A* and II respectively. Thus, 2_1 (2) + 2_1 (3) has now become a mesenterial strand directly linking stomodaea II and *A*. 3_1 (2) and 3_1 (3) form a completely principal couple of II at the opposite end. It is characteristic of *Echinophyllia aspera* (Ell. & Sol.) that mesenteries at each end of the longer diameter of the stomodaeum curve towards the latter. The two mesenteries at each end of the longer diameter may form a couple or belong to different couples.

In figure 6, mesentery 1_1 (1) + 1_1 (2) + 1_1 (3) + 1_1 (4), which is continuous at a higher level and curves towards stomodaeum I, becomes vertically divided lower down at the bend between 1_1 (2) and 1_1 (3), and the two split margins develop filaments; 1_1 (2) and 1_1 (3) form a subsidiary couple of I, 1_1 (1) and 1_1 (4) being the parts of the couple beyond the wall of the calicinal area. Filament epithelium extends up to the bend of the mesentery just above the split. The two end mesenteries 10_2 (subsidiary) and 11_1 (principal) belong to two different couples, whilst the opposite end mesenteries 4_1 (1) and 4_2 (2) form a completely principal couple. 4_1 (3) and 4_1 (4) form a completely principal couple of III. It is, therefore, not unlikely that $4_1\,(1)+4_1\,(2)+4_1\,(3)+4_1\,(4)+4_1\,(5)$ was originally



FIGURES 5, A to D. *Echinophyllia aspera* (Ellis & Solander). Formation of intra-tentacular bud. I, II, III, stomodaea of mother-polyp. *A*, stomodaeum of bud. Dotted areas represent septa.

a mesentery of I forming a completely principal couple with $4_2\,(1)+4_2\,(2)$; if so, it was curved towards stomodaeum III and, by fusion with the latter at its bend between 4_1 (3) and 4_1 (4), was vertically split into two parts, the extra-polypal parts 4_1 (5) and 4_2 (1)

still showing the original coupling. One of the terminal parts of 5_2, viz. 5_2 (5), is a subsidiary mesentery of I, whilst the other terminal part, viz. 5_2 (3), is a principal mesentery of III. 5_1 (1), 12_1 (1), 12_2 (1), 13_1 (1), 13_2 (1), 1_1 (4) and 1_1 (1) extend beyond wall of calicinal area as comparatively straight mesenteries by the side of polyp area III. On the right side of polyp area I is a fairly straight couple 8_1 and 8_2 whose terminal portions are not included in the sectioned piece. In upper sections it is seen that 2_1 (1) + 2_1 (2) + 2_1 (3) + 2_1 (4) becomes a doubly curved mesentery; the first curve between 2_1 (2) and 2_1 (3) has been formed by the upgrowth of its entocoelic septum into polyp area III (the mesentery is

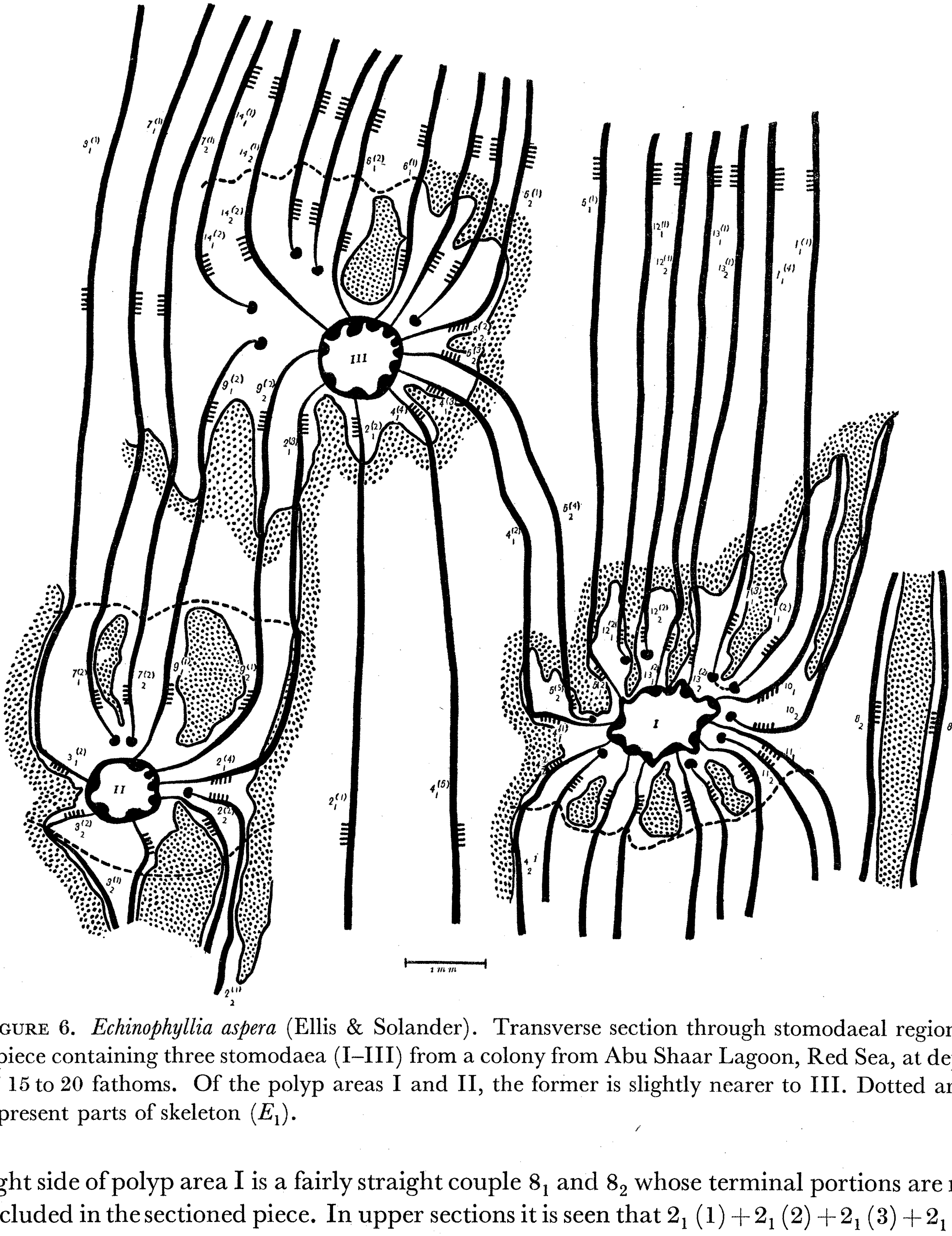


FIGURE 6. *Echinophyllia aspera* (Ellis & Solander). Transverse section through stomodaeal region of a piece containing three stomodaea (I–III) from a colony from Abu Shaar Lagoon, Red Sea, at depth of 15 to 20 fathoms. Of the polyp areas I and II, the former is slightly nearer to III. Dotted areas represent parts of skeleton (E_1).

attached on both sides to the base of the upgrowth), and the mesentery vertically splits where its first bend is fused with stomodaeum III, thus 2_1 (2) and 2_1 (3) form a completely principal couple of III (see also figure 7); the second curve between 2_1 (3) and 2_1 (4) is due to its terminal part being directed towards, and connected with, stomodaeum II. 2_1 (4) and 2_2 (2) form an incompletely principal end couple of II. The extrapolypal part of the mesentery between 2_1 (3) and 2_1 (4) is attached to the adjacent septum by numerous wedge-shaped processes of the middle lamina, but atrophies in the lower sections and finally disappears. 5_2 (1) + 5_2 (2) + 5_2 (3) + 5_2 (4) + 5_2 (5) was probably a straight subsidiary mesentery of I forming an incompletely principal couple with 5_1 (1) + 5_1 (2), and was bent towards and fused at its bend between 5_2 (2) and 5_2 (3) with stomodaeum III, while the latter was being formed by invagination; consequently the mesentery was vertically split at its bend. Thus 5_2 (2) and 5_2 (3) form a completely principal end couple of III, and 5_2 (5) forms with 5_1 (2) an incompletely principal couple of I. Beyond polyp area III, 5_2 (1) still forms a couple with the extrapolypal part of 5_1 (1). The part 5_2 (4) between polyp areas I and III atrophies towards the base. Thus 4_1 (1) + 4_1 (2) + 4_1 (3) and 5_2 (3) + 5_2 (4) + 5_2 (5) form two mesenterial strands that directly link stomodaea I and III, but belong to different couples. 6_1 (1) + 6_1 (2) was a curved mesentery that fused at its bend with stomodaeum III, and has thus been vertically divided into two mesenteries that form a completely principal couple of III (see also figure 7). 9_1 (2) and

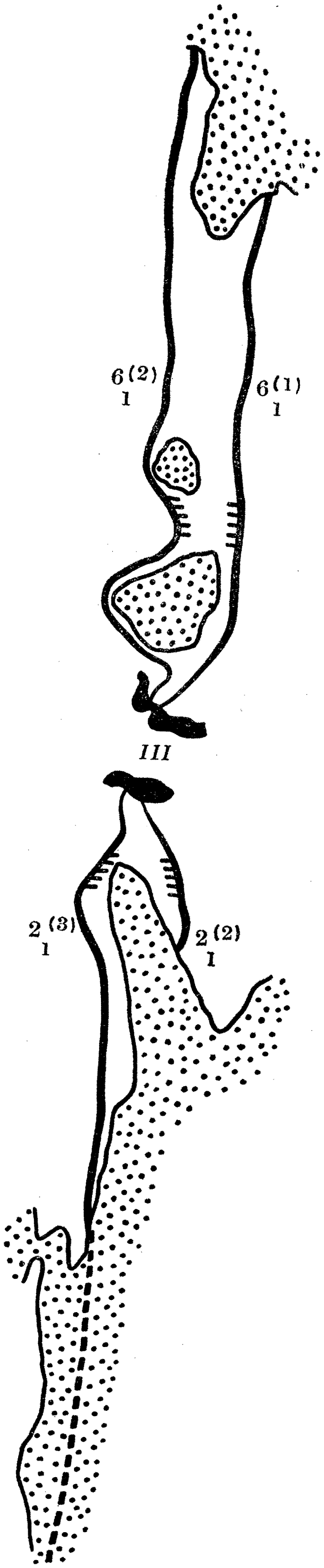


FIGURE 7. *Echinophyllia aspera* (Ellis & Solander). Transverse section of two mesenteries in figure 12, taken at a level showing their curvature towards stomodaeum III (figured in part) from opposite directions. The mesenteries meet stomodaeum at their bends. Vertical division due to fusion has proceeded from below up to this level, resulting in two couples, viz. 2_1 (2) and 2_1 (3), 6_1 (1) and 6_1 (2). Dotted areas represent septa.

9_2 (2) form an incompletely principal couple of III, whilst 9_1 (1) and 9_2 (1) form a completely principal couple of II; in lower sections the two couples become continuous. Thus the two mesenteries 9_1 (2) + 9_1 (1) and 9_2 (1) + 9_2 (2), with 2_1 (3) + 2_1 (4), at first formed three mesenterial strands that directly linked stomodaea II and III, the two former forming a couple but subsequently became discontinuous owing to the formation of corallite walls around I, II and III by the fusion of the upturned ends of the septo-costae. There is no direct linkage between stomodaea I and II. 9_1 (2) and 14_1 (2) are two subsidiary end mesenteries of III, belonging to different couples. 3_1 (2) and 3_2 (2) form a completely principal end couple of II. 3_1 (1) + 3_1 (2), 7_1 (1) + 7_1 (2) and 7_2 (1) + 7_2 (2) are continued from polyp area II alongside of polyp area III. Running more or less parallel to one another are nineteen mesenteries above—three from II, nine from III and seven from I, and fifteen mesenteries below—four from II, two from III and nine from I; the terminal portions of these mesenteries are not included in the sectioned piece. In addition, there are two mesenteries 8_1 and 8_2 (partially included in sectioned piece) outside polyp area I, which belong to this system of parallel mesenteries.

Curvature of certain mesenteries towards newly formed stomodaea is a conspicuous feature of *Echinophyllia* in the early stages of bud-formation. Vertical cleavage takes place by fusion of such mesenteries, at their bends, with the stomodaea. The mesenterial strands so formed for direct linkage of stomodaea may become discontinuous by upraising of septo-costae in the calicinal areas and tendency towards fusion of the upraised ends to form corallite walls. Direct linkage may cease by the atrophy of extra-polypal portions of the mesenterial strands. Interstomodaeal couples of mesenteries have not been observed in the sections; indirect linkage of stomodaea does not, therefore, seem to exist in *Echinophyllia*.

Leptoseris hawaiiensis Vaughan

Short tentacles with terminal batteries are seen in sections, but their exact arrangement can only be determined on living material. Mesenteries follow a straight course towards the periphery corresponding to the direction of the septa, except at the proximal sides of the bases of calicinal areas where corallite walls are formed which interrupt the course of the mesenteries. In the case of incompletely principal and subsidiary couples, one of the mesenteries of a couple is usually much narrower.

Figures 8 A to D show the formation of an intra-tentacular bud. Vertical cleavage of mesenteries of mother-polyp, from below upwards, by the growth of skeletal structures, is frequent and plays an important part in the formation of intra-tentacular diverticula. Couples that are formed by curvature of mesenteries may also become split along their bends prior to stomodaeal formation, if such couples are present in a region where an intra-tentacular diverticulum is to be formed. The split margins, directed towards the diverticulum, develop filaments. The stomodaeum is usually formed by the union of filaments of the broader mesenteries, and subsequently effects an external opening by rupture of the oral disk. Buds may be formed within, or between, concentric rows of polyp areas.

It is seen in sections that most mesenteries in a colony, varying from straight to curved, get split to varying heights from the base, but only in the areas of potential buds do split mesenteries develop filaments along their free margins. New mesenteries may also arise in a bud. Direct or indirect linkage of stomodaea, by mesenterial strands or by inter-stomodaeal couples, has not been observed. In the corallum also there are no septal lamellae between columellar centres.

The appearance of secondary branching of septa is due to vertical splitting of septo-costae, at places where mesenterial cleavage takes place, supplemented by the formation of new septo-costae corresponding to new mesenteries and subsequent fusion, at places, of the outer or inner free margins of new septo-costae with the sides of their neighbours. Since the intervals between concentric rows of calicinal areas are comparatively wide, septo-costae in intervals are correspondingly long and their branching appearance becomes apparent.

Figure 9 shows arrangement of mesenteries in polyp areas, incipient intra-tentacular buds and in intra-tentacular diverticula. Mesentery 1 extends from below polyp area I into intra-tentacular diverticulum *A*, and bears a filament along each free margin; it is vertically divided at a lower level into two parts, viz. *r* 1 (bearing testes) forms a mesentery

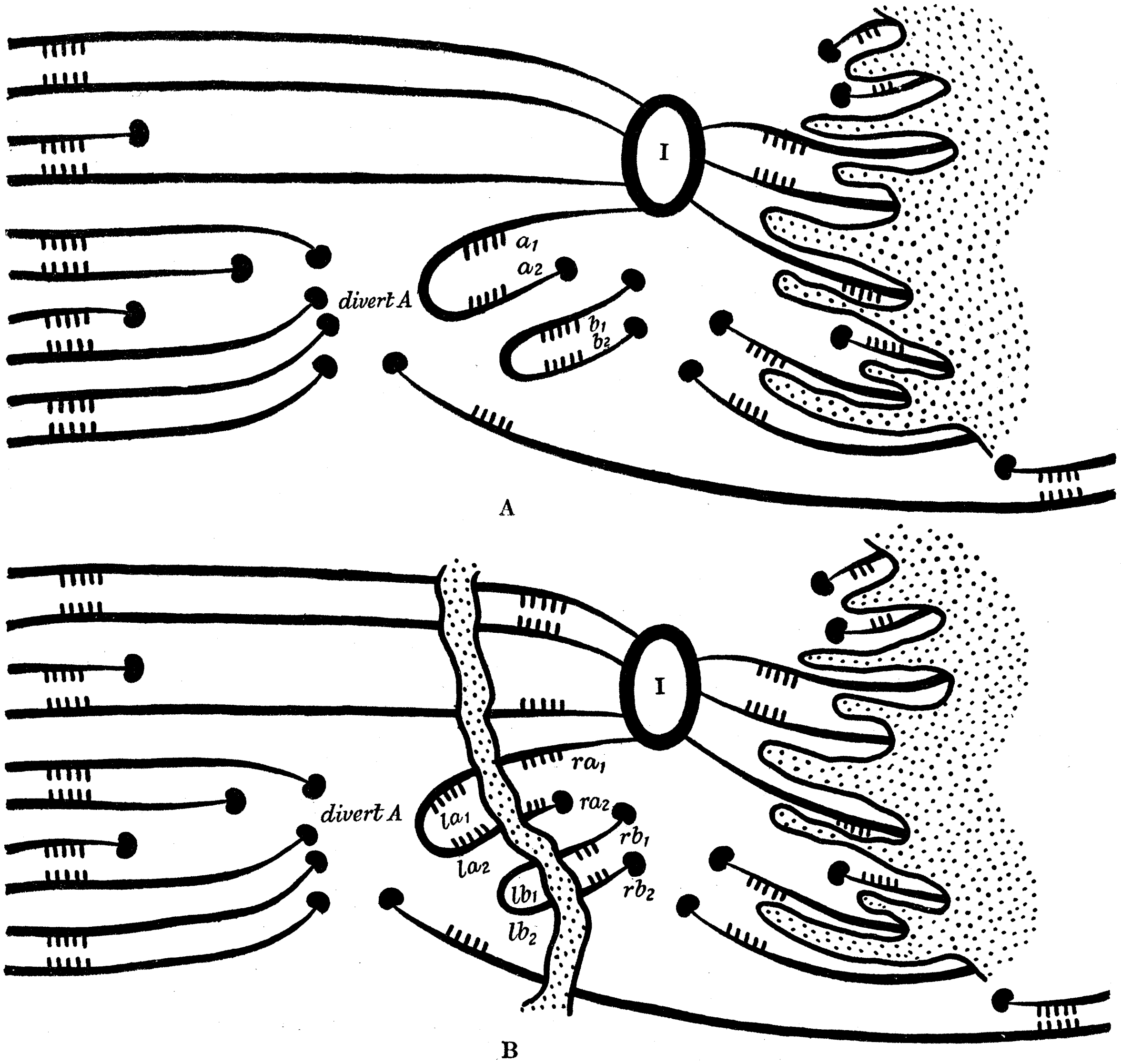
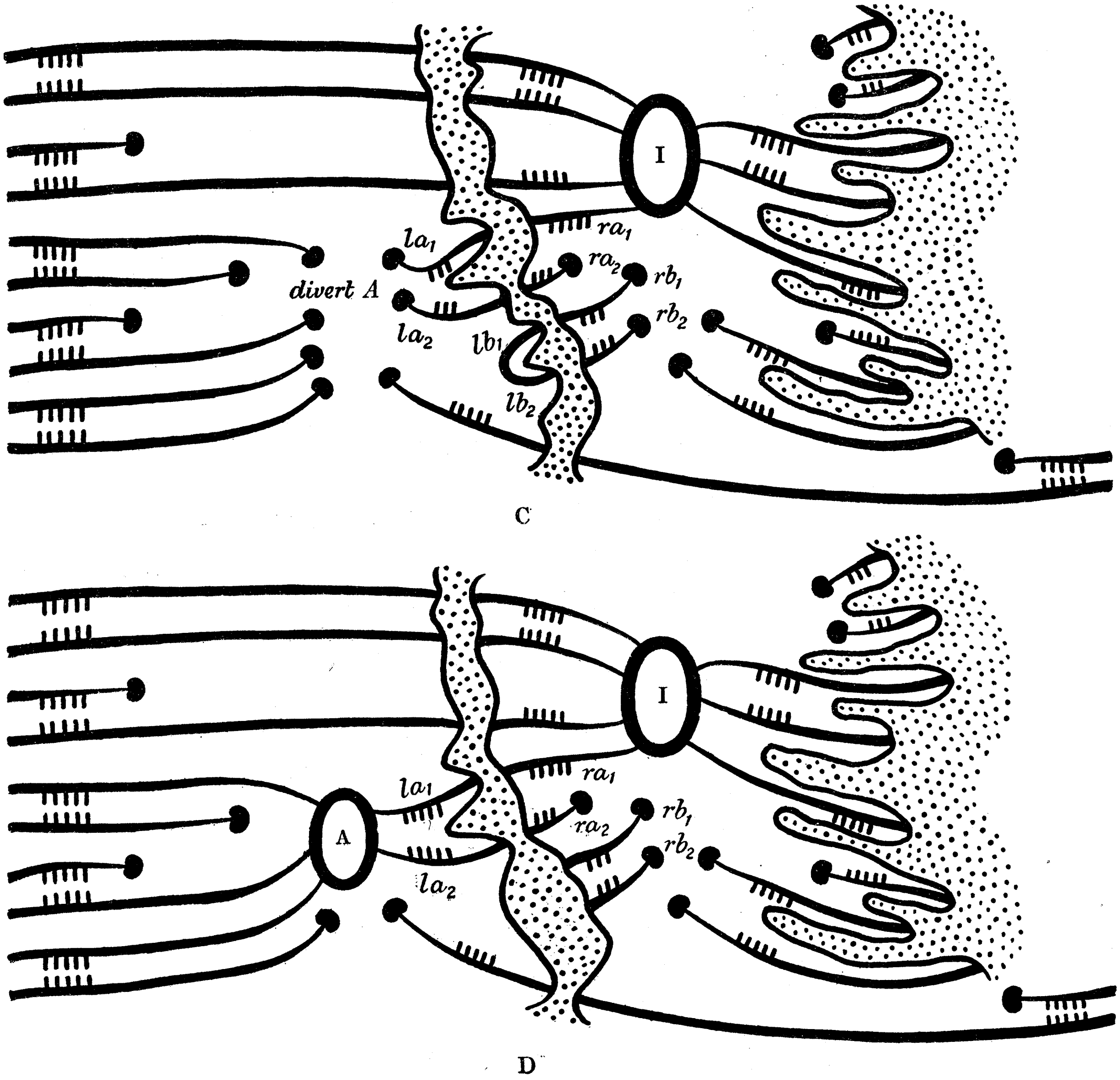


FIGURE 8. For legend see opposite.



FIGURES 8, A to D. *Leptoseris hawaiiensis* Vaughan. Formation of intra-tentacular bud: *divert.* intra-tentacular diverticulum; I, stomodaeum of mother-polyp; *A*, stomodaeum of intra-tentacular bud. Figure 8A, mother-polyp with intra-tentacular diverticulum on the left side. Mesenteries are continuous, except on proximal side where corallite-wall (represented by dots) is present. $a_1 a_2$, $b_1 b_2$, two couples of mesenteries, each formed by curvature of one mesentery. Figure 8B, later stage showing cleavage from below upwards of all mesenteries on left (distal) side of polyp region including the two couples formed by curvature of two mesenteries. Figure 8C, still later stage in which the upper curved mesentery is split again at its bend, thus resulting in two couples of mesenteries whose free margins develop filaments, viz. ra_1, ra_2 in the mother-polyp on the right side and la_1, la_2 in the intra-tentacular diverticulum on the left side. Figure 8D, final bud stage showing formation of new stomodaeum *A* by the union of filaments of five mesenteries. The left part (lb_1, lb_2) of the lower curved mesentery has atrophied, leaving only a right couple of mesenteries rb_1, rb_2 in the mother-polyp.

in region beyond I and *l* 1 in diverticulum *A*. 2_1 and 2_2 are formed by the curvature of the same mesentery which becomes divided at a lower level, the inner parts forming a subsidiary couple of I and the outer bent portion disintegrating towards the base. 3_1 and

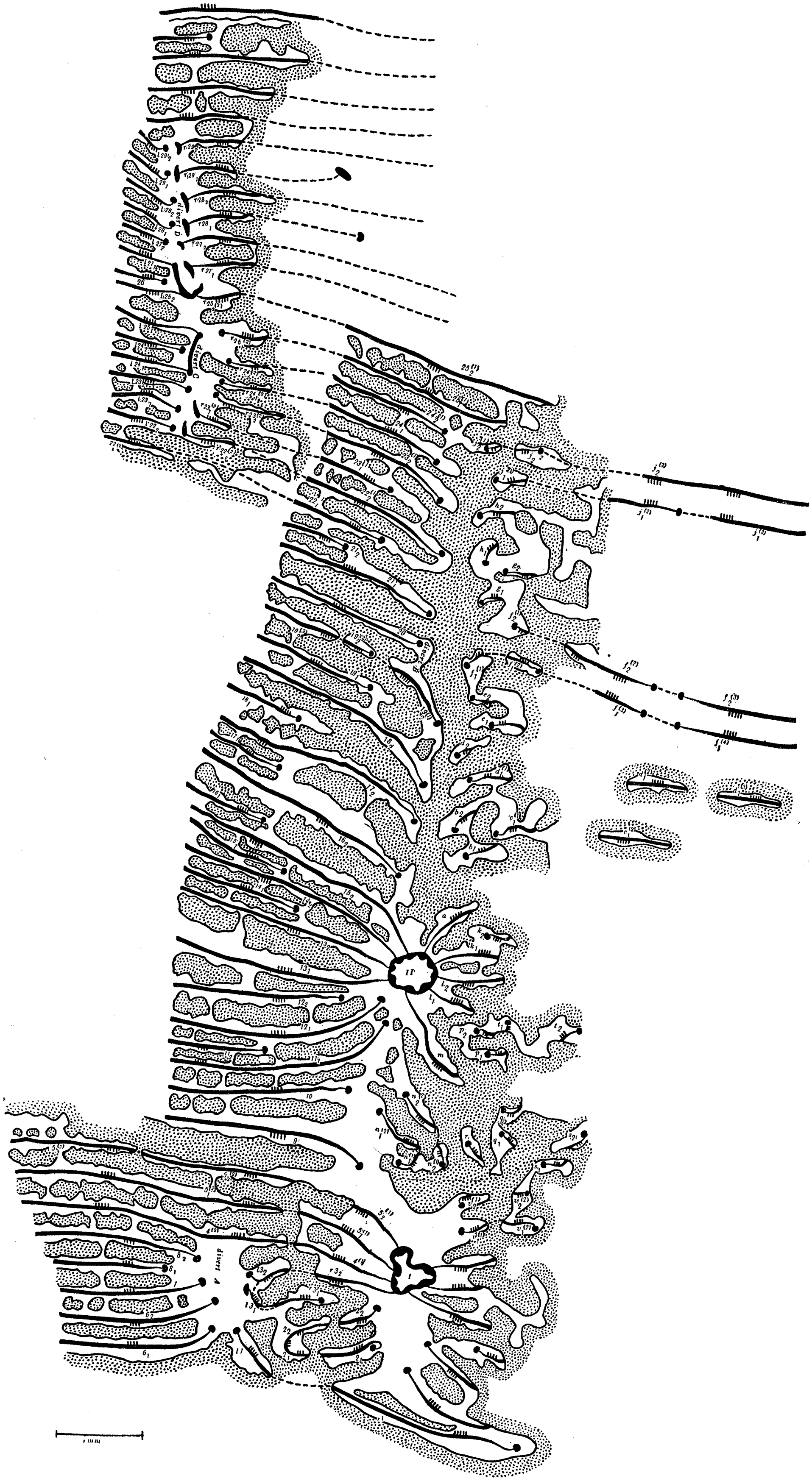


FIGURE 9. *Leptoseris hawaiiensis* Vaughan. Transverse section through stomodaeal region of a piece containing two stomodaea (I and II) and four intra-tentacular diverticula (*divert. A–D*) from a colony from outside Abu Galawa, Red Sea, at a depth of 25 fathoms. Several mesenteries bear testes; the latter form a row in each mesentery, but ova have not appeared in any mesentery. Dotted areas represent parts of skeleton (L_2).

3_2 are also formed by the curvature of a mesentery; by vertical splitting near the middle, the inner parts, $r\ 3_1$ and $r\ 3_2$, become an incompletely principal couple of I; by a similar division at the bend and development of filaments along the free margins thus formed, the outer parts, $l\ 3_1$ and $l\ 3_2$, become a subsidiary couple of diverticulum A. 4 (without fellow in sectioned piece), 5_1 and 5_2 are beyond region of diverticulum A and are vertically divided at a lower level, their inner parts, viz. 5_1 (1) and 5_2 (1) becoming principal mesenteries of I. 6_1 and 6_2, 7 (without fellow), 8_1 and 8_2 are mesenteries of diverticulum A. 9 is directed towards I, and probably belongs to it. V_1 (1) and V_1 (2) become continuous at a higher level; similarly V_2 (1) and V_2 (2), which are now completely separate, might have been originally continuous; V_1 (1) and V_2 (1), V_1 (2) and V_2 (2) form subsidiary couples, the former in polyp area I, the latter in region beyond I. n_1 and n_2 are vertically divided at a lower level, the parts n_1 (1) and n_2 (1) are directed towards I, and probably belong to the latter, whilst n_1 (2) and n_2 (2) belong to II. 10 (without fellow), 11_1 and 11_2, 12_1 and 12_2 probably belong to II. 14_1, 15_1, 16_1, 17_1, 18_1, 19_1, 22_1, 23_1 form a series of narrow mesenteries on the left, whilst 11_1, 12_1, 20, 21_1 belong to the series of broader mesenteries on the same side. An alternation into broad and narrow mesenteries is not seen on the right (proximal) side, owing perhaps to the formation of corallite walls. c_1 (1) and r probably form incompletely principal couples respectively with a and m. p_1 and p_2, q_1 and q_2, s_1 and s_2, t_1 and t_2 are perhaps remnants of mesenteries that have disintegrated to the right of II, and probably form four subsidiary couples, although their pleats are not clearly seen; the first two couples probably belong to II and the last two to region to the right of II. Since corallite walls have been formed on the right (proximal) side of polyp areas I and II, the mesenteries on that side have lost their continuity beyond the polyp areas. The region beyond II contains fifteen couples of mesenteries and one mesentery (viz. 20) without a fellow; of these, 16_2 is directed towards, and may meet, stomodaeum II. It is possible that, in this region, two buds may be formed, although there is yet no indication of stomodaeal formation, i.e. the mesenterial filaments, unlike the condition in C and D, neither show sign of union nor are they broadened. In the upper sections the continuation of f_1 and f_2, j_1 and j_2 into the region to the right of B is visible; the distal margins of f_1 (1), f_2 (1), j_1 (1), j_2 (1) and proximal margins of f_1 (2) and f_2 (2) are attached to corallum, whilst the distal margins of f_1 (2), f_1 (3), f_2 (2), j_1 (2), j_2 (2) and the proximal margins of f_1 (4), f_2 (3) have developed filaments. f_1 (3), f_1 (4), f_2 (2), f_2 (3), j_1 (3), j_2 (2) bear testes. Left and right mesenteries of diverticulum B that face each other are 17_1 and b_1, 17_2 and b_2, 18_1 and d_1, 18_2 and d_2, 19_1 and e_1, 19_2 and e_2, 21_1 and f_1 (1), 21_2 and f_2 (1), 22_1 and g_1, 22_2 (1) and g_2, 23_1 (1) and h_1, 23_2 (1) and h_2, 24_1 (1) and j_1 (1), 24_2 (1) and j_2 (1). Beyond the diverticulum to the right g_1, g_2, h_1, h_2 are not continued, probably because their outer parts have disintegrated with the formation of incipient bud corallite wall on that side. There are two broken pieces of mesentery, d_1 (2) and d_1 (3), bearing testes but not filaments, which probably were originally continuous with d_1 (1), although actual connexions with the latter are not seen in sections. Similarly, there is a broken piece of mesentery, c_1 (2), bearing testes but not filament, probably continuous with c_1 (1), although its connexion with the latter is not seen in sections. 25_1 (1) and 25_2 (1) are beyond the region of B. The appearance in sections of the region beyond B indicates that it is composed of two diverticula C and D. Probably C extends from 22_2 to 25_1, and D from 25_2 to 29_2, in which case

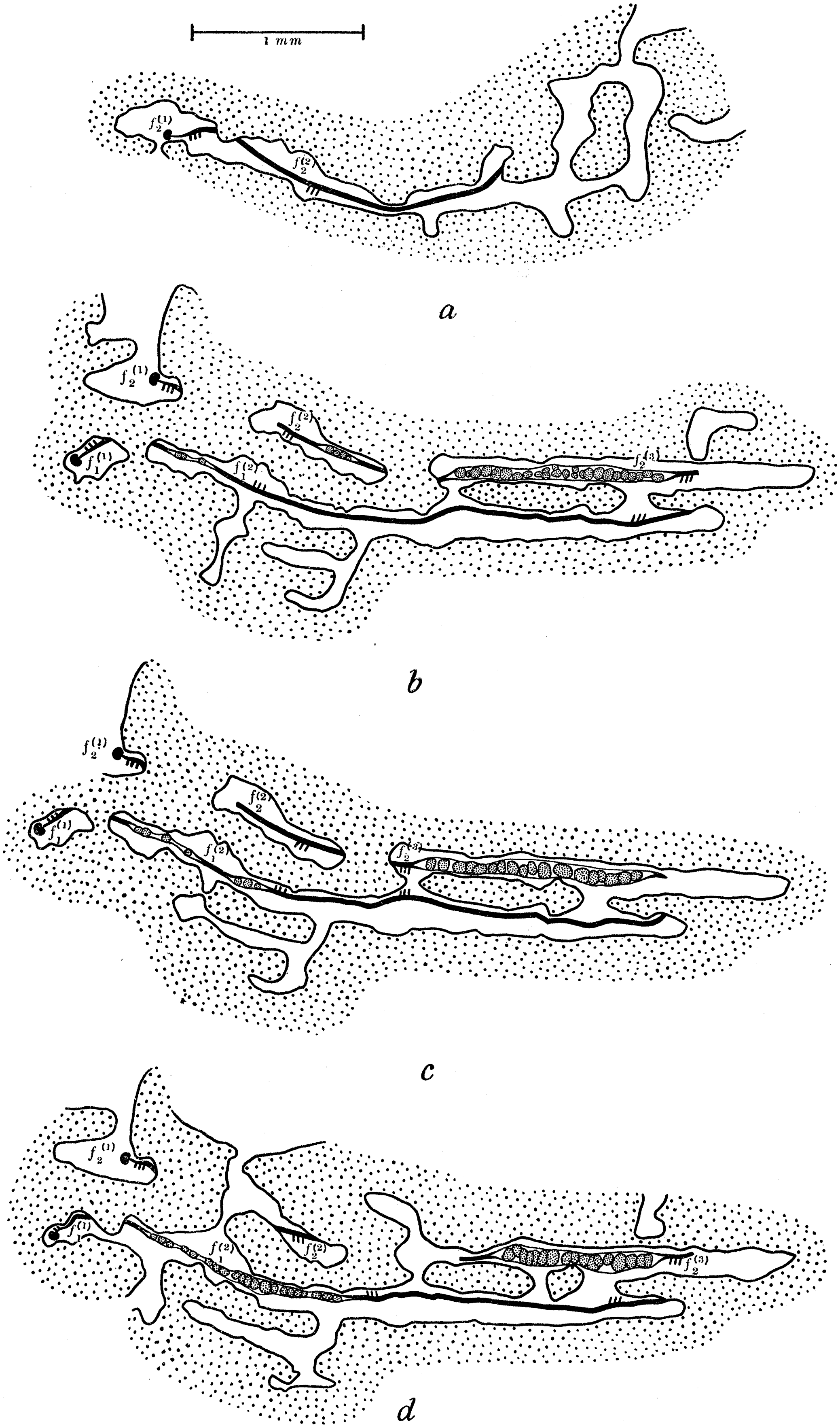
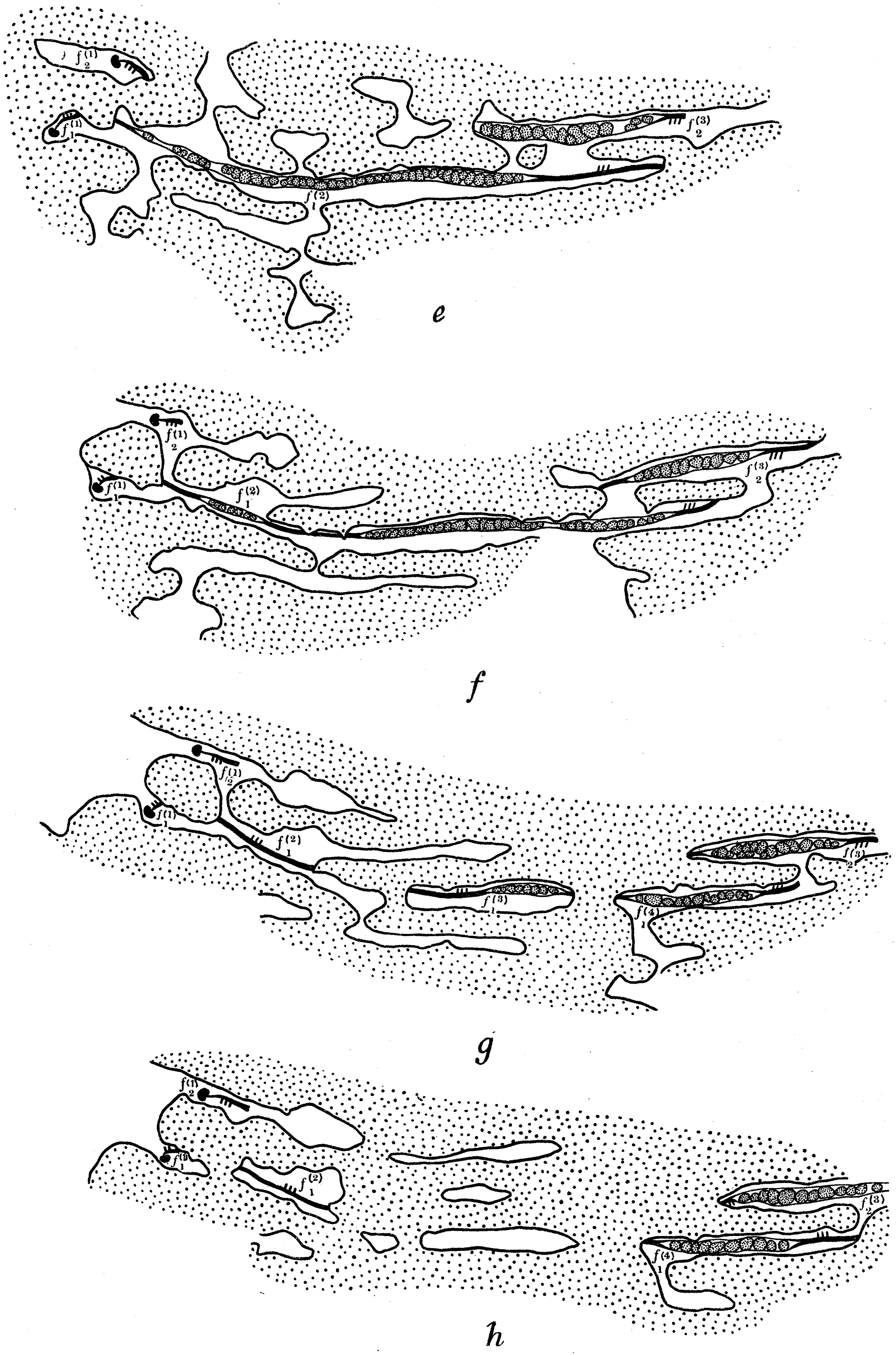


FIGURE 10. For legend see p. 221.



Figures 10, *a* to *h*. *Leptoseris hawaiiensis* Vaughan. Views of series of transverse sections from above downwards, showing vertical cleavage of a couple of mesenteries, f_1 and f_2. Testes represented by dotted sacs within mesenteries, septa by dotted areas. *a*, one of the two mesenteries, f_2, split into f_2 (1) and f_2 (2). *b*, both mesenteries. f_2 (2) divided into f_2 (2) and f_2 (3), both parts bearing testes. f_1 divided into f_1 (1) and f_1 (2), the latter showing commencement of testes. *c*, f_1 (2) bearing testes. *d*, f_2 (2) disintegrating. *e*, f_2 (2) has disappeared. *f*, f_1 (2) showing signs of division. *g*, f_1 (2) divided into f_1 (2), f_1 (3) and f_1 (4). *h*, f_1 (3) has disappeared.

r 25_1 (2) and *r* 25_2 (2), *l* 25_1 and *l* 25_2 may form two interstomodaeal couples of mesenteries. The two diverticula are not in line with each other, *D* being a little external to *C*. The filaments of most of the mesenteries are broadened and those of some adjacent mesenteries have met; this indicates that stomodaea of buds are formed by fusion of mesenterial filaments, mouth-openings being subsequently formed as splits in the oral disk. *r* 22_2 (2) to *r* 24_2 (2) are continuous at a higher level with 22_2 (1) to 24_2 (1) in *B*, but this continuity will get interrupted with the formation of bud corallite wall as in *B*, each mesentery bearing filaments along both free margins. *r* 25_1 (2) and *r* 25_2 (2) are continuous with 25_1 (1) and 25_2 (1), the latter without filaments along their split margins. Mesenteries similarly numbered on the two sides of *C* and *D* face each other, and in each case the two opposing mesenteries are perhaps formed by the splitting of a continuous mesentery, with filaments appearing on the split margins. 26 on the left side of *D* appears to be a new mesentery whose fellow is not seen in the sectioned piece. Diverticula and incipient buds are marked out on the oral disk, but are yet without any trace of mouth-openings. *B* is formed in the same row as polyp areas I and II, whilst *A*, *C* and *D* are outside this row. It seems probable that a new diverticulum will be formed to the right of (proximal to) *D*, as 28_1 and 29_1 are already split and filaments have appeared on their split margins. In regard to vertical division of mesenteries, there are intermediate stages such as $r\,1+l\,1$, $n_1\,(1)+n_1\,(2)$, $n_2\,(1)+n_2\,(2)$ between the straight and bent conditions represented by $f_1\,(1)+f_1\,(2)+f_1\,(3)+f_1\,(4)$ and $r\,3_1+l\,3_1+l\,3_2+r\,3_2$ respectively.

Figures 10 *a* to *h* further show the process of cleavage in a couple of mesenteries, viz. f_1 and f_2 of figure 9.

Coupling by mesenterial curvature usually occurs in *Leptoseris*. But whilst in *Echinophyllia* the mesentery is bent inwards towards the corresponding stomodaeum and usually fuses with the latter at the bend, in *Leptoseris* the mesenterial curvature is directed outwards away from the stomodaeum. In both genera mesenterial cleavage takes place at the bend, and when the resulting margins are free they develop filaments; extra-polypal portions of mesenteries also tend to atrophy.

Psammocora haimiana Milne Edwards & Haime

In this species tentacles with terminal and sub-terminal batteries can be seen in sections, appearing to be arranged around mouth openings; these are mostly entocoelic, but exocoelic tentacles have also been observed.

With regard to *Psammocora gonagra* Klunzinger and *P.* (=*Stephanaria*) *stellata* (Verrill), Yonge (1930, pp. 39–40) remarks as follows:

'The surface is covered with extremely short, blunt tentacles which have the appearance under the binocular of a short brown "fur". The polyps are dotted over the surface, as shown in text-fig. 22, each having a prominent mouth situated on the summit of a relatively large oral cone. The mouth opening is normally small, but capable of great extension; the oral cone is higher than the tentacles and capable of much greater movements. In *P. gonagra* each polyp possesses usually from 4 to 6 tentacles, but in *P. stellata* they are more numerous, between 6 and 9, and have greater powers of expansion. In both species it is difficult often to distinguish to which of adjacent mouths particular tentacles rightly belong.'

The outer parts of some of the intermesenteric spaces, with the subsidiary couples of mesenteries contained in them and the overlying tentacles, are constricted off by interseptal skeletal partitions, and secondarily become extrapolypal. More than one such partitioned off outer region of a polyp, with their mesenteries and tentacles, take part in the formation of a diverticulum as shown in figures 11 A to D. New couples of mesenteries then arise either in the dissociated peripheral parts of intermesenteric spaces or

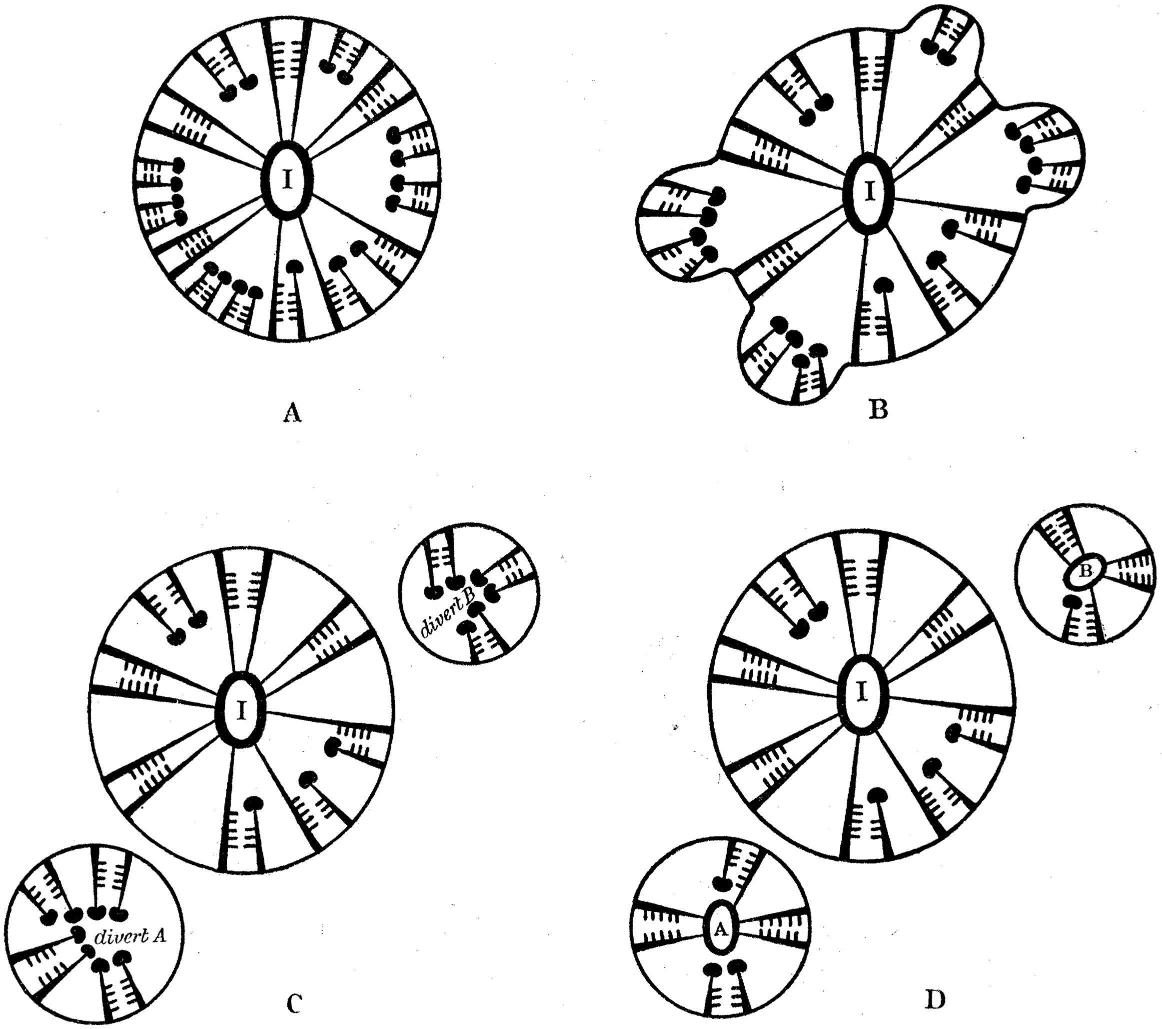


FIGURE 11, A to D. *Psammocora haimiana* Milne Edwards & Haime. Formation of two peripheral intra-tentacular buds from one mother-polyp: *divert. A*, *divert. B*, two peripheral intra-tentacular diverticula; I, stomodaeum of mother-polyp; *A*, *B*, stomodaea of two peripheral intra-tentacular buds. Figure 11A, mother-polyp. Figure 11B, showing constriction of outer parts of four intermesenteric spaces. Figure 11C, showing two peripheral intra-tentacular diverticula, each formed by the union of outer regions of two intermesenteric spaces. Figure 11D, final bud stage showing formation of two new stomodaea *A* and *B*.

after their union to form a diverticulum which becomes a bud by the formation of a stomodaeum as an invagination of the oral disk or by the fusion of filaments of the broader mesenteries. Although the bud, when formed, may appear to be extra-tentacular, owing to its extrapolypal position it has, in reality, an intra-tentacular origin, and therefore directive couples of mesenteries are invariably absent. As buds are formed from peripheral regions that are separated from pre-existing polyp areas, the mesenteries of the former are not usually continuous with those of the latter. Such an unique origin of buds also accounts for the absence, as a rule, of indirect linkage by interstomodaeal couples of mesenteries or direct linkage by mesenterial strands. Vertical cleavage of the outer parts of mesenteries may take place by the formation of partitions across intermesenteric spaces; the outer parts thus separated are subsequently included in diverticula, their free margins developing filaments.

Partitioned off peripheral parts of intermesenteric spaces (with their mesenteries and tentacles) of more than one polyp area may take part in the formation of a bud as shown in figures 12 A to E.

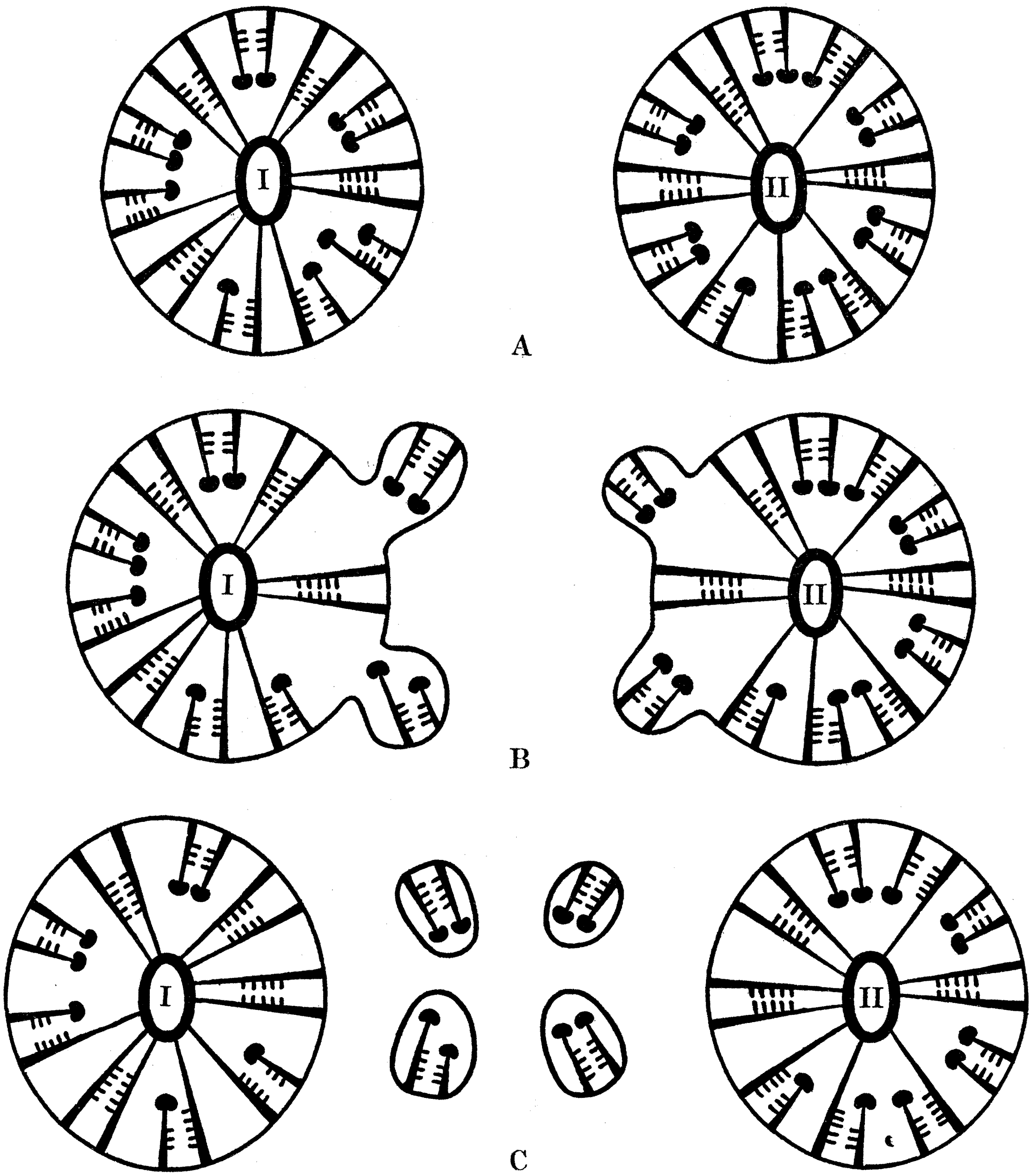
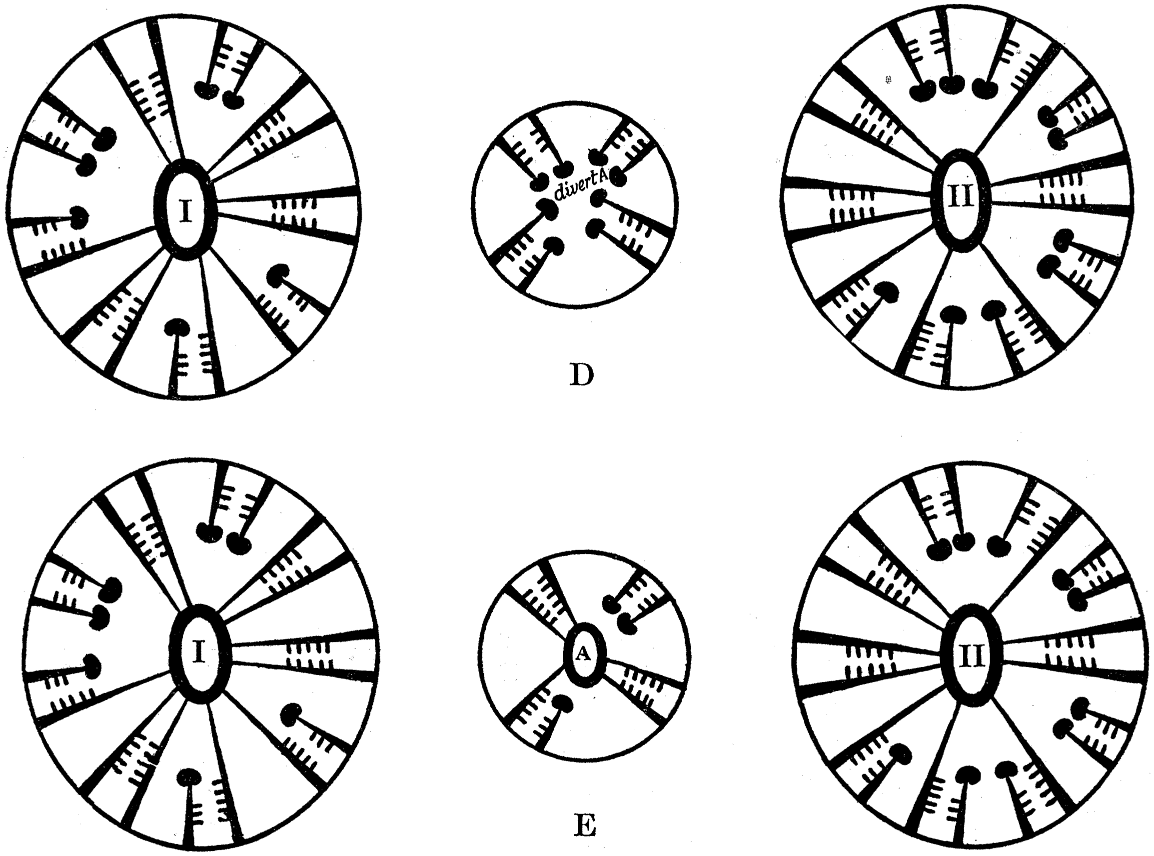


FIGURE 12. For legend see opposite.



FIGURES 12, A to E. *Psammocora haimiana* Milne Edwards & Haime. Formation of a peripheral intra-tentacular bud from two mother-polyps: I, II, stomodaea of mother-polyps; *divert. A*, peripheral intra-tentacular diverticulum; *A*, stomodaeum of peripheral intra-tentacular bud. Figure 12A, two mother-polyps. Figure 12B and C, showing constriction of outer parts of two inter-mesenteric spaces of each mother-polyp. Figure 12D, peripheral intra-tentacular diverticulum formed by the union of the partitioned off outer regions of four intermesenteric spaces. Figure 12E, final bud stage showing formation of new stomodaeum *A*.

Since, as shown above, buds are formed from peripheral regions of pre-existing polyps without direct or indirect linkage, colony formation in *P. haimiana* M. Ed. & H. is by *peripheral intra-tentacular budding*, without linkage. In the absence of direct and indirect linkage *Psammocora* agrees with *Leptoseris*, but in the latter genus budding is not peripheral.

In an adult colony of *Psammocora haimiana* polystomodaeal polyps become sinuous, and therefore newly formed buds do not usually exhibit a cyclic disposition.

In figure 13 there are instances of more than one mother-polyp contributing to the formation of diverticula (between IV and V, XVIII and XIX, XXI and XXV, XXVI and XXXII, XXVII, XXVIII and XXIX, XVI and XXXIV, XXXVI and XXXVII), in addition to several cases of diverticula arising from the same mother-polyp, a good example of which is seen in polyp area XV. An unique feature of *Psammocora* is the presence of interpolypal spaces containing mesenteries, which are the peripheral parts of intermesenteric spaces cut off by the formation of interseptal skeletal partitions. It is seen in sections that the peripheral parts of most mesenteric spaces containing subsidiary couples of mesenteries are in process of being separated and, therefore, appear to project

Table of stomodaea and mesenteries in figure 13

serial order of stomodaea	number of complete principal couples of mesenteries	number of incomplete principal couples of mesenteries	total number of principal couples of mesenteries	number of subsidiary couples of mesenteries	total number of couples of mesenteries	number of principal mesenteries	number of subsidiary mesenteries	total number of mesenteries	number of outlying couples of mesenteries
I	2	2	4	1	5	6	4	10	nil
II	2	6	8	3	11	10	12	22	10
III	4	2	6	2	8	10	6	16	nil
IV	6	nil	6	1	7	12	2	14	10
V	3	2	5	2	7	8	6	14	7
VI	2	3	5	3	8	7	9	16	nil
VII	6	1	7	1	8	13	3	16	1
VIII	6	1	7	3	10	13	7	20	4
IX	4	3	7	3	10	11	9	20	nil
X	3	2	5	3	8	8	8	16	2
XI	4	1	5	3	8	9	7	16	2
XII	2	4	6	nil	6	8	4	12	2
XIII	4	3	7	8	15	11	19	30	1
XIV	2	4	6	2	8	8	8	16	4
XV	2	4	6	2	8	8	8	16	5
XVI	4	1	5	4	9	9	9	18	8
XVII	3	2	5	4	9	8	10	18	3
XVIII	2	3	5	3	8	7	9	16	2
XIX	3	nil	3	4	7	6	8	14	nil
XX	3	nil	3	3	6	6	6	12	3
XXI	4	1	5	5	10	9	11	20	1
XXII	2	3	5	5	10	7	13	20	5
XXIII	3	3	6	14	20	9	31	40	nil

OF *PSAMMOCORA HAIMIANA* MILNE EDWARDS & HAIME

remarks
a young bud
characterized by a large number of mesenterial couples inside and outside polyp area. Outlying couples of mesenteries are arranged in a ring, which will contribute to the formation of more than one diverticulum. The subsidiary mesentery of an incompletely principal couple below and one of the mesenteries of a subsidiary couple above have become outlying mesenteries
one of the subsidiary couples below, which has almost become an outlying couple, is directed towards II
the original subsidiary couples appear to have become outlying couples, arranged more or less in the form of a ring. There is also an additional single outlying mesentery. Five principal mesenteries on the right and nine outlying mesenteries below bear ova. One mesentery of an outlying couple below has not yet been separated. Outlying couples above and below tend to be arranged in an inner and an outer row
there is an additional single outlying mesentery. A diverticulum above seems to be formed of six outlying couples of which three belong to V as they have not yet been separated and three belong to IV; of the latter one couple and one mesentery of each of the remaining two couples have not yet been separated from IV
one of the subsidiary couples has almost become an outlying couple. One subsidiary mesentery of an incompletely principal couple above and an adjacent mesentery of a subsidiary couple have been separated; similarly, a subsidiary mesentery of an incompletely principal couple below has been separated
—
three of the outlying couples form a group, one of which is continuous, at a higher level, with a subsidiary couple of IX. One of the principal couples is continuous with another subsidiary couple of IX; similarly, one outlying couple above is continuous with a subsidiary couple of IX. Such continuity is a rare feature in *Psammocora*. A mesentery of a subsidiary couple to the left has already been separated. Seventeen mesenteries below, including an outlying couple, bear ova
six mesenteries on the right bear ova
one of the subsidiary couples has almost become an outlying couple. Eleven mesenteries on the right, including an outlying couple, bear ova
total number of mesenteries is as in X. A subsidiary couple above has almost become an outlying couple, one of the mesenteries of which has already been separated. Seven mesenteries to the right bear ova
attached outer margin of one of the principal mesenteries is very close to outer margin of a principal mesentery of XXI
number of mesenteries is comparatively large. All subsidiary couples have almost become outlying couples; these, with the existing outlying couple, form a ring, partly in two rows, and will probably take part in the formation of more than one diverticulum. A mesentery of one subsidiary couple above has already been separated. When the peripheral parts of intermesenteric spaces, containing the eight subsidiary couples, are separated by interseptal partitions, XIII and its principal couples will not be affected. Ten subsidiary mesenteries above bear ova
one subsidiary couple below has almost become an outlying couple, a mesentery of which has already been separated. Sixteen mesenteries on the right, including four outlying couples, bear ova
both subsidiary couples have almost become outlying couples. The five outlying couples will probably form one diverticulum. Five mesenteries on the right bear ova
three subsidiary couples to the left will soon become outlying couples. Outlying couples above are arranged in an inner and an outer row. The first outlying couple on the left and three principal mesenteries on the right bear ova
an incomplete principal couple above is formed by the curvature of a single mesentery, which is vertically split at the bend at a lower level. The four subsidiary couples have almost become outlying couples, a mesentery of one of these couples above and another mesentery of a couple below have already been separated. The three outlying couples of XVII are below the two outlying couples of XVIII. An additional outlying couple is directed away from XVII
the three subsidiary couples have almost become outlying couples; an additional single subsidiary mesentery has also become an outlying mesentery
a comparatively young bud. One of the subsidiary couples below has almost become an outlying couple. An adjacent subsidiary couple is directed away from XIX and towards XVIII, and will, with a neighbouring subsidiary couple of XVIII, probably take part in forming a diverticulum
a comparatively young bud. Number of mesenterial couples is as in XIX
an additional principal mesentery forms an interstomodaeal couple with a principal mesentery of XXVIII; this is a rare feature in *Psammocora*. Attached outer margin of one of the principal mesenteries is close to outer margin of a subsidiary mesentery of XXV. Three subsidiary couples below have almost become outlying couples, one of which is directed towards XXV and bears ova
two of the subsidiary couples on the right have almost become outlying couples. A subsidiary mesentery of an incompletely principal couple on the right has been separated.
a completely principal couple above is formed by the curvature of one mesentery which will probably get vertically split at the bend. All fourteen subsidiary couples have almost become outlying couples; those on the left tend to get arranged in an inner and outer row. When the peripheral parts of intermesenteric spaces, containing these subsidiary couples, are separated by interseptal partitions, XXIII and its principal couples will not be affected. A mesentery of a subsidiary couple below has already been separated. Four subsidiary couples below bear ova

Table of stomodaea and mesenteries in figure 13

serial order of stomodaea	number of complete principal couples of mesenteries	number of incomplete principal couples of mesenteries	total number of principal couples of mesenteries	number of subsidiary couples of mesenteries	total number of couples of mesenteries	number of principal mesenteries	number of subsidiary mesenteries	total number of mesenteries	number of outlying couples of mesenteries
XXIV	2	1	3	3	6	5	7	12	nil
XXV	2	3	5	4	9	7	11	18	nil
XXVI	2	1	3	6	9	5	13	18	1
XXVII	1	3	4	4	8	5	11	16	nil
XXVIII	2	3	5	5	10	7	13	20	nil
XXIX	3	nil	3	2	5	6	4	10	5
XXX	2	3	5	2	7	7	7	14	nil
XXXI	3	1	4	3	7	7	7	14	nil
XXXII	3	2	5	6	11	8	14	22	nil
XXXIII	4	5	9	10	19	13	25	38	3
XXXIV	4	2	6	2	8	10	6	16	4
XXXV	2	1	3	nil	3	5	1	6	nil
XXXVI	4	nil	4	13	17	8	26	34	1
XXXVII	3	nil	3	3	6	6	6	12	2
XXXVIII	4	1	5	8	13	9	17	26	5
XXXIX	3	2	5	3	8	8	8	16	nil
XL	4	1	5	5	10	9	11	20	1
XLI	5	nil	5	nil	5	10	nil	10	nil
XLII	4	1	5	2	7	9	5	14	1
XLIII	—	—	—	—	—	—	—	—	4

OF *PSAMMOCORA HAIMIANA* MILNE EDWARDS & HAIME (*continued*)

remarks
a comparatively young bud, somewhat older than I but younger than XIX and XX. A subsidiary couple below has almost become an outlying couple. Filaments have not yet been developed on the free margins of two narrow mesenteries forming a subsidiary couple at the top. Five mesenteries below bear ova
a subsidiary couple on the left is continuous with a completely principal couple of XXVII. One of the subsidiary couples on the right has almost become an outlying couple which, with a neighbouring subsidiary couple of XXI directed towards XXV, will probably take part in forming a diverticulum; compare a similar case under XIX
a subsidiary couple above has been formed by the curvature of one mesentery which will probably get vertically split at the bend. One of the subsidiary couples below has almost become an outlying couple. Only one mesentery of each of the two outlying couples has been separated. One of the mesenteries of the outlying couple below lies in an intermesenteric space of XXXII; a mesentery of a neighbouring subsidiary couple has been separated; these two couples, one belonging to XXXII and another to XXVI, will probably take part in forming a diverticulum
an incompletely principal couple above is formed by the curvature of one mesentery which will probably get vertically split at the bend. The four subsidiary couples will soon become outlying couples; a mesentery of each of two such couples has already been separated
an additional principal mesentery forms an interstomodaeal couple with a principal mesentery of XXI. One of the subsidiary couples below is formed by the curvature of a single mesentery which gets vertically split at a lower level. Four of the subsidiary couples (i.e., except the subsidiary couple on the right) have almost become outlying couples
the two subsidiary couples will soon become outlying couples, and will, with the neighbouring subsidiary couples of XXVII and XXVIII, take part in forming a diverticulum. Some of the outlying couples will, with the top subsidiary couples of XXVIII, probably take part in forming another diverticulum
a comparatively young bud, with few subsidiary couples and no outlying couple
a comparatively young bud. A principal mesentery on the left is continued as a subsidiary mesentery of XXXII; this will probably become vertically split into two mesenteries. The three subsidiary couples, one of which is directed towards XXXVIII, will soon become outlying couples
two subsidiary couples below are formed by the curvature of two mesenteries, each of which will become vertically split at its bend. One of the subsidiary couples above is directed towards XXVI, a mesentery of which has already been separated; this couple, and the neighbouring subsidiary couples of XXVI, take part in forming a diverticulum
large number of mesenteries as in XIII and XXIII. The ten subsidiary couples, with the three outlying couples, form a ring as in XIII. All ten subsidiary couples will soon become outlying couples. When the peripheral parts of the intermesenteric spaces containing the ten subsidiary couples are separated by interseptal partitions, XXXIII and its principal mesenteries will not be affected. A mesentery of the first subsidiary couple on the right has already been separated. Some of the subsidiary couples on the right, with the neighbouring subsidiary couples on the left of XVI, will probably take part in forming a diverticulum. Two subsidiary mesenteries on the left have not yet developed filaments on their free margins
a principal couple above is continuous, at a higher level, with a subsidiary couple of XXXVI. The four outlying couples form a group just above those of XVI. Filaments have not yet appeared on the free margins of the first outlying couple on the left
appears to be a young bud. Some of the mesenteries may not be included in the piece sectioned
a principal mesentery at the top is continued as a subsidiary mesentery of XXXVIII; this will probably become vertically split into two mesenteries. To the left of this is a subsidiary couple formed by the curvature of a single mesentery which will probably become vertically split at its bend. The subsidiary couples form a ring; most of which will probably become outlying couples; in that case XXXVI and its principal mesenteries will not be affected. A mesentery of each of the two adjacent subsidiary couples at the bottom left corner has already been separated
a young bud with comparatively few mesenteries. A completely principal couple above has been formed by the curvature of a single mesentery which will probably become vertically split at its bend. A subsidiary couple is also similarly formed by the curvature of a single mesentery. The subsidiary couple below will soon become an outlying couple. Four outlying couples on the left might have been formed after the separation of the peripheral part of an intermesenteric space. The two outlying couples below, with some of the neighbouring subsidiary couples of XXXVI, probably take part in the formation of a diverticulum
two principal, and two subsidiary, couples are formed by the curvature of four mesenteries, which are vertically split at a lower level. Most subsidiary couples will become outlying couples; when that separation takes place, there will be two rows of outlying couples on the left. A mesentery of a subsidiary couple on the left has already been separated. Filaments have not yet been developed on the free margins of a subsidiary couple at the upper right-hand corner
the three subsidiary couples will soon become outlying couples. A mesentery of a subsidiary couple below has already been separated; similarly, a subsidiary mesentery of an incompletely principal couple on the right has been separated
the five subsidiary couples will soon become outlying couples. Three of these couples on the left might have been formed after the peripheral part of an intermesenteric space had been separated. These, with the outlying couple, make a group and will probably take part in forming a diverticulum
neither subsidiary nor outlying couples. Such couples, if present, might not have been included in the piece sectioned
some mesenteries might not have been included in the piece sectioned
only partially included in the piece sectioned. The four outlying couples are in two rows of two couples each

beyond their respective polyp areas. When the peripheral parts are finally constricted off, they appear like isolated spaces lying among polyp areas. By such separation the polyp areas and their principal couples are not altered to any appreciable extent (XIII, XXIII and XXXIII). New mesenteries may subsequently arise in these interpolypal spaces (XXXVII, XL). There is also evidence of vertical cleavage of mesenteries which, however, is a rare occurrence as compared with this phenomenon in *Leptoseris*. It is possible that such separated parts of mesenteries may, by subsequent formation of filaments on their free margins, appear as outlying subsidiary mesenteries within interpolypal spaces (VIII and IX). Such an outlying couple may be composed of two mesenteries derived from two neighbouring parents (IV and V). Not infrequently outlying couples are arranged in more than one row (IV, XIII, XVI and XXIII). When all subsidiary couples of a polyp area have been separated, they form a complete ring of outlying couples around the latter (II, IV, XIII and XXXIII). Sometimes a mesenterial couple is formed by the curvature of the same mesentery which, subsequently, becomes vertically split at its bend (XVII, XXIII, XXVI, XXVII, XXVIII, XXXVI, XXXVII, XXXVIII). Rarely a mesentery is continued into an adjacent polyp area, but never connected to two stomodaea (VIII and IX, XXV and XXVII, XXXI and XXXII, XXXIV and XXXVI, XXXVI and XXXVIII). Occurrence of interstomodaeal couples is very rare (XXI and XXVIII). Indirect or direct linkage of stomodaea is not, therefore, a feature of *Psammocora*.

Coupling by mesenterial curvature occurs less frequently in *Psammocora* than in *Echinophyllia* and *Leptoseris*. As in the latter genus, the curvature is directed outwards away from the corresponding stomodaeum. Vertical cleavage also takes place at the mesenterial bend as in *Echinophyllia* and *Leptoseris*, but whilst in these genera the split margins develop filaments, in *Psammocora* they are attached to the corallum.

This work was commenced in 1938 in the Zoological Laboratory of Government College, Lahore, where serial sections of polyps were prepared, and continued during 1938–9 in the Department of Zoology at Cambridge. At the outbreak of war, the late Professor J. Stanley Gardiner, F.R.S., advised postponement of the work till my return to Cambridge after the cessation of hostilities.

The polyp material for this paper was taken from colonies collected by the late Dr C. Crossland from Tahiti and the Red Sea and fixed and preserved by him.

The figures accompanying this paper were constructed from camera lucida tracings of transverse sections of polyps. Each figure belongs to a single series of sections, although often drawn at different levels.

I am indebted to the late Professor J. Stanley Gardiner, F.R.S., for much helpful criticism and advice during the progress of this work, Professor J. Gray, F.R.S., and Mr F. R. Parrington, M.A., for laboratory and library facilities and for accommodation in the Museum, the Royal Society for a grant in aid of this work and to the Governing Body of Emmanuel College, Cambridge, for hospitality during the academic year 1938–9 and from 20 May to 30 June 1946.

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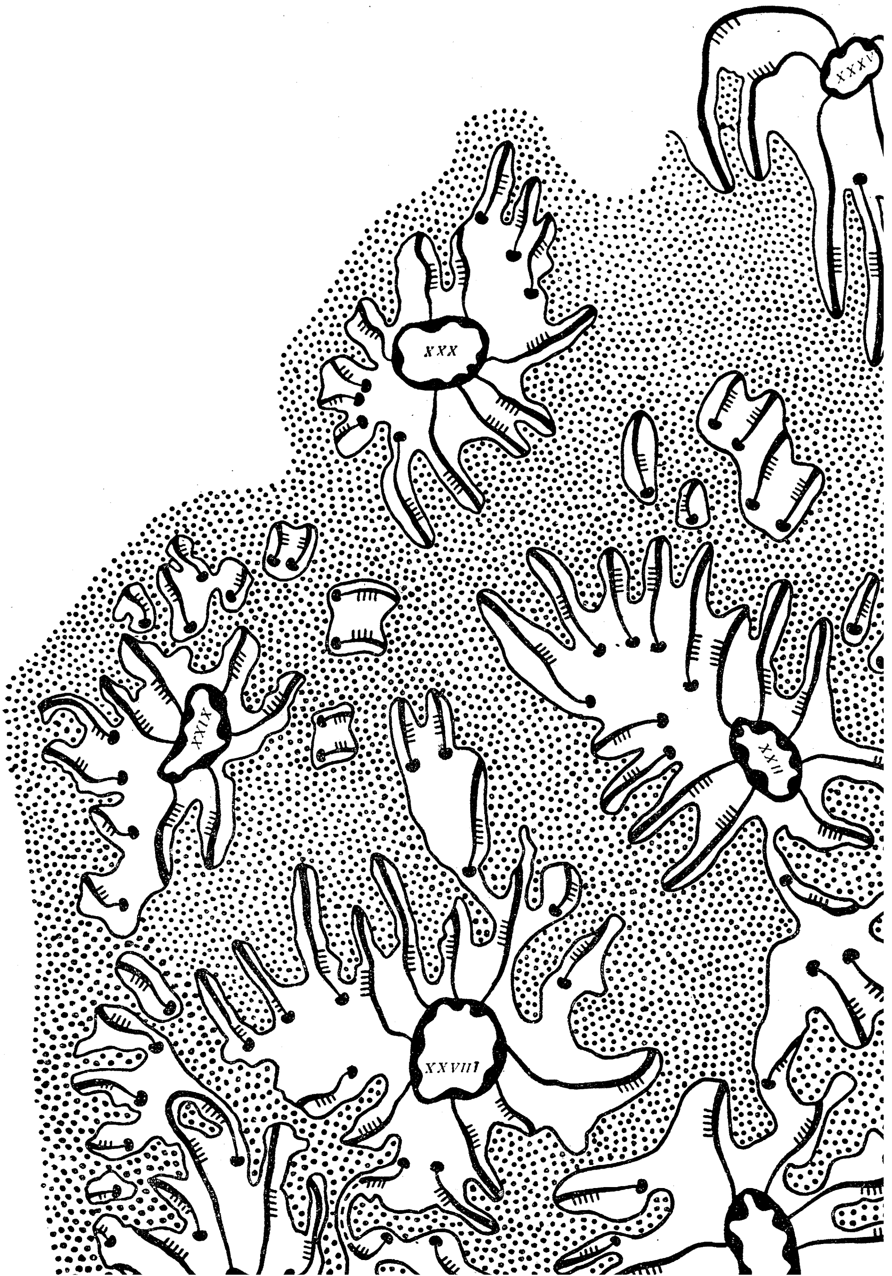

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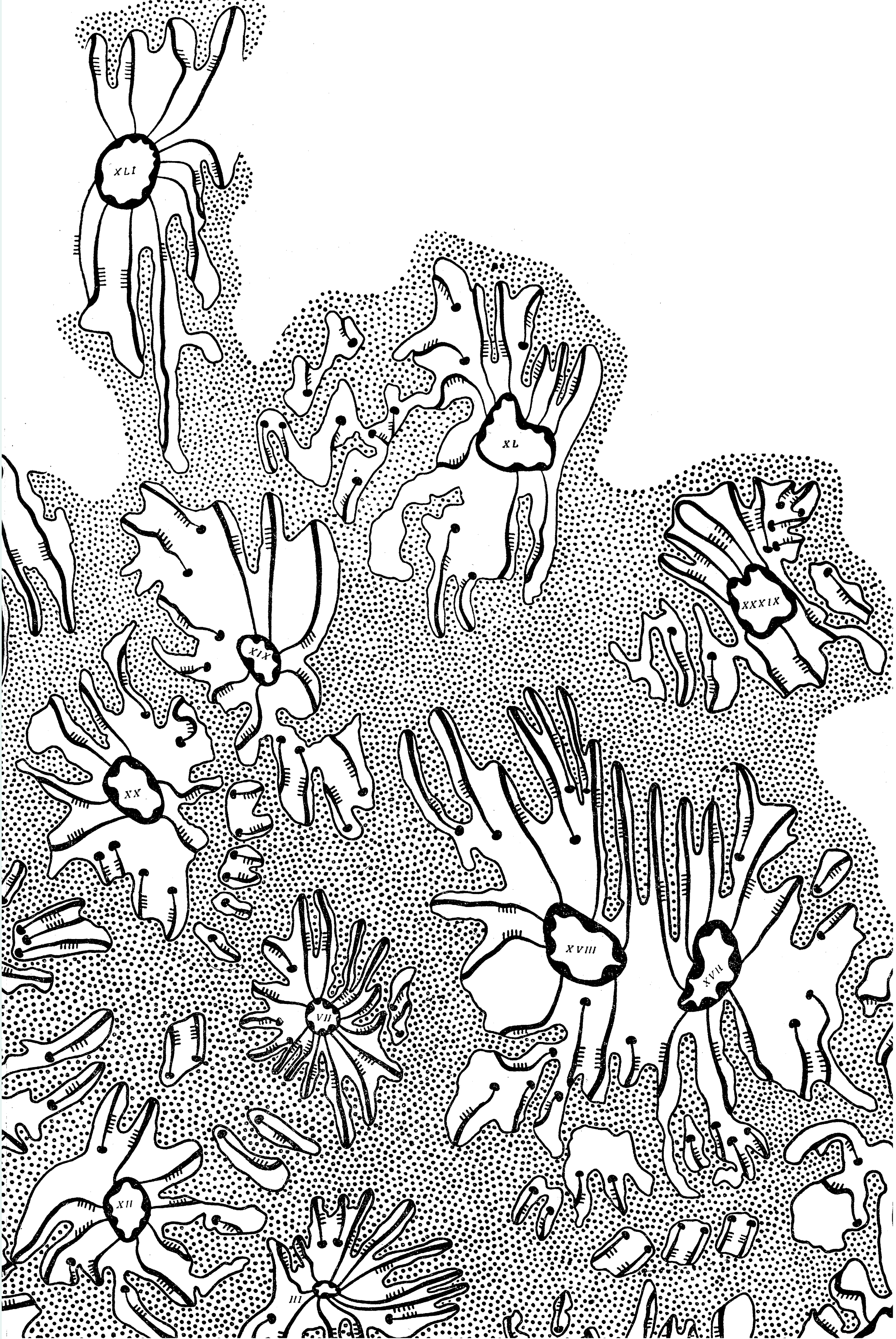

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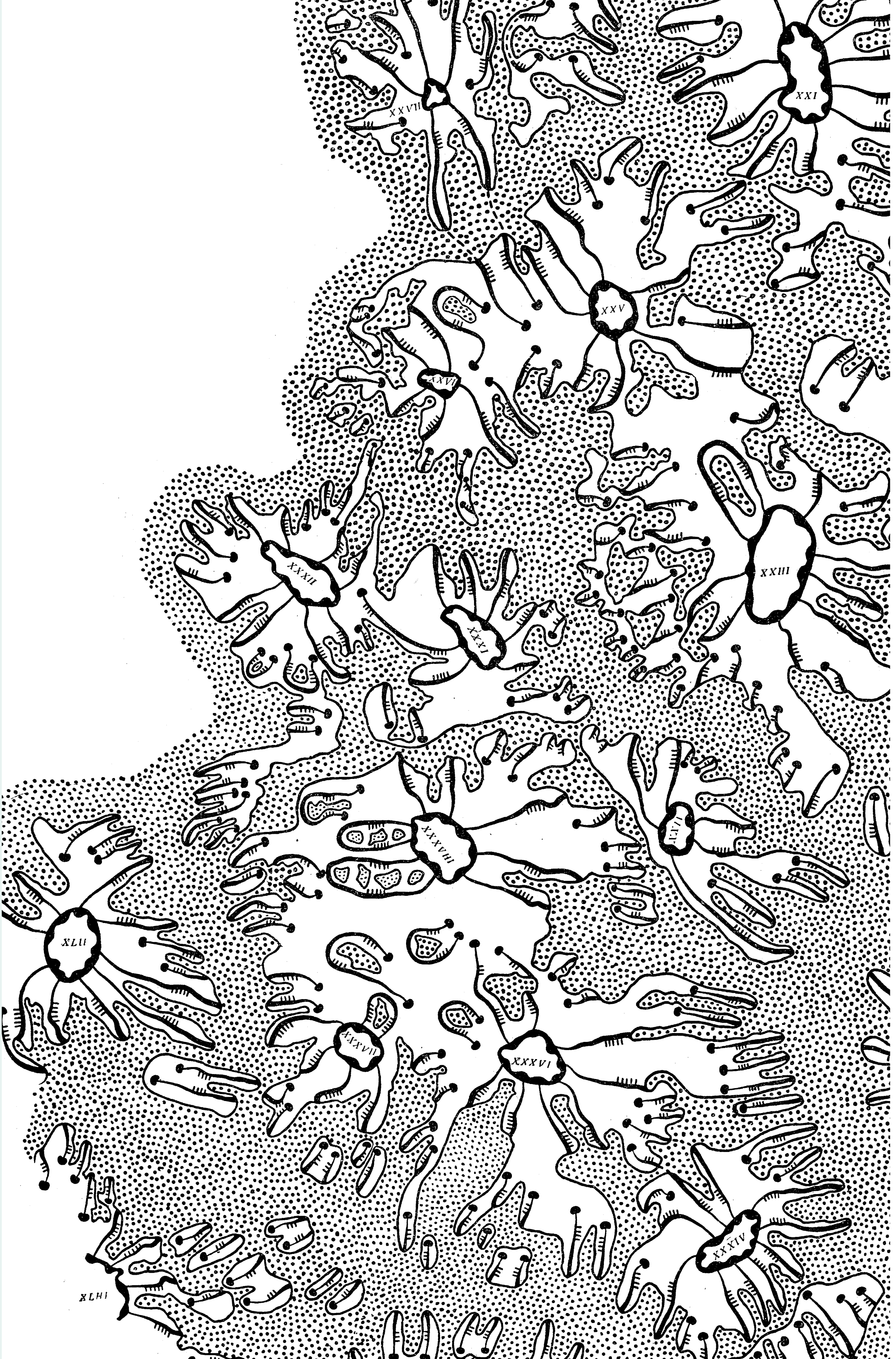

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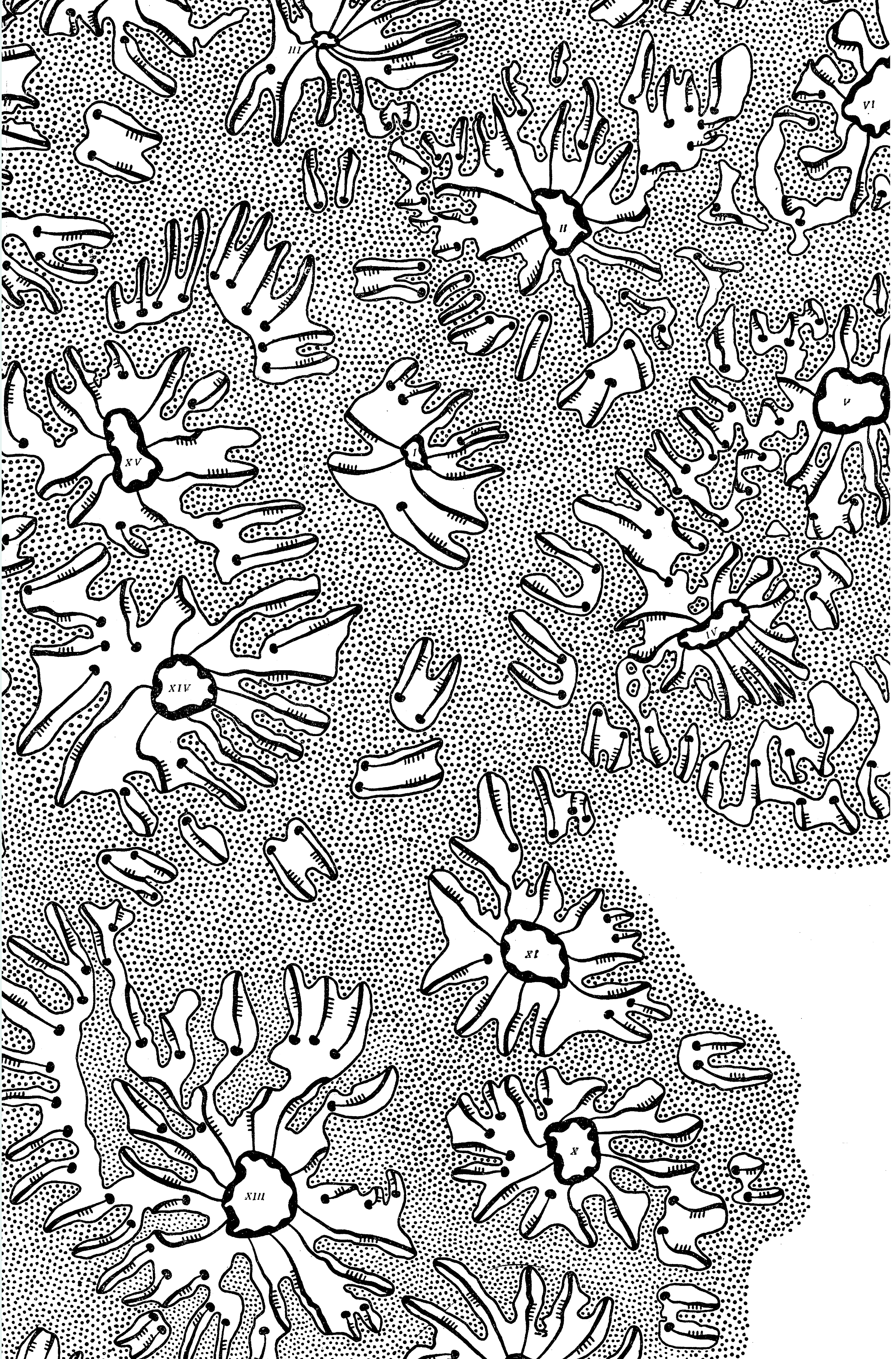

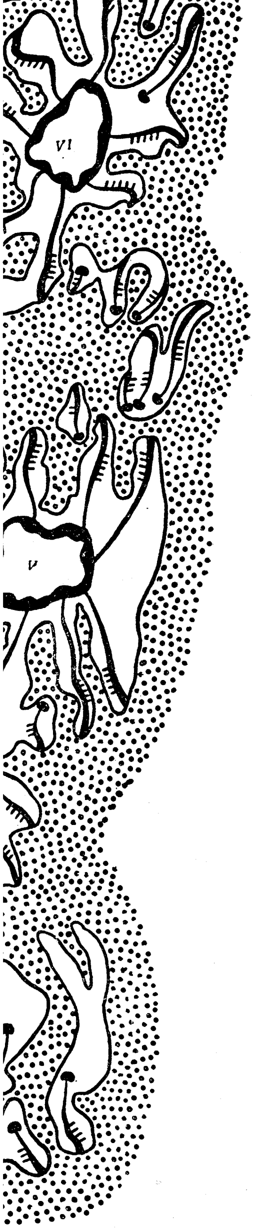

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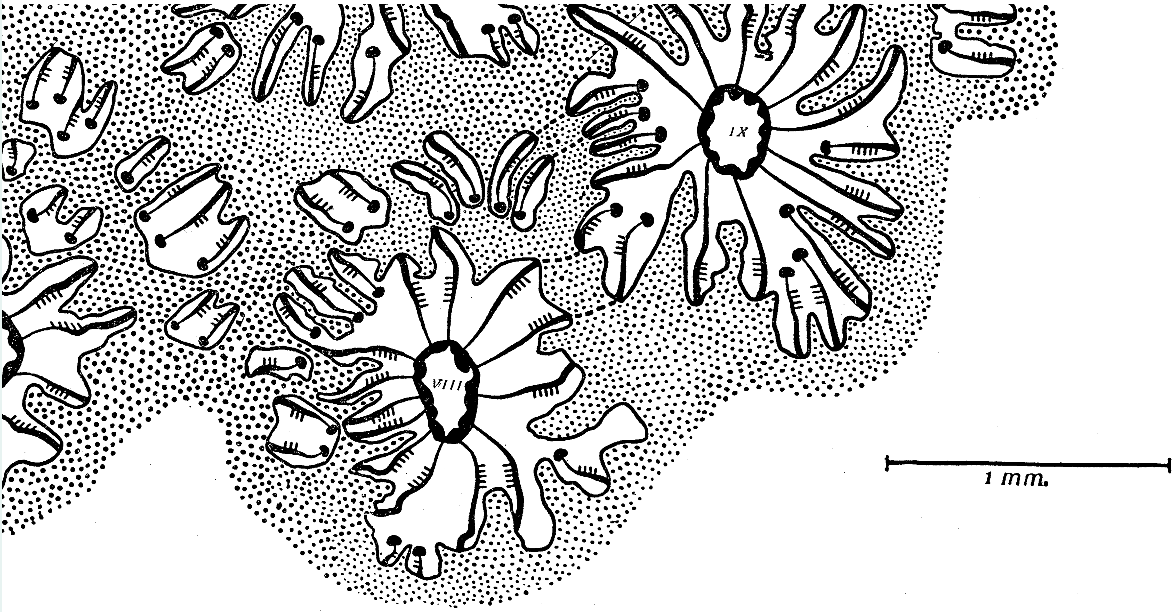
FIGURE 13. *Psammocora haimiana* Milne Edwards & Haime. Transverse section through sto
Dotted areas repre

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



omodaeal region of a piece containing forty-three stomodaea (I–XLIII) from a colony from Tahiti.
esent parts of skeleton (Ps_1).

ahiti.

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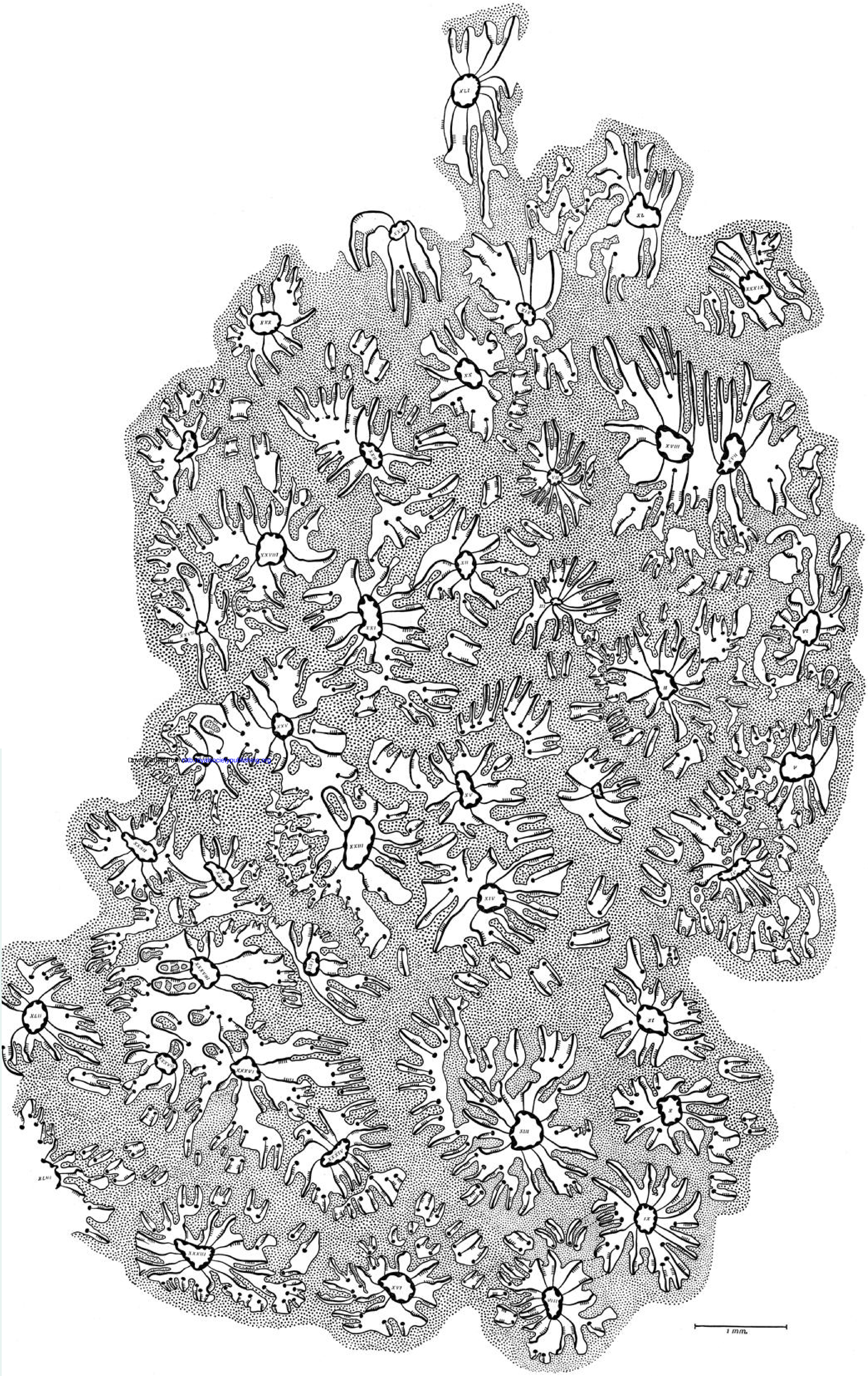

FIGURE 13. *Psammocora haimiana* Milne Edwards & Haime. Transverse section through stomodaeal-region of a piece containing forty-three stomodaea (I–XLIII) from a colony from Tahiti. Dotted areas represent parts of skeleton (Ps_1).