SOUTH AFRICAN CORALS OF THE GENUS *FLABELLUM*, WITH AN ACCOUNT OF THEIR ANATOMY AND DEVELOPMENT,

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1. INTRODUCTION.

The present paper forms the first part of an account of a remarkably fine collection of corals from the Cape of Good Hope, entrusted to me for identification. Most of the specimens appear to have been preserved in *formalin*, an excellent reagent, but one which is somewhat uncertain in its results. To give an instance, corals of the genus *Flabellum* are almost uniformly well preserved, while those of *Caryophyllia* are almost useless for anatomy. In any case the examination of more than the gross anatomy of the polyps of the various species, or forms, in the different genera is not, in view of the results obtained in the present genus, particularly to be desired.

The collection is of peculiar interest from the fact that the same forms have been repeatedly dredged in slightly or considerably different localities. Thus the variation due to different habitats may subsequently be worked out, and correlated perhaps with the physical and other conditions. For this purpose accurate charts for each locality of the temperature of the sea, of the character of the bottom, and of the currents both on the surface and to the bottom are desirable, as well as a knowledge of the topography and the fauna and flora. The present and further collections will give a correct knowledge of the "normal" or "continuous" variations in each species, and it may be hoped that the presence and nature of "discontinuous" or "specific" variation in the group may be elucidated. At the same time the accurate knowledge of the coral fauna in any one locality *in relation to its environment* must necessarily be of immense value in deducing the conditions under which tertiary and earlier coralline deposits have been formed, in effect in studying the history and geography of the earth.*

Most workers on the systematic side complain of the enormous difficulty of determining the species of corals. This seems to me to be more apparent than real. It has probably arisen largely owing to the not-unnatural desire to refer each specimen to a species—to give each a convenient handle by

* The above paragraph was written before I received the "Report of the Government Biologist for the Year 1900." I find therein most or all the information I desire as to the environment, physical conditions, etc.

which to grasp it—while nothing may be known of its habitat, its locality alone being broadly indicated. Most collections, too, if they contain many colonial forms, are small in specimens, so that variability cannot be properly studied. Lastly, it must be recognised that sedentary animals vary in accordance with their surroundings in the same way as do trees and other plants.

Having determined which are the species in any collection, it is necessary to examine into the question as to whether these species are already known or new. This is a far more perplexing and arduous task.* So far as my experience goes, I find that there are in each genus only a limited number of characters, which vary in a species-making manner. Most of the other characters are those of the family and genus, and require no particular remark. The rest are of but small importance, and belong rather to the individual than the species. They become eliminated necessarily as a larger and larger number of examples is studied. In the earlier descriptions the recorded characters often do not include those on which the species are necessarily founded at the present day. Later workers may have recorded these from an examination of the same specimens, or elucidated them from others. In the latter case there must always be some element of doubt, but this is unavoidable. Again, if the variability *owing to environment* may be expressed as from 1 to 100, the original specimens—especially if few in number, as is usually the case—may be placed between 1 and 10 or 90 and 100, while the great bulk of subsequent collections will be about 50. Specimens may in the first place be put as species at every tenth, but as more specimens are examined the intermediate forms must be necessarily joined together, until finally the limits of the real species are elucidated.

The personal element of each worker in the field is—and must always be—enormous, but the remedy lies in the systematic study of the normal variation of different species, particularly in relation to the physical and biological characters of its environment. It may then be possible to separate the variability of the species *per se* from that due to external causes, by this means possibly arriving at some more accurate conception of the formation of the species themselves.

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* Vide "Some Fossil Corals from the Elevated Reefs of Curacoa, etc.," by T. Wayland Vaughan, Samm. des Geol. Reichs-Mus. Leiden, Ser. II., Bd. II., Heft I. (1901).

2. GENERAL.

The genus *Flabellum* is characterised among the Turbinolidae by having a well-defined "epitheca," and together with this the absence of any structure, which may be termed a "theca." The genus *Antillia* shows typically the difference between "theca" and "epitheca." The first is the wall—be it formed as a basal deposit or by thickenings of the septal sides—surrounding the digestive cavity of the polyp, while the latter closes off such parts of the anemone as may lie outside the "theca" from the external medium, *i.e.*, the sea-water. According to this definition the "theca" should be covered on and formed from both sides by the tissues of the polyp, while the "epitheca" is only so covered on and formed from one, *i.e*, the inner side. Accepting the fact that the skeleton lies completely external to the polyp—a reality not within the knowledge of the proposers of the terms—the above forms a reliable and indeed the only distinction, unless it be subsequently shown that the two are formed essentially differently from one another.

"Costae" correspond to the septa, and are their continuations outside the theca. The theca is not formed before the septa, but may be built up *pari passu* with their formation. More often the septa are formed first, and from the beginning project above the theca, *i.e.*, are "exsert." In *Antillia* the edges of the "costae" are fused with the epitheca, but in most forms there is no such epitheca, and they are hence covered over outside by the soft tissues. Where epitheca alone is present—as in *Flabellum*—there can be no costae, although raised ribs of the epitheca may simulate them. The term "exsert" applied to the septa also bears relation to the presence of a theca, and cannot properly be applied where none such is present.

The only case, where there can in practice be any doubt between theca and epitheca, is where a theca without costae has been formed. In such a case, if the edge-zone of the polyp—that part which lies external to the theca—withdraws completely, there may actually be no tissues external to the wall. The latter, if a theca, always shows in section a definite dark line along its centre, and in a living polyp some of the top or upper part of the wall would still necessarily be covered by an edge-zone. There would further be no distinction between the inner and outer sides of such a theca. A possible extreme case would be where the calicoblastic ectoderm of the edge-zone in its retreat deposited a special coating of carbonate of lime. The glassy appearance of *Desmophyllum* in its lower parts indicates the downward extent of the edge-zone, and may be due to such a deposit. This, however, does

not really in any way resemble a true epitheca, and the presence or absence of a central dark line in section can leave no doubt as to its homologies.

Where an epitheca is present, there can be no budding from outside the same, no external tissues existing. If buds are found, as are stated to exist in *Blastotrochus*, they must be due to the epitheca being imperfectly formed, so as to allow the tissues of the polyp to project freely at certain parts of the surface.

The "columella" may be "essential" or "parietal," true or false. In the first case, it arises on the basal plate as a central deposit, to which the septal edges may secondarily be attached. A "parietal columella" has no such basal deposit, but is formed by the tissues which cover the larger septa, fusing across the coelenteric cavity and joining them by trabeculae of corallum. The two modes of formation are morphologically quite distinct from one another. I, hence, apply the name only to the "essential" or true columella. In many genera, the development being unknown, it is not clear whether there is a true columella or not. In such, as the deposition of a central pillar of carbonate of lime must be regarded as the more primitive mode of formation, I assume the presence of a true columella.

"Pali" also are of two kinds, true and false. The former arise as deposits on the basal plate, while the latter are the mere thickened edges of the septa, or formed by trabeculae from the same. The true pali are often, and indeed generally, secondarily joined to the septal edges either by trabeculae or along their whole length. Where a coral is truncated, it follows that true pali *can* only be present in front of those septa which are primarily formed on the basal plate. Additional orders of septa, added during growth, can have no pali, unless (as is conceivably the case in some of the Astraeidae) the original pali become branched.

3. **The Genus** FLABELLUM.

Flabellum Lesson, Illustr. de Zool., 1831.

Flabellum Milne Edwards et Haime, Ann. des Sc. nat., 3e ser., t. IX., p. 256 (1848) and Coralliaires, t. II., p. 79 (1857).

Blastotrochus Milne Edwards et Haime, Ann. des Sc. nat., 3e ser., t. IX, p. 284 (1848) and Coralliaires, t. II., p. 99 (1857). Semper, Zeit. für. wiss. Zool., Bd. XXII., p. 237 (1872).

Rhizotrochus Milne Edwards et Haime, Ann. des Sc. nat., 3e ser., t. IX., p. 281 (1848) and Coralliaires, t. II., p. 97 (1857).

Flabellum, *Blastotrochus* and *Rhizotrochus* Duncan, Jour. Linn. Soc., vol. XVIII., pp. 13-15 (1885).

Duncan divided the Turbinolidae into a number of "alliances" of which the second is the "Flabelloida," comprising the recent genera *Flabellum*, *Rhizotrochus* and *Blastotrochus*. These are characterised by being "simple forms with no theca and hence costae. There is no true columella, but the septal edges may fuse by trabeculae and fill up the axial fossa. The forms are fixed or free, with or without rootlets, and generally more or less compressed." As above defined the group is perfectly and morphologically distinct from any other division of the Turbinolidae.

The fossil genus *Thysanus* I have not been able to examine, but the three recent genera do not seem to me to present any real points of difference. *Blastotrochus* is said to differ from *Flabellum* by budding occurring at the sides between the calicular margin and the base, the buds falling off and growing. Of *Flabellum rubrum* I have examples with young individuals growing similarly to the above between the calicular margin and the base. They are attached principally to one or other end of the calicle, but may lie on the sides as well. All are completely cut off from the soft tissues of the polyp, and there are no indications in any single case as to whether they have been definitely budded off, or whether they have been formed by the attachment of free-swimming larvae. If the former be the case, a small portion of the polyp must have been cut off by the advancing epitheca of the parent, as there is now no trace of any connection, even the youngest having indications of its own basal plate separating it from the epitheca of the older corallite. In two *supposed* specimens of the original type *B. nutrix* from the Phillipines I can find no indication of definite budding, nor of any difference between the mode of attachment of the buds to that found in *F. rubrum*. In reference to Semper it is necessary to point out that he presumably supposed the corallum to be of endoderm formation, and it is interesting to note that his specimens of *B. nutrix*, *F. irregulare* and *F. variabile* all came from the same habitat, *i.e.*, the channel of Lapinig from 6-10 fathoms. The presence of young attached forms appears to me to be perhaps an accidental circumstance. In any case I cannot deem it of sufficient importance to separate *Blastotrochus* from *Flabellum*.

Rhizotrochus has hollow rootlets communicating with the coelenteron of the large polyp, or with the interior of the calicle of the dried corallites. I shall subsequently in *F. rubrum* have occasion to show that in some specimens there are rootlets found, precisely similar to these. Duncan states as a further character that "the columella is absent, and the

septa either unite by a few trabeculae or join across the axial space." In *Flabellum* there is no columella, but the septal edges unite by trabeculae in absolutely the same way. In *F. rubrum* there is often very little such fusion of the septal edges, indeed not more than is found in some specimens of *R. fragilis* Pourtalès and *R. tulipa* Pourtalès. In *R. typus* Ed. & H., *R. affinis* Duncan and *R. levidensis* Gardiner there is no such fusion, but the above species of Pourtalès are in this respect intermediate. Ed. & H. remark that in *R. typus* the larger septa have in the young traces of trabeculae, which disappear in the adult. How far the presence or absence of a false columella can be regarded at all as a generic character is doubtful, but certainly in this case there is no valid reason for separating *Rhizotrochus* from *Flabellum*.

The characters of the genus *Flabellum* would be practically synonymous with those of the alliance Flabelloida, as given above, and hence need not be repeated.

The chief distinguishing characters of species within the genus *Flabellum* appear to be (1) shape as seen in side view and looking into the calicle as well as in transverse sections of the calicle: (2) if the corallum be free, whether there has been a distinct rupture of the stalk, leaving a scar or not: (3) the number of septa fusing together by their septal edges or the number of equal septa of the lowest cycles: (4) if compressed, the presence or absence of wings or hollow epithecal processes, or possibly both, or if round, the presence or absence of root-like processes. As Semper has shown, and as will be subsequently seen in *F. rubrum*, (3) and (4) may require a large number of specimens to ascertain definitely these characters, but in some forms they become of primary importance (those cited above formerly placed in genus *Rhizotrochus* and others). (2) appears to be correlated with changes of shape. (1) varies considerably in any species, but the vast majority of specimens in each species approach to a distinct, central type. The shape within the genus varies greatly, some species being compressed, others round or angular. In some species the epitheca, as a flat plate, joins the outer edges of the septa and in others forms festoons between the same. In some the upper edge of the epitheca follows regular curves, the septa all attaining the same height, and in others is quite irregular, some cycles of septa rising higher than others.

Of supplementary characters the septal contours depend largely on the shape of the corallite, but the distances between the spined ridges on the septal sides may be of some importance. The latter vary somewhat in individuals of presumably the same age—judging by their accretion-lines—and of similar size and shape. Much more then do they vary

in specimens of different rates of growth. Measurements are unreliable, as would also be any dealing with the distances between accretion-lines, unless several hundred specimens of each species had been examined.

The consideration of the specific variability of the polyps must be deferred to the last section of this report, when the anatomy of our species will have been dealt with.

4. FLABELLUM PAVONINUM. (Plate IV., figs. 18—21).

Flabellum pavoninum Lesson, Illustr. de Zoologie, pl. 14 (1831), Ed. et H., Ann. des Sc., nat., 3e ser., t. IX., p. 260 (1848), and Cor., t. II., p. 80 (1857).

Euphyllia pavonina Dana, Zoophytes, p. 159, pl 6, fig. 6 (1846).

Flabellum distinctum Ed. et H., Ann. des Sc. nat., 3e ser., t. IX., p. 262 (1848) and Cor, t. II., p. 80 (1857); Duncan, Trans. Zoo. Soc., Lond., qto., p. 322, pl. XXXIX., figs. 1-13 (1871).

Flabellum patens et *australe*, Moseley, Challenger Report, pp. 172-3, pl. VI., figs. 4, 4a, 5, 5a and pl. VII., figs. 4, 4a, 5, 5a, 5b (1881).

Flabellum paripavoninum Alcock, Madreporaria, Calcutta Museum, qto., p. 21, pl. II., figs. 3, 3a, 3b (1898).

The collection obtained nine specimens of this species made up of (1) five from 6½ miles E. b. S. of Cape Natal, 54 fathoms, bottom "fine sand and algae"; (2) one 5½ miles S.E. ½ E. from the same, 62 fathoms, "sand, gravel and rock"; (3) one 9½ miles S.S.W. ¼ S. from Cape Vidal, 80-100 fathoms, "rocky" bottom; (4) one 9½ miles S.E. ¼ E. of O'Niel Peak, 90 fathoms, "broken shells"; and (5) Umhloti R. Mouth N.W. ½ W. 15½ miles, 100 fathoms, "sand, shell, hard ground."

The corallum of this species is characterised by its much compressed calicle with flattened, pointed ends. The mouth of the calicle in longitudinal section of its longer axis or as seen in side view varies from two-thirds to a full semi-circle, so that the two end wings make an angle of from 120° to 180° with one another. In the centre there is a short cylindrical pedicle, which only in the smallest specimen (long axis of calicle 13·5 mm.) still remains attached.

The measurements of eight of the specimens are as follows :—

I. Number of Specimen	1	2	3	4	5	6	7	8[1]
II. ,, Dredging	1	1	1	2	3	1	4	5
III. Length of Calicle..	47*	48	48	33	34	29	20	13·5
IV. Breadth of do. ..	21	22	22	12·5	14·5	12·5	9·5	6
V. Height of do. ..	34	37	36	25	24	25	17·5	10
VI. Length of perpendicular from base of pedicle to line joining ends of calicle	6·5	7	7·5	2·5	3	1·5	2	6
VII. Septa fusing by trabeculae	52†	48	48†	40	38	40	26	16
VIII. Total Septa ..	220†	212	100†	152	100	152	104	58

The measurements in lines VI. and III. taken together give the angle, which the wings form with one another.

By comparison with Lesson's figure it will be seen that Nos. 1 and 2 are almost absolutely similar in shape. Dana figures two specimens, one with basal angle approaching two right angles, and a second resembling No. 3, 1 and 2 being intermediate. *F. distinctum* Ed. and H. differs in having cycles I.-III. equal in size, whereas *F. pavoninum* has cycles I.-IV. equal; the fusion of the septa by trabeculae is presumably the same in both cases. The septa of cycles III. and IV. can be easily distinguished in No. 2 and in Nos. 4 7 are very distinct. Yet at the same time cycles I. to IV. are "sensiblement égales." In No. 3 the distinction is much more pronounced and "les trois premiers cycles seulement sont égaux entre eux." Indeed, there is no difference between Edwards and Haime's two species. So far as Duncan's figures of *F. distinctum* are concerned, there is obviously no separation between his species and my specimens, some of which show the intermediate characters to *F. pavoninum*. The figures of the two species, however, present marked differences in the smoothness of the external epitheca, but Nos. 1 and 2 above resemble *F. pavoninum* in being quite smooth, while in the rest lines of growth and, in some cases, distinct ribs can be seen. (Figs. 18–21).

F. patens and *F. australe*, both Moseley, have, so far as I could see from an examination of the specimens, no specific differences from the species under consideration. No. 2 above shows a cutting away of the septal borders close to the margin of the calicle, a character not found in the other specimens from the same dredging. In the specimens enumerated it is

* Measurements in millimetres. † These numbers, being taken from spirit specimens, possibly slightly exceed those here recorded. [1] This specimen was brought up together with a large number of corallites of *F. rubrum*, its external resemblance to small specimens of which is at once apparent from the measurements.

clear that the number of septa increases markedly with the lengthening of the calicle. The larger number of septa—268 and 248—found in *F. australe* is undoubtedly due to the extra size and length of the calicle, 55 mm.

F. paripavoninum Alcock is apparently founded on a single specimen. It has a "sessile scar of attachment but no pedicle." No stress is laid on this point, and as all other forms of this shape have a pedicle, it must be regarded as purely accidental, until more specimens are discovered. For the rest its characters are not such as would not include it within the range of variation of this species.

The species, as above constituted, has been obtained from Singapore, China and Japan (Ed. and H.), Ki Islands, 129 *f.* (fathoms) and New South Wales 120 *f.* (Moseley), North Atlantic 994, 364 and 304 *f.* (Duncan), Laccadives 636 *f.* (Alcock) and Cape of Good Hope 50 to 100 *f.*

5. FLABELLUM RUBRUM. (Pl. IV., figs. 22-34).

Turbinolia rubra Q. et G., Voy. de l'Astrolabe, Zoophytes, p. 188, pl. 14, figs. 5-9 (1833).

Flabellum rubrum, cumingii, elongatum, crassum, crenulatum elegans et *profundum* all Edwards and Haime, Ann. des Sc. nat., 3e sér., t. IX., pp. 265-280, pl. 8 (1848) and Cor., t. II, pp. 89-97 (1857)

Euphyllia spheniscus Dana, Zoophytes, p. 160, pl. 6, fig. 1 (1846).

Flabellum irregulare Semper, Zeit. für wiss. Zool., Bd. XXII., pp. 242-5, pl. XVI., figs. 7-17 (1872).

Flabellum transversale Moseley, Challenger Report, p. 174, pl. VI., fig. 6, 6a (1881).

The collection contained over five hundred specimens of this species, made up as follows :—

	Number of Specimens.	Depth.	Locality.	Character of Bottom.
1.	1	27	Lat. 33° 50' S., long. 25° 54' 30" E.	Sand.
2.	6	30	Lat. 33° 53' S., long. 25° 51' 20" E.	Mud, sand and specks.
3.	26	32	Lat. 33° 3' S., long. 27° 57' E.	Sand, shell and rock.
4.	185	47	Cape Natal W. b. N. 4½ miles	Sand and shell.
5.	258	54	Cape Natal W. b. N. 6½ miles	Fine sand and algae.
6.	2	27	Morewood Cove (Natal) NW b N ¾ N 3 miles	Sand and shell. Hard ground.
7.	11	100	Umhloti R. Mouth N.W. ½ W 15½ miles	Sand and shell. Hard ground.
8.	35	40	Off Umhloti R. Mouth	Sand and shell. Hard ground.
9.	5	90	O'Neil Peak, N.W. ¼ W. 9½ miles	Broken shells.
10.	1 (dead)	250	Port Shepstone, N.W.b. W. 11 miles	Rock and coral.
11.	5	45	Lat. 32° 53' S., Long. 28° 12' E.	Coralline material.

TABLE OF MEASUREMENTS, ETC., OF THE COLLECTION.

Numbers of the Dredgings.	Number of Specimens Examined.	1. No. of specimens. 2. No of septa fusing by trabeculae. 3. Total number of septa. 4. Average breadth of calicle, when the length of the same measures—																			
		9-11·5 mm.				12-14·5 mm.				15-17·5 mm.				18-20·5 mm.				21-25 mm.			
		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
5	60	4	15	56	5·9	26	20	73	7·6	22	21·1	77·2	8·6	7	23·1	85·1	9·1	1	24	100	9·5
4	82	12	15·1	55·8	5·6	32	19·2	69·8	7·1	31	20·4	77·6	8·1	7	21·1	78·6	8·7	0	—	—	—
8	16	4	13·5	53	5·5	9	19·7	66	7·3	3	20	72	8·8	0	—	—	—	0	—	—	—
1, 2 and 3*	20*	0	—	—	—	2	17	71	7	6	19	80·3	9·6	3	2 2	85	10·3	4	22	99	12·1
Rest ×	20	2	14	48	4·5	10	18·9	63·2	7 9	4	20	68	8·3	3	21·3	73·3	10·3	1	24	84	10·5

× Comprises 3 obtained in a separate haul of 5, 2 of 6, 5 of 7, 5 of 9 and 5 of 11.

* Made up of 17 of 3, 2 of 2 and 1 of 1. Five of these are too large to be included in this list; their enumeration with length of calicle first in place of number of specimens is as follows:—26·5, 22, 102, 13; 27, 24, 100, 15; 28, 24, 102, 15; 33, 24, 140, 17; 37, 24, 168, 18.

The species, as may be seen from the accompanying table, is extremely variable, but its main characters would seem to be as follows :—

"Corallum conical or wedge-shaped, generally compressed, usually with a distinct scar below, 2 to 7 mm. in length and showing 12 to 24 septa. Sides of the corallum commonly with curved transverse bands, corresponding to intervals of growth, often at the narrow sides opposite the ends of the calicle carried out into small wings. Wings sometimes replaced by hollow root-like processes near the scar, perhaps also with additional roots at the sides; in large specimens wings generally absent. The calicle is elliptical, the top of the long axis not more than 1 to 3 mm. below that of the short. Relation of axes very variable, about 2 to 1.

"The centre of the calicle a deep fissure, the larger septa ending almost perpendicularly against it, filled in below by trabeculae in medium-sized specimens from 20 septa and in large from 24. In all free specimens septa of cycles I. to IV. present, cycles V. and VI. depending on the size of the individuals.

"Height of free corallites from 4-35 mm.; long axes of same from 9-37 mm."

The septa, as in most or all species of the genus, have radially set fine ledges with spines at intervals, and the larger against the axial fossa are often much broadened at their edges where the trabeculae come off.

Although there are only three specimens in the collection, which appear to be absolutely the same as *F. rubrum*, this name has the priority. All the young corallites are of course fixed. They break off generally when their calicles have attained a length in their long axes of about 9 mm., the free corallites being about 5 mm. high. Some, however, are attached considerably longer, the largest attaining a height of 23 mm. Three of the specimens could not ever have become free, the central stalk being still perfect and surrounded on all sides by rootlets, numbering 7, 8 and 8. One of the specimens is attached to a small piece of decaying serpulid tube, and a second to a mere fragment of coral. Both supports seems to have been free, and suggest a possible reason for the throwing down of extra rootlets. The edges of the septa of these specimens further do not show through the epitheca. The calicles of two are scarcely compressed, and these two, taken alone, would undoubtedly have been placed in the former genus *Rhizotrochus*. Each rootlet communicates with two interseptal spaces on opposite sides of a septum. The latter bisects the rootlet where it joins the large corallite, and thence continues into the rootlet for some distance as a ridge on its lower side.

The species of Edwards and Haime differ from one another mainly in the shape of the calicle, presence or absence of spines near scar of corallite and systems of septa. The first of these varies greatly in my specimens. The compression in some is very slight, the angle made by the two flattened sides with one another being from 15° to 60° or 70°. Taking the long axis as 100, the short axis varies in No. 5 from 44 to 66, in No. 4 from 37 to 71, and in No. 3 from 43 to 83.

The wings are at first hollow, but owing to deposition of corallum inside become more or less solid. They are quite distinct in 80 per cent. of Nos. 4 and 5. Sometimes they continue up evenly on both sides, but generally there are small wings only at the end of the accretion lines, which probably show periods of rest; the two sides are not usually by any means symmetrical. In the larger specimens they are not so clear, but still traces are commonly present near the basal scar. With growth, in some cases, there seems to have been a certain amount of solution of the epitheca outside and deposition of corallum within. The wings might by this means become blunt spines. This may be partially the case in Nos. 1, 2 and 3. Of these, two have clearly wings, four are rounded at their ends, and ten have at least a pair of spines near their basal scars. Five smaller specimens of other dredgings have also paired spines, not wings. Three of these are very small, and without the specimens of Nos. 1, 2 and 3, it would naturally have been stated, when the corallum was thought to be of endodermic origin, that spines are characteristic of young individuals.

The septa vary with age up to 168, the maximum found. No less than 105 out of 188 specimens recorded in the table had 20 fusing by trabeculae, thus corresponding to *F. irregulare* Semper. This, however, appears to be only a stage of growth as any of the septa of cycle III. may be among the four, which fail to fuse by their trabeculae. The two sides of the calicle do not necessarily correspond, and every possible variation is found, in one with 24 large septa, the number being made up by the enlargement of 2 septa of cycle IV. In the majority of cases with 20 large septa it is the two central side pairs of cycle III. that fail to fuse.

In some cases the horizontal upper edges of the septa rise above the upper edge of the epitheca, while usually they lie in the same plane. In No. 1 they rise above it, but in some specimens of No. 3 lie about 1·5 mm. below, the appearance being as if their edges had been shaved down near the borders of the calicle.

An examination of the type specimen of *F. transversale* Moseley showed that it belonged to the same species, being merely a single corallite that had not lost its stalk. *F. thouarsi*

Ed. and H. probably is merely another form with stalk still intact, but I have no specimen directly comparable. Septal cycles I. and II. are described as equal, the calicle being 25 mm. long by 16 mm. broad. One specimen of No. 3 similarly has only 12 septa fusing in the axial fossa, its calicle being 15 by 12·5 mm.

In the table of measurements, given above, it may be observed that Nos. 1, 2 and 3 differ from the rest far more than the latter do from one another. The corallites obtained in these dredgings were overgrown outside by Polyzoa, weed and barnacles right up to the edge of the calicle, while on the rest isolated serpulid tubes or small masses of *Polytrema* alone were found. In addition to differences in size* the corallum is denser and thicker†; the calicles are more rounded at their ends, and there is a tendency to form spines rather than wings. Indeed the appearances are such as to point to these forms constituting a distinct local race or even a variety. Against this view most of these specimens show 7 to 9 accretion lines, while in Nos. 4 and 5 these number only 4 to 5.‡ These bands are so regular in different specimens that it is quite clear that they indicate periods of growth. These periods must be annual, as there are no changes in currents or other oceanic conditions in the region except such. Hence it is possible that the differences are due only to age, the polyps having started on different years, when the conditions were not quite the same. Again the conditions of the various habitats may have differed, and partially caused the variation. Only one specimen of these three dredgings has a young form attached to it. This has 12 septa, and differs in no respect from those of other dredgings.

The group placed by Ed. and H. under § AA and FFF, called by Semper *F. variabile*, appears to be connected with *F. rubrum* by individuals. Some of Semper's figures have wings and others spines. The scars of all are larger than in the same author's figures of *F. rubrum* (= *irregulare*). This is probably due to the corallites breaking off in different accretion bands. In the present collection five specimens are doubtful. Most specimens from the Maldives in my posses-

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* The corallites of Nos. 7 and 9 are also markedly larger than those of Nos. 3, 4 and 8.

† This is perhaps due to the stimulation of the incrusting organisms. In one corallite there is a distinct ring where the latter began to overgrow the calicle, when a fresh growing period seems to have set in, allowing the polyp to resume its sway. In some corallites the epitheca has been broken, and healed or rebuilt. In these the new epitheca is generally thicker than the old.

‡ The severance of the corallite usually takes place in the thinner basal part of one of these bands, a series of punctures being formed round the corallite.

sion belong to *F. variabile**, but a few more nearly approach *F. rubrum*. In the anatomy of the polyps I can find no constant differences. Semper evidently found few intermediates, but such do exist, so that his second species appears to be only a variety. It should be noted that both of Semper's species of *Flabellum* and his species of *Blastotrochus* were all found in precisely the same habitat. The latter does not differ except in its so-called generic characters from the two *Flabellum*. I would hence suggest that here we have a case of three true varieties of a single species with extremely rare intermediates, living together in the same locality, breeding together, but yet the vast majority preserving their parent forms.†

The species, as above constituted, has been obtained from New Zealand (25 *f.*), Bass Straits (38 *f.*), Phillipines (6-10 *f.*), China, Singapore (2-3 *f.*) and Cape Colony (27-100 *f.*). *F. stokesi* (= *F. variabile* Semper), if regarded as a variety, gives in addition the Arafura Sea (28 and 49 *f.*) and Maldives (20-50 *f.*). In the British Museum I have seen a number of specimens of which six (close to Nos. 1, 2 and 3) were obtained by Captain Sir E. Belcher at the Cape of Good Hope. Of species doubtfully the same *F. thouarsi* comes from the Falkland Islands, and *F. braziliense* Pourtalés (Memoirs Mus. Comp. Zool. Harvard, vol. IV., p. 33) was founded on a single *dead* specimen from 40 *f.* off the Brazil coast.

6. GENERAL ANATOMY OF THE POLYPS OF *F. RUBRUM* (Figs. I. and II.).

Polyp.—The polyp is seated as it were in a cup, formed by the corallite. It lies completely inside the skeleton and does not extend down in any way on the outside of its walls, forming an edge-zone. In the expanded condition the polyp would rear itself for at least 5-6 mm. above the epitheca. The tentacles would then be set as in a solitary Actinian round the top of the mouth-disc in a broad, double band separated by the peristome from an elongated stomodoeum. The contracted polyp, however, does not rise above its skeletal wall.

* The proper name of this species or variety should be *stokesi*, as Moseley has suggested, or some other of Ed. and H.'s names proposed at the same time. Its synonyms would appear to be *F. oweni*, *aculeatum*, *spinosum*, *debile*, *sumatrense* and *candeanum*, all Ed. and H., and *F. variabile* Semper.

The only other living species of Ed. and H. not already dealt with is *F. compressum* (Lamarck), of which there can be little doubt *F. affine* and *F. bairdi*, both Ed. and H., are synonyms.

† Such varieties are common enough in other groups of the animal kingdom, but this is the first suggested case in Madreporaria, or, I believe, Coelenterata. The bringing together of the male and female elements is a passive act, so that it is a fair inference that the three varieties would breed together.

The tentacles, or the pores of the retracted tentacles, form a circlet half-way between the epitheca and the stomodoeum, and the peristome is irregularly contracted into ridges between the attachments of the mesenteries. The stomodoeum may be either extremely reduced or enormously enlarged, the former if the polyp has been slowly killed in spirit or chromic acid, the latter if more rapidly fixed in formalin. To a certain extent the appearance and size of the stomodoeum depends on the state of retraction of the tentacles, being much larger when the latter are but partially invaginated.

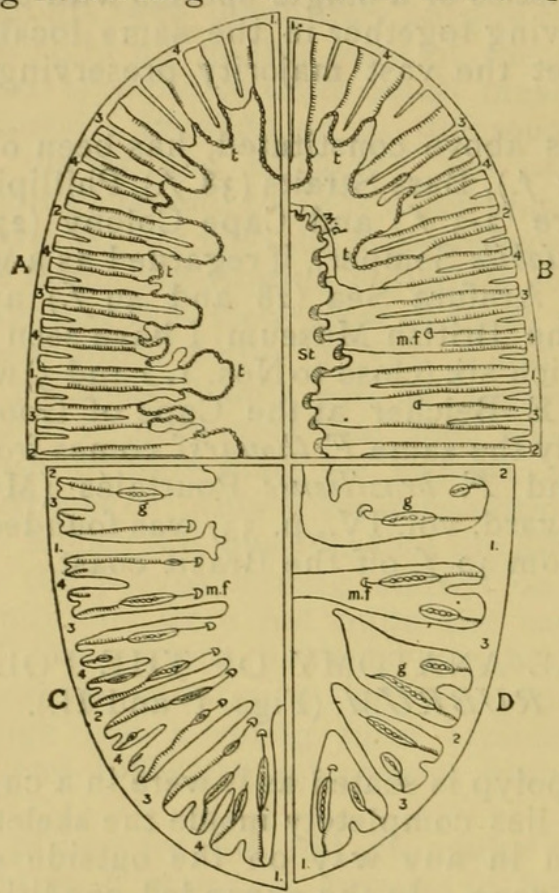

Fig. I. Partly diagrammatical transverse section through a single completely retracted specimen of *F. rubrum* in different planes:—A. Through the top of the epitheca a little below its edge: B. Through the stomodoeum, cutting the basal contracted ends of some of the tentacles: C. Through the top of the masses of generative organs: D. Through the bottom part of the generative organs.

The numerals refer to the cycles of the septa. *t.* Tentacles. *st.* Stomodoeum. *p.w.* Peristome wall. *m.f.* Mesenterial filaments. *g.* Testicular masses.

The sections were slightly simplified from camera lucida drawings. In addition to the general anatomy they show the decrease in size and disappearance of the mesenteries and septa lower down in the corallite. One of the mesenteries of a pair bounding a septum of cycle 4 reaches the stomodoeum (see B) and is so represented, although it is very unusual for such an one to do so.

Septa and Mesenteries.—When decalcified, the polyp is divided up into as many chief segments as there are larger septa. These are joined over the open mouth of the calicle by

the body-wall of the polyp, but are free below, where the septa fuse with one another. Each segment is further subdivided by the smaller septa, typically three in number. The septa throughout alternate with mesenteries. The latter are in pairs with their muscles—except on the directives—on the sides facing one another. It follows hence that half the septa are entocoelic and half exocoelic (Fig. I.). As already seen the orders of septa vary greatly in individuals, so that it is impossible to characterise any one order as exocoelic. From the alternate arrangement of mesenteries and septa it follows that the highest numerical order in any part is the exocoelic one. As the growth of any corallite proceeds, more and more septa up to six cycles appear. The former exocoelic order of septa becomes entocoelic by the development of new pairs of mesenteries. The increase of mesenteries takes place *pari passu* with the formation of new septa. An examination of 16 corallites has failed to reveal a single case of the growth of the new septa preceding that of the new mesenteries or *vice versa*. The mesenteries in every case are perfectly distinct on the external body-wall between the tentacles and the upper edge of the epitheca. The mesenterial filament is developed very shortly after the mesentery is formed, but the definite formation of the muscular fibres takes place later, and they gradually increase throughout life.

Tentacles.—The tentacles arise over the entocoelic septa alone, and are accordingly half as numerous as the whole body of septa. An inner cycle of larger tentacles, corresponding to the septa which reach the columella, and an outer cycle may usually be traced. The tentacles are retracted by the longitudinal muscles of the mesenteries in an acrecbolic manner (Fig. II.). The invagination is never complete, a central portion and two pockets on either side of the septum beneath being found. Secondary pockets also occur, the muscles seeming to be attached in clumps. A pair of mesenteries passes across towards the stomodoeum on each side of the base of a tentacle, some of their longitudinal muscles continuing a direct course up the tentacle. Below the outer cycles the mesenteries may to some degree extend into the tentacles, but with increase of size even in the expanded polyp come to pass around the base.

All the tentacles are covered with round, knobbed batteries of nematocysts, which gradually decrease in size from their tips. At the base these pass imperceptibly into the ectoderms of the external body wall and peristome, and except in the youngest tentacles do not cover over the attachments of the mesenteries.

Stomodoeum.—The stomodoeum is a slit, one-third to two-fifths of the long diameter of the calicle in length, with no

trace of any marked grooves at either end (Fig. I.). Its surface is owing to thickenings of its walls ridged over those mesenteries, which are attached to it. If 24 septa fuse in the axial fossa, there should be 48 mesenteries of a first order reaching the stomodoeum and corresponding to ridges. If a less number fuse, there should be a proportionately lesser number of mesenteries with ridges on the stomodoeum, but this is not so, three polyps with 18, 20 and 21 such septa having 48 mesenteries with ridges and one with 24 septa 50 such mesenteries. In a case with 20 septa (Fig. I.) two of the mesenteries out of pairs on each side of tertiary septa have failed to reach the stomodoeum, but their places have been taken by others bounding quaternary septa.

The lower edge of the stomodoeum is ill-defined and often in the contracted polyp somewhat turned outwards (Fig. II.). Its thickenings pass directly into the filaments of the corresponding mesenteries, which form a first order.

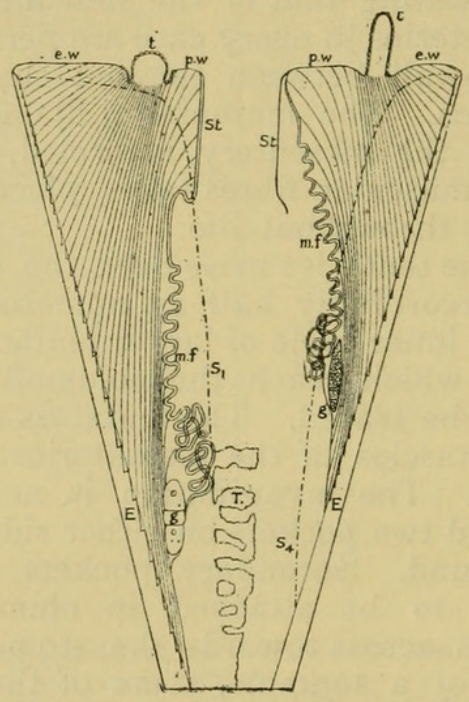

Fig II. Diagrammatical longitudinal section of a partially retracted specimen of *F. rubrum*, the left half cutting a tentacle over a primary septum, exposing the face of one of the bounding mesenteries, and the right half cutting a less retracted tentacle over a quaternary septum and likewise exposing the face of one of the bounding mesenteries.

The longitudinal lines on the faces of the mesenteries represent the distribution and course of the muscular fibres. Against the epitheca their attachment in clusters is, to some degree, shown.

e. w. External body wall. *t.* Tentacles. *p. w* Wall of the peristome. *st.* Stomodoeum. *m. f.* Mesenterial filaments. *g.* Generative organs (ovary on the left and testis on the right mesentery). *E.* Epitheca. *S* 1 and *S* 4 septa of cycles I. and IV., represented by incomplete lines. *T.* Trabeculae from the septal edge.

Muscles.—The muscles are of the usual Actinian type, but the circular sphincter is absent. The longitudinal muscular

fibres are set on plates of the structureless lamella, but the transverse, which are very slightly developed, have no such folds. The origin and course of the longitudinal muscles may be seen in Fig. II. The separate fibres never cross one another, but below the filaments muscle-plates are found on both sides of the mesentery, some of the most deeply attached muscles crossing the free edge of the mesentery to its opposite side. The fibres end at the attachment of the mesenteries more or less in clumps, which seem to be connected with a similar mode of attachment of the mesentery to the corallum (see Fig. II.).

The transverse muscular fibres, lying on the opposite faces of the mesenteries to the longitudinal, do not appear to me to extend more than half-way down the stomodoeum. They run outwards mainly to the body-wall external to the tentacles, and have no connection with the attachment of the mesenteries to the corallum. The tentacles being entocoelic cannot be connected with these muscles in any way.* The longitudinal muscles alone contract the polyp, the expansion being due to the elasticity of the polyp following the relaxation of the same muscles. The transverse muscles would seem to be present solely for the purpose of opening the stomodoeum for the reception of food, though they might, by drawing together the external body-wall and stomodoeum, assist slightly in pushing out the tentacles.

Mesenteries.—The first cycle of mesenteries—48 in number, all reaching the stomodoeum—should be the pairs on either sides of primary, secondary and tertiary septa. There are then typically 48 further mesenteries of a second order, 24 pairs on either side of quaternary septa. These do not reach the stomodoeum, but start from the peristome near the mouth, only very exceptionally being attached to the stomodoeum for the whole or part of its length. I have not cut serial sections of any polyp with a third cycle of mesenteries, but from dissections it is clear that the latter are attached almost in the same position as the secondary mesenteries.

The mesenteries vary considerably in size, but their general appearance may be seen in figures I. and II. In any polyp the secondary mesenteries are usually nearly of the same size, but the primary may vary somewhat, *in the smaller polyps* 24 being sometimes larger and extending deeper into the calicle marking out the original primary and secondary septa.

The filaments of the primary mesenteries extend down from the thickenings of the stomodoeum, and form an irregular

* The tentacles over the primary septa at each end of the calice, hence between the two pairs of directive mesenteries, are never contracted to the same extent as the lateral tentacles, being drawn in principally by the general contraction of the polyp.

series of loops down the edges of the mesenteries (Fig. II.). The character of looping depends on the state of retraction of the polyps, but normally alternates from side to side. Below they end in a massed series of larger loops, irregularly arranged. The end of the filament is not free. The mesentery between the massed portion of the filament and the longitudinal muscles is no doubt enormously extensile, but there is no part which could be shot out as an acontium (see Pl. III, fig. 17). The filaments of the secondary mesenteries commence right from their attachment to the stomodoeum or peristome, and, enlarging somewhat, extend down straight for some distance, still deeper forming similar loops.

Generative Organs.—The presence or absence in an individual of generative organs on any mesentery depends entirely and solely on its size. In the youngest male state single round or oval acini are found just behind or sometimes a little below the massed end of the mesenterial filament. In the next stage a few widely separated masses may be seen, forming with the thickened endoderm a narrow band. This increases in length and breadth, so that in the largest mesenteries an oval-shaped mass, 5 mm. long by 1·5 mm. broad, is found. The whole then consists of closely-packed spermagens, which vary considerably in size and shape, some being branched, others round or oval, and yet others nearly polygonal.

The ovaries are similar in size and position to the testes. In the ripe condition on the larger septa they have a row of up to about seven ova, the end ones oval in shape, the central one round, but all flattened where they touch one another. Fresh ova—at first small round bodies with no food yolk—generally appear in the structureless lamella each between a riper ovum and the free edge of the mesentery, but in one case, where the central of three nearly ripe ova seems to have been dehisced, three small ova have appeared in its place.

In 11 polyps of dredging No. 4 and 3 of No. 5 that I have examined the whole or main bulk of the mass is testicular on the primary mesenteries. On all the secondary mesenteries, where the development may be traced, the whole is always so. In one series of sections across a polyp of No. 4 (calicle 17 mm. long) I have found in the inner part of the testicular masses on the primary mesenteries a few relatively small isolated ova without food yolk. In one mesentery of a still larger polyp of the same dredging there are three ova on the inner edge of the testicular mass at its top end behind the massed loops of the mesenterial filament (Pl. III, fig. 17) and in all the other primary mesenteries of the same polyp ova were found as well. In two small polyps of No. 3 the mass is

testicular, and in two larger polyps (calicle about 23 mm. long, entirely formed of ova.

I had not sufficient examples of larger sized corallites as obtained in dredging No. 3, which I could decalcify so as to trace the changes in generative organs with increase of size. I am, however, impelled to consider that there must be protandry. The polyp first produces testicular elements, which are replaced as it grows by ova; a regular crop of these are then ripened. With increase of size the rate of growth of the corallite seems to gradually lessen. This is correlated with the production of ova, the increase in the number of which causes cessation of growth and finally the death of the parent polyp*.

Note on F. PAVONINUM.—I have only been able to afford to use one polyp between Nos. 6 and 7 of the table of measurements on p. 124 for the study of the anatomy of this species. Tentacles are present over all the septa, and the latter are all entocoelic, there being thus relatively twice as many mesenteries as in *F. rubrum*. Those pairs of mesenteries, which lie on either side of the septa fusing by trabeculae in the axial fossa, alone appear as a rule to depend from the stomodoeum.

In all other respects the anatomy is the same as above described in *F. rubrum*. The polyp is in the male condition. The spermagens are tightly packed together, and present in side view a round to branched appearance.

7. MINUTE ANATOMY OF THE POLYPS OF *F. RUBRUM*. (Pl. I and II, figs. 1—9).

Calicoblastic Ectoderm (figs. 1-3).—The layer of ectoderm separating the polyp from the corallum is everywhere complete, and even in the most roughly decalcified specimens is not torn away. It varies considerably in accordance as it may be in any position an active secretory layer or not. No definite cells can in any part be distinguished. Over the greater part of the corallum it is an extremely thin, finely granular layer, slightly thickened where nuclei are present. The latter are generally slightly oval in shape with granules but seldom a network. It only differs from the same layer in other corals in being better defined and more definite.

Near the base of the polyp and on the sides of the septa the calicoblastic layer simulates the appearance of a pavement epithelium, nuclei joined together by finely granular

* Since the above was written I have examined a large number of specimens of the same Coral from other localities. *Vide* "Some Notes on Variation and Protandry in *Flabellum rubrum* and senescence in the same and other Corals." *Proc. Camb. Phil. Soc.*, vol. XI, pp. 463-71 (1902).

protoplasm (fig. 3). As the edges of the septa are approached the layer thickens. Nuclei become more frequent, and tend to exhibit a definite network. The protoplasm forms, as it were, two layers, the one against the structureless lamella, the other with a ragged edge against the corallum, joined by a series of bridges between large vacuoles. The nuclei commonly lie in the outer layer or in these bridges (fig. 1). At the edge of the septum the ectoderm is still thicker, but the large vacuoles are nearly absent, and towards the outer side (*i.e.*, against the septum) the protoplasm is almost hyaline. The same, too, is the case at the upper edge of the epitheca, where the ectoderm forms practically a thick hyaline pad, seated on the corallum.

The calicoblastic ectoderm is also thickened greatly, where the mesenteries are attached to the corallum and on each side of the same (fig. 2). Its edge against the corallum is very ill-defined, indeed ragged and broken. The protoplasm is densely granular, often with relatively large granules. The processes which attach the structureless lamella to the corallum (desmocytes) do not materially differ from what Bourne, Fowler and others have described. They are especially well developed at the attachments of the mesenteries (fig. 2), but may occur in any part, small bunches being in particular scattered over the septal sides. Their development was quite clear, and did not differ materially from Bourne's description.[1] The first appearance of any *desmocyte* could be seen in a granular mass of protoplasm against the corallum, to which from the first it seemed to be attached. Subsequently by growth inwards it joins the structureless lamella, which may be thickened so as to meet it. At its base or side is always a nucleus with a well-defined network, but otherwise the same as those of the layer.

My researches add little to Bourne's most admirable and lucid account of the formation of the skeleton. There are no "scales,"[2] nor is there any indication of the possible formation and shedding of any such. The appearance of the layer in a few preparations of both hard and soft parts only showed that the structure in the decalcified sections had in no way changed. The layer had in all cases become slightly separated from the corallum—perhaps by killing—except where the desmocytes attached themselves.

The thickening of the ectoderm on the septal edges was found everywhere, but it varied enormously, at intervals being extremely thick and much more hyaline. Where secretion

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1. *Quart., Jour. Micro. Sci.*, vol. 41, pp. 499-547 (1899).
2. *Vide* "Microscopic and Systematic Study of Madreporarian Types of Corals," by Maria M. Ogilvie, *Phil. Trans. R.S.*, vol. CLXXXVII., p. 83 (1896).

may be supposed to be going on especially actively, the layer is more hyaline and where not granular. The distances between the thickenings of the ectoderm on the septal edges correspond more or less to the distances between the ridges on the sides of the septa, and seem to lie over their ends. They would hence fall on the so-called "centres of calcification." When I first examined microscopically the skeletons of corals, I thought that these centres corresponded to the tubes of boring organisms, which became densely packed with the dust caused by grinding. Such organisms do tend in colonial reef-corals to bore along these centres, indicating perhaps that they are lines of least resistance. May not these centres be directly due to the thickenings of the calicoblastic layer? I can only regard the layer as an enormous syncitium, and for the growth of a septum there would seem to be a flowing up of the protoplasm on either side. Where the two layers of protoplasm fuse, *i.e.*, immediately over the "dark line" joining the "centres of calcification" there is an extensive formation of corallum. This takes on the crystalline form, but the regular arrangement is not seen until after the formation of the "growth lamellae" of the septal sides. The "centres of calcification" would, on this view, represent aggregations of crystals of carbonate of lime not arranged in any determinate direction. The radiations from these would then represent lines of irregularly arranged crystallisation.

General Ectoderm (figs. 4-8).—The ectoderm is everywhere extremely well preserved and shows its structure admirably. It varies in different polyps only in accordance with their state of contraction, outside the tentacles often appearing as if knobbed (fig. 4). Cell outlines cannot usually be distinguished, but it is an epithelium of a narrow, elongated, columnar facies with a broad, crowded layer of rod, or oval-shaped, densely granular nuclei. The latter vary considerably with the amount of vacuolation and the presence or absence of gland cells, but are for the most part found in the outer half of the epithelium. The outer or free edge presents an appearance of longitudinal striation, so that it is probably in life ciliated all over. Over the structureless lamella the protoplasm forms a finely granular network, in or above which a few rounder nuclei may be distinguished. These belong to irregularly-shaped sense cells, some of which are represented in the figures.

Gland cells occur of two kinds, mucous and granular, and can be best distinguished in tissues stained with thionin and orange green. The mucous cells stain deep blue, and the granular in accordance with their ripeness from yellow to black. The mucous cells are of the typical goblet-shape, and are situated in the outer half of the layer. Most of the

granular cells lie on the contrary in the inner half of the epithelium below its layer of nuclei; but many have definite necks extending through the epithelium to the exterior. While the oval-shaped nuclei of the mucous cells are situated at the base of their secreted mass, the nuclei of the granular cells lie in the middle, and are generally round with well-defined membranes and a few granules. In the earliest state the cells stain of a homogeneous yellow colour. Fine granules appear in this and give rise to larger spherules or masses. These become concentrated towards the outer part of the cell, which then sends a process to the exterior. At the same time the granules become more and more deeply stained and smaller (figs. 4-8).

The Ectoderm of the External Body Wall (fig. 4) is rather more vacuolar than the same layer elsewhere and slightly thinner. Granular cells are relatively rare and generally appear ripe. The basal nervous layer is usually distinct, and presents the punctate arrangement of the Actiniaria. Nerve cells are here and there present. A few nematocysts of the regular tentacular kind, but always much smaller, occur in places.

The **ectoderm of the tentacles** (fig. 5) differs only in being packed with the nematocysts in batteries. Mucous cells are less common than elsewhere, and granular cells about as numerous as in the ectoderm of the external body-wall. The nervous layer is concentrated under the batteries, three or four of its nuclei being often visible in a single section through the middle of a battery. No definite muscles can be distinguished, but the epithelium appears to give off processes which are joined to special attachments of the structureless membrane.

The nematocysts are the same as I found in the tentacles of *Coenopsammia* (Willey's Zoo. Results, p. 368). Each has about 30 turns of the thread, which in the fully ripe body lies immediately under its external wall, so that it projects spirally. The development of the thread follows the same lines as in *Coenopsammia*, the reduction in size taking place *pari passu* with the formation of the thread.

The **ectoderm of the peristome** differs only from that of the external body-wall in being less vacuolated and having the nuclei still more massed together. The nervous layer is always distinct, and the granular gland cells are fairly common. Nematocysts are not found.

The **stomodoeal ectoderm** (figs. 6 and 7) exhibits the same structure as that of the peristome. It is thickened over the attachments of the mesenteries (fig. 6), but between these is not so thick as on the peristome. In the latter position the nuclei form a broad line broken only where the

gland cells project towards the exterior. The nervous layer is little marked. Over the mesenteries (fig. 6) the appearance is as if the whole had been pressed together to give the enhanced thickness. The rod-shaped nuclei of the layer are closely packed together. The whole is evidently densely ciliated. The outer part is set with large mucous cells, and granular cells extend up from the base. These latter cells are very numerous and lie internally to the layer of nuclei, and, unless actively secreting, do not seem to have processes to the exterior. At the base they are connected by protoplasmic strands to the nerve layer, and in some sections appear to be connected with the protoplasm immediately around definite nervous nuclei. It is characteristic of these gland cells in this and the next part of the ectoderm to be considered that they usually have their nuclei quite distinct—more or less round with a few granules—and exhibit all phases from rest to active secretion.

The **mesenterial filaments** (fig. 8) are presumably ectodermic in origin, as they certainly are in structure. They are of the usual form, a central rounded part (the filament proper) set on the somewhat broadened end of the structureless lamella. The thickenings of the stomodoeal ectoderm gradually narrow as they pass into the filaments. Allowing for their necessarily constricted base the latter differ in no respect from these thickenings. They have the same thickness, the same gland cells and nuclei, the nervous layer alone perhaps not being so well marked. They also seem to be ciliated. On the straight upper edge of the mesentery gland cells are not so numerous, and the nuclei are very dense. In the central half the whole of the inner part is crowded with granular gland cells, while towards the lower end the filament is more vacuolated.

Endoderm (figs. 2, 3, 7 and 8).—Generally cell outlines could not be distinguished in the endoderm, but in some sections near the attachment of mesenteries the protoplasmic areas had become partially separated from one another. In this position (fig. 2) the layer consisted of low columnar cells with large, flattened, basal processes, spreading outwards on the structureless lamella. Their nuclei were nearly round with well-defined membranes and network. Between the cells were a number of large vacuoles, but in this position no glands of any sort could be distinguished.

More often, except where especially thickened, the endoderm appears to consist of a vacuolated epithelium of more cubical facies with slightly oval nuclei (fig. 7). In certain positions, where the body-wall immediately overlies the corallum, it is thinner and more homogeneous. On the sides of the mesenteries and under the peristome and tentacles it is

thicker and more vacuolated, and in the latter position the cells appear to be directly attached to low processes of the structureless lamella. Over the muscles the layer is thicker with more oval nuclei (fig. 2).

Under the mesenterial filaments the endoderm is as it were concentrated to form two great pads to support the filament, generally as broad or broader than the filament itself (fig. 8). These are formed of granular protoplasm scattered with the regular endodermic nuclei, and with small, round, deeply staining granules, appearing almost like nuclei of a second order. There is here little vacuolation and no definite contour against the coelenteron, the edge being drawn out into ragged processes. In this position, though indeed they may be found sparsely distributed over the whole endoderm, are a few mucous cells of small size and a large number of round homogeneously staining bodies of about twice the diameter of the nuclei. The latter take up all stains fairly evenly, and exhibit no trace of structure. When teased out they appear as round refractive bodies, and are, I have no doubt, of a fatty nature. In the same position at the base of the filament I have also found diatoms and other algal matter inthe endoderm.

A number of oval bodies generally occur in the endoderm on each side of the upper top ends of the septa, forming almost a layer (fig. 3). In a polyp with calicle 17 mm. long they are only present in this position, but in smaller polyps isolated ones are found anywhere over the corallum. They generally do not stain, or stain very imperfectly, and appear in section to have a number of pieces of a thick filament. When reconstructed, a spirally coiled thick thread is found (fig. 9). The various coils, about 12 to 15, are in contact, and extend diagonally around the whole. The appearance approaches that of the mesenterial nematocysts of *Cocnopsammia* (*loc. cit.*, p. 370), but with enormously swollen threads and no discharging apparatus. Most are in the same condition as in the figures, but I have found a few with as yet no thread developed. Some have no nuclei, but where present they are oval and densely granular. There are no indications of any having been ejected, nor of any possibility of ejection. There can, however, be no doubt, but that they are nematocysts, perhaps rudimentary or reduced. As such their position, especially on the upper free edges of the septa, is probably not devoid of morphological significance.

Generative Organs.—In the young stage the testes are composed of small cell masses, forming follicles in the structureless lamella. Later, as described by Hickson in Alcyonium,* each follicle consists of a dense mass of granular nuclei surrounding a small open central coagulum.

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* *Quart. Jour. Micr. Sci.*, vol. 37, p. 343 (1895).

The ova have a large round nucleus with nucleolus set in a mass of yolk spherules, the whole sometimes reaching 1·5 mm. in length by nearly 1 mm. in breadth. The nucleus is usually situated in the upper part of the cell, and in a fortunate series of sections I found near the base of two ova small canals extending through the endoderm. These open from the exocoelic side, and reach down to the surface of the ova, one of which seems to have partially flowed into its canal. The diameter of the canals is in each case about that of a human, red blood-corpuscle, and the sections, which are not quite so thick, appear in both cases to have been cut almost longitudinally through the centre of each channel. The bounding endoderm shows longitudinal striae in the walls, but the existence of canals is quite clear under a high power. Although I have examined many other ova I have not found these oviducts elsewhere, and I suspect that they are merely temporary structures for the escape of the ova. They have not been previously described, so far as I am aware, in the Madreporaria, and are almost certainly what the Hertwigs described as the "Fadenappart" of the ova in the Actimaria *

The single polyp of *F. pavoninum*, that I examined, is in rather a different condition, so far as digestion is concerned, to any of those of the above species that I have worked over. It, however, only differs in its minute anatomy from *F. rubrum* in that mucous gland cells are more conspicuous and numerous both in the ectoderm, and more especially in the endoderm.

8. ON THE POST-LARVAL DEVELOPMENT OF *F. RUBRUM*. (Pl. III, figs. 10-16.)

Dried Coralla.—The corallites of dredgings 4 and 5 in particular have various stages of the development of the species growing upon them. In the earliest stage found there is a distinct round basal plate with 6 septa radiating from the centre, but not meeting one another. There is no trace of epitheca. As yet it is uncertain whether the young corallite belongs to *Flabellum* or to a fungid coral, which I have also found growing on some of the specimens. The earliest undoubted stage is that of a corallite, nearly 2 mm. in diameter, with a distinct epithecal rim, ·2-·4 mm. high, and 6 primary and 6 secondary septa (fig. 10). Another, almost similar, has the epitheca ·5 mm. high showing the

* *Die Actinien* [1879].—Plate vii., Fig. 13, very closely resembles the appearance If ound, but the membrane of the ovum in my section is distinct and the nucleus at the opposite end of the cell (Fig. 2).

early growth lines; the diameter is 2 mm., and the septa are practically the same as in the previous stage (fig. 11). A third is 1·5 mm. high with a very marked looping outwards of the epitheca between the septa, of which the primaries extend further into the corallite.

In fig. 12 is represented a stage where the primary septa are beginning to give off trabeculae; the specimen is 1·75 mm. high and 2·5 mm in diameter, and has well-marked growth-lines on its epitheca. In fig. 13, a specimen 1·5 mm. high by 2 mm. in diameter, the primary septa have all fused with one another by trabeculae, but as yet there are no signs of any tertiary septa. The latter have appeared in the next stage (fig. 14a) 4 mm. high by 3·5 mm. in diameter. The calicle has begun to elongate the terminal septa of its long axis belonging to the first cycle. The six primaries are still distinctly the larger, but six secondaries have fused with them and with one another. The corallite in side view (fig. 14b) shows marked accretion lines and the characteristic wavy structure of the epitheca. The former represent slight additions to the epitheca, and do not correspond to the lines of growth in the older specimens, which are markedly larger and consist of many such.

The further changes lie in the gradual fusion of the tertiary septa to those of cycles I. and II. by trabeculae. This does not take place generally until there has been a very marked and considerable increase in the size of the corallite, nor usually until after it has become free. Fig. 15 represents a free specimen 6 mm. high, 9·5 mm. long axis of calicle, and 4·5 mm. short axis of same. Only one septum of cycle III. has as yet become fused with those of I. and II. This is situated in an end space between septa of cycles I. and II., and it will be noticed that the tertiary septa in these four spaces are larger than in the side ones, being indeed the first to fuse. Those in the next four spaces are larger than those in the central ones, which are naturally from the method of growth of the corallum the last to join up, only indeed fusing in the largest corallites. In the figure it may be observed that in two of the end spaces of the calicle between septa of cycles I. and III. quinary septa have appeared on either side of the quaternary, which are everywhere complete.

The corallum, where it breaks off from its pedicle, varies considerable, but is usually in the stage with 12 septa fusing with only traces of the tertiary septa (fig. 16). A series of perforations appear right round the corallite in one of the accretion bands near the base, but what causes these I have been quite unable to determine. In no case is there any

regeneration from the still attached stalk as in *Fungia*, *Cycloseris** and probably many other genera.

Polyps —(Text-Figures III. and IV.).—The greater part of the collection was forwarded to me in formalin. For the determination of the species it was necessary to dry and clean a considerable number of the adult specimens. To study the development of the septa and corallum I had to do the same to some of the smaller forms. The earliest of these with 6 large and 6 small septa appeared, as if the tissues of the polyp had been torn off the mouth of the calicle.† All the specimens of the young forms seemed to have suffered greatly, and I rejected one after another as useless for section cutting, placing them in the cleaning bath. Finally I selected a young polyp, which from surface view appeared to have been torn around the base of the tentacles where they run into the external body wall, there being no visible trace of tentacles, peristome or stomodoeum. The central part of the calicle was filled in with a mass of the irregularly coiled mesenterial filaments, which I hoped might show the structure. On cutting a series of transverse sections the whole polyp turned out to be thoroughly well-preserved. So far as I can see, there is no trace whatever in the polyp of any rupture or tearing off of any part of the body wall, beyond what is clearly due to the perforation of the latter by the upper, sharp edges of some of the septa.

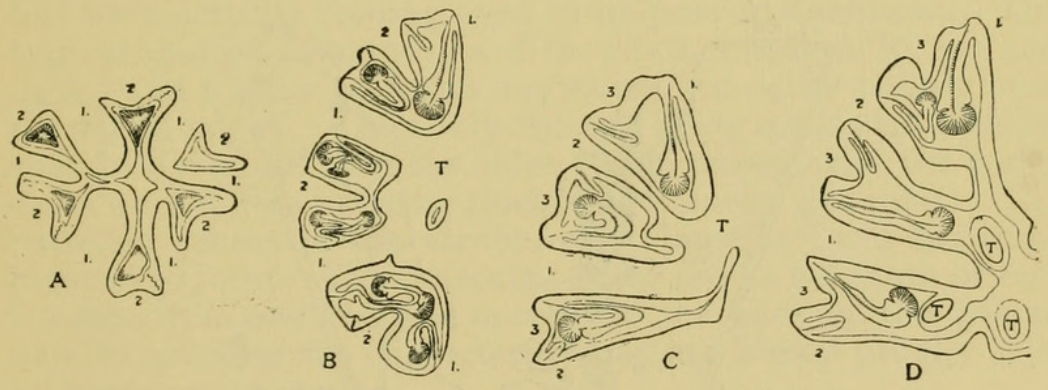

Fig. III. Transverse sections through the attached post-larval stage of *F. rubrum*, described in the text, in four different planes, shown approximately in Fig. IV. (drawn under the camera lucida).

A. shows the connection of the cavities of the different systems at the base of the polyp. Only traces of mesenteries are present by three of the septa. B. represents half the same at a higher level. The primary septa alone fuse in the axial fossa. The first 12 mesenteries are complete and the second 12 have commenced. C. and D. represent the same quadrant, C. where the primary and secondary septa both fuse by trabeculae and D. a little higher.

The numerals refer to the cycles of the septa. *T.* Trabeculae from the septal edges.

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* *Vide Willey's Zoological Results*, pp. 171-180 and plates XIX and XX.

† Two other specimens, since found, corroborate the development as described in the following pages. They are both of a considerably earlier stage.

The general structure of the polyp may be best seen by reference to Figs. III. and IV. The corallite has 12 septa fusing by trabeculae in the axial fossa, the septa of cycles I. and II., alternating with the 12 septa of cycle III., which are extremely small, only just having made their appearance. The stage then is about that shown in fig. 14. The mesenteries number 24, 6 pairs of larger situated on either side of the primary septa and 6 pairs of smaller against the secondary septa. The filaments of the former mesenteries form great bunches of coiled loops, but of the latter are very slightly developed (Fig. IV.) In one or two of the exocoeles traces of the tertiary mesenteries are found in prolongations of the structureless lamella, which have as yet no trace of filaments.

All the mesenteries are attached above to the body wall, which forms a rim around the mouth of the corallite of about one-fifth its breadth. The mesenteries hang from this, their free edges being continuous with its edge (Fig. IV.), but their filaments do not appear until some little distance below the same. On the larger mesenteries the muscular filaments have developed in the typical manner, most originating near the edge of the body-wall; on the smaller mesenteries they are as yet scarcely noticeable. *There is no trace of any tentacles in any area of the body-wall, having nematocysts or otherwise, nor of any stomodoeum.*

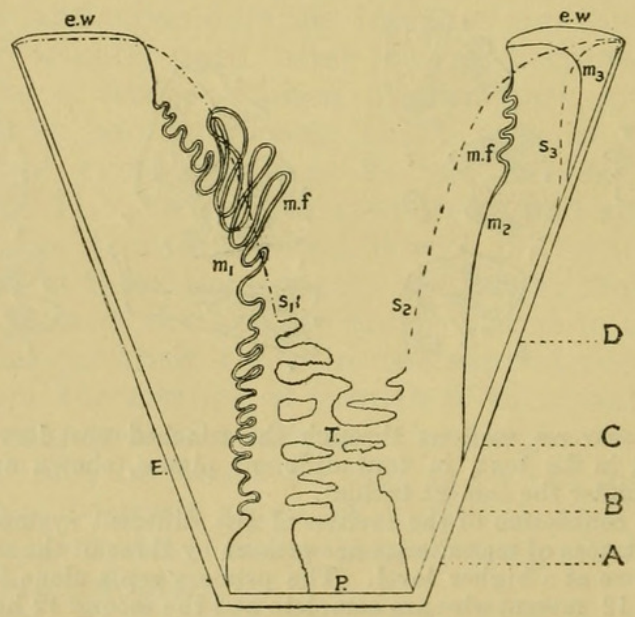

Fig. IV. Diagrammatical longitudinal section through the attached post-larval stage of *F. rubrum* described in the text. The left side represents one of the mesenteries bounding a primary septum, and on the right side mesenteries bounding secondary and tertiary septa are shown.

A.—D. sections shown in Fig. III.

e. w. External body-wall. *m. f.* Mesenterial filaments. m_1, m_2 and m_3. Mesenteries bounding septal cycles I., II. and III. S_1, S_2 and S_3. Septa of cycles I., II. and III., represented by incomplete lines. *T.* Trabeculae from the septal edges. *E.* Epitheca. *P.* Basal plate.

As the series of sections show (Fig. III.), the primary and secondary septa fuse with one another by their edges, so as to close in the axial fossa at a certain depth with a mass of trabeculae (Fig. III. C.). Lower down the secondary septa become smaller, and the fossa is closed in by processes from the primary septa alone (Fig. III. B.). Indeed the latter processes form almost a solid mass closing in the axial fossa. Still lower, the primary septa themselves become reduced so that the axial fossa is quite open (Fig. III. A.). The tissues of the different segments between the primary septa fuse across, and place the whole coelenteron in free communication. In the lower half of the polyp the coelenteron is, however, much reduced—in many places almost obliterated—by the convolutions of the mesenterial filaments.

Besides the above points, the bearing of which will be considered later, there is little to note about the polyp. The enormous thickness of the body-wall, as seen in the camera lucida drawings (Fig. III.), is due to the relatively great thickness everywhere of the endoderm. The layer is coarsely granular, and somewhat similar to the same layer at the base of the mesenterial filaments in the adult (p. 142, and fig. 8); cell outlines may, however, be distinguished in some places at the free edge of the layer. Fat cells are present here and there, and foreign bodies (principally algal) are found near the bases of the mesenterial filaments, showing that the polyp has been actively feeding even in its present condition. The typical aborted nematocysts of the adult endoderm (p. 142 and figs. 3 and 9) may be found anywhere, but occur mainly near the septal edges. They only differ in being somewhat smaller than in the adult. On the sides of the mesenteries the endoderm only differs in being thicker and more granular. The flattened plates of the structureless lamella have but commenced to form. The muscular fibres are as yet more or less isolated from one another, except at the base of the polyp, and do not form the characteristic square blocks usually seen in a transverse section.

The mesenterial filaments are of the same structure as in the adult, but rather more granular. The structureless lamella is extremely thin, in many places scarcely existing as a distinct layer.

The calicoblastic ectoderm varies from a columnar to a cubical facies, and is everywhere a well-defined hyaline layer with little or no granulation. The "desmocytes," except at the base of the polyp, are not yet attached to the structureless membrane. The whole layer is noticeable for its hyaline appearance and well-defined edge against the corallum, never having a ragged surface except near the attachments of the mesenteries. Above the corallum the

calicoblastic ectoderm merges gradually into the external ectoderm, which only differs from that of the adult in being less vacuolated and in the comparative absence of mucous and granular gland cells.

A later stage, which I have also examined by serial sections, is that of a still attached polyp, long axis of calicle 5 mm., and short axis 2·5 mm. It has 48 septa, of which 12 alone fuse in the axial fossa, the stage being hence a little earlier than fig. 15. The stomodoem is an extremely shallow invagination. There is as yet no trace of generative organs, the polyp being otherwise, even in its minute anatomy, similar to the adult. The tissues surrounding the septa fuse across below the mass of trabeculae in the axial fossa, thus extending to the very bottom of the corallite. The minute examination has shown no cause which can in any way produce the breaking-off of the calicle from its stalk. Some of the tissues would undoubtedly seem to remain in the pedicle, but, as already mentioned, I have found no evidence of its possible future growth to form a fresh corallite.

9. CONCLUSIONS RELATING TO THE GENUS *FLABELLUM*.

In the preceding pages an attempt has been made to investigate and determine as far as possible the variation in the skeleton of two very dissimilar species of the genus *Flabellum*. The variation is of two kinds, specific and normal.* The latter may be best seen by reference to the synonomy. It is in these two species enormous, and the study affords some data for considering the possible and probable variations not only in the same but in other genera. In *F. rubrum* there appear to be three distinct specific or discontinuous variations, between which the intermediates do not form more than 1·2 per cent. of the total number of specimens. This, so far as I am aware, is the first suggestion of the presence of distinct varieties in the Madreporaria.

The question as to whether the skeleton in the axial fossa represents a true columella, built by deposition on the basal plate, or is merely formed by trabeculae from the septal edges appears to me of morphological and generic importance. The development shows clearly that there is no such true columella in *Flabellum*.† Trabeculae

* See "Heredity, Differentiation and other Conceptions of Biology," by W. Bateson, *Proc. R. Soc*, vol. 69, p. 193.

† In this connection it is interesting to note that series of sections of even moderate sized attached corallites show at different heights the development of the septa equally as well as separate corallites in different stages. There is in *F. rubrum* no obliteration of the axial fossa by corallum between the earliest trabeculae that arise and the basal plate.

are merely formed by the fusion across the axial fossa of the body-wall, covering the septal edges, and may arise in any corallite of any genus. The origin of rootlets has been clearly shown by Lacaze Duthiers* in *F. anthophyllum.* They seem to arise as a flowing over the edge of the cup of the tissues of its polyp, probably brought about by the absence of favourable circumstances for the deposition of the skeleton and the presence of more suitable conditions for the increase of the polyp itself. These considerations lead to the absorption of the genus *Rhizotrochus*, while the close resemblance between the buds of *Blastotrochus* and *Flabellum* scarcely allow of their being distinct genera.

The comparison of the anatomy of the polyps of *F. pavoninum* and *F. rubrum* show that they are separated by the fact that all the septa in the former are entocoelic and have tentacles over them, whereas half the septa of the latter are exocoelic, with no correspondingly situated tentacles. The mesenteries of the former are hence twice as numerous as the septa, and of the latter the same in number.

Moseley's account† of the anatomy of the genus is rather confused. A generalised transverse section, Moseley's fig. 10 shows twice as many mesenteries as there are septa in the genus, and it is stated that there are the same number of tentacles as there are septa. This, as a generic character, is contradicted by the same author's fig. 12 of *F. japonicum*, which shows 48 tentacles corresponding to septal cycles I.—IV., while cycle V. is also stated to be present. From this figure the presumption is that the septa and mesenteries alternate in this species as in *F. rubrum.* A figure of a longitudinal section of *F. alabastrum* shows three orders of mesenteries, attached (1) to the lower edge of the stomodoeum, (2) to the junction of stomodoeum and peristome, and (3) to the peristome near the bases of the tentacles, an arrangement similar to that found in both *F. rubrum* and *F. pavoninum.* The ova occur on all the mesenteries according to size, but are not represented in any determinate series, being scattered all over the lower parts of the mesenteries.

In *F. anthophyllum*, according to Lacaze Duthiers (*loc. cit.*), the tentacles and septa correspond in number. The mesenteries likewise are of the same number, and the arrangement accordingly is such that half the septa and tentacles are exocoelic. The testes consist of polyhedral masses, and the ovaries each of 4-5 ova placed in a row, a similar arrangement to *F. rubrum.*

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* "Evolution du Polypier du *Flabellum anthophyllum*," *Arch. de Zool. exp. et gén.*, 3e ser., t II., p. 445 et seq. (1894).

† Challenger Report on Corals, pp. 162-4, pl. xvi., figs. 10-12 (1882).

In his description of *F. patagonichum* Fowler* has woefully confused theca and epitheca, and septal trabeculae with columella. There are 4 orders of septa, all entocoelic and with tentacles. Mesenteries I. and II. (on either side of septa I. and II.) are alone attached to the stomodoeum, while in *F. rubrum* and *F. pavoninum* I.-III. are so attached. The stomodoeum is stated to have well marked gonidial grooves and "Through periphery of mouth-disc (peristome) protrude the acontia" through "definite openings." †

The above short *resumé* of our present knowledge of the anatomy of the polyps shows that the differences in the corallites are correlated with differences in the polyps. For a thoroughly scientific classification a knowledge of the polyp anatomy is essential. In the case of *F. rubrum* it confirms the diagnosis of the species and its variations, which was first studied on the dried coralla alone. If there is so much specific variability in the polyps of one genus as implied by the above, why not in all genera. Of the specifically variable polyp characters I would only draw further attention to the number of mesenteries meeting the stomodoeum and depending from it. My experience in *F. rubrum* is that this character is much less variable than any founded on numbers of septa of different sizes, etc. Indeed, it seems to me to be probably one likely to be of no inconsiderable value for separating our species from one another.

The importance of the development of the corallite lies in the fact that the regular 6-system radial arrangement of septa is found dominating the early stages, whereas with growth the calicle becomes elongated, bilaterally symmetrical with 20—24 equal septa. However the mesenteries may develop, the septa in all genera of Madreporaria support Milne-Edwards and Haime's views on radial symmetry being primitive in the group; that in effect the group was evolved from forms with pronounced radial symmetry.

The minute anatomy in different polyps varies enormously in accordance with the state of the polyp so far as feeding is concerned. In one polyp I found large numbers of a Foraminiferan, which Mr. J. J. Lister has referred to the genus

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* "The Anatomy of the Madreporaria," *Quart. Jour. Micro. Sci.*, vol. XXV., p. 577, pl. XL. (1885.)

† Fowler's description of anatomical details is meagre and the figures are diagrammatical. According to Fowler's account there are a few points of difference from *F. rubrum*. The mesenterial filaments are said to be found on the whole free edges of the mesenteries, even below where the ova are situated and the acontia given off. The oblique exccoelic muscles of the mesenteries—presumably traversing the structureless lamella—become (according to Fowler) the external longitudinal coat of the tentacles, and the longitudinal muscles of the mesenteries the circular fibres of the same. The acontia are said to be set with both tentacular and mesenterial nematocysts, while Fowler's figure of the section of one is peculiar in only showing a single thread-cell.

Operculina, and in others quantities of diatoms and algal growths. Where such are present the stomodoeal epithelium and the mesenterial filaments are reduced in size, the granular gland cells having sunk down, after secretion, towards the structureless lamella, and not showing the swollen out appearance seen in the figures. Every stage of ingestion and protusion of foreign matter could be seen in the swollen out endodermal bases of the mesenterial filaments, but elsewhere was not observed. The storing up of round, fat globules, not only in the endoderm at the bases of the mesenterial filaments, but anywhere in the endoderm, indicates that there must be a true digestion—due to the secretion of the gland cells of the mesenterial filaments—and absorption over the whole endoderm, as well as ingestion at the bases of the filaments. No absorption would, however, seem to occur in the mesenterial filaments, the concentration of fat, etc., in the endoderm at their bases being correlated with this.*

It is unnecessary to repeat my views on the layers in the Actinozoon polyps.† There can be no doubt, if the descriptions and figures be carefully examined, that the external, tentacular, peristomial, stomodoeal and mesenterial filament epithelia of *F. rubrum* all belong to the same layer. The formation of the corallum, the apparent protandry of the generative organs, and the presence of a distinct canal leading through the endoderm to the ova have already been considered, and require no further reference here.

The post-larval stage in the development of the polyp, which I have described above, is remarkable in many ways. I have been over the anatomy many times, and I cannot see that there is or can be any error in the account of its gross anatomy. The main point of interest, a mouth almost as large as that of the calicle, I have found also in two younger stages, not however so well preserved. Such a stage is absolutely without parallel among the described developments of the Actinozoon polyps, which, from the first, have well-defined stomodoea. In the adult the stomodoeal wall is ridged over the attachments of the mesenteries, and in the stage described the mesenteries present are only such as in the adult depend from the stomodoeum. *The only logical method of conceiving the formation of the stomodoeum 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*

* *Vide* "La Digestion chez les Actinies," by Victor Willem, *Bull. Sc. Médecine de Gand*, p. 295 (1892), and p. 375 of my paper "On the Anatomy of a Supposed New Species of Coenopsammia from Lifu," *Willey's Zool. Results*, pp. 357-380 (1899).

† *Loc. cit.* p. 374-5.

together, assisted by the downgrowth of the body-wall form the stomodoeum. The latter increases in depth with the size of the polyp, and the process probably goes on to some extent throughout life.

It is necessary to lay strong emphasis on the fact that *this is a larval development.** The organs are functional, and the conditions of life are not quite the same as in the adult. All the organs are correlated with one another; the endoderm is digestive and everywhere ingests foreign particles.† In this stage there is a necessity for a rapid growth, for an abundant nutrition, which might he assisted by the widely open mouth. Perhaps there is no need of protection, so that the tentacles only appear later on to guard the polyp when it is producing generative organs. On the other hand the endodermal nematocysts are possibly now or were in the evolution of these forms at one time functional.

If a large number of the madreporaria be examined, I believe that in a not inconsiderable number a corresponding development will be found. The condition was probably brought about by an enormous enlargement of the gastropore in the first place, the stomodoeum then becoming of secondary formation. In the adult the stomodoeum is probably a definite morphological entity. Primitively it arises as an inpushing or ingrowth of the ectoderm at a very early stage of development. The adult stage is necessary to the organism. The variation has been produced and perpetuated in the young stage alone. This larva cannot be held to indicate in any way an ancestral stage of structure that has been hit upon by natural selection. It shows rather a variation on an entirely new line. The case is one which markedly emphasises the fact that the tendency in development is "to directness and abbreviation and to the omission of ancestral stages of structure," which here is as true for larval as for embryonic development.

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* *Vide* "On the Law of Development commonly known as Von Baer's Law, and on the Significance of Ancestral Rudiments in Embryonic Development" by Adam Sedgwick, *Quart. Jour. Micro. Sci.*, vol. 36, and *Studies Morph. Lab. Camb.*, vol. vi., pp. 75-92 (1896).

† Perhaps the n matocysts in the endoderm at the edges of the tentacles were once functional at this stage in protecting the tissues of the polyp.

EXPLANATION OF PLATES I-IV.

All the figures refer to *Flabellum rubrum* unless otherwise stated. *ect.* Ectoderm. *c. ect.* Calicoblast ectoderm. *end.* Endoderm. *s. l.* Structureless lamella. *n. l.* Nervous layer of the ectoderm. *t. n.* Tentacular nematocysts. *end. n.* Reduced endodermal nematocysts. *m. g. c.* Mucous gland cells. *g. g. c.* Granular gland cells. *f. b.* Ingested foreign bodies. *f. g.* Fat globules. *m. f.* Muscular fibres.

Fig. 1. Section of the calicoblastic ectoderm on the side of a septum about 1 mm. inside the edge against the axial fossa.

Fig. 2. Section of the attachment of the body-wall to the corallum at the base of a mesentery.

Fig. 3. Section of the body-wall over a septum near its upper free edge.

Fig. 4. Section of the ectoderm of the external body-wall. (The section is that of a knob caused by the contraction of the polyp. It serves to show the constituents of the layer, but does not give in any way a real idea of its true appearance. It was chosen only after a prolonged search, no other section in this position showing more than 1 nerve cell and 2 or 3 granular gland cells. The vacuolated nature of the layer does not appear).

Fig. 5. Section through a battery of nematocysts on a partially retracted tentacle.

Fig. 6. Section through the ectoderm of the stomodoeal wall over the attachment of a mesentery.

Fig. 7. Section of the stomodoeal wall between the attachments of two mesenteries.

Fig. 8. Transverse section of the mesenterial filament and edge of a primary mesentery at about the middle of its course. (For the sake of clearness no tone has been placed over the structureless lamella).

Fig. 9. Reduced endodermal nematocyst, reconstructed from a series of sections.

Figs. 10-15. Various stages in the development of the corallite. The numerals where present refer to the cycles of the septa.

Fig. 16. Scar of a broken-off corallite. The dark lines in the septa are depressions, due to the eating away of the corallum along the central "dark lines" of the septa.

Fig. 17. Side view of a mesentery from a polyp of about 20 mm. in length, showing the coiled loop of the mesenterial filament, generative mass and arrangement of the muscular fibres. The filament is reversed so that the upper end is actually the more deeply situated in the corallum. The sperm acini contain ripe spermatozoa and on the inner side are seen three ova. To the right of the figure the clumped attachments of the muscular fibres to the corallum are seen.

Figs. 18-21. Views of four South African specimens of *F. pavoninum* from the side to show the general shape, accretion lines, wings, etc.

Figs. 22-34. Various corallites of *F. rubrum* from side view to show the variations in the shape of the corallum.

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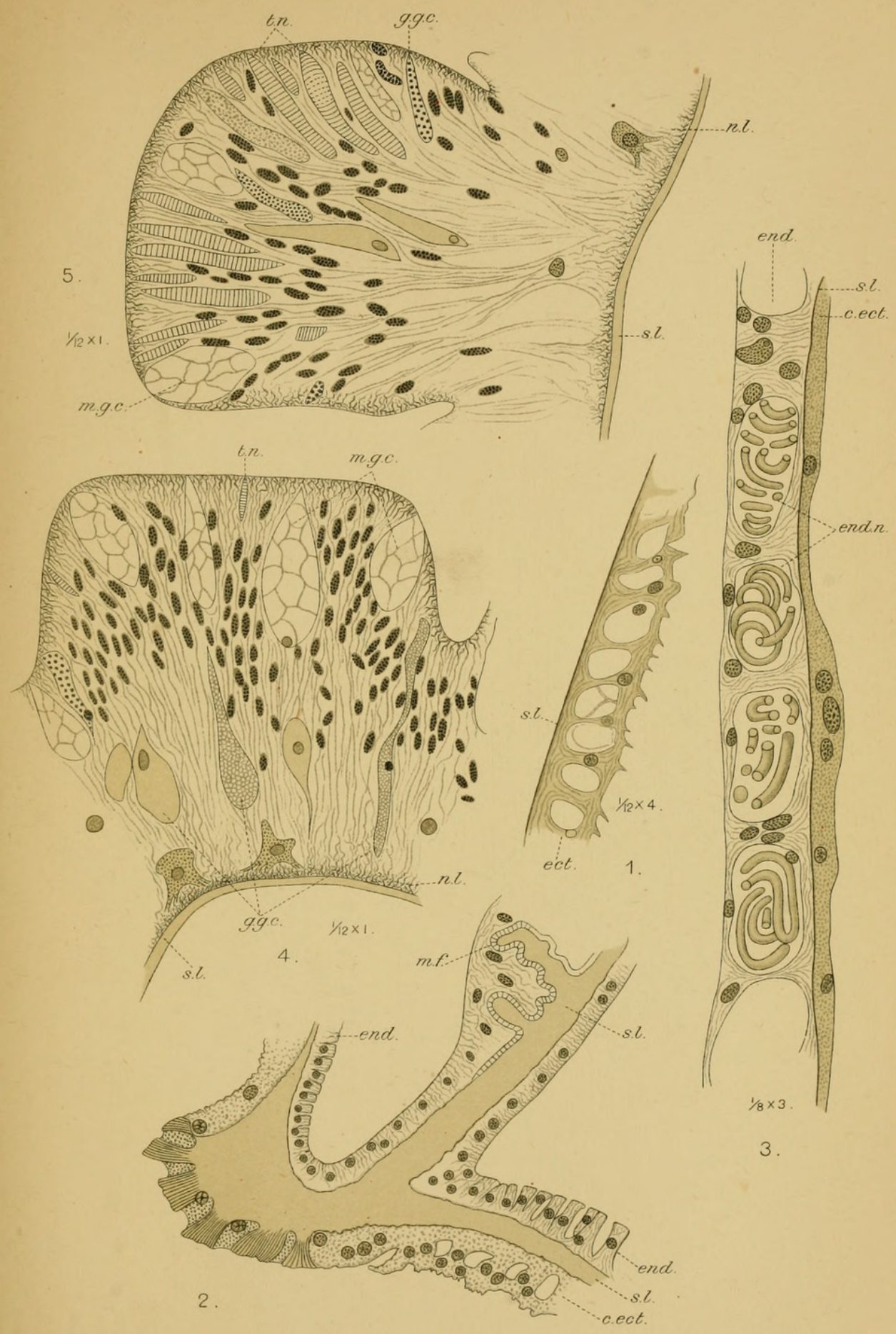
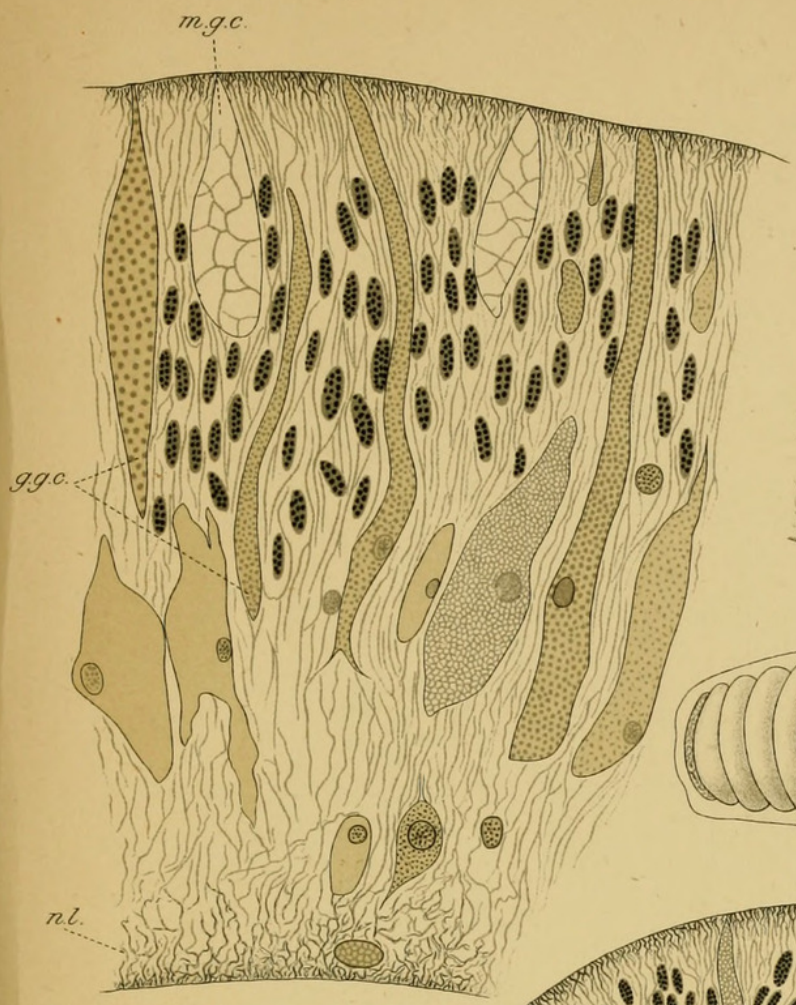


STANLEY GARDINER - FLABELLUM.

E. Wilson del. et lith. Cambridge.



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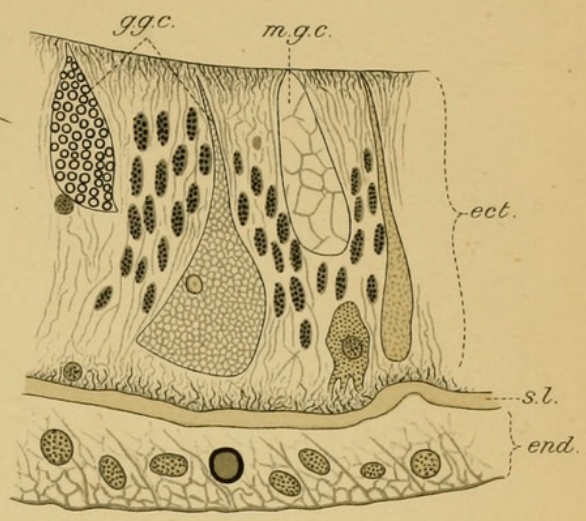

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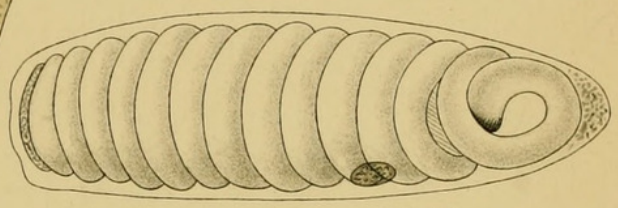

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1/12 × 1. 8.

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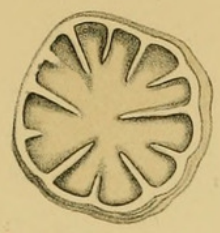
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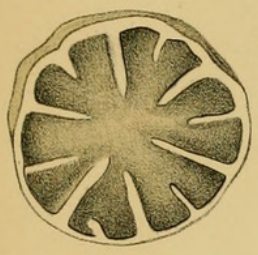
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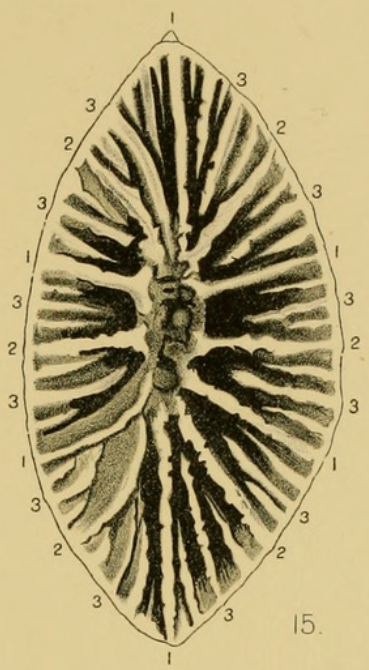
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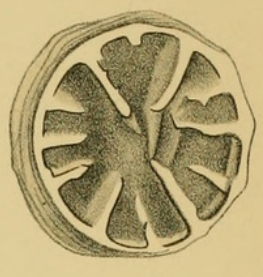
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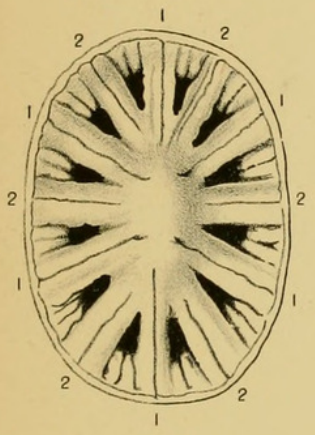
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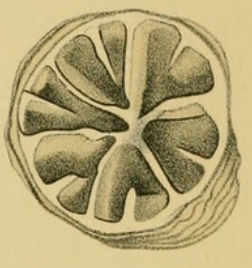
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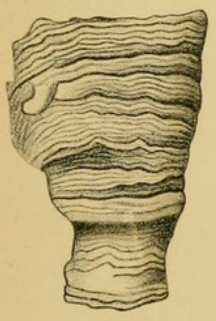
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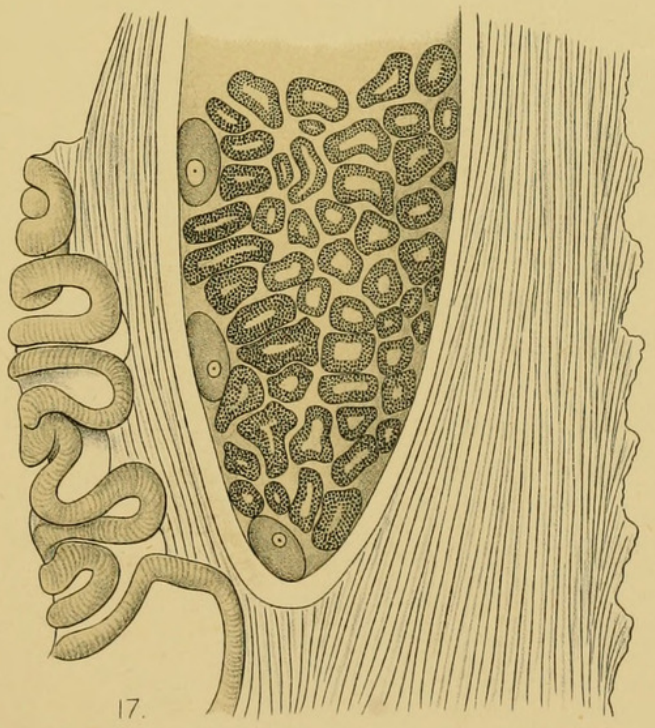
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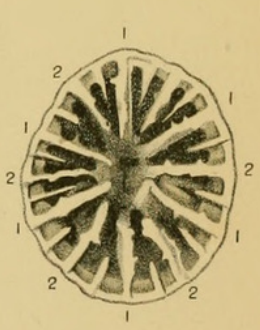
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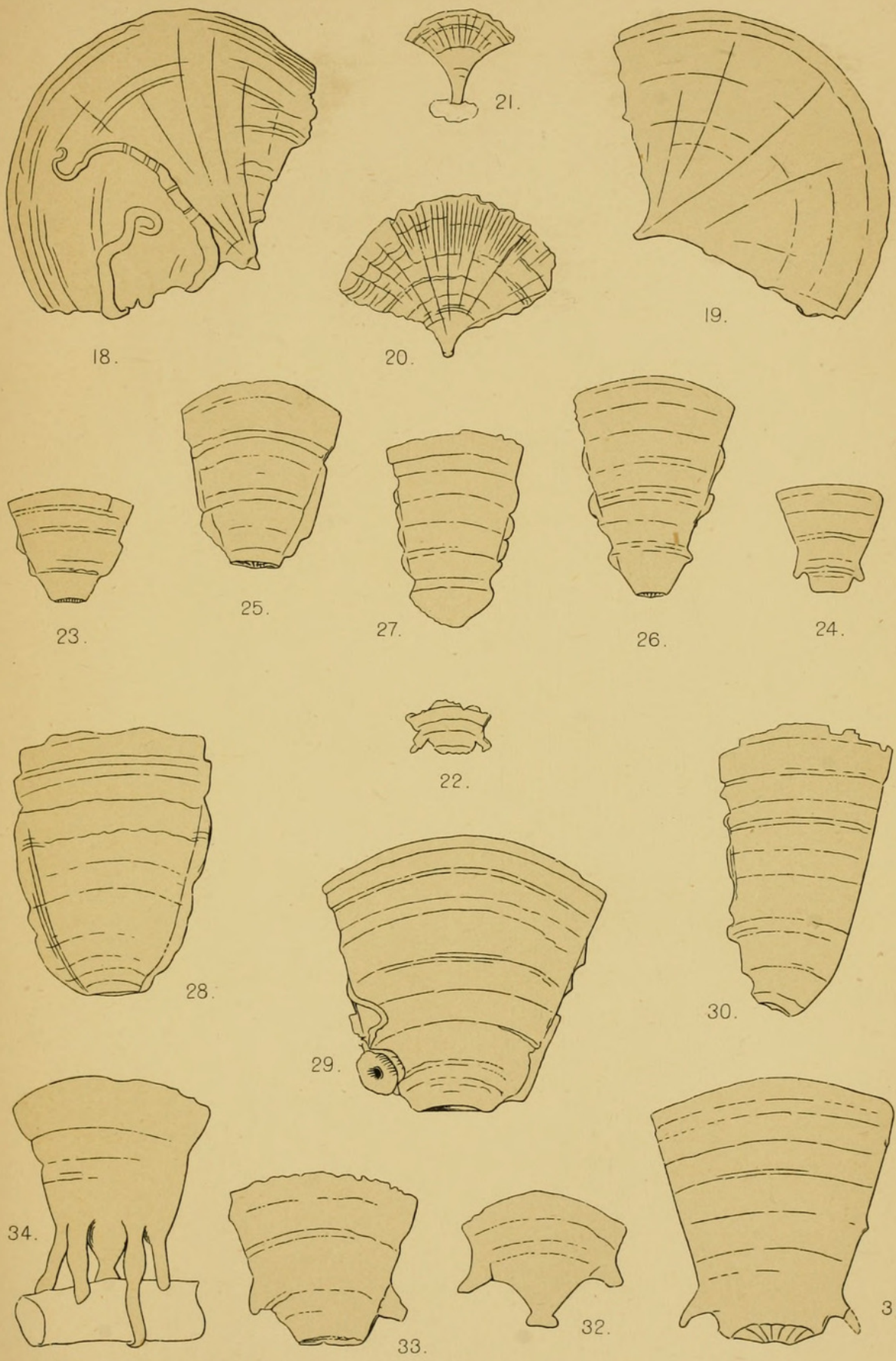

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Gardiner, J. Stanley. 1902. "South African Corals of the Genus Flabellum, with an account of their Anatomy and Development." *Marine investigations in South Africa* 2, 115–154. https://doi.org/10.5962/p.366551.

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