STUDIES ON THE PHYSIOLOGY OF CORALS.

I. FEEDING MECHANISMS AND FOOD.

BY

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WITH THIRTY-FOUR TEXT-FIGURES AND TWO PLATES.

GENERAL INTRODUCTION.

Few subjects of such obvious zoological importance are so obscure as the nutrition of corals and the significance of their zooxanthellæ. Until these problems are fully elucidated, knowledge of the fundamental conditions controlling the formation of coral reefs must remain imperfect. Necessarily, therefore, work along these lines formed an important part of the programme of the Expedition. The work carried out was so extensive and so varied in character that I have judged it best to present the results in a series of six papers, each complete in itself. The results of the various researches and of those of other members of the Expedition which throw light on the problems concerned will be discussed in a final, seventh, paper, when their bearings upon one another will be pointed out and final conclusions reached. The papers are presented in the logical sequence: Feeding mechanisms and food; digestive enzymes; structure of the gut, absorption, storage and excretion; structure, distribution and physiology of the zooxanthellæ; experiments dealing with zooxanthellæ as a possible source of food for the corals; production of oxygen by the zooxanthellæ and its relation to the respiratory processes of the corals.

While this work was carried out under my general direction, it was only rendered possible on the scale on which it is here presented by the constant assistance of Mrs. Yonge and Mr. A. G. Nicholls, whose names appear as collaborators in a number of the papers, but who assisted in a greater or less degree in all stages of the work. Much advice was also received from other members of the Expedition, notably from Mr. A. P. Orr, and considerable practical help from Mr. G. W. Otter. After my departure from Australia I was able to carry out some further experiments, confirming and extending previous work, at the Marine Laboratory of the University of Hawaii, at Honolulu. This was made possible only by financial assistance provided by the Balfour Managers and by the Bernice P. Bishop Museum, Honolulu, to which bodies, and to Prof. C. H. Edmondson, the Director of the Marine Laboratory, I have pleasure in here recording my gratitude. Since my

return to the Plymouth Laboratory I have been able to carry out a little further work of a confirmatory character on British representatives of the Madreporaria, Alcyonaria and Actiniaria.

CONTENTS.

1. INTRODUCTION.

So little work has been done on the feeding of corals, such discordant conclusions drawn from the results obtained, and so much emphasis laid on the supposed inability of some, if not all, genera of corals to capture living prey, that the fullest possible survey of the manner of feeding of corals and the type of food which they are capable of securing was clearly of primary importance. With this purpose in view the feeding mechanisms of as many genera as could be obtained were examined. Many came from Low Isles Reef, others as a result of dredging operations within the Barrier, others again from Maer (Murray) Island in the Torres Strait, from the Island of Oahu (Hawaii) and from Plymouth. In every case the locality from which the coral was obtained is noted. I have to thank Prof. G. Matthai for naming many of the corals. Most of the others were identified by reference to the descriptions and figures of Vaughan (1918). Help was also obtained

from a named collection of duplicate Barrier Reef corals received from the British Museum (Natural History).

Prof. T. Wayland Vaughan has very kindly given me full details of his notes on the feeding of West Indian corals, a condensed account of which he published in 1912. Relevant matter from these notes is introduced into the text at the appropriate places, thus enabling the survey of feeding mechanisms to embrace Atlantic as well as Indo-Pacific genera.

2. LITERATURE.

The literature on the mode of feeding of corals and on their food is very scanty. Consisting as it does of work on a few scattered genera, the papers concerned will be most conveniently referred to when discussing my own experiments on allied genera or species. A good review of the subject is provided by Boschma (1925*b*).

3. MATERIAL AND METHODS.

Corals were obtained from Low Isles Reef by collecting at low tide or by the use of the diving helmet. Some collected during the various dredging operations were kept alive until they could be examined. Since the majority of corals do not expand in daylight, considerable difficulties were experienced in studying the behaviour of the expanded polyps. The corals were kept in large glass tanks containing sea-water in the aquarium behind the laboratory until the evening, when they were brought into the laboratory and examined under the binocular dissecting microscope. This necessitated the use of a powerful light concentrated on the animal and observations had to be made very quickly, and often repeated trials were necessary before the desired information was obtained. There is thus no doubt that the efficiency of coral polyps under natural conditions as securers of living prey is much greater than is indicated by the experiments carried out under these abnormal conditions. Corals were fed with freshly collected plankton, usually obtained by Mr. A. G. Nicholls by tow-netting in the anchorage after dark, and with pieces of mollusc meat. To determine the direction of beat of the cilia, carmine and, more usually, the finest grade of carborundum powder were employed. As indicated in the introduction, every effort was made to examine species of all the available genera. The illustrations are essentially diagrammatic, though in all cases drawn approximately to scale.

4. CLASSIFICATION ADOPTED.

The work of the physiologist and experimentalist on corals is not rendered easier by the uncertainty which exists as to the classification of certain groups of corals. In this present work, in particular, the results have to be presented in rational systematic form, and the classification used by Vaughan (1907, 1918) and Hoffmeister (1925) is adopted. As will be noted later, this classification (based entirely on the form of the skeleton) does agree closely with the observed differences in the nature and behaviour of the living polyps.

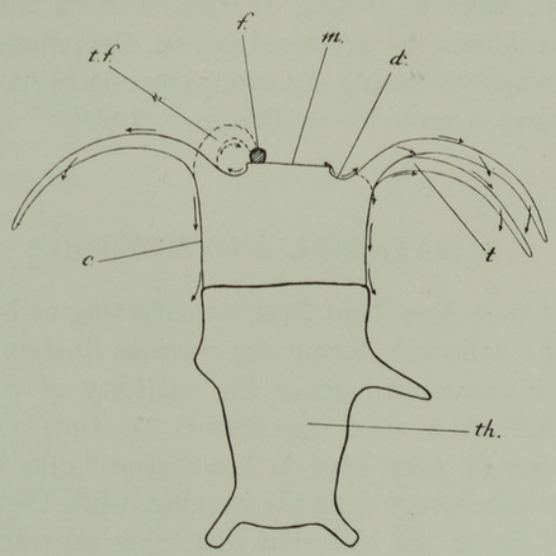
5. REVIEW OF FEEDING MECHANISMS.*

A. MADREPORARIA.

I. Flabellidae.

Flabellum rubrum.—Dredged 19 fathoms, near Lizard Island.

Polyp.—This is capable of considerable expansion above the calix; thus in the specimen shown in text-fig. 1, where the skeleton was 2·1 cm. long, the polyp could be raised 1·2 cm. above it, and the maximum expansion of the tentacles was 3·2 cm. The polyp is exceptionally sensitive. Seen from above the disc is oval, the large mouth



Text-fig. 1.—*Flabellum rubrum*, viewed laterally. ×1½. Arrows indicate direction of ciliary currents. For explanation of letters, see footnote.*

forming a slit along the longer axis, and being 1·2 cm. long in an animal with a disc 2·1 cm. wide. The tentacles are arranged in two rows, the inner somewhat the larger, and numbering about 24, and the outer numbering 36. They are very thin and transparent and covered with opaque spots.

Calix.—The septa are comparatively low and the columella small, a considerable cavity being thus formed.

Ciliary Currents.—Material is carried outward from the surface of the disc, and thence between the tentacles and down the column. Ciliation of the tentacles is slight, but material is carried to the tip on the inner side and outwards laterally, in both cases being speedily rejected.

Seizure of Food.—Meat is seized firmly by the tentacles the moment it touches them, the tentacle then immediately bending inward and passing the food to the mouth, which opens and swallows it. The entire ring of tentacles, which normally droop downward, turn upward and a little inward as soon as food touches any one of them. Both

* The letters given below are used frequently in the figures. Their meanings are as follows: *c.*, column; *ce.*, coelenteron; *cs.*, coenosarc; *d.*, disc; *e.z.*, edge-zone; *f.*, food mass; *m.*, mouth; *m.f.* mesenterial filament; *o.*, oral cone; *s.*, septum; *st.*, stomodaeum; *t.*, tentacle; *t.f.*, tentacle contracted after taking food; *th.*, theca; *w.*, waste matter.

living *Sagitta* and Copepoda are seized immediately they touch the tentacles and are carried to the mouth.

Remarks.—*Flabellum* possesses a highly efficient feeding mechanism for capturing living animal prey, and ciliary currents for removing waste material from the surface. The great powers of expansion of the polyp and depth of the " cup " result in the formation of a large coelenteric cavity, into which large prey can be passed and there digested.

II. Caryophylliidae.

Caryophyllia smithii.—Dredged 10 to 20 fathoms, off Stoke Point, near Plymouth.

This species is too well known to require description. Its mode of feeding has been examined by Carlgren (1905). Animal prey or pieces of meat are seized firmly by the tentacles and passed to the mouth. The cilia on the disc beat outwards except in the inner region round the mouth, where they beat inwards. Particles removed from the disc are carried between the bases of the tentacles and down the column. Carlgren states that the tentacles are not ciliated ; my own observations fail to confirm this, but ciliation is certainly extremely sparse, or else the beat exceptionally weak. The polyp expands above the cup to a height almost as great as that of the skeleton beneath, and the tentacles elongate until as long as, or longer than, the diameter of the disc.

Remarks.—Here again the polyp is very well adapted for the seizure of animal prey, the coelenteric cavity large, and ciliary currents, not well developed, dispose of waste material.

III. Oculinidae.

Acrhelia horrescens.—Fringing reef, Maer Island.

The structure and behaviour of the polyp is identical with that of *Galaxea* (p. 24) and description is therefore unnecessary, particularly in view of the possibility that this genus should properly be placed in the Orbicellidae.

Atlantic Species.

Oculina diffusa.—Tortugas.

> Prof. Vaughan, in his notes, states that the polyp has two rows of tentacles. Material is removed from the surface of the colony by ciliary activity, meat is seized and swallowed, but diatoms refused.

Lophohelia prolifera.—*ca.* 200 fathoms, Trondhjem Fjord, Norway.

This species possesses a large polyp capable of great expansion above the calix, and also a double ring of long tentacles. In 1926 I observed the readiness with which meat is seized and swallowed, but no observations were made on the ciliary currents.

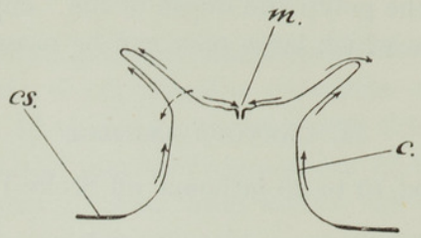
IV. Seriatoporidae.

Seriatopora hystrix.—Fringing reef, Maer Island.

Polyp.—When expanded there is a short column with a single row of 12 short tentacles, as shown in text-fig. 2, though the latter are probably capable of much greater

expansion. The disc is relatively large with a central mouth at the summit of a small oral cone.

Calix.—The cavity is almost completely blocked by the six well-developed septa and the thick columella.



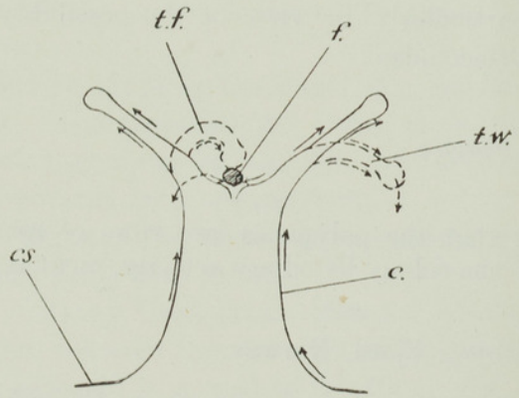
Text-fig. 2.—*Seriatopora hystrix*, vertical section. ×16. For explanation of letters, see p. 16.

Ciliary Currents.—Material passes *up* the column, and up both inner and outer sides of the tentacles, to be rejected at the tips if useless. Cilia on disc *all* beat towards the mouth, into which carmine or carborundum powder is passed to be later rejected. Cilia between bases of tentacles beat outwards. Material is quickly removed from the surface of the colony.

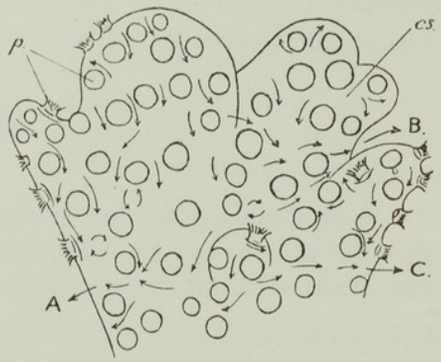
Seizure of Food.—Meat is taken by the tentacles and passed to the mouth, but it is difficult to obtain normal reactions in the laboratory.

Pocillopora bulbosa.—Low Isles reef.

Polyp.—Very similar to that of *Seriatopora* but taller, expanding readily even in daylight, and with 12 long, rather blunt-ended tentacles in a single row (see text-fig. 3). The whole polyp is very sensitive, frequently closing up immediately when a little carborundum is dropped upon it.



Text-fig. 3.



Text-fig. 4.

Text-fig. 3.—*Pocillopora bulbosa*, vertical section. × 16. *t.w.*, tentacle bent outwards so as to dispose of waste matter. For other lettering, see p. 16.

Text-fig. 4.—*Pocillopora bulbosa*, surface view of terminal portion of branch. ×4. A., B., C., regions where waste material removed from surface; *p.*, polyps. For other lettering, see p. 16.

Calix.—The septa and columella being rudimentary or obsolete, the cavity is relatively large.

Ciliary Currents.—These are identical in nature with those of *Seriatopora*, and are shown in text-figs. 3 and 4. The tentacles bend outward to allow waste matter passed

to their tips to be dropped off on to the surface of the colony, whence they are carried away by very rapid currents, as indicated in text-fig. 4, which shows the side of a terminal branch. Material is thrown off the colony at definite places, three of which A., B. and C., are present in the portion figured.

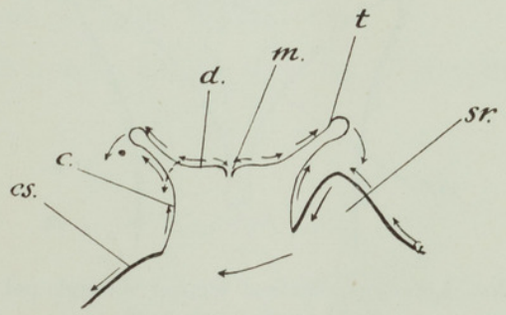
Seizure of Food.—Meat is taken by the tentacles and passed to the mouth. Living plankton is captured at once by polyps much smaller than itself. Thus a crab Zoea three times as long as the diameter of a polyp was secured, the tip of the abdomen being swallowed and, in spite of the continuous struggles of the prey, it was gradually pulled into the coelenteron, the polyp expanding to a relatively great size in the process. In the same way small *Sagitta* were captured and swallowed in about thirty seconds. Copepoda and a variety of small planktonic crustacea were captured immediately they touched the polyps and passed by the tentacles to the mouth, which has an almost indefinite power of expansion. Vegetable matter, if swallowed, was invariably quickly rejected.

Remarks.—In spite of its small size the polyp of *Pocillopora* (and presumably under natural conditions also that of *Seriatopora*) is capable of capturing and swallowing comparatively large animal prey. A large additional collecting surface is provided by the coenosarc, since material there collected passes up the column and so to the tentacles, which convey it to the mouth if of food value, while all waste material is quickly removed from the surface of the colony. Since the small disc and polyp can contract very quickly, there is no need for any ciliary currents to remove waste matter from the disc.

V. Stylophoridae.

Stylophora pistillata.—Low Isles reef.

Polyp.—Very similar to *Seriatopora* and *Pocillopora*, but with a shorter column than either, having a height not greater, under normal conditions, than one-third the diameter of the disc and tentacles. The tentacles are short with knobbed ends, 12 in number and in a single row. The disc is round, with a small mouth on the summit of an oral cone.



Text-fig. 5.—*Stylophora pistillata*, vertical section. ×16. *sr*, spur on skeleton above polyp. For other lettering, see p. 16.

Calix.—The primary septa are thick and there is a well-developed columella, the cavity being comparatively small. On the side above the polyp is a small projecting spur (*sr.*, text-fig. 5).

Ciliary Currents.—Exactly as in *Seriatopora* and *Pocillopora*, but material, if passed to the mouth by ciliary currents, is *not* invariably swallowed. If useless, *e. g.* carborundum, carmine or vegetable matter, it collects into a ball at the summit of the

oral cone, until large enough to be caught by the outward beating cilia on the sides of the tentacles, which quickly dispose of it. It seems possible that the presence of the spur above the polyp is of assistance by deflecting waste matter completely over the polyp beneath.

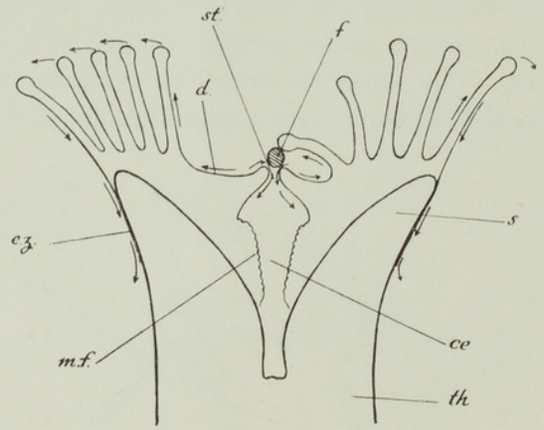
Seizure of Food.—Both meat and zooplankton are captured by the tentacles, conveyed to the mouth and swallowed slowly. On one occasion when meat was given to one polyp four neighbouring polyps were seen to lean towards it, mesenterial filaments were projected from the mouths of all of them, and these extended towards the food mass and finally wrapped round it.

Remarks.—The nature and behaviour of the polyp is very similar to that of the polyps of the Seriatoporidae. It appears, however, that *Stylophora* has not the same power of swallowing large food masses as *Pocillopora*, presumably because its powers of expansion are much less ; also there is a smaller cavity in the calix. To overcome this disadvantage the mesenterial filaments are extended through the mouth.

VI. Eusmiliidae.

Euphyllia glabrescens.—Batt reef.

Polyp.—Very large, and only capable of partial retraction. The tentacles are very numerous, consisting of some four or five rows (see text-fig. 6), all approximately the same size, and occupying so much of the upper side of the polyp that the central disc is comparatively small and usually obscured, except when the polyp is fully expanded and the tentacles bent outwards. Tissue covers the upper region of the theca ; this is the edge-zone tissue (*e.z.*).



Text-fig. 6.—*Euphyllia glabrescens*, vertical section through polyp and calix. × 2½.
For lettering, see p. 16.

Calix.—Except during the process of division, the calices are separated from one another, though in life the whole surface of the colony is covered with a mass of tentacles and the individual polyps and underlying calices cannot be distinguished. The septa, though prominent, leave a large cavity, which is unoccupied by a columella, as shown in text-fig. 6.

Ciliary Currents.—On the disc, except for the region immediately around the oral cone, the cilia beat outwards. On the tentacles currents pass up the inner sides and down

the outer, and currents also pass down the edge-zone. Material in process of removal is conveyed from the disc, up the inner row of tentacles, and thence is passed over the tips of the tentacles to be discarded from the outermost row. Should food be dropped on to the disc the same thing happens, but when it reaches the tip of the inner tentacles, these curl over and convey it to the mouth.

Seizure of Food.—Meat is immediately taken by the tentacles, which then contract, hiding it. The tentacles bend towards the mouth, which inclines towards them, the mouth opening at the same time and exposing the downward beating cilia which line the stomodaeum. As in all corals, much mucus is extruded during feeding, and inedible material, such as carmine, etc., may be caught in these mucus strings and passed into the mouth. Vegetable matter and starch are rejected even if placed directly on the mouth, which contracts downward, and the material is carried away in the manner described under "Ciliary Currents." A piece of meat placed on the mouth causes it to open and the meat is slowly drawn in by ciliary activity, the mouth finally shutting firmly over it. Much excretory and indigestible matter is rejected through the mouth within twenty-four hours after feeding.

Remarks.—The large size of the polyp and the numerous tentacles of *Euphyllia* enable it to capture large prey, which can be taken into the large coelenteron.

Atlantic Species.

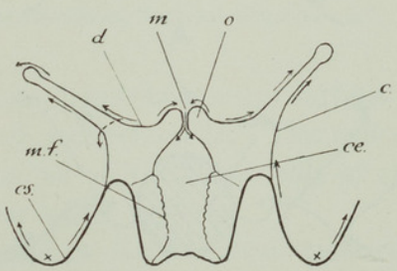
Eusmilia aspera.—Tortugas.

From Prof. Vaughan's notes, it appears that the polyp of this coral is very unlike *Euphyllia*, possessing small knobbed tentacles, "barely visible to the naked eye," and consisting of three rows with an incomplete fourth row. Meat and plankton were taken in the usual way, and waste material removed from the surface by ciliary currents. Diatoms were refused.

VII. Orbicellidae.

Leptastrea agassizi.—Island of Oahu, Waikiki Reef.

Polyp.—Round, with a short column (text-fig. 7) never observed higher than about



Text-fig. 7.—*Leptastrea agassizi*, vertical section through polyp and calix. × 8. *x.*, site of ciliary currents, removing material from the surface of the colony in a plane vertical to that of the section. For other lettering, see p. 16.

1 mm. in the aquarium, though it probably expands more in nature. Tentacles in a single row, 24 to 28 in number; those over the primary septa bend a little inward, at any rate when the polyp is partially expanded, and between them are usually three rather smaller

and outwardly directed tentacles. They are capable, even in the laboratory, of expanding to about 5 mm. The disc is round and the mouth a transverse slit at the top of a comparatively large oral cone.

Calix.—Raised 1 to 2 mm. above the surface of the coenosteum. The primary septa are slightly exsert, but do not project far into the cavity, which is somewhat shallow owing to the presence of a low " false " columella.

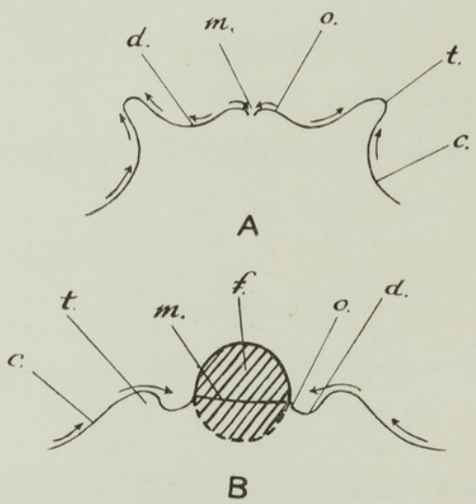
Ciliary Currents.—Except around the oral cone, the cilia on the disc beat outwards, the currents being continued between the tentacles and up their inner sides. Material is carried up the column and up the outer side of the tentacles. The coenosarc, as always, is ciliated, but material is not removed from it readily, but embedded in mucus and raised clear of the surface. There is practically no passage for material between the calices, everything being conveyed up to the surmounting polyps.

Seizure of Food.—Meat taken at once and very tenaciously by the tentacles, the polyp at the same time contracting, the food being conveyed to the mouth and immediately swallowed. The mouth can extend very greatly, enfolding or " flowing over " the relatively large pieces of meat.

Remarks.—*Leptastrea* has a well-developed polyp capable of capturing animal prey with ease, material caught on the surface of the coenosarc being also passed to the polyps by ciliary activity. The removal of waste material from the surface, after it has been lifted clear, is presumably by water movements—a satisfactory mechanism in the case of this coral which lives on the wave-swept surface of the reefs.

Cyphastrea chalcidicum.—Low Isles reef.

Polyp.—Never observed well expanded, it possesses a round disc and 24 short tentacles, the whole forming a flat plate as shown in text-fig. 8A.



Text-fig. 8.—*Cyphastrea chalcidicum*, vertical section. × 20. A, normal polyp ; B, polyp when swallowing food. For lettering, see p. 16.

Calix.—This is slightly raised above the general surface of the coenosteum, the cavity being almost obscured by the prominent primary septa. A columella is present.

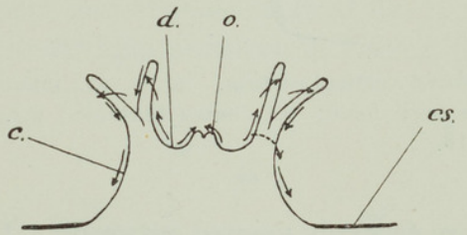
Ciliary Currents.—Disposed exactly as in *Leptastrea*, but material is carried quickly off the disc and over the tentacles and thence off the coenosarc at very great speed. The calices not being placed so close together as in *Leptastrea* there is a clear passage for waste material between them.

Seizure of Food.—Meat is not taken with any great readiness by the tentacles in the semi-contracted state they invariably present in the laboratory. When seized it is passed to the mouth which, as shown in text-fig. 8B, may expand greatly till it occupies more than half the normal area of the disc, the food being swallowed very quickly, the disc sinking while the oral cone rises, and the mouth, as in *Leptastrea*, enfolds the food. During this process the contracted tentacles bend inwards as shown in the figure, and inedible matter, such as carborundum, may then pass directly up the column, along the tentacles and over the small, contracted disc to the mouth, into which it passes with the food. This was at first thought to be due to a reversal of the ciliary current. Any carborundum not swallowed with the food is removed as soon as the act of swallowing is completed and the disc regains its normal shape, when the outwardly beating cilia are again exposed.

Remarks.—Conditions approximate closely to those described in *Leptastrea*, but there is a more efficient means of clearing the surface of the colony by means of ciliary currents.

Echinopora lamellosa.—Low Isles reef.

Polyp.—Round, with a column of medium height when fully expanded, as shown in text-fig. 9. Usually 24 tentacles, arranged in two rows and capable of considerable extension. Mouth on the summit of a prominent oral cone.



Text-fig. 9—*Echinopora lamellosa*, vertical section. ×7. For lettering, see p. 16.

Calix.—Raised about 2 mm. above the general surface, the cavity occupied by three cycles of septa and a well-developed columella. The calices are widely but irregularly spaced out and are more numerous on the upper side of the thin skeleton, being often absent altogether from the under side.

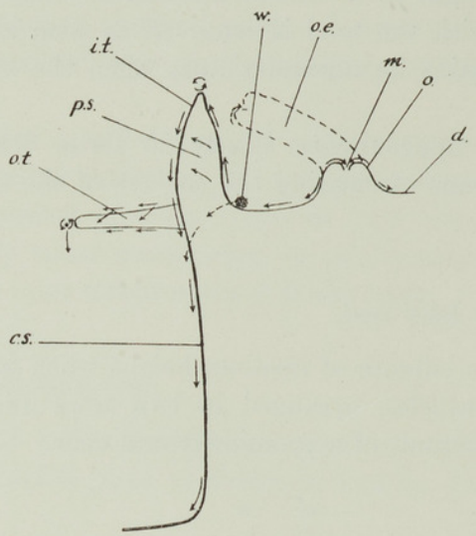
Ciliary Currents.—The cilia on the disc beat outwards except in the region of the oral cone ; on the tentacles material is carried upward on the inner sides, and downward on the outer, the latter current being continued down the side of the column. Over the general surface of the coenosarc are cilia which carry away material very rapidly.

Seizure of Food.—Meat is taken with the greatest readiness by the tentacles, which at once bend inward over the mouth, the entire polyp contracting at the same time. A little later the polyp expands again to its maximum extent, and adjacent polyps, which may originally have been contracted, also expand.

Remarks.—The polyps are comparatively large and well disposed for the capture of living prey, and this fact, combined with the danger from the falling of silt on the wide horizontal lamella which composes the skeleton, is probably responsible for the differences between *Echinopora* and both *Leptastrea* and *Cyphastrea* in the beat of the cilia on the column.

Galaxea fascicularis.—Low Isles reef.

Polyp.—Round or oval in cross-section. It is difficult to distinguish the extent of the column even when the polyp is fully expanded, owing to the shape of the calix. A large, exposed disc with a prominent oral cone is surrounded by a ring of 24 tentacles. The 6 tentacles corresponding to the six primary septa are brown, and stand erect owing to the presence within them of the prominent, exsert primary septa (text-fig. 10, *p.s.*); the



Text-fig. 10.—*Galaxea fascicularis*, vertical section. × 8. *i.t.*, inner tentacle; *o.e.*, oral cone expanded after stimulation with food; *o.t.*, outer tentacle; *p.s.*, exsert primary septum. For other lettering, see p. 16.

remaining 18 are green, and are normally pointed outwards. These tentacles have remarkable powers of expansion; on one occasion in the aquarium a colony was observed with the majority of the tentacles at least 2·5 cm. long and the longest 5 cm. Even in daylight the polyps are usually partially expanded.

Calix.—Stands, on the average, 4 to 5 mm. above the perithecal surface, the exsert primary septa rising another 2 mm. above this. The secondary septa are also slightly exsert. There is a deep-seated columella, but the septa are so wide that comparatively little space is left within the calix.

Ciliary Currents.—These are identical with those of *Echinopora*, except that on the 18 outer tentacles the cilia on the outer side beat upwards and not downwards. Material is carried diagonally outwards and upwards over the sides of the tentacles.

Seizure of Food.—Meat is taken readily by the tentacles, passed to their tips by ciliary activity, and then pushed over to the mouth, which can be protruded to an exceptional extent on the end of the oral cone, as shown in text-fig. 10. A copepod was seized immediately and then passed round the inner ring of tentacles, mainly by ciliary action,

being finally passed to the mouth, which had extended and turned in the direction from which it was to receive the food as soon as this was captured. During swallowing movements the animal temporarily contracts, the tentacles bending in over the mouth. A large *Sagitta* was taken in the same way and a quarter swallowed, the mouth then opened to its fullest extent, and mesenterial filaments were protruded which gradually wrapped round the prey. *Cavolinia*, some 2 mm. in diameter, were swallowed completely, the disc rising up around and over them. Diatoms and starch were both refused.

Remarks.—The polyp of *Galaxea* is thoroughly adapted for the capture and digestion of living prey, the comparatively small coelenteric cavity, due to the limited powers of expansion above the skeleton, being in effect increased when necessary by the protrusion of the mesenterial filaments.

Atlantic Species.

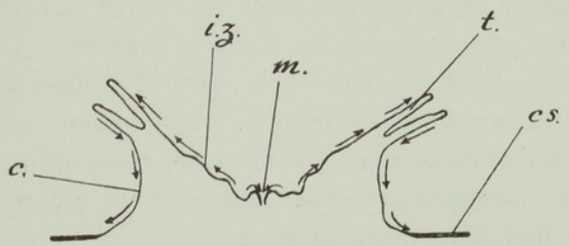
Orbicella annularis and *O. cavernosa*.—Tortugas.

I find in Prof. Vaughan's notes that in both species sand was removed, though somewhat slowly, from the general surface, much mucus being extruded. Meat was readily taken and swallowed, and *O. annularis* was observed to capture a Copepod. Mesenterial filaments were protruded freely though the column-wall in *O. cavernosa*. Diatoms and chopped algae were invariably refused.

VIII. Faviidae.

Favia pallida.—Low Isles reef.

Polyp.—Round in cross-section, with numerous tentacles arranged in a double row. The column is short and the disc depressed, the region around the oral cone being covered with irregular mounds and depressions (text-fig. 11, *i.z.*). Species of *Favia* were occasionally seen expanded in daylight as shown in Plate I, fig. 1.



Text-fig. 11.—*Favia pallida*, vertical section. × 4. *i.z.*, irregular, rugose area on disc.
For other lettering, see p. 16.

Calix.—The columella is depressed and surrounded by the paliform teeth, 18 of the septa running in to meet it. There is thus only a small, shallow cavity.

Ciliary Currents.—These were difficult to observe owing to the sensitiveness of the polyps, which frequently contracted on the addition of traces of such a light substance as carmine. The general arrangement of the ciliary currents is the same as in *Echinopora*, and is indicated in text-fig. 11. Particles falling on to the oral cone may be drawn into the mouth, but if so are invariably rejected with mucus, and carried away by ciliary currents on the disc. There is a confusion of currents in the irregular zone of the disc,

with frequent eddies, but no evidence of any reversal of ciliary currents. Duerden's observations (1906) on a change of ciliary beat in the stomodaeum could not be confirmed. Powerful currents on the coenosarc rapidly clean the surface of the colony.

Seizure of Food.—Meat or active zooplankton organisms, such as copepods and *Sagitta*, were seized with the greatest avidity, the tentacles curling inward the moment food is taken, and the entire polyp retracting. The same reaction was observed when vegetable matter was given, but invariably after a few minutes the polyp expanded again, and the plant material was ejected from the mouth.

Remarks.—*Favia pallida* and many other species of *Favia* examined were all characterized by the exceptional sureness and speed with which zooplankton and meat were seized and swallowed. Prof. Vaughan, in his notes, states that *Favia fragum* from Tortugas takes meat, but not diatoms, with great readiness, sand being removed quickly from the surface of the colony. He considers that ciliary reversal may take place, but this was certainly not so in the Indo-Pacific species of *Favia* which I examined.

Favites spp. and *Goniastrea* spp.—Low Isles reef and Maer Island.

Several species of these two genera were examined ; their polyps closely resemble those of *Favia* in both structure and behaviour.

Coeloria and Maeandra spp.—Low Isles reef and Maer Island.

Although the polyps of *Coeloria* are elongated in the typical meandrine fashion, their behaviour is identical with that already described for *Favia*. Species of this genus were observed at night on the reef flat with tentacles expanded to a length of 2 to 3 cm., and with mesenterial filaments extruded.

Vaughan (1912, 1919) has described in detail the feeding of *Maeandra areolata*.* Small crabs, amphipods, crab zoea, *Sagitta*, salps, small fish and meat were all captured and digested readily. When placed on a region of the edge zone beyond reach of the tentacles, ciliary currents were observed to reverse and the food brought within reach of the tentacles. After a certain time, however, this reaction could no longer be brought about, food matter being carried away in the same manner as inedible matter. A reversal of ciliary beat was also found on the disc, waste matter such as sand-grains being carried out, but, if mixed with meat, being drawn into the mouth. The process of feeding was exactly as in *Favia*, the tentacles bending downward and the edge-zone sphincter contracting thereby, closing the polyp. Ciliary currents over the surface of the colony caused it to be rapidly cleared after sand-grains had been dropped upon it.

Platygyra [=*Leptoria*] *phrygia*.—Low Isles reef.

Polyp.—This is a typical meandrine with frequent mouths along the narrow disc region, which is fringed with a single row of numerous tentacles. When expanded the tentacles of adjacent " valleys " interdigitate, the interpolypal region being entirely hidden. The mesenterial filaments were frequently extruded through the mouth.

* Matthai (1928) places this species, found only in the Atlantic, in the genus *Manicina* (see below, p. 30). It seems probable that the structure of the polyp is different from that of the Indo-Pacific *Coeloria*—a fact which may account for the differences between my observations on the feeding reactions of *Coeloria* and those of Vaughan on *Maeandra*. When fully expanded, the tentacles of *Coeloria* cover the entire surface of the colony ; in *Maeandra areolata*, judging from Vaughan's photograph (1919, Pl. XVII), this is not so, a fact which probably accounts for the presence of reversal of ciliary currents in this species.

Calix.—A prominent lamellar columella effectively blocks the cavity.

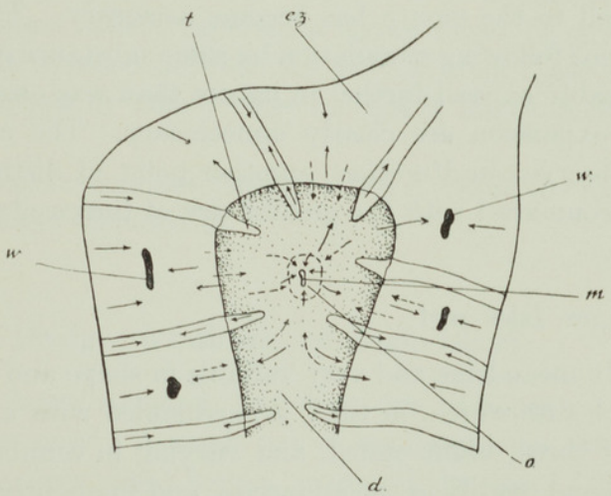
Ciliary Currents.—Material placed on the disc, irrespective of the presence of food, is quickly removed. Waste matter is carried over the tentacles, the cilia on which beat upwards on the inner side and downwards on the outer side, and then caught in the rapid and powerful ciliary currents of the coenosarc, and so removed from the surface of the colony. Ciliary currents immediately around the oral cone beat towards the mouth

Seizure of Food.—Meat is taken with great tenacity by the tentacles, an exceptional amount of mucus being secreted in the region round about. This accumulation of mucus inhibits ciliary activity and makes observations difficult, but it is quite certain that no reversal of the ciliary currents occurs. Comparatively little effort is made to swallow the food, or even to pass it to the mouth. But this coral does not expand well under laboratory conditions. Mesenterial filaments are protruded freely through the mouths immediately food is given, and wrap round the food masses. This may be a perfectly normal procedure.

Remarks.—Although difficult to observe, there can be no doubt that *Platygyra* has an efficient mechanism for the capture and disposal of animal prey.

Merulina ampliata.—Low Isles reef.

(Although this genus is not referred by Vaughan (1918) to any family—it is, of course, a meandrine coral—I have introduced it here because of the superficial resemblance of its skeleton to that of *Platygyra*, and the striking differences in the structure and behaviour of the polyps between the two species.)



Text-fig. 12.—*Merulina ampliata*, surface view. × 8. For lettering, see p. 16. Dotted arrows indicate reversal of ciliary currents after stimulation with food.

Polyp.—Superficially very like *Platygyra*, having the same meandrine form with discs and intervening collines of about the same size, and with frequent mouths along the disc. The tentacles are much fewer in number, and are arranged in a single row with wide intervals between them, as shown in text-fig. 12.

Calix.—Easily to be distinguished from *Platygyra* owing to the absence of the lamellar columella. The columella is more spongy in character and often low enough to leave a small cavity.

Ciliary Currents.—Waste material is removed very quickly from the disc, passing over the tentacles and the tissue between them, and on to the interpolypal region, in the centre and highest point of which it collects in masses (text-fig. 12, *w.*), to be removed by water currents. Immediately around the mouth the cilia beat inwards.

Seizure of Food.—When meat is placed on the tissue surface midway between two polypal grooves, the tissue immediately contracts both where the meat is placed, and also on one of the adjacent discs. The nearest mouth opens wide and leans over in the direction of the food, while a great deal of mucus is extruded, strings of which are drawn into the mouth. The tentacles in the vicinity contract out of sight, never making any attempt to curl over and seize the food. After a short period the food slides over and into the mouth. This was observed repeatedly, and is undoubtedly due to a reversal of ciliary current, carborundum or other inedible matter put on at this time being also carried to the mouth. This reversal of current is maintained during the slow process of swallowing, when the mouth expands, if necessary, to a vast extent. After the food has been swallowed, the direction of the ciliary currents gradually changes back to normal. When meat is placed directly on the tentacles it is taken by them with great tenacity being pulled from a needle with ease. The tentacle then contracts and passes the food to the mouth, which extends greatly and finally swallows it. In this case also there is a great production of mucus, and a temporary reversal of ciliary currents in the region which serves this particular mouth. Even copepods can be caught easily by the nematocysts on the interpolypal surface, entangled in mucus and carried to the mouth by ciliary action.

Remarks.—The tentacles in *Merulina* are so small and so much of the interpolypal tissue is exposed even when the tentacles are fully expanded, that some additional method for the bringing of food to the mouth has become necessary. This has been found in a reversal of ciliary current following stimulation by some substance of food value. Although the tentacles can probably expand further in nature than was observed in the laboratory, yet great powers of expansion are clearly unnecessary. The extrusion of mesenterial filaments was never observed in *Merulina*—another point of distinction from *Platygyra*—a fact which may be connected with the greater size of the cavity underlying the mouth.

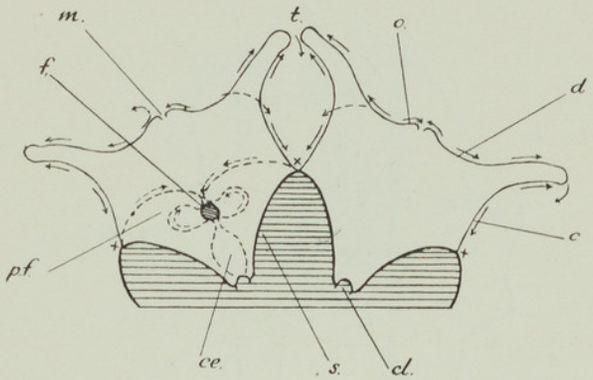
Hydnophora exesa.—Low Isles reef.

Polyp.—Typically meandrine and very variable in shape and size. There are usually several mouths to each disc which, in turn, is surrounded with a single row of tentacles, arranged in groups of three, blunt ended, and varying in number according to the size of the disc. They expand readily in the aquarium, and frequently in daytime on the reef, completely obscuring when they do so the intercalysal projections which are so characteristic of this genus. The tentacles of adjacent polyps interdigitate as indicated in text-fig. 13.

Calix.—The prominent, spongy columella so characteristic of many meandrines completely occupies the cavity, the wide septa ascending almost vertically to form the erect, isolated collines which cover the surface of the skeleton.

Ciliary Currents.—As usual the currents beat outwards on the disc surface, except in the region of the oral cone, being continued up the inner surface of the tentacles and between them. Outside currents pass up the tentacles and down the column. Material is quickly removed from the colony by currents on the interpolypal tissue (text-fig. 13, *x.*).

Seizure of Food.—Meat is taken firmly by the tentacles, which, together with the underlying disc, then contract to the extent shown by the dotted lines in text-fig. 13. It was never possible to follow the process of swallowing. When contracted in this manner inedible matter flows over the outer surface as indicated by the dotted arrows, *i. e.* the currents on the column wall are apparently reversed. This may, however, be due to the practical obliteration of the column wall, the cilia on the outer side of the tentacles being



Text-fig. 13.—*Hydnophora exesa*, vertical section through two polyps and calices. × 8. *cl.*, columella ; *p.f.*, polyp contracted after seizure of food ; *x.*, ciliary currents for removal of waste matter. For other lettering, see p. 16.

alone responsible for the passage of material. There is no apparent reason for a reversal of ciliary current—a process which experience shows never occurs without due cause. Meat placed on the tissue exposed between the polyps when these are partly contracted is never moved to the polyps by ciliary currents, but is finally secured by an extended, reflected tentacle.

Remarks.—*Hydnophora* resembles *Platygyra* and *Favia* in the readiness and efficiency with which food is seized and disposed of.

Tridacophyllia lactuca.*—Dredged 6 fathoms, off Eagle Island.

Polyp.—There is a large rounded disc with one or more mouths, that shown in text-fig. 14 possessing one only. A single row of small tentacles, which were seldom seen expanded to more than a very slight degree, surround the disc. The collines separating the calices are of great height and very thin, the coenosarc covering them being smooth with faintly marked vertical ridges.

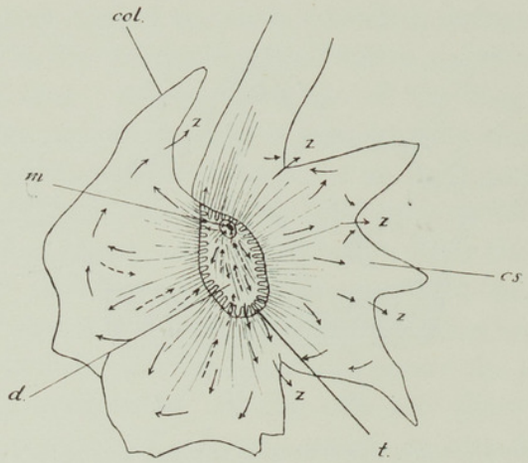
Calix.—The septa, which continue up the collines for a considerable distance, are particularly broad in the region of the calix, where they are in contact with the large, spongy columella, the cavity being entirely blocked in this manner.

Ciliary Currents.—It was never possible to observe with accuracy those on the tentacles, which probably agree with those described for the other meandrines. On the remainder of the tissue the currents carry material outwards except immediately round

* I am uncertain whether this genus should be considered here or under the Mussidae ; in any case the two families have a great deal in common.

the mouth, as shown in text-fig. 14. On the collines waste matter is conveyed to the depressions, there to be rejected (*z.* in text-fig. 14).

Seizure of Food.—When meat is placed upon the disc or the coenosarc, the ciliary currents are reversed and material carried to the mouth, which opens and swallows it. This ciliary reversal is local only, waste material in this region being also carried to the mouth.



Text-fig. 14.—*Tridacophyllia lactuca*, surface view. × 1½. *col.*, collines between polypal areas ; *z.*, regions where waste matter removed from surface. For other lettering, see p. 16. Dotted arrows indicate reversal of ciliary currents after stimulation with food.

Remarks.—Here again the presence of very small tentacles and a large area of exposed coenosarc is correlated with a reversal of ciliary current following stimulation with food material.

Atlantic Species.

Manicina gyrosa.—Tortugas.

In his notes Prof. Vaughan states that the tentacles of this species are extraordinarily small, being barely visible to the naked eye, and not reaching from the edge-zone to the mouth. They are in two rows and have the tips knobbed. Solid food is seized by them, but is carried from them to the mouth by inwardly directed ciliary tracts on the disc. It is noteworthy that in this species the oral discs are not arched over in the usual manner by the margins of the edge zone. Mesenterial filaments were extruded outside the tentacular rows. Sand was rapidly removed from the surface of the colony, also diatoms, but when meat was added the ciliary currents were reversed and the diatoms drawn into the mouth, to be later ejected. Seaweed was invariably rejected.

[Astrangiidae.]

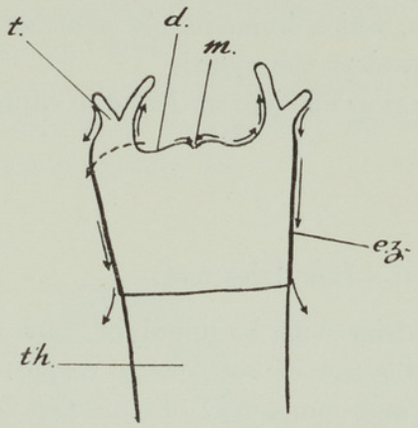
Astrangia danae.—Woods Hole.

Boschma (1925*b*) has examined the feeding of this species, and states that it will capture small copepods with its tentacles, after which the mouth with the central part of the disc forms a conical protuberance which moves towards the prey. The tentacles at the same time bend downwards, and when the two meet the prey is released and falls into the stomadaeum, and thence to the gastric cavity.

IX. Mussidae.

Caulastrea furcata.—Dredged 20 fathoms near Lizard Island.

Polyp.—This was never seen in a greater state of expansion than that shown in text-fig. 15. The tentacles are arranged in a double row, surrounding a large disc with a



Text-fig. 15.—*Caulastrea furcata* vertical section. ×3. For lettering, see p. 16.

prominent oral cone. The polyps are separated, except when undergoing division, the edge-zone tissue continuing for some distance down the outer wall of the calix. The septa are prominent and exsert, broadening proximally to meet the central, spongy columella, and so forming a shallow, cup-shaped cavity.

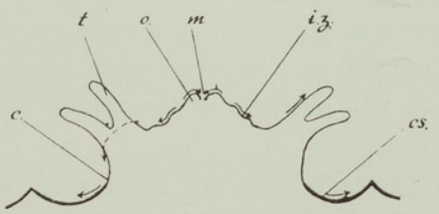
Ciliary Currents.—Carborundum and similar inedible matter is carried outwards on the disc, up the inner side of the tentacles, down their outer sides and down the edge zone and so rejected. Currents beat inwards around the oral cone.

Seizure of Food.—Meat is taken with avidity by the tentacles, even when they are half contracted ; the mouth is capable of very great extension and may occupy almost the entire area of the disc. The act of swallowing is very rapid.

Remarks.—The tentacles here are solely responsible for food capture.

Acanthastrea echinata.—Maer Island.

Polyp.—The general appearance resembles that of *Favia* closely. The polyps are rounded with a short column. The disc, which had many rounded protuberances, contains a very prominent oral cone, and is surrounded by a double row of tentacles (see text-fig. 16).



Text-fig. 16.—*Acanthastrea echinata*, vertical section. × 4. *i.z.*, irregular rugose area on disc. For other lettering, see p. 16.

Calix.—Of the same type as *Favia*, but with the septal margins typically spinose.

Ciliary Currents.—On the oral cone currents beat towards the mouth; on the disc round about material is carried outwards by rather devious routes around the tissue protuberances, with many local vortices, and up the inner side of the tentacles. The currents on the outer side of the tentacles and on the column could not be observed with certainty. Waste matter is rapidly removed from the coenosarc.

Seizure of Food.—Meat and living zooplankton are seized with exceptional speed and sureness by the tentacles, which immediately contract. The polyp contracts at the same time and the food is passed to the mouth.

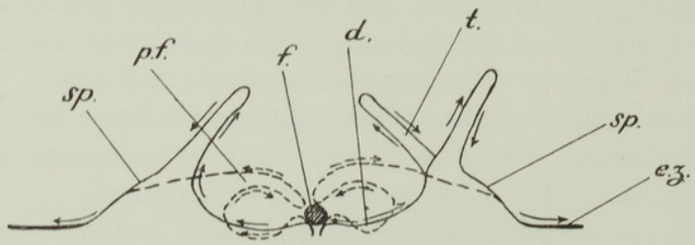
Remarks.—*Acanthastrea* is as efficient as *Favia* in capturing living prey, the tentacles alone being used.

Symphyllia recta [= *S. nobilis*].—Low Isles reef.

Polyp.—A typical meandrine with large polyps, each disc containing many mouths, and being fringed with a double row of tentacles. When fully expanded the tentacles of adjacent polyps interdigitate and completely obscure the fleshy coenosarc.

Calix.—The broad collines are high with deep intervening valleys, the bases of which are composed of septa and spongy columella of about the same height.

Ciliary Currents.—As shown in text-fig. 17, material is carried outwards on the disc, over and between the tentacles, and thence on to the edge-zone, where it is caught in powerful currents, which remove it from the surface of the colony.



Text-fig. 17.—*Symphyllia recta*, vertical section. ×3. *p.f.*, polyp contracted after seizure of food; *sp.*, sphincter muscle. For other lettering, see p. 16.

Seizure of Food.—Living zooplankton or meat is taken with the greatest readiness by the tentacles, which at once pass it to the mouth, the whole polyp contracting at the same time, as a result of the closure of the sphincter (text-fig. 17, *sp.*). The oral cone elongates during this process, while the disc descends. The food is passed to the mouth, where it is swallowed. If meat is placed on the exposed disc, it is carried outwards till it meets the tentacles; if placed on the coenosarc when the colony is only partially expanded, it is removed from the surface as though it were inedible matter. There is never any reversal of ciliary currents.

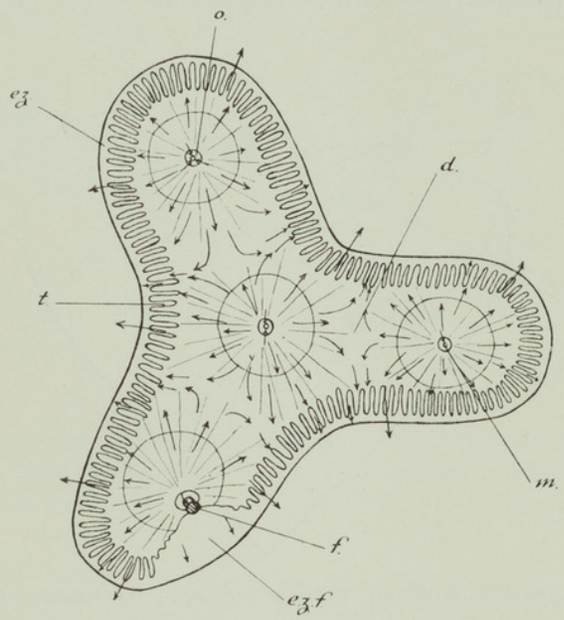
Remarks.—Here again the tentacles are large and, when fully expanded, cover a large area. They alone are concerned with food capture, which they carry out with great efficiency.

Lobophyllia corymbosa.—Low Isles reef.

Polyp.—The polyps of this species are of great size, as shown in Plate I, fig. 2, and text-fig. 18, and largely separated from one another. These characters with the larger and more spiny septa form the principal distinctions between this and the preceding genus. There is a great expanse of disc tissue containing one or more mouths, and surrounded with a double row of tentacles which were observed expanded to an average length of 1·5 cm. The edge-zone tissue is continued for some distance down the outer side of each calix, and is exceptionally thick and fleshy.

Calix.—In essentials the same as that of *Symphyllia*, only on a rather larger scale.

Ciliary Currents.—Exactly as in *Symphyllia*; the course of the currents on a disc containing four mouths is shown in text-fig. 18.



Text-fig. 18.—*Lobophyllia corymbosa*, surface view. Nat. size. *e.z.f.*, edge-zone curled over towards mouth after stimulation with food. For other lettering, see p. 16.

Seizure of Food.—Meat and zooplankton are taken by the tentacles readily, and with results similar to those already described for *Symphyllia*. If large pieces of meat are given which the mouth is apparently too small to swallow, then mesenterial filaments are freely extruded and wrap round the food. After about one hour they were observed to withdraw slowly, carrying the food, now somewhat reduced in bulk and generally softened, with them. The mesenterial filaments are very frequently extruded through the mouth for no apparent reason. Meat placed on the exposed disc is carried outwards till it touches the tentacles, which secure it and carry it to the mouth in the usual manner. No evidence of a reversal of ciliary current was obtained.

Remarks.—Conditions are essentially similar to those in *Symphyllia*.

Trachyphyllia geoffroyi.—Dredged 19 fathoms near Lizard Island.

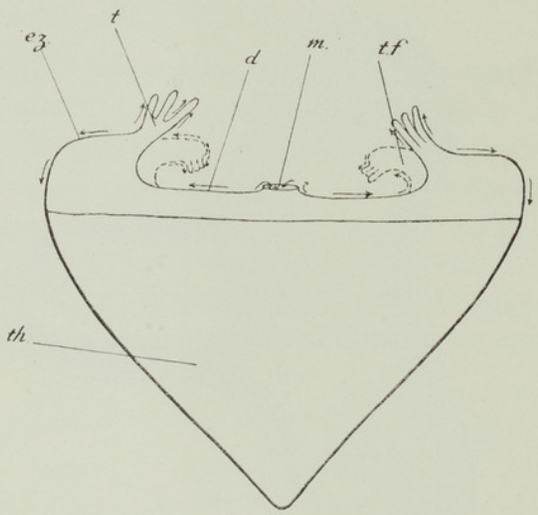
Polyp.—All the specimens obtained consisted of solitary polyps, each with a single mouth. The polyp is circular, with a large centrally placed mouth, a wide disc fringed

with numerous tentacles arranged in approximately three rows (but these were never seen well expanded), and a well-developed edge-zone, all of which are shown in text-fig. 19.

Calix.—Of the same type as *Lobophyllia* and *Symphyllia*, with a shallow cup, the base of which is occupied by a very large, spongy columella.

Ciliary Currents.—As indicated in the figure, these follow the usual course with the exception of the currents on the outer side of the tentacles, which beat upwards instead of downwards.

Seizure of Food.—Meat placed on the disc is carried outwards till it reaches the tentacles, which curl over in manner shown by the dotted lines in text-fig. 19. The meat is then moved around in a clockwise direction by the ciliary currents, the polyp contracting at the same time and decreasing the area of the disc. In the laboratory this process was never observed to lead to the swallowing of food, but, as already stated, this coral was never observed fully expanded under these conditions.



Text-fig. 19.—*Trachyphyllia geoffroyi*, vertical section. Nat. size. For lettering, see p. 16.

Remarks.—There seems no reason to doubt that, under normal conditions, *Trachyphyllia* will feed in the same manner and as efficiently as the previous meandrines possessing large tentacles which were studied. There was no evidence of any reversal of ciliary currents.

Atlantic Species.

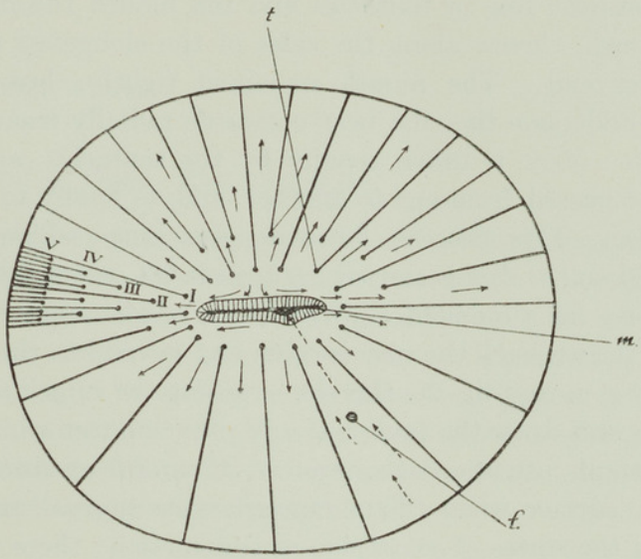
Isophyllia dipsacea.—Bermuda.

The feeding reactions of this coral have been described in great detail, and well illustrated by Carpenter (1910). Plankton is seized by the tentacles, a contraction of these and of the oral disc following. The same process follows the application of concentrated meat extract. The edge zone, by folding inward as a result of the contraction of the sphincter, finally roofs in the tentacles and oral disc, thereby forming a superficial chamber into which the stomodaeum and the mesenterial filaments project. Digestion and absorption by the filaments takes place, Carpenter thinks, exclusively in this chamber, *i. e.* extra-coelenterically. Cilia normally beat so as to clear the surface even when mixed with meat juice, but occasionally they reverse their effective beat. Conditions, except in the latter respect, are thus closely equivalent to those found in *Lobophyllia*.

X. Fungiidae.

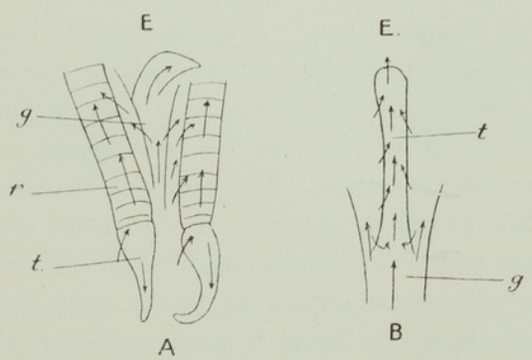
Fungia danai—Low Isles reef.

Polyp.—Probably no coral is better known. The upper surface is covered with small tentacles, which arise above the ends of the septa as indicated diagrammatically in text-fig. 20. These have a maximum power of expansion of not more than 1 cm. in



Text-fig. 20.—*Fungia danai*, surface view, diagrammatic. Nat. size. I–V, primary to quintary cycles of septa. For lettering, see p. 16. Dotted arrows indicate reversal of ciliary currents after stimulation with food.

a specimen with a greatest diameter of 15 cm. They rarely, if ever, expand during the day, their usual appearance then being shown in Plate I, fig. 3. The mouth is large with smooth lips, beneath which is a grooved stomodaeum. The surface of the disc between the tentacles is smooth.



Text-fig. 21.—Ciliation on tentacles of *Fungia*. A, *Fungia danai*. × 7. B, *Fungia actiniformis*. × 4. E, direction of edge of disc; *g.*, groove between underlying septa; *r.*, ridge over septum beneath. For other lettering, see p. 16.

Calix.—There are five cycles of septa, of approximately the same height, surrounding a deep, central fossa.

Ciliary Currents.—The direction of ciliary currents, as indicated by the removal of carborundum dropped upon the surface of the polyp, is shown in text-fig. 20, and, for a small region of the disc embracing two tentacles, in text-fig. 21A. The currents beat outwards everywhere on the surface of the disc, both on the grooves between the septa beneath and the ridges which overlie these. On the tentacles material is carried backward round the base, but upwards on the tentacles themselves. On the smooth area between the innermost row of tentacles and the mouth the currents pass inwards to the edge of the mouth, thence along the sides of the elongated mouth and outwards and away from either end. The mouth remained tightly shut during the time of observation. On the underside the cilia beat outwards radially from the centre.

Seizure of Food.—Meat is taken readily by the tentacles, and may, if these are very well expanded, be passed from one to another, and so finally to the mouth, without ever touching the disc. This process, however, was very seldom observed. Almost invariably, meat placed on the disc is carried backwards till, stopped by the first tentacle it meets, it remains passive for a moment and then, as a result unquestionably of a reversal of ciliary current, it is drawn back the way it came and beyond to the mouth. This opens to receive it, as indicated in text-fig. 20, thereby exposing the ridged stomodaeum, the cilia of which beat inwards and draw the food and any other matter which may be caught in the same reversed current into the coelenteron. A careful examination of the grooves and ridges on the disc surface when ciliary currents were normal and reversed failed to show any difference in the states of expansion or contraction; there is no evidence for the bringing into play of different tracts of cilia. Plankton organisms were caught and swallowed in a similar manner, but vegetable matter was invariably rejected.

Fungia cyclolites.—Dredged 19 fathoms, near Lizard Island.

This small species, characterized by its pronounced concavo-convex shape, the disc being on the convex side, was used for more exact work on ciliary reversal. It lives well in the aquarium, is small enough to be easily observed under the binocular dissecting microscope, and, unlike *Fungia danai* under similar conditions, its feeding reactions are performed with unfailing regularity. The tentacles are very short and were never seen expanded more than 1·5 mm. where the diameter of the disc was 4 cm. Ciliary currents were exactly as described in *Fungia danai*. A great deal of mucus was extruded when the food was placed on the disc—more than when inedible matter was added. Following stimulation by meat, the ciliary currents reverse not only in the groove where the food lies, but also in the grooves on either side and the intervening ridges; the currents on the tentacles in this region are also reversed. The effect is transmitted in either direction, radially, so that the direction of ciliary currents on the entire length of these grooves and ridges is affected in the same way. Thus meat may be placed on the disc near the mouth, but carborundum placed on the outer extremity of the same sector of the disc is drawn inwards. Observations, tabulated in Table I, were made on the length of time which elapses between stimulation and ciliary reversal, and between the withdrawal of the stimulation and the return of the currents to their normal beat, the periods being accurately determined by means of a stop-watch.

TABLE I.—*Experiments on Time Factor in Ciliary Reversal, the same specimen of* Fungia *being used for all experiments, but stimulated in different regions.*

Length of period between placing of food on disc and reversal of ciliary current.	Length of period between swallowing of food and return of ciliary currents to their normal direction.
1. 2 min.	31 sec.
2. 2 ,, 5 sec.	29 ,,
3. 2 ,,	28 ,,
4. 1 ,, 50 ,,	22 ,,
5. 1 ,, 50 ,,	22 ,,
Average : 1 min. 57 sec.	Average : 26·4 sec.

Fungia scutaria.—Island of Oahu, Kaneohe Reef.

This species behaves in a similar manner, Prof. C. H. Edmondson informing me that he frequently demonstrates the reversal of ciliary currents to his students. The attempt was made while at Honolulu to discover whether ciliary reversal could be brought about by potassium chloride, as was shown to be the case in the anemone *Metridium marginatum* by Parker (1905). Six small specimens were taken and placed in separate containers, to each of which was added 200 c.c. of sea-water, containing varying percentages of potassium chloride, carmine and carborundum powder being placed on the disc. The results of this experiment are tabulated in Table II. :

TABLE II.

Percentage KCl.	Result.
2·5	Some material removed from disc, but never into mouth ; remainder still there after 20 hours and the coral dead.
1·5, 1·0	Great extrusion of mucus, but material all removed from the disc after 3 hours.
0·5, 0·25, 0·0	In all three cases material rapidly removed from the disc.

It is clear that potassium chloride does not have the same effect on the cilia of *Fungia* as on those of *Metridium*, the concentration of KCl (2·5) which Parker employed killing *Fungia*, and lower concentrations increasing mucus secretion, but not affecting the direction of the ciliary currents.

Fungia actiniformis var. *crassitentaculata.*—Low Isles reef.

This species, a photograph of a typical specimen of which is shown in Plate I, fig. 4, is characterized by the presence of very large tentacles which are never retracted, even in the brightest light. Thus in a specimen whose greatest diameter was 7 cm., the tentacles measured, on the average, 4·5 cm. It is difficult to see the disc tissue or even the mouth, owing to the great size and constant movements of the tentacles.

Ciliary Currents.—Though difficult to observe, apparently exactly as in the other species. The tentacles have powerful currents beating towards the tips, as shown in text-fig. 21B.

Seizure of Food.—Meat or zooplankton is taken with exceptional tenacity by the tentacles, the tissue of which will suffer tearing rather than surrender it. After seizure of food, the tentacle contracts to its minimum size, as do the adjacent tentacles, and the underlying area of the disc contracts tightly against the skeleton. The mouth gapes and bends towards the food which is transferred into it, the process being again difficult to follow, owing to the covering mass of writhing, contracted tentacles. *There is never any reversal of ciliary current in this species*, carborundum and other inedible matter being carried outwards even though food is given at the same time. Carborundum mixed with meat-juice causes the tentacles to contract and move actively, and induces an abundant secretion of mucus, but never causes a reversal of the ciliary currents.

Herpetolitha stricta.—Low Isles reef.

Polyp.—Essentially the same as *Fungia danai* except that it is elongated with a series of mouths running down the middle line. The tentacles are very short and blunt ended.

Calix.—Of essentially the same type as *Fungia.*

Ciliary Currents.—These beat away from the mouths radially along the line of the underlying septa.

Seizure of Food.—When meat is placed on the disc, the direction of the ciliary current reverses after a comparatively long interval, after which the food and any other matter lying in the zone of reversed ciliary current is carried towards the nearest mouth, which opens on that side exactly as in *Fungia.* Ciliary reversal extends to the two or three grooves on either side of the one on which the food lies.

Döderleinia irregularis.—Maer Island.

Polyp.—Of the same general type as *Herpetolitha*, but with a central mouth and very many smaller ones (about half the size of the central one) dotted over the surface. Thus a polyp 13 cm. long and 9·5 cm. across at the widest place had a central mouth with 168 smaller ones. Each of these is surrounded by a series of short, blunt tentacles, some 20 in number for the principal mouth, and 10 each for the others.

Calix.—Smaller, but otherwise similar to those of other fungids.

Ciliary Currents.—Inedible matter is removed with great speed from the surface. Starting from the central mouth, it is carried to the edge by tortuous courses, being usually deflected clear of the numerous subsidiary mouths. Occasionally matter in mucus strings is carried clear over these mouths. As in *Fungia*, ciliary currents on the underside beat radially outwards from the centre.

Seizure of Food.—Meat placed on the disc causes a reversal of ciliary current. The process is essentially similar to that observed with *Fungia* and *Herpetolitha*, but, owing to the nature of the coral, more complex. Reversal is slow after the meat is placed on the disc, the food being first carried away and then, as a result of the reversal of the currents, deflected into one of the mouths, which opens to receive it in the usual manner. The change of ciliary current affects also the region around the two or three adjacent

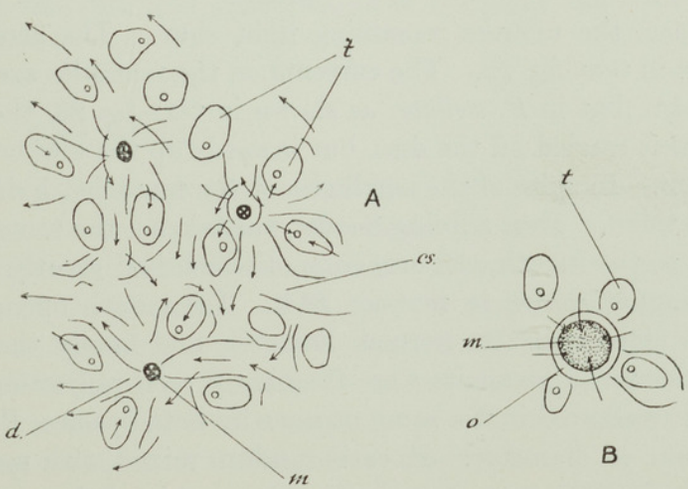
mouths, which all open, the oral cones extending and bending towards the food. After food is swallowed the ciliary currents return somewhat slowly back to normal. When meat or plankton organisms are given to the tentacles they are taken securely, but are never passed to the mouth ; the tentacle and the underlying disc contract, and the food slides over the tentacle and into the mouth exclusively under ciliary action.

Remarks on the Fungiidae.—Observations on species of the three genera, *Fungia*, *Herpetolitha* and *Döderleinia* have shown clearly that in the Fungids food is captured by the nematocysts on the tentacles or disc surface, and then carried to the mouth as a result of a reversal of the normal direction of the ciliary currents. The one exception to this is found in *Fungia actiniformis*, where alone the tentacles are large enough to perform their usual function of carrying food to the mouth. Duerden (1906) obtained similar results with experiments on *Fungia* at Hawaii, but explains them differently. He concluded that " the outer surface of *Fungia* is not ciliated, and that any motion of particles upon the disc or in its vicinity is entirely due to currents of water produced by the cilia lining the stomodaeum." He found that mucus is freely secreted by the surface of the disc when food is placed upon it, and considered that the opening of the mouth and the pulling in of these strings of mucus with the entangled food by the cilia lining the stomodaeum was alone responsible for the carriage of food into the coelenteron. Inedible matter dropped upon the disc was caught in a thin sheet of mucus, which later, he states, was carried gradually away as a result of exhalant currents proceeding from the stomodaeum. It is very doubtful whether Duerden would have expressed similar views had he had the advantage of observing his *Fungia* with a modern binocular dissecting microscope.

XI. Agariciidae.

Psammocora gonagra.—Low Isles reef ; *Psammocora* [= *Stephanaria*] *stellata.*—Island of Oahu, Waikiki reef.

Polyp.—The surface is covered with extremely short, blunt tentacles which have the appearance under the binocular of a short brown " fur." The polyps are dotted over the surface, as shown in text-fig. 22, each having a prominent mouth situated on the

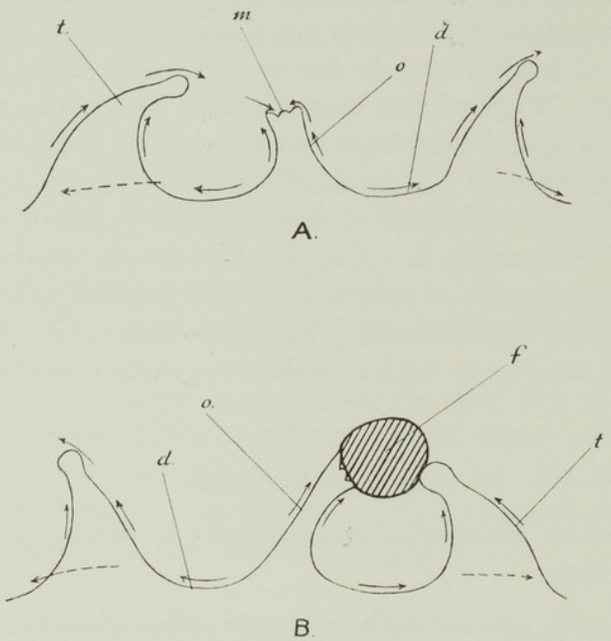


Text-fig. 22.—*Psammocora gonagra*, surface view. × 20. B, polyp A after stimulation by food ; mouth opening greatly extended. For other lettering, see p. 16.

summit of a relatively large oral cone. The mouth opening is normally small, but capable of great extension; the oral cone is higher than the tentacles and capable of much greater movements. In *Psammocora gonagra* each polyp possesses usually from 4 to 6 tentacles, but in *P. stellata* they are more numerous, between 6 and 9, and have greater powers of expansion. In both species it is difficult often to distinguish to which of adjacent mouths particular tentacles rightly belong.

Calix.—Although the septa are usually so disposed as to leave a moderate-sized cavity, the centre of this is occupied by a well-developed columellar tubercle.

Ciliary Currents.—Carborundum powder is rapidly removed from the surface of the colony, usually avoiding the polyp mouths. If, however, a thick sheet of carborundum is placed on the surface, the entire sheet is removed as a whole and carried indifferently



Text-fig. 23.—*Psammocora stellata*, vertical sections. × 25. A, normal polyp; B, polyp taking food. For other lettering, see p. 16.

over the entire surface, the mouths remaining tight shut. The general distribution of the currents is shown in text-fig. 22. The currents on the tentacles are difficult to observe in *Psammocora gonagra*, but in *P. stellata*, as shown in text-fig. 23, they pass upwards on either side. Material is carried off the disc, but inwards up the oral cone.

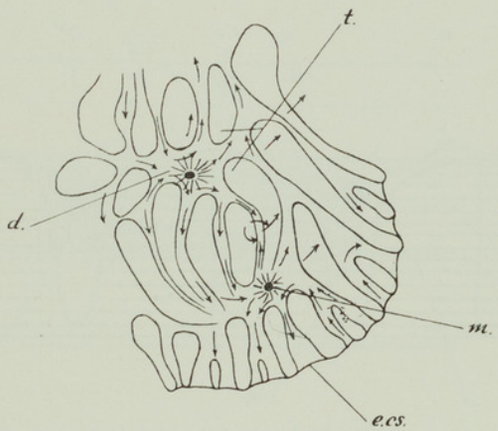
Seizure of Food.—In spite of the small size of the tentacles, living zooplankton was secured with ease by them. Thus a living *Sagitta* was taken; the tentacle then contracted and passed the food to the mouth, the oral cone of which had greatly elongated and bent towards it in the manner shown in text-fig. 23 B. The mouth opened to a remarkable extent, no less than eight times its normal diameter, and finally the entire *Sagitta* was swallowed. The mesenterial filaments were frequently seen projecting from the mouths. Meat was seized and swallowed in the same manner by both species, *P. stellata* swallowing with ease pieces 1 mm. in diameter. If carborundum mixed with meat-juice was given, an *apparent* reversal of ciliary current took place, everything being swallowed, the mouth opening to the size indicated in text-fig. 22B. The explanation of this apparent reversal

is shown in text-fig. 23A, the left-hand tentacle in which is bent towards the mouth, when the ciliary currents running up its outer side carry material over it, and so into the mouth, which leans towards the tentacle. The disc is, as it were, short-circuited.

Remarks.—In spite of the small size of its polyps and their apparent inefficiency as agents of food capture, *Psammocora* is excellently equipped with the means for capturing and disposing of living animal prey.

Pavona danai.—Low Isles reef; *Pavona varians.*—Island of Oahu, Waikiki reef.

In structure and mode of functioning this genus closely resembles *Psammocora.* The general disposition of the colony is shown in text-fig. 24. There are frequent mouths surrounded by a very variable number of low tentacles. In neither of the species examined were these ever seen well expanded, and in consequence the normal feeding reactions could not be obtained. On one occasion only was food seen to be swallowed, when the



Text-fig. 24.—*Pavona danai*, surface view. × 16. *e.cs.*, edge of coenosarc. For other lettering, see p. 16.

mouth distended greatly. Material dropped on the surface of the colony is removed with the same speed and efficiency as in *Psammocora*; so far as could be determined, the ciliary currents on the disc and tentacles have the same direction of beat as those of *Psammocora.*

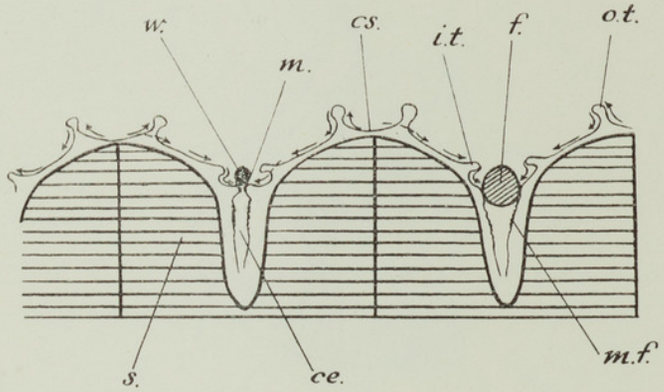
Coeloseris mayori.—Maer Island.

Polyp.—This coral, a new genus described by Vaughan (1918) from the locality where these observations were made, is of exceptional interest. The polyps are polygonal and of an average diameter of 5 mm., even when fully expanded they are raised but slightly above the surface of the skeleton. Two rows of very short, blunt tentacles surround each polyp, each row consisting of about 26 members. Their arrangement in relation to the polyp is shown in text-fig. 25. The disc lies in a depression with the small mouth in the centre. As shown in the figure, the tentacles of adjacent polyps are so close together that the intervening coenosarc is reduced to a minimum.

Calix.—The septa of adjacent calices are continuous. There is no columella, so that the cavity is exceptionally open and very deep.

Ciliary Currents.—*All* material placed on the surface of the colony is carried to the polyps. This is shown clearly in text-fig. 25. Ciliary currents carry material from the coenosarc up the inner side of the outer row of tentacles, or else between adjacent tentacles, and thence over the disc and second row of tentacles to the mouth. If it is inedible the mouth remains tightly shut and it gradually accumulates into a rounded mass with much mucus (see text-fig. 25, left hand polyp), being revolved the whole time by the cilia until it becomes too heavy to be moved in this way. The mouth remains tightly shut and no muscular movements take place. A specimen covered with carborundum in a dish of sea-water was left overnight, and in the morning the carborundum was found still on the colony, but all collected into rounded balls over the polyps.

Seizure of Food.—Meat is taken firmly by the tentacles, which then, together with the underlying disc tissue, contract. The disc practically disappears in the cavity of the calix. The food is then carried down by ciliary activity (never passed down by the tentacles, the sole reaction of which is to draw the food down on to the tissue and so within



Text-fig. 25.—*Coeloseris mayeri*, vertical section through two polyps and calices. ×7. *i.t.*, inner tentacle; *o.t.*, outer tentacle. For other lettering, see p. 16.

the range of the ciliary currents). The food sinks lower and lower and gradually the disc reappears, the mouth having closed over the food. The mouth is capable of expanding until its orifice is as great as that of the calix, so that relatively large masses can be swallowed.

Remarks.—The capture of food is brought about by tentacular action, and its transference to the mouth by ciliary action—essentially the same process which takes place in the Fungiidae, but without any reversal of ciliary currents. As in *Leptastrea agassizi*, waste matter must be removed by wave action. As pointed out by Mayer (1918), *Coeloseris* is a typical shore coral exposed to continual water movements. A second point of great interest is the size of the opening within the calix, which permits food to be taken into it, so that there is no necessity in this coral for the tissue to be raised high above the skeleton before an adequate coelenteric cavity can be formed. Probably also in consequence of this fact, mesenterial filaments were never seen extruded.

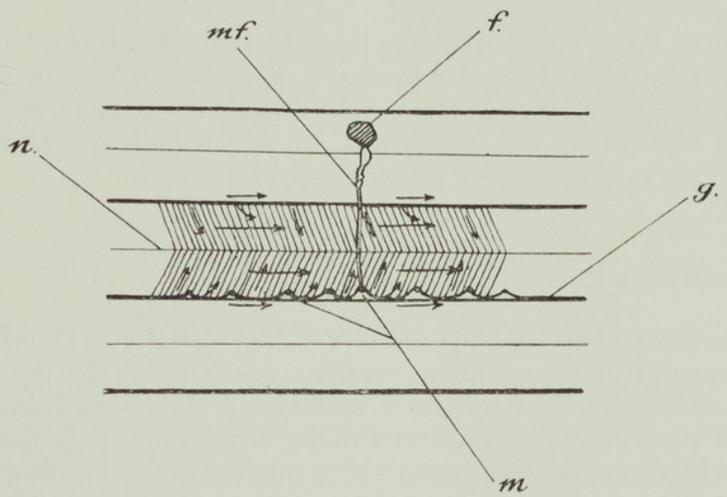
Pachyseris speciosa.—Low Isles reef.

Polyp.—The polyp and underlying skeleton of this genus are altogether unlike those of any other coral. The surface of the colony, as can best be realized by reference to

Plate II, fig. 5, is covered with a series of parallel ridges and grooves. Polyp mouths, so small as to be difficult to see except when the oral cones are expanded under the stimulus of food, occur at intervals along the grooves. There are *no tentacles*. The surface of the ridges is transversely grooved as shown in text-fig. 26, and covered with a brown coenosarc.

Calix.—The ridges are formed of parallel lines of septa which, are continuous from one groove to another. The cavity at the base of the grooves is occupied completely by a false columella.

Ciliary Currents.—Material dropped on to the surface of the colony is carried round in the grooves and on the surface of the ridges until finally removed, water movements doubtless assisting. There are different tracts of cilia on the small transverse ridges and in the intervening grooves which cover the surface of the large ridges, those on the former beating horizontally in the same direction as the currents in the grooves and those in the latter beating upwards, and so carrying material out of the main grooves on to the



Text-fig. 26.—*Pachyseris speciosa*, surface view. ×3. *g.*, groove on surface; *n.*, summit of ridge, itself transversely grooved. For other lettering, see p. 16.

surface of the ridges. Both are shown in text-fig. 26. When the mouths are open the ciliary currents on the oral cone carry material upwards and then pass it into the mouth.

Seizure of Food.—When meat is placed on the surface of the colony there is never any change in the direction of the ciliary currents. The food is carried in the same currents as the waste material. But the mouths, previously hardly perceptible, now become apparent owing to the elevation of the oral cones in the neighbourhood. Food was *never* seen to be swallowed, the mouths having apparently relatively small powers of expansion. But mesenterial filaments are freely extruded as shown in the figure. Food is carried along in the ciliary currents until it is carried to a mouth, seldom the first met, by one of two methods. It may be caught by a mesenterial filament which may pass over one or two ridges to seize it, or it may be entangled in a mucus string, the other end of which is in process of being drawn into the mouth by the action of the cilia lining the stomodaeum. In either case the food comes to rest over the mouth, out of which mesenterial filaments are protruded in large numbers to wrap securely round it. Plankton organisms are secured in this manner. They are apparently paralysed by the nematocysts on the coenosarc as soon as they touch it; mucus is at once secreted, entangling the animal, which is then carried to a mouth by one of the two methods described. The mesenterial filaments of

this coral are exceptionally long, and there is strong evidence that they play an important *rôle* in the capture of prey, and carry out their normal functions of digestion and absorption largely outside the coelenteron.

Remarks.—Alone amongst the corals examined *Pachyseris* possesses no tentacles, the capture of food being carried out by a combination of the nematocysts of the coenosarc acting in co-operation with mucus secretion and the mesenterial filaments. The coelenteric cavity is so small, even when the coral is fully expanded, that digestion and absorption by the mesenterial filaments takes place extracoelenterically. *Pachyseris torresiana* was also examined with similar results.

Atlantic Species.

Agaricia purpurea.—Tortugas.

In his notes Prof. Vaughan states that the tentacles of this coral are short, and arranged in at least three irregular cycles. Meat was seized by them in the usual way, but all vegetable matter refused. Sand-grains were removed, but poorly from the surface of the colony—a fact which he thinks indicates that this coral is ill adapted for living in areas where much silt falls.

Siderastrea radians.—Tortugas.

Prof. Vaughan states that the tentacles of this species are knobbed, and consist of three complete and one incomplete crown corresponding to the septa. The two inner cycles are composed of bifurcate tentacles. Meat was taken by them in the usual way and they were even observed to capture a small jelly-fish (*Linuche*). The mouth is greatly elongated and expanded during the act of swallowing. Mesenterial filaments were frequently extruded. Vegetable matter was not taken. A mixture of carmine and meat-juice was drawn into the mouth exclusively by ciliary action (probably as in *Psammocora*), but sand-grains and carmine alone were slowly removed from the surface of the colony. Duerden (1902) states that *Siderastrea* can capture with its tentacles small annelids.

XII. Eupsammiidae.

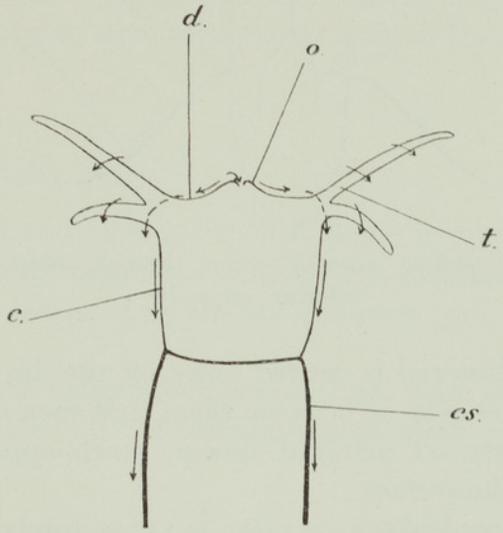
Dendrophyllia nigrescens.—Dredged 14 fathoms, Penguin Channel.

Polyp.—The polyp of this species is large, and capable of great expansion above the skeleton. Thus a polyp 2 cm. in diameter can expand to about that height, as shown in text-fig. 27. There are two rows of tentacles, the inner zones being the larger, but less numerous, there being approximately 18 inner tentacles and 27 outer ones. The mouth is a large transverse slit on the summit of the oral cone.

Calix.—There is a deep cavity with a low but well-developed columella at the base.

Ciliary Currents.—Material is carried off the disc, except on the oral cone region, and away between the tentacles and down the column. The tentacles are very weakly ciliated, the direction of the currents being difficult to determine accurately; they *probably* beat round the tentacles from the inner to the outer side.

Seizure of Food.—Meat is taken readily by the tentacles which contract downward holding it. This applies only to those tentacles in the immediate vicinity of the food ; the others and the polyp generally do not contract. The food is moved in the direction of the mouth, but only slightly, for the oral cone elongates and leans towards the food, which passes down the greatly extended mouth.



Text-fig. 27.—*Dendrophyllia nigrescens*, vertical section. × 2. For lettering, see p. 16.

Balanophyllia regia.—Rock pools near Plymouth.

Apart from its solitary habit this coral is very like *Dendrophyllia*. The polyp has the same characteristics and habits—a large mouth and oral cone, two rows of large tentacles varying in number between 27 and 36 in the specimens examined, and considerable powers of expansion. Food is taken with the same ease as in *Dendrophyllia*, large pieces of meat being swallowed. The ciliary currents agree with those described above, the currents on the tentacles again being weak and beating a little upward on the inner sides, but mainly round to the other side.

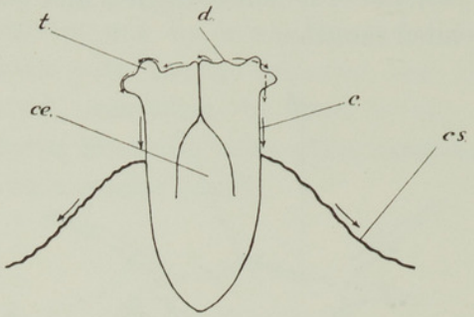
Remarks on the Eupsammiidae.—These corals have large polyps capable of capturing large prey, and relatively weak ciliary currents. They are not true reef-builders (although species of *Dendrophyllia* are common on certain reefs, *D. manni* being conspicuous on the fringing reef at Kaneohe, Island of Oahu, this coral is to be regarded as a deep-water type which has extended its vertical range), and the weakness of the ciliary currents here, as in *Caryophyllia*, are to be attributed to that fact.

XIII. Acroporidae.

Astreopora ocellata.—Low Isles reef.

Polyp.—The maximum degree of expansion observed was about 3 to 4 mm. above the opening of the calix. There are 24 tentacles arranged in two rows and never seen as more than the blunt and stubby protuberances shown in text-fig. 28. The disc is flat or convex, with a small transverse mouth on the summit of a small oral cone. The stomodaeum is very conspicuous owing to its opaque colour, and showing up as a thin, white tube in the centre of the polyp, ending in a white spot at the mouth.

Calix.—There is no columella and the septa are very narrow. As a result the cavities are of exceptional capacity and may measure 6 mm. in depth and 2 mm. in diameter. Each is raised on a protuberance above the general surface of the colony.



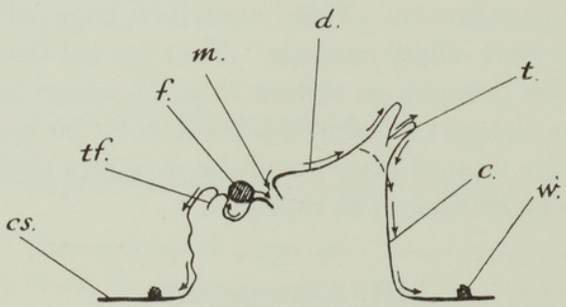
Text-fig. 28.—*Astreopora ocellata*, vertical section through polyp and calyx. × 10. For lettering, see p. 16.

Ciliary Currents.—Material is carried away off the disc, up the inner side of the tentacles and down the outer side, or between them, and then down the column. On the coenosarc the currents carry off material slowly, much opposition being encountered from the rugose nature of the surface.

Seizure of Food.—Zooplankton or meat is taken firmly with the tentacles, which curl inwards, the polyp contracting at the same time. When the tentacles have fully overarched the disc, the polyp by a sudden contraction draws itself completely within the calix, the final process of swallowing being thus hidden from view.

Turbinaria spp.—Low Isles reef.

Polyp.—Several species of this genus were examined, the polyps of all having the same characteristics. They expand freely even in full daylight, forming a cylinder about as high as it is broad, fringed at the top with two rows of small, but very numerous tentacles. The oral cone is unusually small.



Text-fig. 29.—*Turbinaria sp.*, vertical section. ×4. For lettering, see p. 16.

Calix.—Although the calices are large the cavity, owing to the size of the septa and columella, is small.

Ciliary Currents.—Exactly as in *Astreopora*; material is, however, carried away from the surface of the colony more quickly.

Seizure of Food.—Meat is taken by the tentacles, which contract and bend inwards; the disc at that side also contracts, as shown in text-fig. 29, thereby drawing the mouth

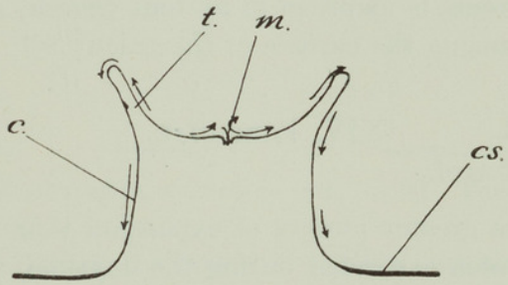
towards the food. Finally the tentacles touch the mouth, which opens; the tentacles are then withdrawn and the food is very quickly swallowed. A more common reaction was the complete contraction of the polyp after food has been taken. If meat is placed on the disc it is carried outwards by the cilia until it meets the tentacles. After contraction the polyps very quickly expand again. The same reaction was obtained with meat-juice, but none with starch or vegetable matter. Living zooplankton, such as copepods, *Sagitta*, medusae and pteropods, were captured as soon as they touched the tentacles and conveyed to the mouth.

Montipora ramosa.—Low Isles reef.

Polyp.—This is small and rounded with a single row of 12 tentacles, as observed never very long, but probably capable of considerable expansion.

Calix.—The cavity is bordered by the six spiniform, principal septa, but within it is relatively capacious.

Ciliary Currents.—As indicated in text-fig. 30, these are exactly as described for *Astreopora*; material is cleared off the coenosarc moderately quickly.



Text-fig. 30.—*Montipora ramosa*, vertical section. ×30. For lettering, see p. 16.

Seizure of Food.—This coral is not easy to observe under laboratory conditions, meat being seldom taken with any readiness. The mesenterial filaments are often extruded in the presence of food.

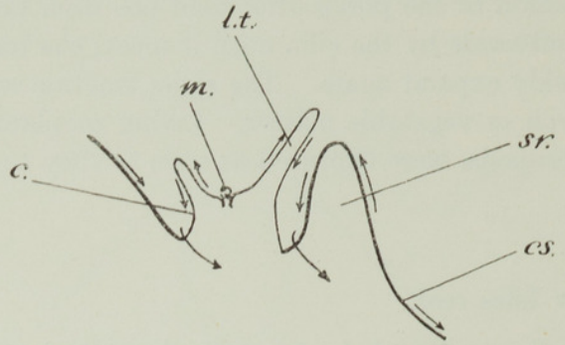
Acropora hebes.—Low Isles reef.

Polyp.—Expands readily, but difficult to observe owing to the quickness with which it contracts while under the binocular. The polyp is rounded, projecting above the skeleton to a height approximating to its diameter. The tentacles vary in number between 6 and 12, according to the position of the polyp. The lowest tentacle, *i. e.* the one opposite to the middle of the cup which surrounds the polyp on its underside, is always larger than the others, as shown in text-fig. 31.

Calix.—The septa are very low and there is no columella, so that a large cavity is provided.

Ciliary Currents.—Exactly as in *Astreopora*, but material is removed from the colony at very great speed, being deflected clear of the polyps. On the cup beneath the polyp currents pass upwards on the outer side and downward on the inner, as shown in the figure. There is an exceptional secretion of mucus in all species of this genus.

Seizure of Food.—Meat or zooplankton is taken by the tentacles immediately it touches them. The polyp then contracts, but expands again directly after.



Text-fig. 31.—*Acropora hebes*, vertical section. ×12. *l.t.*, long tentacle; *sr.*, cup shaped spur on under side of polyp. For other lettering, see p. 16.

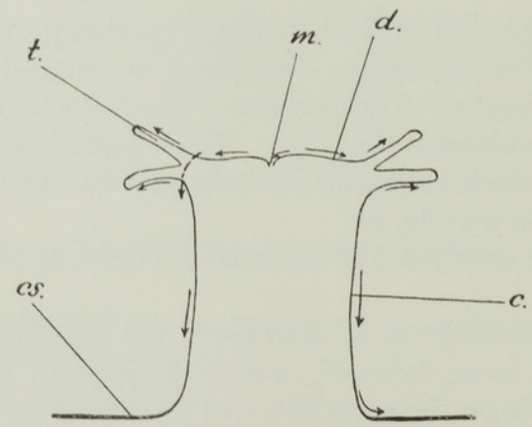
Remarks on the Acroporidae.—All four genera here examined show similar characteristics. Their polyps are well adapted for the seizure of prey without any assistance from the ciliary mechanisms, the comparatively small degree of expansion of the polyps being compensated for in all but *Turbinaria* by the large size of the cavity of the calix. The direction of ciliary currents is identical in all four genera, *Acropora* having the most efficient mechanism for cleansing the surface of the colony.

XIV. Poritidae.

Goniopora tenuidens.—Batt reef.

Polyp.—This possesses greater powers of expansion than probably any other coral polyp. It was frequently seen expanded during the daytime, with the column anything up to 5 cm. long. The polyp is round, with a ring of 24 tentacles arranged in two rows and having an observed power of expansion of up to 0·5 cm. The mouth is a transverse slit on a small oral cone. When the polyp contracts it does so by turning itself inside out, its former bulk disappearing within the calix. Plate II, fig. 6, gives some indication of the appearance, under water, of an expanded colony.

Calix.—This takes the form of a flat depression with almost straight sides and of considerable area, the base being formed of a small central columella and the paliform lobes of the septa.



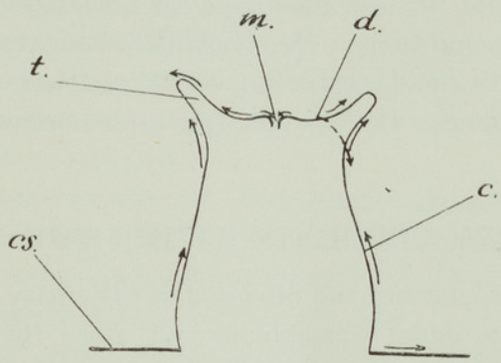
Text-fig. 32.—*Goniopora tenuidens*, vertical section. × 10. For lettering, see p. 16.

Ciliary Currents.—These are indicated in text-fig. 32, and have the usual arrangement, the one point of interest being that on the outer side of the tentacles the currents pass upwards. Material which collects at the tips of the tentacles is either dropped off or else transferred to the outgoing tracts between the tentacles.

Seizure of Food.—This coral does not lend itself to experimentation. Meat is taken by the tentacles and passed to the mouth, which has great powers of expansion, the polyp contracting at the same time. When a comparatively large piece of meat was placed on the mouth mesenterial filaments were extruded. Vegetable matter was refused.

Porites solida.—Low Isles reef.

Polyp.—In spite of its very small size, this has considerable powers of expansion, as indicated in text-fig. 33. There are 12 tentacles in a single row, a flat round disc and a small transverse mouth on a very small oral cone.



Text-fig. 33.—*Porites solida*, vertical section. ×30. For lettering, see p. 16.

Calix.—Of the same type as *Goniopora*, a shallow depression, but somewhat deeper, relatively, and much smaller.

Ciliary Currents.—Exactly as in *Goniopora* except that, as shown in the figure, the currents on the column carry material upwards and not downwards. Material is removed with moderate speed from the coenosarc.

Seizure of Food.—Here again the polyps contract so readily that it is difficult to observe the feeding processes in the laboratory. Meat-juice mixed with carborundum was seen to be taken into the mouth mixed with mucus in long strings.

Prof. Vaughan in his notes states that in *Porites calvaria* meat-juice and carmine are drawn in, the tentacles bending inward. The process is clearly the same as that described for *Psammocora*, material being drawn up the column and then over the outer sides of the tentacles and so to the mouth. He also saw a small worm caught, killed and swallowed by a polyp of *Porites asteroides*. Vegetable matter was invariably refused.

Remarks on the Poritidae.—Prof. Vaughan's observations and my own are in agreement, showing that these corals can secure their food by means of their tentacles, aided somewhat in the case of *Porites* (a small polyped coral with a smaller range of activity) by the cilia on the column and outer side of the tentacles.

B. ALCYONARIA.

Representatives of two genera of alcyonarian corals, *Heliopora* and *Tubipora*, were obtained. Although polyps of the first-named were seen, it was never possible to study them under the microscope. *Tubipora* did not occur on Low Isles, and failed to stand

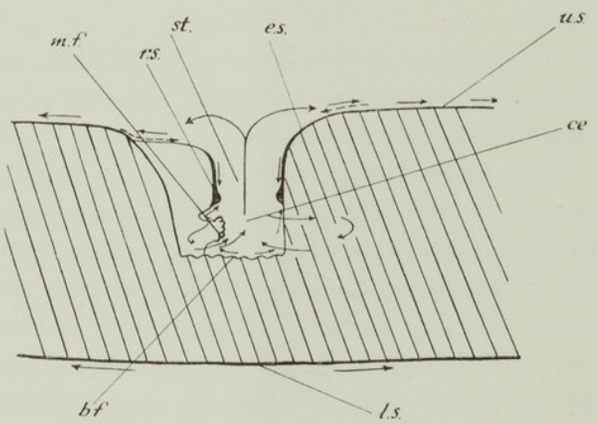
transportation from Batt reef, seven miles away. There is, however, no reason for thinking that these polyps are in any way different from those of other Alcyonaria. Pratt (1905) found that after a colony of *Alcyonium digitatum* had been for some time in water containing great quantities of zooplankton, " the surface of the tentacles was dotted with hundreds of paralysed Nauplii and Copepods. Occasionally a tentacle would curl inwards and deposit its captured prey within the mouth. Usually, however, the zooids, with tentacles outspread, remained expanded for quite an hour, then the colony slowly contracted. . . ." I have been able to confirm these observations at Plymouth, and to note in addition the absence (or very weak development) of cilia upon the zooids and general surface of the colony. The polyps of *Tubipora* are invariably expanded, even in the brightest light.

C. HYDROZOA.

Millepora was abundant in the anchorage at Low Isles. It refused, however, to expand under laboratory conditions. Mr. Nicholls when examining *Millepora* for zooxanthellae found in one case a small crustacean, 0·176 mm. long, which completely occupied the coelenteron of a gastrozooid. Beutler (1926) has demonstrated the carnivorous nature of the hydroids.

6. CILIARY CURRENTS WITHIN THE POLYP.

In order to determine the nature and direction of the ciliary currents within the polyp, a large specimen of *Fungia danai* was split in half along the long axis of the mouth, and then embedded upright in plasticene with the exposed coelenteron uppermost, as shown in text-fig. 34. It was then just covered with sea-water and the ciliary currents examined under the binocular.



TEXT-FIG. 34.—*Fungia danai*; individual split along the long axis of the mouth to expose the coelenteron. × 1½. *b.f.*, base of fossa; *e.s.*, edge of septum; *l.s.*, lower surface of animal; *r.s.*, ridge at base of stomodaeum; *u.s.*, upper surface. For other lettering, see p. 16.

As shown in the figure, the ciliary currents on the stomodaeum carry material downwards as far as the thickened lower margin (*r.s.*). Food is then seized by the filaments. There is a definite circulation within the coelenteron. Material is drawn in between the septa immediately beneath the lower end of the stomodaeum and circulates in the interseptal spaces beneath the disc. It is finally conveyed back to the base of the central fossa, as shown in the figure. Currents beat outwards from the centre of the base of the fossa and

then upwards on the edges of the septa ; on the mesenterial filaments particles are carried to the thickened, glandular margin and thence upwards. Inedible matter thus gradually accumulates beneath the base of the stomodaeum. A great deal of mucus is secreted, and sooner or later this material is lifted clear of the surface by this means. It then comes under the influence of the upwardly directed, compensating current in the centre of the coelenteron. Long mucus strings are drawn out of the mouth in this manner and conveyed on to the surface of the disc, where they are carried away by the outgoing tracts of cilia. If the mucus strings are long, as soon as the one end falls on to the disc the remainder is pulled out over the stomodaeum. In *Fungia* no outgoing tracts of cilia were found on the stomodaeum, nor was any reversal of cilia noted. It is generally true that when waste matter is removed from the coelenteron of any coral the mouth opens wide so as to permit the development of powerful outward currents.

A specimen of *Lobophyllia corymbosa* was examined in the same way, and with results of a similar character. On certain regions of the endoderm below the stomodaeum there appeared, however, to be a rhythmically reversible beat of the cilia, which carried particles first in one direction and then in the other. It did not appear to be influenced by the pull of adjacent cilia on mucus strings, or by muscular contractions. On the remainder of the endoderm the cilia beat upwards.

When the almost transparent polyps of *Pocillopora* are fully expanded, balls of matter can be seen passing up and down the hollow tentacles, rotating the whole time, and spinning round when they reach the blind, distal end. A similar up-and-down movement was also seen within the coelenteron.

Within the polyp, therefore, material is circulated freely, the mesenterial filaments seizing anything of food value and the remainder being finally ejected through the widely opened mouth.

7. DISCUSSION.

In spite of the difficulties of observation outlined in Section 3, the nature of the feeding processes in corals has been considerably elucidated. Corals feed on living animal prey, capturing it by means of the nematocysts on the tentacles, on the general surface of the coenosarc and on the mesenterial filaments. It is then conveyed to the mouth by means of tentacles, ciliary currents or mesenterial filaments. Mucus, as always in animals with a great development of cilia, is secreted in large quantities and plays an important *rôle* both in cleansing the surface and in entangling food.

The feeding reactions of typical Madreporaria, by which is meant the deep- or cold-water cup corals, such as *Flabellum*, *Caryophyllia* or *Balanophyllia*, and reef builders with large polyps and prominent tentacles, such as *Euphyllia*, *Echinopora*, *Favia* or *Goniopora*, are essentially the same as those of the Actiniaria, which have been described in detail by Parker (1917). Duerden (1902) has described the musculature and some of the reactions of the polyps of West Indian corals. Following stimulation by food the tentacles bend inwards as a result of muscular contraction. At the same time the disc sinks in the region beneath, the result of contractions of the vertical muscles in the mesenteries beneath. Contractions of the horizontal muscle strands in the mesenteries cause the mouth and stomodaeum to open. The extension of the oral cone, so pronounced in certain corals, *e. g. Galaxea*, is associated with a contraction of the disc and the forcing out of the cone by water pressure, the direction in which it turns being conditioned by local contractions of

the radial muscles. In certain corals, the meandrines in particular, the circular musculature of the column is especially thick near the base of the tentacles, forming a well-marked sphincter, the contractions of which cause the edge-zone tissue to overarch the disc, the tentacles contracting and being folded underneath. Carpenter (1910) has described in detail the operation of the sphincter in *Isophyllia*. Food is carried into the coelenteron by the ciliary currents on the walls of the stomodaeum, and once within it is seized by the mesenterial filaments. Smaller particles are circulated through the cavity in currents created by ciliary activity, and are grasped by the mesenterial filaments if of food value, or rejected, together with the indigestible residue of the food, in the compensating outward current through the mouth. Madreporarians are, like Actinians, in the words of Parker (1917), " more nearly a sum of parts than a unit."

The most conspicuous difference between such corals and actinians is the greater development in the former of cilia. These cover the surface of the ectoderm and, with the exception of those on the oral cone and in the stomodaeum, are used, in co-operation with mucus, for cleansing the surface of the body. Thus they are more powerfully developed in the reef builders, such as *Favia* and *Echinopora*, which live in shallow water, where there is a greater fall of silt, than in the deep-water corals, such as *Flabellum* and *Balanophyllia*.

Many reef building corals are undoubtedly specialized. The deep- or cold-water coral, whether it be imperforate, such as *Flabellum*, *Lophohelia* or *Caryophyllia*, or perforate, like *Dendrophyllia* or *Balanophyllia*, has large polyps and a relatively small skeleton. The reef builders have massive skeletons and frequently small and very numerous polyps. Further evidence of specialization is afforded by the development of ciliary currents, first as more efficient cleansing mechanisms, and then as an aid to, and finally as an essential part of, the feeding processes. The result of these specializations is to fit reef corals for the capture of zooplankton organisms of all sizes. Since these are, on the average, small and the total supply is, though adequate, never excessive, highly specialized feeding mechanisms are essential for the capture of the necessary quantity of food.

Corals with small polyps, such as *Seriatopora*, *Pocillopora*, *Stylophora*, *Leptastrea*, *Cyphastrea* or *Porites*, have upwardly directed ciliary currents on the column and the outer sides of the tentacles, so that food captured by the nematocysts on the surface of the coenosarc between the polyps is conveyed in this manner to the mouth. In the same way in *Psammocora* and (presumably) *Pavona*, where there is no column, the tentacles by bending inward towards the mouth cause food to be conveyed to it in the ciliary currents on their outer sides. In all these cases ciliary currents aid in food collection, but the tentacles retain the controlling influence, being able to pass the food to the mouth or to reject it according to the state of contraction or expansion. This results frequently in an erroneous impression of ciliary reversal. In the above instances the cleansing function of the cilia, as revealed by observations under the binocular microscope, is not apparently seriously impeded except in *Leptastrea*, where water movements are probably partially responsible for the efficient cleaning of the surface of the colony. It will be shown, however, in a later paper in this volume by Marshall and Orr, that, unless they are aided by water movements, corals with small polyps such as *Porites* and *Psammocora*, do not cleanse themselves so efficiently under natural conditions, as those with large polyps like *Favia*, *Symphyllia* and *Fungia*.

This utilization of the cilia without any reversal of their currents as a means of food

conveyance is most highly developed in two genera of the Agariciidae, *Coeloseris* and *Pachyseris*. In the former all material which falls on to the surface of the colony is carried to the polyps, the tentacles merely assisting in a minor degree and never selecting or rejecting matter for conveyance to the mouth. Water movements are essential for the cleansing of the surface, the cilia having lost that function except in so far as inedible matter is accumulated in balls over the polyps and so rendered the easier to remove. In *Pachyseris* tentacles have been lost, their place being taken in part by the mesenterial filaments, the importance of which in food capture will be discussed a little later. Material is carried over the surface of the colony by ciliary action and so passed close to many mouths which, if it is edible, may take it in, either in mucus strings or by means of the filaments. Here again waste matter is largely removed by water currents.

A second type of ciliary feeding mechanism is found exclusively in the meandrines and in the Fungiidae. Though the currents are normally concerned with the removal of material from the surface of the colony, yet after stimulation with food they reverse, and food, with any other material in the vicinity, is carried to the mouth. Although now discredited for all other metazoan phyla, the reversal of ciliary currents in Actiniaria has been established with certainty by Parker (1896, 1905) and Parker and Marks (1928), who worked on *Metridium*. A local reversal of ciliary current follows stimulation with meat-juice or potassium ions and, as Parker (1928) has more recently found, also glycogen. The significance of this last finding will be discussed in the next paper in this series.

In Madreporaria reversal of ciliary current only occurs in genera or species with tentacles too small to range over the surface of the disc or the adjacent coenosarc or to convey food to the mouth. Thus in the meandrines reversal was found in *Merulina* and *Tridacophyllia*, where the tentacles are sparse and minute, and also by Vaughan (1912, 1919) in *Maeandra* [=*Manicina*] *areolata*. In the fungids all species examined, whether of the genus *Fungia*, *Herpetolitha* or *Polyphyllia*, showed reversal except the one species, *Fungia actiniformis*, where, alone in the Fungiidae examined, the tentacles are of great size. There seems no doubt that the reversal of ciliary currents in the Madreporaria is correlated with a reduction in the size of the tentacles, although as we have seen, these may be reduced without ciliary reversal being developed.

The size and nature of the cavity within the calix has been emphasized, and with intent, in the review of feeding mechanisms. It has been shown that when normally expanded the great majority of corals have a coelenteric cavity raised above the skeleton and large enough to accommodate a relatively large animal of the plankton. In cases where there is no columella and the cavity consequently large, *e. g.* in *Euphyllia*, *Coeloseris*, *Astreopora* and the fungids, the polyp is never raised to any great height above the skeleton. Where, on the contrary, there is a large columella and practically no cavity, as in *Echinopora*, *Hydnophora* or *Goniopora*, the polyp raises itself relatively high above the surface of the skeleton. In other cases mesenterial filaments are freely extruded and digestion and absorption are carried out in part or wholly extra-coelenterically. This appears to be the normal procedure in *Pachyseris*, and occurs also in *Stylophora*, *Galaxea*, many meandrines, and *Montipora*. Carpenter (1910) and Vaughan (1912) have both emphasized the importance of this extrusion of the filaments in Atlantic genera.

This capacity for raising their tissues high above the skeleton and of extruding, if necessary, mesenterial filaments, renders valueless any conclusions drawn from the structure of the calix as to the ability or inability of corals to swallow food. Thus

Matthai (1914) states that in *Galaxea musicalis* the primary septa press against the stomodaeum and almost occlude the lumen, and suggests that this implies "an imperfect functional capacity" which he correlates with the great abundance of zooxanthellae.

Vegetable matter is invariably refused by corals, Vaughan's observations on Atlantic corals and the present ones on Indo-Pacific corals agreeing completely in this. Meat of any kind or living zooplankton is invariably taken if the coral is sufficiently expanded. The latter form the natural food of the corals, for the capture of which they are admirably equipped, as the foregoing review of feeding mechanisms has, it is hoped, made abundantly evident. A point of the very greatest importance is the extent of the *capturing surface* which is far greater in proportion to the bulk of the tissues than in any other group of animals. When fully expanded the tentacles of such genera as *Galaxea*, *Favia*, *Coeloria*, *Lobophyllia* or *Symphyllia* cover the entire surface of the colony and may elongate till from 3 to 5 cm. in length. Large planktonic organisms are caught with ease and sureness. The fungids can secure prey equally well by means of the short tentacles and the wide surface of the disc. Corals with small polyps expose a surface almost as great but, as it were, without the same depth, and are specialized for the capture of smaller organisms.

The colony must be considered as an individual possessing many mouths and an equal number of digestive systems, and not as so many individual polyps. The actual amount of tissue is very small, a thin skin over the surface of the colony, with fine internal extensions in the case of the perforate corals, and the amount of food required must be very small. Although corals grow with considerable speed, the increase in the tissues is more apparent than real, for the increase in the size of the skeleton, the result of calcium metabolism within the tissues, is separate process from that of tissue growth.

A considerable controversy exists regarding the food of Madreporaria which possess zooxanthellae, that is the reef builders. Gardiner (1899, 1901, 1902–3, 1904, 1928), Gravier (1908) and Boschma (1924, 1925*a*, 1925*b*, 1926) all consider that the algae form a part at least of the food, while Murray (1889), Duerden (1902, 1906), Carpenter (1910), Vaughan (1912) and Mayer (1918) all hold the opinon that zooplankton exclusively form the food of corals. This is not yet the time to enter into this controversy. It has been shown in this paper that corals *do* possess the necessary feeding mechanisms for the capture of living zooplankton. The vexed question of the absence of animal food in the coelentera of corals, on which Gardiner in particular lays great stress, will be discussed in the light of the results of work on the digestive processes, which forms the subject-matter of the next paper in this series. The significance of the algae will be discussed later still.

Corals, as a general rule, expand only at night when, as the results of the investigations on plankton will make abundantly clear, their food is most abundant. There are a few exceptions which are always expanded in the daytime. Some of them have been noted in the course of this paper, *Pocillopora*, *Euphyllia*, *Fungia actiniformis* and *Goniopora* being the most conspicuous. On occasion colonies of *Seriatopora*, *Favia* (see Plate I, fig. 1), *Hydnophora*, *Herpetolitha*, *Pavona* (once only) and *Porites* were seen expanded in the light. *Tubipora* and the other alcyonarians are regularly expanded during the day—a fact which may be correlated with the more passive nature of the capturing surface.

In conclusion it seems advisable to stress a fact too often overlooked, namely, that when an animal possesses an organ or set of organs which perform certain functions with perfect efficiency, it can be taken as axiomatic that such organs are used.

8. SUMMARY.

1. The feedings mechanism of species of forty genera of Madreporaria have been examined.

2. In all cases satisfactory evidence was found that such corals capture and devour living zooplankton.

3. Vegetable matter was invariably refused, in almost all cases by the tentacles, but failing them by the mouth or the coelenteron.

4. In the less specialized corals with large polyps the tentacles exclusively are concerned with food capture.

5. The ectoderm of all corals is thickly ciliated. The original function of the currents created by the beating of the cilia is the removal of silt and waste material from the polyps and the general surface of the colony.

6. In a number of cases these ciliary currents also assist in the transport of food to the mouth (apart from the cilia on the oral cone and on the walls of the stomodaeum, which are always concerned with the transport of food).

7. In such cases the removal of material from the surface may be assisted by water movements.

8. In certain of the Agariciidae, where the tentacles are reduced or lost, ciliary currents are exclusively concerned with the transport or presentation of food to the mouth, water movements being alone responsible for the cleansing of the surface of the colony.

9. Where tentacles are very small the reversal of ciliary currents may follow stimulation by food. The currents have thus a double function. Reversal was observed only in the meandrines and in the Fungiidae and only in genera or species with small tentacles, the correlation between the two being clear.

10. The power of expansion above the skeleton is such that a large coelenteric cavity may be formed even though the cavity within the calix is obliterated by large septa or a prominent columella.

11. Mesenterial filaments are freely extruded in certain genera where the power of expansion is limited, or where the food is too large to be swallowed at once. Digestion and absorption in these cases take place, in part or wholly, extra-coelenterically.

12. There is a definite circulation within the coelenteron caused by ciliary currents ; any food material is seized by the mesenterial filaments and the remaining material with excreta is rejected through the mouth-opening.

13. Like actinians, Madreporaria are " more nearly a sum of parts than a unity " (Parker), prey being paralysed by the nematocysts on the tentacles or other regions of the ectoderm and conveyed to the mouth by local muscular or ciliary action, with the assistance of mucus in the latter case.

14. Corals are carnivores with highly developed feeding mechanisms, those of the different genera of reef builders being specialized for dealing with zooplankton of all sizes.

15. A few genera are always found expanded in the daytime, others very occasionally, but the great majority only expand in the darkness, when alone zooplankton is abundant.

9. REFERENCES.

Beutler, R. 1926. Beobachtungen an gefütterten Hydroidpolypen. Z. vergl. Physiol. III (= Abth. C. Z. wiss. Biol.), pp. 737–775, pl. iv, text-figs. 1–12.

Boschma, H. 1924. On the Food of Madreporaria. Proc. Akad. Wet. Amst. XXVII, pp. 13–23, text-figs. 1, 2.

—— 1925*a*. On the Symbiosis of Certain Bermuda Coelenterates and Zooxanthellae. Proc. Amer. Acad. Arts Sci. LX, pp. 451–460, text-fig. 1.

—— 1925*b*. On the Feeding Reactions and Digestion in the Coral Polyp *Astrangia danae*, with Notes on its Symbiosis with Zooxanthellae. Biol. Bull. Wood's Hole, XLIX, pp. 407–439, text-fig. 1.

—— 1926. On the Food of Reef-Corals. Proc. Akad. Wet. Amst., XXIX, pp. 993–997.

Carlgren, O. 1905. Über die Bedeutung der Flimmerbewegung für den Nahrungstransport bei den Actiniarien und Madreporarien. Biol. Zbl. XXV, pp. 308–322, text-figs. 1–6.

Carpenter, F. W. 1910. Feeding Reactions of the Rose Coral (Isophyllia). Proc. Amer. Acad. Arts Sci. XLVI, pp. 149–162, pl. i, text-figs. 1, 2.

Duerden, J. E. 1902. West Indian Madreporarian Polyps. Mem. Nat. Acad. Sci. Washington, VIII, pp. 399–597, pls. i–xxv, text-figs. 1–18.

—— 1906. The *Rôle* of Mucus in Corals. Quart. J. Micr. Sci. XLIX, pp. 591–614, text-figs. 1–6.

Gardiner, J. S. 1899. The Building of Atolls. Proc. Fourth Int. Congr. Zoology, pp. 118–123, pl. i.

—— 1901. On the Rate of Growth of some Corals from Fiji. Proc. Camb. Phil. Soc., XI, pp. 214–219.

—— 1902–03. The Maldive and Laccadive Groups with Notes on other Coral Formations in the Indian Ocean. The Fauna and Geography of the Maldive and Laccadive Archipelagoes, I, Parts 3 and 4.

—— 1904. The Formation of Coral Reefs. Nature, Lond. LXIX, pp. 371–373, text-figs. 1–4.

—— 1928. Coral Reefs and Islands. Science of the Sea, 2nd edition, edited by E. J. Allen, pp. 121–149, text-figs. 13–29.

Gravier, C. 1908. Sur quelques traits de la biologie des récifs coralliens. Bull. Soc. philom. Paris, ser. 9, X, pp. 144–162.

Hoffmeister, J. E. 1925. Some Corals from American Samoa and the Fiji Islands. Pap. Dept. of Mar. Carn. Instn. Biol. XXII, pp. 1–90, pls. A and i–xxiii.

Matthai, G. 1914. A Revision of the Recent Colonial Astraeidae possessing distinct Corallites. Trans. Linn. Soc. Lond. Zool. XVII, pp. 1–140, pls. i–xxxviii.

—— 1928. Catalogue of the Madreporarian Corals in the British Museum (Natural History). Vol. VII. A Monograph of the Recent Meandroid Astraeidae. British Museum, London, 288 pp., pls. i–lxxii, text-figs. 1–35.

Mayer, A. G. 1918. Ecology of Murray Island Reef. Pap. Dept. of Mar. Biol. Carn. Inst. IX, pp. 1–48, pls. i–xix, text-figs. 1–9.

Murray, J. 1889. Structure, Origin and Distribution of Coral Reefs and Islands. Nature, Lond. XXXIX, pp. 424–428.

Parker, G. H. 1896. The Reactions of *Metridium* to Food and other Substances. Bull. Mus. Comp. Zoöl. Harv. XXIX, pp. 107–119.

—— 1905. The Reversal of Ciliary Movement in Metazoans. Amer. J. Physiol. XIII, pp. 1–16.

—— 1917. Actinian Behaviour. J. Exp. Zool. XXII, pp. 193–229.

—— 1928. Glycogen as a means of Ciliary Reversal. Proc. Nat. Acad. Sci. Wash. XIV, pp. 713–714.

Parker, G. H., and Marks, A. P. 1928. Ciliary Reversal in the Sea Anemone *Metridium*. J. Exp. Zool. LII, pp. 1–6.

Pratt, E. M. 1905. The Digestive Organs of the Alcyonaria and their Relation to the Mesogloeal Cell Plexus. Quart. J. Micr. Sci. XLIX, pp. 327–362, pls. xx–xxii.

Vaughan, T. W. 1907. Recent Madreporaria of the Hawaiian Islands and Laysan. Bull. U.S. Nat. Mus. No. 59, pp. ix + 427, pls. i–xcvi, text-fig. 1.

—— 1912. Studies of the Geology and of the Madreporaria of the Bahamas and of Southern Florida. Yearb. Carnegie Inst. No. 11, pp. 153–162.

—— 1918. Some Shoal-Water Corals from Murray Island (Australia), Cocos-Keeling Islands and Fanning Island. Pap. Dept. of Mar. Biol. Carn. Instn. IX, pp. 49–234, pls. xx–xciii, text-figs. 1, 2.

—— 1919. Corals and the Formation of Coral Reefs. Annu. Rep. Smithson. Inst. 1917, pp. 189–276, pls. i–xxxvii, text-figs. 1–16.

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DESCRIPTION OF PLATE I.

FIG. 1.—*Favia sp.*; expanded in daylight, upper portion of colony out of water. × $\frac{1}{3}$.

FIG. 2.—*Lobophyllia corymbosa*; flashlight photograph when expanded at night. × $1\frac{1}{2}$.

FIG. 3.—*Fungia danai*; normal appearance in life. × $\frac{1}{4}$.

FIG. 4.—*Fungia actiniformis*; normal appearance in life. × $\frac{1}{2}$.

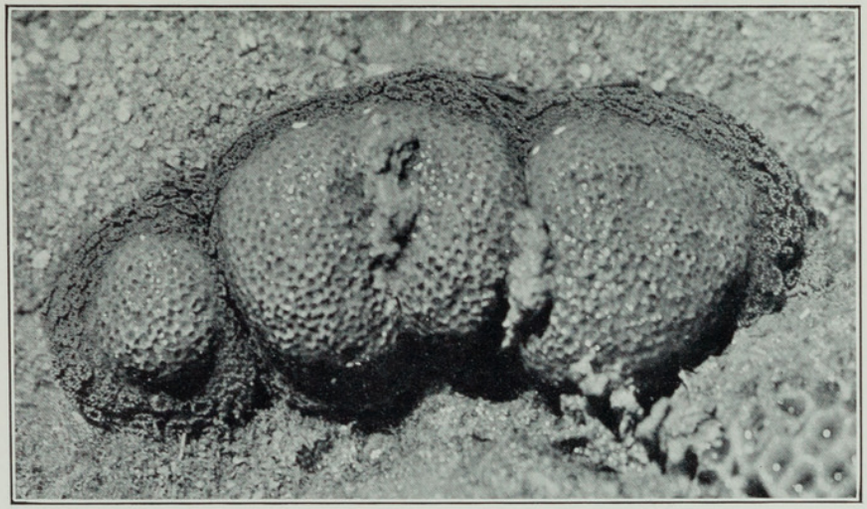

Photo G. W. Otter.] FIG. 1.

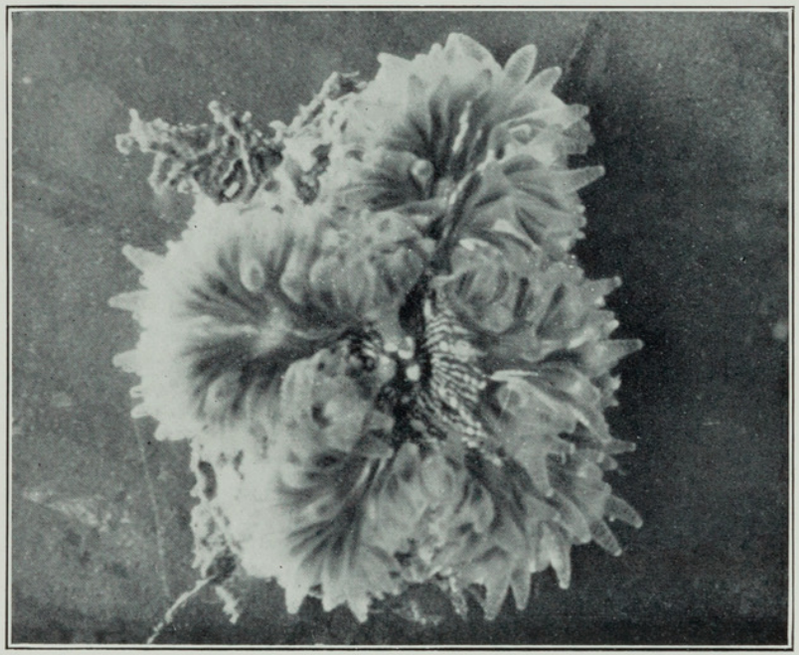

Photo S. M. Manton.] FIG. 2.

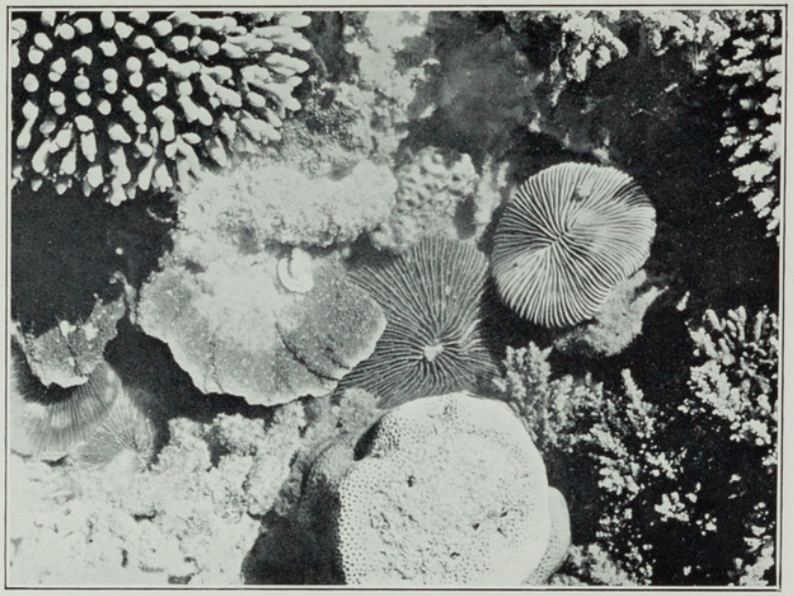

Photo G. W. Otter.] FIG. 3.

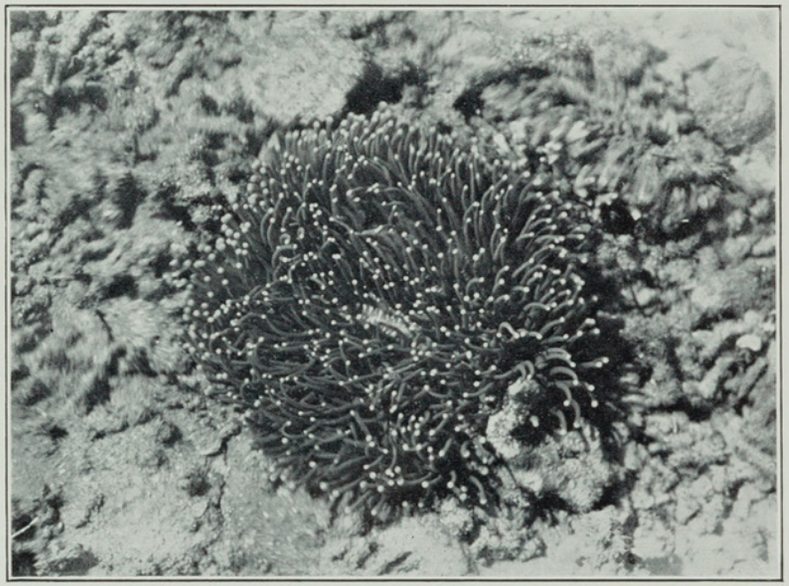

Photo G. W. Otter.] FIG. 4.

[*Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE II.

FIG. 5.—*Pachyseris speciosa*; upper surface of skeleton, showing arrangement of ridges. × 1½.

FIG. 6.—*Goniopora tenuidens*; colony expanded in daylight under normal conditions. × ½.

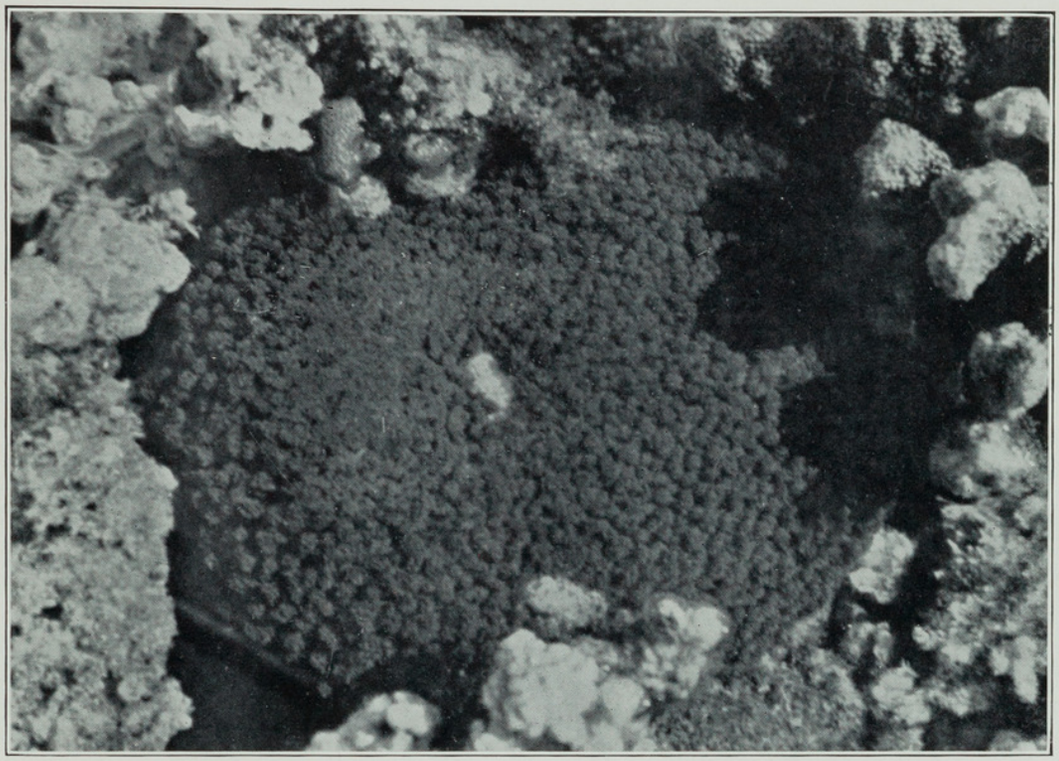

Photo M. J. Yonge.] FIG. 6.

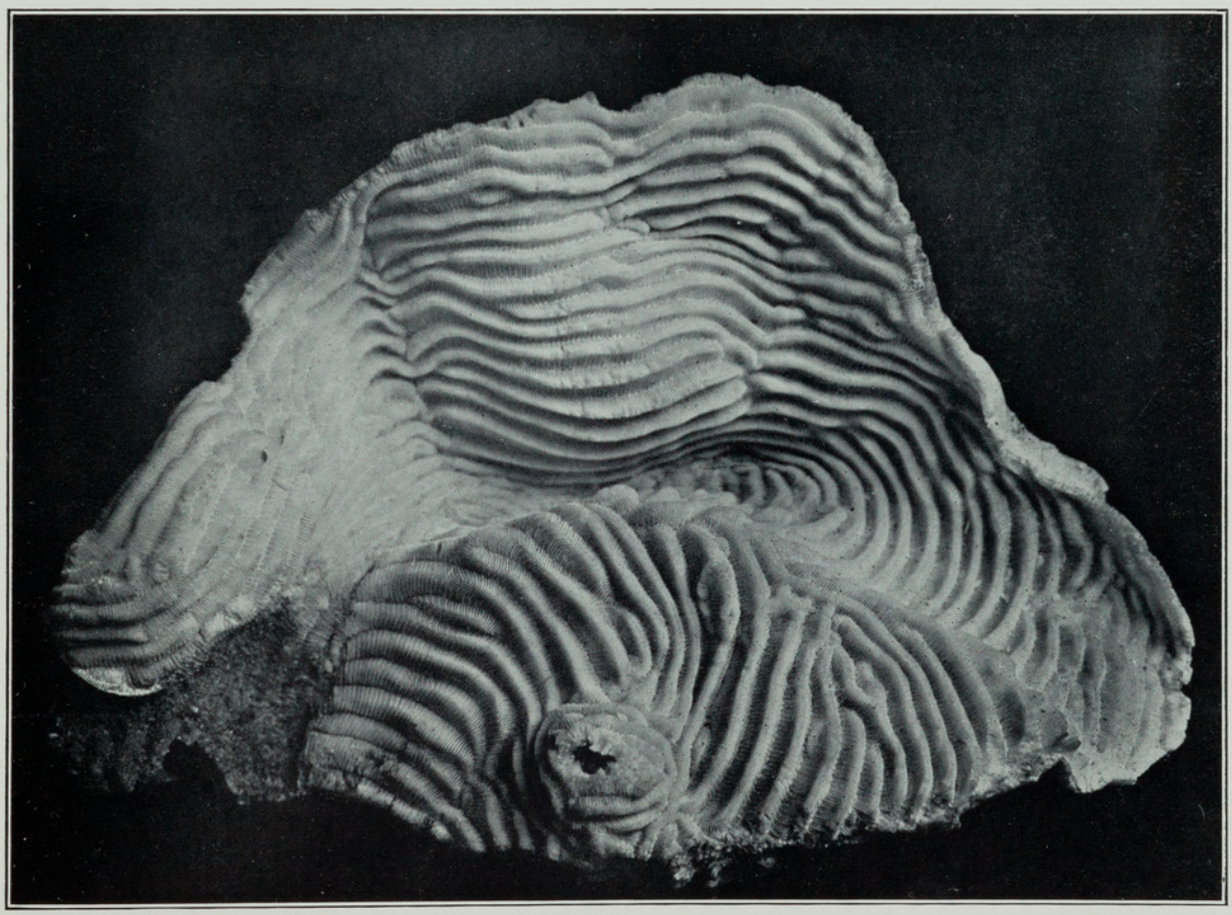

Photo Heath & Stoneman.] FIG. 5. [*Adlard & Son, Ltd., Impr.*