CORALS AND THE FORMATION OF CORAL REEFS.[1]

By Thomas Wayland Vaughan.

[With 37 plates.]

CONTENTS.

INTRODUCTION.

Corals have long attracted the attention and excited the interest of scientific men, observant laymen, and poets. For some hundreds of years they were thought to be marine plants and were termed "Zoophytes," a name said to have been given them in the sixth century by Sextus Empiricus and Isodore of Seville. Notwithstanding that Ferrante Imperato in 1599 advocated that corals were animals, naturalists persisted in believing that they were plants until

---

[1] In the present article only a few specific references to the literature on corals and coral reefs have been introduced. However, in my memoir entitled "Fossil corals from Central America, Cuba, and Porto Rico, with an account of the American Tertiary, Pleistocene, and Recent coral reefs," in press as a part of U. S. National Museum Bulletin 103, I have given fairly full bibliographic citations and have called attention to certain publications, particularly those by W. M. Davis and R. A. Daly, in which there are elaborate reviews of the literature on coral reefs.

Peysonnel announced the results of his laborious investigations in the West Indies, and even after his observations were published in 1753, a few perverse individuals continued to adhere to the old views. It now seems strange that Peysonnel's researches constituted one of the important advances in our knowledge of the animal kingdom.

Of the early savants, Patrick Brown in his "Civil and Natural History of Jamaica," 1756, Seba in his "Locupletissimi rerum naturalium Thesauri accurata descriptio," 1758, Knorr in his "Deliciae selectae naturae," 1771, and many others described and figured many corals; and much pleasure may be derived from the text and the carefully executed figures of these authors. One of the most delightful of story-tellers and lyric poets, Adelbert de Chamisso, exiled from France as a result of the French Revolution and a refugee in Germany, was one of the early contributors to coral-reef theories. He described one species of stony coral and published exquisite figures of it based on his own drawings. Though the enthusiasm of many of the early writers on this subject is inspiring and their charm is great and though the temptation is strong to yield to their spell and consider the subject only as they so fascinatingly present it, attention must be diverted from them and directed toward the objects themselves.

WHAT ARE CORALS?

Since the days of Peysonnel all informed students, except the few perverse individuals to whom allusion has been made, have believed that corals are not merely animals but that they are animals closely akin to the sea anemones. Like sea anemones, they are, at least while young, more or less cylindrical in form; the lower end, called the foot, is attached to some object; around the margin of the flattish upper end there are tentacles that can be extended or retracted; and near the middle of a flattish area within the tentacles there is a slit-like mouth that can be widely opened or closely shut. Below the fleshy floor between the tentacles and the mouth there are folds of soft tissue, known as mesenteries, that are attached to the wall on their outer ends, but on their inner ends they are free below a rather short tube, called the gullet or esophagus. On the edges of the mesenteries there are often curled filaments, called mesenterial filaments. Figures 1 and 2 on plate 1 are illustrations of two Blaschka glass models of sea anemones.

One of the peculiarities of corals and related animals is that the outer surface of the animal tissue, including the tentacles and the mesenterial filaments, are beset with lasso stinging-cells (see text fig. 4, p. 207), each of which may shoot out a small dartlike object that at one end is attached by a thread. Another peculiarity is that their outer surface secretes slimy mucus; and a third attribute is that their surfaces are covered with small short processes, termed cilia, which under certain conditions beat so as to move the mucus and whatever may be embedded in it toward the mouth, while under other conditions they beat so as to move things away from the mouth.

Sea anemones and corals are alike in the characters so far considered. They differ in that sea anemones have only soft tissues, while the lower surface of corals secretes a skeleton, called the corallum, composed mostly of carbonate of lime. Coral larvae, called planulae, are small, pear-shaped or cylindrical objects, about half a millimeter in diameter and about a millimeter long, and their outer surface is covered with cilia by means of which they can move rapidly. After a time, ranging from a day or two to two or three weeks, the larval corals settle and attach themselves to some object. At first a flat basal plate is secreted by the bottom end, and on this are laid down radial plates that grow upward within or between the mesenterial folds. Above each of the radiately arranged plates, known as septa, there is a tentacle. At their outer ends the septa are joined together by a wall, differing in character according to the kind of coral, and at the inner ends of the septa there is usually, but not always, a central columella, which likewise differs in character according to the kind of coral. In the spaces between the septa peculiar structures that are of much value in classifying corals may develop.

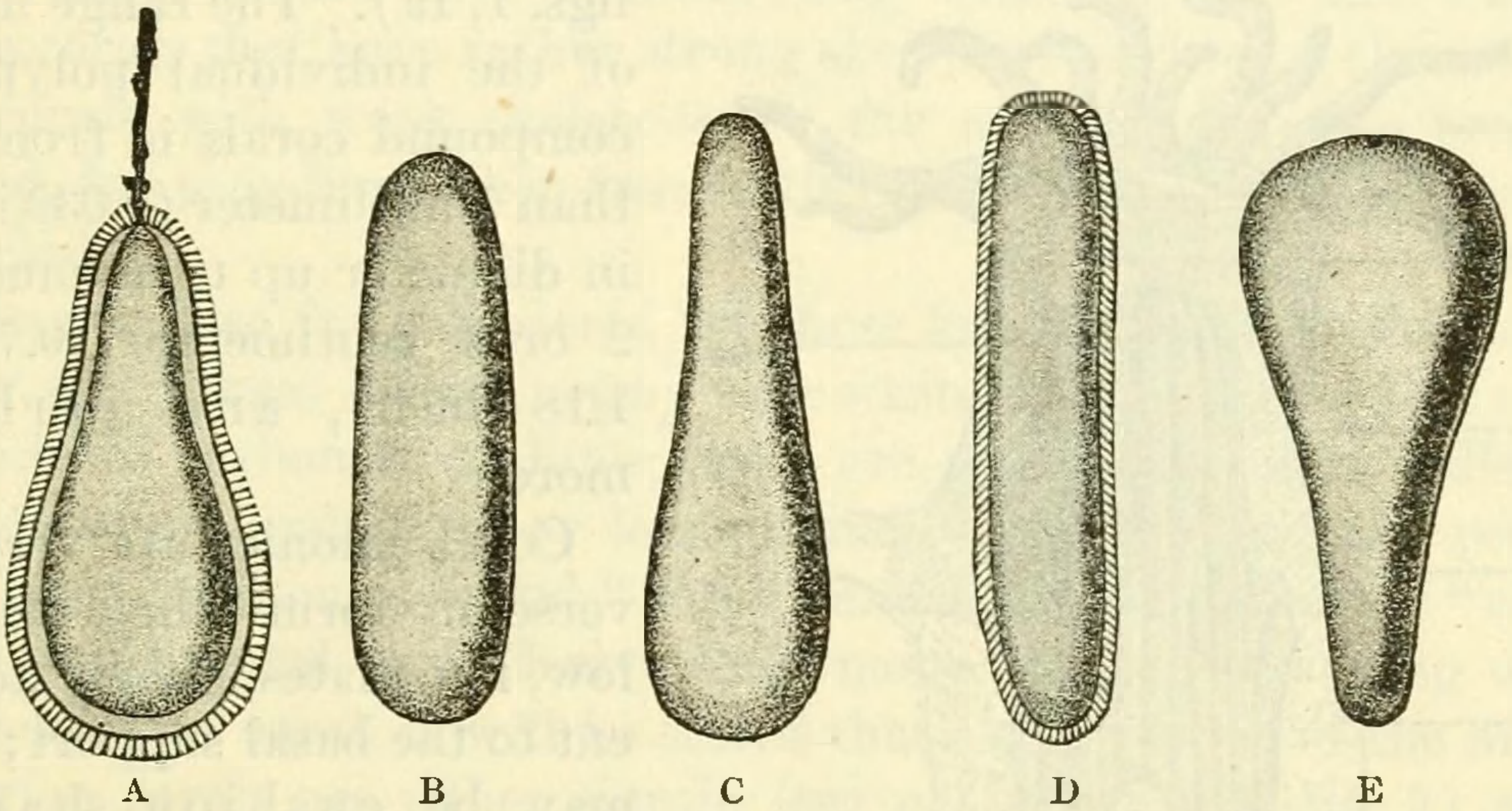


FIG. 1.—LARVAE OF THE CORAL. *Favia fragum* (ESPER), MUCH ENLARGED. AFTER DUERDEN. THE VARIOUS FORMS OF THE LARVAE IMMEDIATELY AFTER EXTRUSION ARE REPRESENTED. A IS VIEWED AS A TRANSPARENT OBJECT; B TO E ARE REPRESENTED AS SEEN BY REFLECTED LIGHT. THE EXTRUSION OF CELL DÉBRIS THROUGH THE ORAL APERTURE OF A IS SHOWN.

Some corals remain simple, that is solitary, throughout their lives (some of these are shown on pls. 3 and 12 to 14); while others multiply asexually and form colonies. There are two kinds or methods of asexual reproduction recognized by students of these organisms. One of these methods, termed budding or gemmation, is by a bud appearing on the surface of the soft tissues outside the circle of tentacles (pl. 2, fig. 1); the other method, known as fission, is by a mother coral polyp dividing equally or unequally and forming two or more polyps (pl. 2, fig. 2). Budding or fission may be repeated until from an initial polyp only 1 or 2, or perhaps 5 millimeters in diameter, a colony, a compound coral, many feet in diameter may result, with thousands of individual polyps, each having its own more or less clearly recognizable mouth, but all joined together by communal soft tissue known as coenosarc.

Corals that remain simple may be small, 5 or 6 millimeters (about one-fifth inch) in diameter, or they may be rather large, up to as much as 250 millimeters, nearly a foot, in diameter, as in some species of the genus *Fungia* (pl. 3, figs. 1, 1a). The range in size of the individual polyps in compound corals is from less than 1 millimeter (0.039 inch) in diameter up to as much as 2 or 3 centimeters (0.78 or 1.18 inch), and perhaps more.

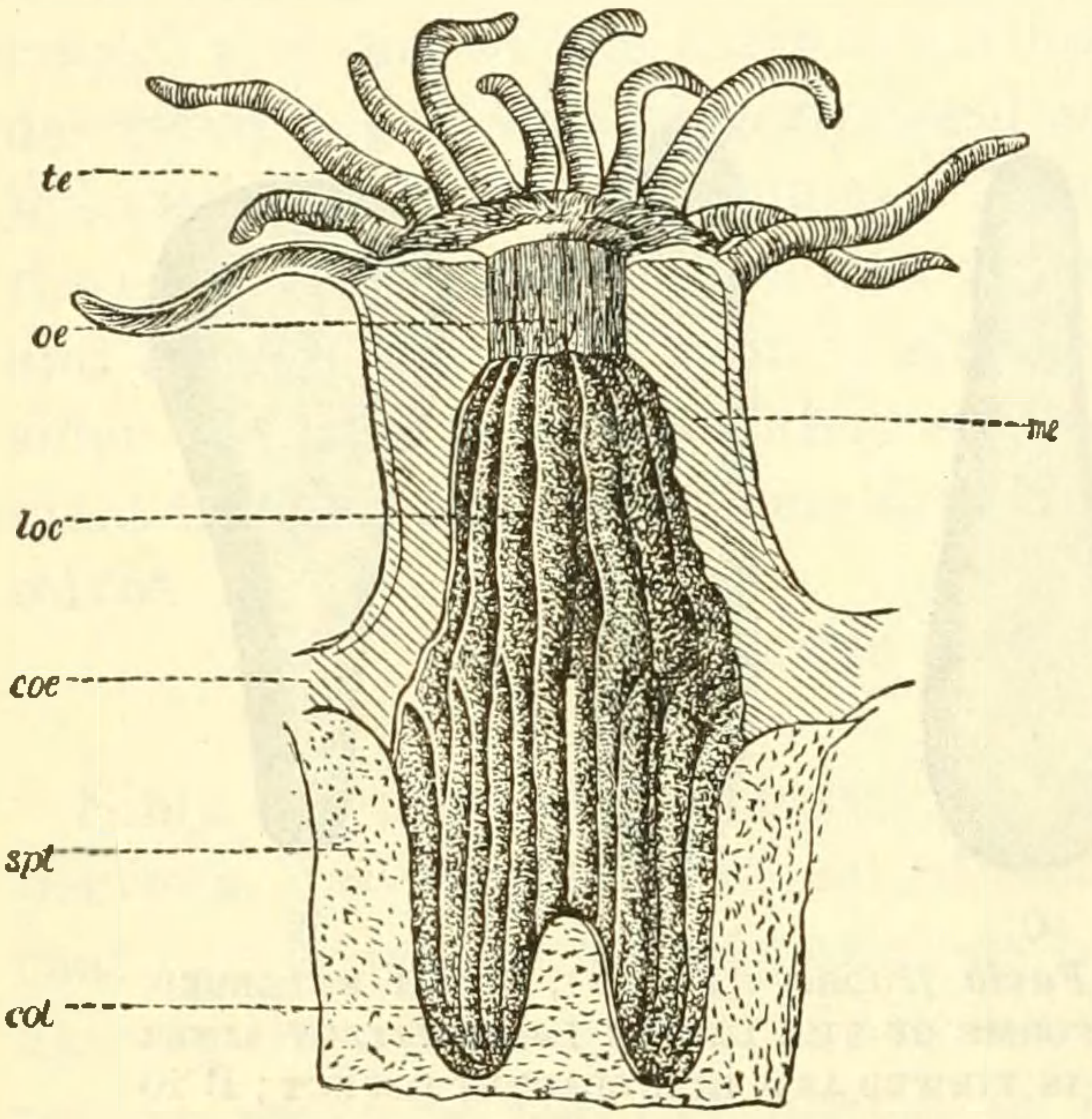


FIG. 2.—ENLARGED LONGITUDINAL SECTION OF ASTREOIDES CALYCULARIS (PALLAS). AFTER LACAZE-DUTHIERS. *te*, TENTACLES; *oe*, OESOPHAGUS; *me*, MESENTERY; *loc*, MESENTERIC POUCHES; *coe*, COENOSARC; *spt*, SEPTUM; *col*, COLUMELLA.

Coral colonies are very diverse in form—they may be low, flat plates, closely adherent to the basal support; they may be cushion-shaped; they may form more or less perfect hemispheres or spheres; or the outer surface may be variously lobed. Some corals form simple or divided columns; others form elongate, round branches, which range from only a few millimeters to several centimeters in diameter; the branches of other corals are more or less compressed and platelike. Other growth-forms are erect or subhorizontal, thick or thin plates and vases, which may be small and shallow or large and deep. Some colonies are tuftlike. In colonies that are formed by budding, the individual corallites and polyps are usually subcircular in outline and are separated from one another by interspaces that range in width from mere dividing walls up to several centimeters across. But in colonies formed by fission, the corallites often occur in series which may contain two or three, or very many corallites in rows; when the series are long they may wind and twist so as to warrant bestowing such names as *Maeandra* and *Meandrina* on certain genera. One genus of corals in which the corallum forms tall, more or less divided columns, has long, winding series and is appropriately named *Dendrogyra.* In such series the polyp mouths occur along longitudinal depressions, called valleys, which may be narrow or wide, shallow or deep, and adjacent valleys may be close together with very narrow interspaces or they may be relatively far apart.

It will be shown in remarks to follow that the growth-form is of much importance in considering the relations of corals to the physical conditions under which they live. The flattish, cushion-shaped, and hemispherical corals, that are attached by wide bases, have the strongest structures; those corals composed of thick plates or thick platelike branches rank next in strength; while those that form thin, erect laminæ and slender, long branches are the weakest. Some corals that have rather strong skeletons need to be classed with the corals with weak skeletons, so far as their habitats are concerned, for they live either free on the sea bottom or are very weakly attached.

The corals so far considered are those known as the Madreporaria. Their soft tissues secrete nearly pure white skeletons composed almost entirely of carbonate of lime; there are pitlike calices or valleys in the skeleton; and more or less distinctly radial septa are present. The hard skeleton is called "coral" and this is the kind of "coral" from which coral reefs derive their name. Before speaking of another kind of coral, it will be stated that the tentacles of the Madreporarian corals are either simple (see pl. 17 and text fig. 2) or are bifurcate or trifurcate—they are *never* pinnate; and it will also be said that in the Madreporarian corals now living, the septa and mesenteries are arranged on a plan of six or in multiples of six, except where the plan has been obscured by fission. Because of this arrangement of septa and mesenteries, this group of corals is called *Hexacoralla.* Ages ago, geologically speaking, the predominant corals had their septa arranged on a basal plan of *four* or *multiples of four* and these have been called *Tetracoralla*, the other highest subdivision of the Madreporaria.

The Alcyonaria, constituting a group of corals of the same rank as the Madreporaria, comprise the precious coral, *Corallium rubrum*, and other species from which jewelry is made, the sea fans, sea feathers, and sea whips, some of which are among the most beautiful objects in the ocean. The tentacles of these corals are pinnately fringed or plumose, and, because their mesenteries and tentacles are arranged on a plan of eight, they have been called *Octocoralla.* The skeleton of the Alcyonaria is unlike that of the Madreporaria, in that it usually consists of a horny axis, more or less completely calcified, surrounded by horny material in which spicules are embedded.

The skeletons of Alcyonaria of this kind further differ from those of the Madreporaria in possessing, according to F. W. Clarke and W. C. Wheeler, from 6.18 to 15.73 per cent of carbonate of magnesia. In the red organ-pipe coral, genus *Tubipora* (pl. 4, figs. 1, 1*a*), the spicules are sufficiently cemented together to form tubes. The skeleton of the blue coral, *Heliopora coerulea* (pl. 4, figs. 2, 2*a*), looks very much like one of the Madreporaria, and it is composed of almost pure carbonate of lime, but the polyps have the anatomical characteristics of the Alcyonaria.

One of the hydroids, *Millepora* (pl. 2, figs. 3, 3*a*), is usually considered with the corals, although zoologically it is not one of them. The figures of the skeleton show that it has no distinct septa, and that there are two kinds of pores corresponding to two kinds of polyps, also called zooids. The larger pores, the gastropores, lodge the larger nutritive polyps; while the smaller pores, dactylopores, lodge the smaller, the food-capturing, zooids. The skeleton of *Millepora*, according to Clarke and Wheeler, is composed of almost pure carbonate of lime.

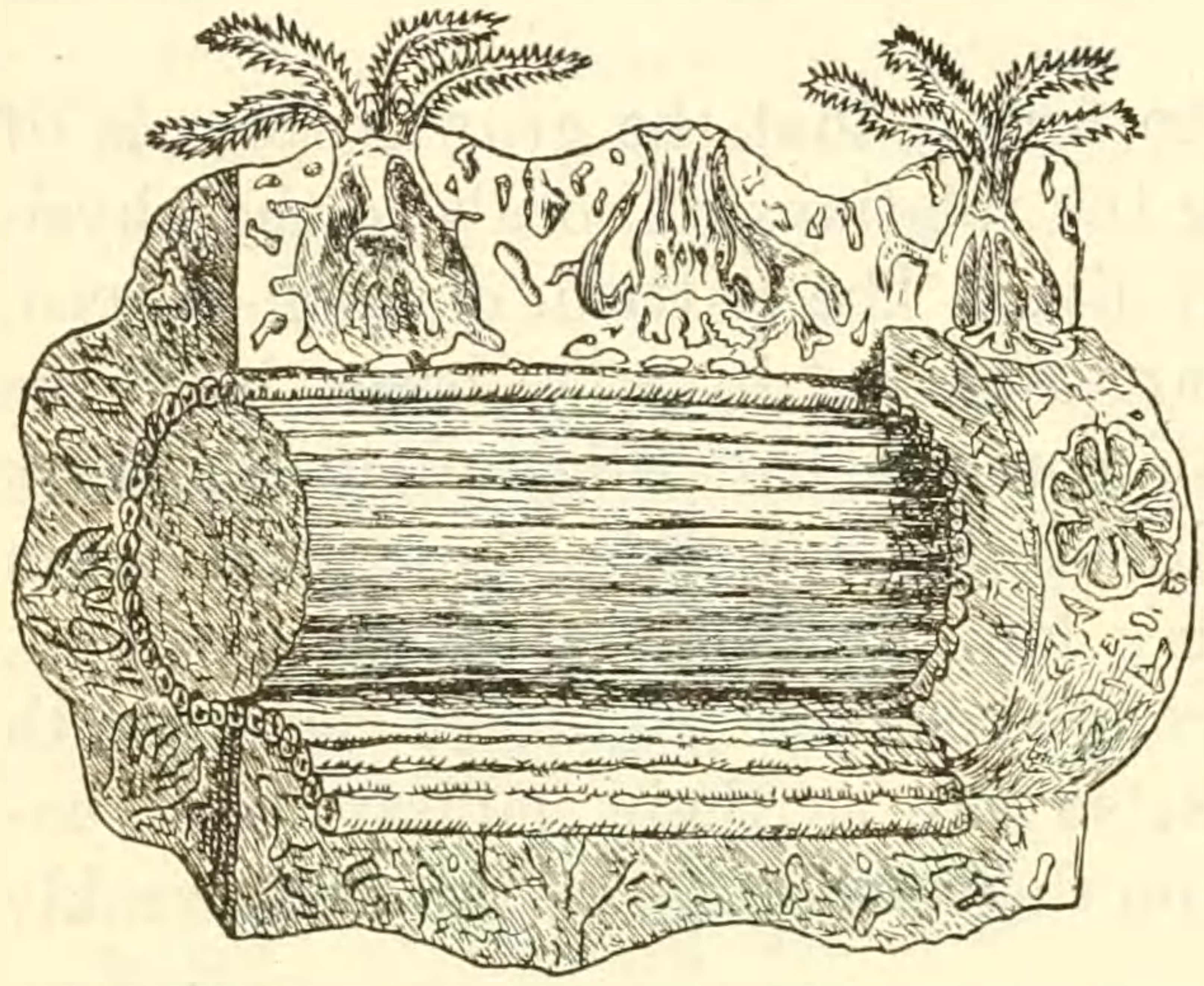


FIG. 3.—*Corallium rubrum* LAMARCK. AFTER LACAZE-DUTHIERS.

DIFFERENCES IN THE CORALS ON THE LAGOON (THE QUIET WATER) AND ON THE EXPOSED (THE ROUGH WATER) SIDES OF A CORAL REEF.

Darwin in his Structure and Distribution of Coral Reefs, [1] gave an excellent description of the difference between the corals in the lagoon of Keeling atoll and those on the exposed reef. A few years ago Dr. F. Wood Jones spent 15 months in the Cocos-Keeling Islands, and in his book, Coral and Atolls, produced a far more detailed account of the relations of the corals in those islands to their environmental conditions than that of Darwin, but what Darwin said is correct. Dr. Wood Jones sent me his collection, which is now the property of the United States National Museum, and I have been able to publish a detailed account of it.[2] The Cocos-Keeling Islands are classic ground for the students of reef corals and coral reefs, and it seems appropriate to begin the consideration of the relations of

---

[1] See 3d ed., pp. 1–19, 1889.

[2] Vaughan, T. W., Some shoal-water corals from Murray Island (Australia), Cocos-Keeling Islands, and Fanning Island: Carnegie Institution, Washington, Publ. 213, pp. 49–234, pls. 20–93, 1918.

corals to their environment with an account of conditions there. The following table shows the relations:

Relations of growth-form of Cocos-Keeling corals to habitat.

Habitat.	Free corals.	Fragile branches or folia.	Stout branches and lobate columns.	Growth-form massive.
Lagoon	2	11	5	5
Barrier pools and barrier flat	2	6 (mostly on lagoon edge of flat)	4	8
Exposed side of barrier			3	13

Within the lagoon free corals or corals that form fragile branches or folia are predominant; on the barrier flat and in the barrier pools the forms with stronger skeletons are more numerous; while on the exposed barrier there are only corals that have a massive growth-form or are composed of stout branches. One of the species, *Pocillopora elegans* Dana, which forms compressed branches, occurs within lagoons and on barriers. The branches of the specimens in the lagoon are tall and rather weak, while specimens on the barrier have the branches aborted into slightly protuberant nodules. Plate 6 illustrates a corallum of the lagoon kind, and plate 5, figure 2, illustrates a specimen Dr. Wood Jones collected on the Cocos-Keeling barrier.

Six specimens of *Pocillopora bulbosa* Ehrenberg taken by Dr. Wood Jones from a floating log are very interesting in this connection (pl. 5, fig. 1). He says regarding these specimens:

> In the lagoon, a large portion of a tree trunk was floated, and made fast to an anchor and chain; the wood was used to float a ship's moorings, and remained just two years in the water. When it was removed in 1906, several colonies of *Pocillopora* had started growths upon it, and they had taken up different positions around its circumference. The colonies growing above were flattened bosses; those on the sloping sides showed more tendency to branch; and those below its convexity were delicate branched forms.
>
> Now the environments of these colonies were very different, and they were absolutely constant. At all stages of the tide waves broke upon its upper surface, whilst the sides were in gently moving unbroken water, and the bottom was in comparative calm. * * *

Dr. A. G. Mayer made a very interesting collection of corals at Murray Island, Australia, and I have described them in my paper above cited. Preceding my paper, Doctor Mayer has given in the same volume an account of the ecology of the Murray Island reef, in which he presents a statistical statement of the number of coral colonies according to species in successive squares across the reef. I based the following table on Doctor Mayer's collection:

Table showing distance from shore, depth of water, character of bottom, number of species, and growth form of the colonies, for each station on line I, southeast reef, Murray Island.

Distance from shore (in feet)	Depth of water at low tide (in inches).	Character of bottom.	Number of species at each station.	Number of species according to growth form.		
				Fragile branches and free disks.	Stout branches.	Massive or incrusting.
300	2 - 4	Hard limestone mud over lava rock.	1	....	....	1
400	4.5- 5	Firm limestone mud	7	3	....	4
450-550	6 -12	Sand and mud, rock	10	3	....	7
600-650	6.5-10	Sandy	18	7	....	11
800-820	10 -11	Broken coral	[1] 20	6	1	12
1,000-1,020	14 -17	Rocky	21	10	1	10
1,200-1,250	12 -16	Rocky	18	6	2	10
1,400-1,445	14 -15	Rocky, broken coral	24	10	2	12
1,600-1,675	10 -16	Hard, rocky, broken coral	32	4	2	26
1,720-1,775	2.5- 3	Hard, rocky, with crevice like tide pools.	13	....	6	7

[1] *Acropora pectinata* (Brook), which is of discoid corymbose growth form, is not counted in the tabulation.

Comparison of this with the preceding table reveals precisely the same principles.

The collection made by Doctor Mayer at Murray Island contains an excellent illustration of the variation of *Stylophora pistillata* (Esper) according to environment. The branches of a specimen from a depth of 18 fathoms, northwest of Murray Island, where the water is not violently agitated, are slender, elongate, and fragile (pl. 7, fig. 1), while a specimen from the exposed reef has very short, stumpy branches (pl. 7, fig. 2). Plate 8, figure 2, illustrates *Porites porites* from the exposed reef at Tortugas, Florida, while plate 8, figure 1, illustrates the growth form assumed by a fragment broken from the exposed reef and then attached to a terra-cotta disk and planted within Tortugas lagoon.

In shallow water, corals which have fragile skeletons or which are weakly attached to the bottom predominate in lagoons, where the water is not violently disturbed; and usually conditions favorable for the life of corals having these kinds of growth habits are present outside lagoons in depths between 18 and 25 fathoms. But on the exposed sea-sides of reefs, where the surf is strong and storm waves break, all the corals have strong skeletons, mostly of massive growth form. If the same species of branching coral occurs both in places protected from the beat of the surf and in those exposed to the breakers, the colonies in the exposed situations adjust themselves to their environment by strengthening their skeletons. The preceding paragraphs show that these adjustments take place in the Cocos-Keeling Islands, on the Great Barrier of Australia, and in Florida, and warrant the conclusion that the phenomena are of general occurrence. As there are, particularly along the sides of channels through which water flows into and out of lagoons, situations intermediate in condition between those in the lagoons and those on the exposed sea-sides of reefs, there are areas in which there is more or less commingling of the two kinds of corals, and in them both massive reef-building forms and fragile lagoon forms live side by side.

RELATION OF CORALS TO DEPTH OF WATER.

A great deal of information has been accumulated on the relation of corals to depth of water. Among those who have particularly studied this subject are Darwin, Dana, Pourtalès, Quelch, Moseley, Stanley Gardiner, and myself. Usually massive reef builders are mostly found in water 27 meters or less in depth, but some species extend to depths between 37 and 48 meters, and a few reach depths as great as 74 meters. The available evidence indicates a depth between 37 and 46 meters as the maximum at which a true coral reef will form.

At depths slightly greater than 46 meters, between 46 and 74 meters, there are in coral-reef areas corals that differ somewhat from the shoal-water fauna and from the true deep-sea corals. These corals naturally resemble more closely those found in the deep water of the lagoons than those on the exposed sides of reefs or the flats just behind exposed reefs. Stanley Gardiner appears to have been the first clearly to recognize this bathymetric faunal zone, and in his work on the Maldive and Laccadive Archipelagoes very properly emphasized its importance. In my own work on the living corals of the Hawaiian Islands, I recognized the presence of a rather distinctive fauna at these depths. Illustrations of it are given on plates 9–11.

Between 74 and 183 meters in depth corals of deep-sea facies commingle in the Hawaiian Islands with the fauna found principally between 46 and 74 meters in depth. Deep-sea corals, those found in water 183 meters or more in depth, are mostly simple, cup corals, and many have very delicate, fragile, even lacelike skeletons. Several species from the Hawaiian Islands are illustrated by plates 12–15. A species that closely resembles the one illustrated by plate 14, figures 3, 3a, was dredged off Callao, Peru, in water 3,209 fathoms (=19,254 feet=5,892 meters) deep. Other deep-sea corals are compound forms that have delicate, elongate, attenuate branches. Three species with this kind of growth habit are illustrated by plate 15.

The following tables present the results of a study of the distribution of Hawaiian corals according to depth. Similar relations prevail in the Indian Ocean, the Central Pacific, and in the Gulf of Mexico and the Caribbean Sea. Although these tables apply specifically to the Hawaiian Islands, they really illustrate certain of the broad principles underlying the relation of coral faunas to depth of water.

Bathymetric distribution of corals in the Hawaiian Islands—Table showing the numerical distribution of forms according to depth.

(Depths in meters.)

Depth in meters	0–46	46–74	74–183	183–366	366–549	549–732	732–915	915–1,098	1,098–1,281	1,281–1,464	1,464–1,647	1,647–2,105
Number of forms found at that depth	77	14	7	21	13	8	0	0	1	0	2	1
Number of forms confined to that depth	70	5	2	14	6	5	....	....	0	0	1	1
Number of forms ranging into the next deeper	7	2	4	5	3	0	....	....	0	0	0	....
Number of forms occurring in next shallower	....	7	2	4	5	3	....	....	0	....	0	....
Number of forms occurring in both shallower and deeper water	....	0	1	2	1	0	....	....	....	....	....	....

Bathymetric distribution of coral genera in the Hawaiian Islands.

(*Depths in meters.*)

0–46	46–74	74–183	183–366	366–549	549–732	732–915	915–1,098	1,098–1,281	1,281–1,464	1,464–1,647	1,647–2,105
Pocillopora. Leptastrea. Cyphastrea. Coelastrea. Fungia. Pavona. Leptoseris. Stephanaria. Psammocora. Dendrophyllia. Montipora. Porites. Alveopora.	Pocillopora. Pavona. Leptoseris. Montipora. Porites.	Madracis. Fungia. Leptoseris. Stephanophyllia Balanophyllia.	Flabellum. Placotrochus. Paracyathus. Deltocyathus. Caryophyllia. Cyathoceras. Anthemiphyllia. Madracis. Leptoseris. Stephanophyllia Endopachys. Balanophyllia. Dendrophyllia.	Flabellum. Gardineria. Desmophyllum. Paracyathus. Trochocyathus. Caryophyllia. Cyathoceras. Madracis. Leptoseris. Anisopsammia.	Desmophyllum. Caryophyllia. Cyathoceras. Ceratotrochus. Madrepora. Mussa? Anisopsammia.	None.	None.	Flabellum.	None.	Flabellum. Caryophyllia.	Bathyactis.
TOTAL NUMBER OF GENERA.											
13	5	5	13	10	7	0	0	1	0	2	1

RELATION OF CORALS TO TEMPERATURE.

In the foregoing pages the relations of corals to violently agitated or relatively quiet water and to depth of water have been particularly discussed. The relations of corals to the temperature of the water will now be considered, and it will be introduced by a table showing the distribution of the genera of Hawaiian corals according to temperature. The surface temperatures in this table are for the period between March 27 and August 29, 1902, and, therefore, do not represent the minimum temperature for the year. The temperature relations of reef-corals will be considered later. If this table is compared with the table showing the bathymetric distribution of coral genera in the Hawaiian Islands, it will be evident that the names in the first column of each table are the same. A further examination of the table showing the distribution of genera according to temperature will reveal that a temperature of about 22.8° C. is the boundary between the shoal-water and the deep-water faunas. The names of the genera that were obtained at temperatures above 15.6° C., but not so high as 22.8° C. and above 4.5° C., are those that appear in the columns 183 to 732 meters in depth; the genera dredged between temperatures of 4.5° and —1.12° C. were those collected between 1,464 and 2,105 meters in depth. The temperature of the deep-sea fauna ranges between somewhat less than 22.8° C. (about 15.6° C.) and —1.12° C., with the maximum development between 10° C. and 4.5° C.

Distribution of genera of corals according to temperature in the Hawaiian Islands.

25.6° to 22.8° C.	22.8° to 15.6° C.	15.6° to 10° C.	10° to 4.5° C.	4.5° to —1.12° C.
Pocillopora.	Flabellum.[1]	Flabellum.	Flabellum.	Flabellum.
Leptastrea.	Placotrochus.[1]	Cyathoceras.	Gardineria.	Caryophyllia.
Cyphastrea.	Paracyathus.[1]	Madracis.	Desmophyllum.	Bathyactis.
Coelastrea.	Caryophyllia.[1]	Stephanophyllia.	Paracyathus.	
Fungia.	Cyathoceras.[1]	Balanophyllia.	Deltocyathus.	
Pavona.	Anthemiphyllia.[1]		Trochocyathus.	
Leptoseris.	Madracis.[1]		Caryophyllia.	
Stephanaria.	Fungia.[2]		Cyathoceras.	
Psammocora.	Leptoseris.		Ceratotrochus.	
Dendrophyllia.	Stephanophyllia.[1]		Madrepora.	
Montipora.	Balanophyllia.[3]		Madracis.	
Porites.	Dendrophyllia.[1]		Mussa? sp. juv.	
Alveopora.			Leptoseris.	
			Stephanophyllia.	
			Endopachys.	
			Balanophyllia.	
			Dendrophyllia.	
			Anisopsammia.	
Total number of genera.				
13	12	5	18	3

[1] Not obtained at a temperature so high as 21° C.=70° F.
[2] Not obtained at a temperature so low as 21° C.=70° F.
[3] Temperature range doubtful.

North and south of coral reef areas it seems that the deep-sea corals live in shallower water, because the temperature of the water at and near the surface in higher latitudes is colder than at the surface in the Tropics. For instance, some years ago a species of *Caryophyllia*, one of the cup corals, which was collected along the shore in Alaska, was submitted to me by the United States Bureau of Fisheries. It is an unnamed species, but in its general aspect it resembles the deep-sea forms of the Tropics. There is much scattered evidence of this kind, for example, the corals living on the shores of southern California, but it has never been assembled and systematically presented. There is in the United States National Museum a large amount of material, for which there are records of the depth and temperature of the water and the character of the bottom, that could serve as the basis for such a study. It is my belief that the great gap in present information on coral faunas is the dearth of information on the relations between the deep-sea faunas of the Tropics and the shoal-water faunas of the colder parts of the ocean, both northward and southward from the Tropics. For a long time it has been my desire to make a special study of this important problem, and, unless some one else undertakes it, I still hope to be able to give it the attention that, in my opinion, it deserves.

With regard to the temperature relations of reef-forming corals, it will be said that, except on very shallow flats where the water is stagnant at times and the temperature at such times may range between 33° and 38° C., the upper limit of the temperature endurance of such corals is rarely reached. It is therefore rather to the lower limit of temperature that reef-corals can withstand, that attention should be directed.

A series of experiments, conducted by A. G. Mayer to ascertain the higher and lower limits of temperature the common corals around the Tortugas can endure, indicate that a lowering of the temperature to 13.9° C. would exterminate the principal Florida reef corals, while the most important inner flat corals would survive. He obtained similar results on the corals around Murray Island, Australia. But, actual reef records show that reef corals do not naturally withstand so much cooling as in the laboratory experiments.

Temperature records made at lighthouses along the Florida reef, communicated to me by Dr. H. F. Moore of the United States Bureau of Fisheries show that vigorous reefs will endure a temperature as low as 18.15° C., the minimum at Carysfort Light between the years 1879 and 1899; but at Fowey Rocks, where the minimum drops to 15.6° C., although there are some corals, there is no thriving reef. The species found at the north end of the reef line are those which Mayer's experiments showed capable of withstanding the lowest temperature. The temperature records for the reef line indicate 18.15° C. as the minimum temperature which a reef will survive—this is 1.85° C. lower than the figure given by Dana. It is not probable that a reef could withstand a continuous temperature so low as this. Wherever the depth of water is great enough to lower the bottom temperature below 18.15° C., more probably about 22° C., reef corals will not live. This temperature appears to be attained around the Hawaiian Islands within a depth of 183 meters. According to Agassiz's "Three Cruises of the Blake" the bottom temperature in the Gulf of Mexico and the Caribbean Sea is usually too low for the growth of reef corals at a depth of 183 meters, and in places it is too low at a depth of 87 meters. Recent records of temperature near Bermuda, the Bahamas, and Florida, show that in those areas the temperature at 300 meters is uniformly too low for the life of reef corals; it is usually too low at 200 meters; and occasionally too low at 100 meters, in an area where the surface temperature is high enough for the life of reef-forming corals.

RELATION OF CORALS TO SEDIMENT.

One of the important factors affecting the life of corals is their relation to sediment. Of course any coral permanently buried in sediment would be killed, but nearly all corals can remove some sediment from their surfaces, and some can rid themselves of considerable quantities. The outer-reef corals proper have their surfaces kept clean by the movement of the water, that is, by waves, surf, and currents; but as the species living on the inner flats and in the lagoons have not sufficient assistance of that kind, they require special adaptations for keeping their surfaces clean. One of these adaptations is for the colony to be divided into upward-pointing branches, which present very small or no flat areas on which sediment can lodge. Other corals, *Maeandra areolata* for example, has greatly developed cilia, which move the sediment toward the periphery of the colony and cause it to drop off. Some species, *Siderastrea radians* for instance, can stand temporary burial. A. G. Mayer discovered that those corals that can withstand the highest temperatures can endure the longest burial. The capacity to resist the effects of high temperature and that to resist the effects of burial are, therefore, brought into relation, and one seems to be the correlative of the other. According to Mayer, high temperature produces death by asphyxiation, as also does burial.

RELATION OF CORALS TO LIGHT.

Light is another factor that affects corals. Plate 16, figure A, represents the wharf at old Fort Jefferson, Tortugas, Florida. Coral larvae have attached themselves to the peripheral piers and many thriving colonies have resulted, but the more central piers bear few or no corals. Light is the only factor I have been able to imagine to be the cause of this result, for the water under the middle of the wharf is of the same temperature as that outside and the food supply is the same both under and outside the wharf.

Dana says:

> The range of temperature 85° to 74° F. gives sufficient heat for the development of the greater part of coral reef species; and yet the temperature at the 100-foot plane in the middle Pacific is mostly above 74°. The chief cause of limitation in depth is the diminished light, as pointed out by Prof. T. Fuchs.[1]

Hjort says in his article on "The *Michael Sars* North Atlantic Deep-Sea Expedition:"[2]

> * * * Now, if we calculate the depth to which the rays of the sun penetrate, after passing through the same distance in the water, assuming always that the rays are direct, and that the rate of absorption is the same, we find that the rays will have passed through the same distance to reach a depth of 500 meters in 50° north latitude that they will pass through to reach 650 meters in 33° north latitude, or 300 meters in 67° north latitude.
>
> However, the transparency of the water varies greatly in different regions. If we take the results of previous observations during different expeditions, we may set down the visible depth in the open sea as being, roughly, 50 meters in 33° north latitude, 40 meters in 50° north latitude, and 25 meters at the outside in the Norwegian Sea in 67° north latitude. Taking this into consideration, we find that there will be the same *intensity* from the rectilinear rays—
>
> In 33° north latitude, at about 800 meters' depth.
> In 50° north latitude, at about 500 meters' depth.
> In 67° north latitude, at about 200 meters' depth. * * *
>
> During the Atlantic cruise of the *Michael Sars* we undertook a series of measurements of the intensity of light with a photometer constructed by Doctor Helland-Hansen; to determine the intensity of the different color rays, Doctor Helland-Hansen made use of panchromatic plates and gelatine color-filters. The observation south and west of the Azores (that is to say, at the southern stations) showed that the rays of light strongly affected the plate at a depth of 100 meters. The red rays were weakest here, while the blue and ultra-violet rays were strongest. At a depth of 500 meters the blue and ultra-violet rays were still distinctly visible, and at a depth of 1,000 meters the ultra-violet rays were yet perceptible. In 1,700 meters, however, there was not the faintest trace of light, even after the plates had been exposed for two hours in broad daylight.

The observations recorded in the foregoing quotation show a distinct decrease in the intensity of the red rays of light at a depth of 100 meters. As the maximum development of the deep-sea fauna off the Hawaiian Islands is between depths of 183 and 732 meters and at temperatures between 10° and 4.5° C., depth, temperature, and intensity of light are correlatives. The deep-sea fauna mostly lives at depths too great for the penetration of the red rays, but, where

---

[1] Corals and coral islands, 3d ed., p. 118; see also Vaughan, U. S. Nat. Mus. Bull. 59, p. 46, 1907.

[2] Geographical Journ., vol. 37, pp. 505–506, 1911.

most luxuriant, it is reached by the blue and ultra-violet rays; but many deep-sea species live in utter darkness. In higher latitudes the deep-sea fauna of the Tropics, it seems, may live in shallower water, where the light is stronger than in the deep water nearer the Equator.

At the Tortugas I made experiments on 17 species of shoal-water corals to ascertain their relation to light. The specimens were placed in a live car, specially constructed so as to be entirely dark after shutting a trapdoor. At the end of 14 days one species, *Acropora muricata*, apparently had died, and the specimens of all the other species were pale, the green plant cells in the coral tissues having died or lost their color; at the end of 28 days specimens of *Favia fragum* and *Agaricia purpurea* had died; at the end of 43 days one specimen of *Eusmilia aspera* had died, and most of the polyps of *Oculina diffusa* were dead. The notes at the end of 43 days were kindly made for me by Dr. A. G. Mayer, who put on the rocks, under the landing for the laboratory pump wharf, those specimens that withstood the exclusion of light. About a year later I found seven of them and made notes on them on July 21, 1915. These specimens not only survived being in the dark for 43 days, but before the end of a year were again very nearly or quite normal. The fact that shoal-water corals are not normal in the dark, although they will endure the exclusion of light for a considerable period, and the fact that they are absent on the central piers under Fort Jefferson wharf where the light is weak, while they are abundant on the peripheral piers, is strong evidence in favor of light being one of the ecologic factors determining the locus of species of corals. The commensal green algae, known as Zoanthoxellae, that as a rule are embedded in the tissues of shoal-water corals, set free oxygen which is intimately available for use by the corals, as it is in immediate contact with the animal tissues. Since these plants while in the dark cease to set free oxygen, and the corals under such circumstances are deprived of oxygen from that source, it may be that the poverty of coral growth in dark places is due to the suppression of the activities of these plants.

Notwithstanding the high degree of probability that this inference is correct, additional accurate photometric records at depths from about 37 to 183 meters are necessary before completely convincing results may be obtained.

CAPACITY OF CORALS TO WITHSTAND EXPOSURE IN THE AIR.

As the corals that live in very shoal water may be above water level during low-tide periods, it is of interest to know how long they can endure being out of their natural medium. I made a number of experiments on the species common in the Tortugas, Florida, to ascertain how long they can live out of the water and found that all can withstand limited exposure in the air, but, of course, none of them can live permanently out of water. Colonies of the same species were placed in both the sun and shade on glass plates; and in both the sun and shade in vessels containing enough sea-water to keep the bases of the colonies wet. The death of colonies exposed to the air naturally depends on the rate of the desiccation of the soft animal tissues. As heat accelerates drying, the specimens in the sun are more quickly killed than those in the shade; and, as both the soft parts and the skeletons of all corals are more or less porous, a colony whose base is immersed in sea water will live longer than one lying on a glass plate. Although not precisely, almost generally, those corals with the most porous skeletons can longest endure being out of the water, for such skeletons dry more slowly than those that are more compact, and, if the bases are wet, they rapidly absorb water through capillarity. Any one of the sixteen species of Tortugas corals used in the experiments will endure half an hour's exposure on a glass plate in the shade without apparent damage; nearly all will stand one hour's exposure under such conditions; while some survived such exposure for four hours. Colonies of a number of species were badly damaged but were not entirely killed after lying for one and a half hours on a glass plate in the sun. Of the species experimented with *Favia fragum*, *Porites porites*, and *Porites astreoides* have the greatest capacity for withstanding exposure in the atmosphere, while that of *Maeandra areolata* and *Siderastrea radians* is almost as great. Usually the species that form the exposed reefs can not withstand being out of the water so long as those that live on the shallow flats behind the reefs. Doctor Mayer made a series of exposure experiments on the corals at Murray Island, Australia, and obtained similar results.

RELATION OF CORALS TO CONCENTRATION OF SALTS IN THE OCEAN.

The following is Dittmar's mean of 77 analyses of sea water:

Cl	55.292
Br	.188
SO_4	7.692
CO_3	.207
Na	30.593
K	1.106
Rb	----
Ca	1.197
Mg	3.725
Fe, SiO_2, PO_4	----
Fe, NH_4, NO_3	----
Al_2O_3, Fe_2O_3, SiO_2	----
	100.00

The ratio of the weight of the salts in the sea water to any given weight of water is expressed as parts per thousand and is called the salinity of the water, for instance, a salinity of 36 means that there are 36 pounds of salt in 1,000 pounds of water.

The factors affecting the life of corals, so far considered, are all more or less correlated; for instance, at great depths in the ocean the temperature is low, there is no light, and surface agitation of the sea is not felt. The relative salinity of the ocean differs from these factors in that it is not definitely related to any one of them, except that in the Tropics the surface concentration of sea salts is somewhat greater than that at depths considerably below the surface, and that there the concentration is somewhat greater than that on the surface in higher latitudes. In other words, there is in the surface waters of the Tropics some concentration of salts due to evaporation, but the difference in the salinity of the different parts of the ocean, away from the mouths of great rivers, is not sufficient to affect the life of corals. Notwithstanding these facts, it is important to know the maximum and minimum salinities that corals can endure.

The average salinity of the Tortugas water according to Dole is 36.01. Of the 17 species of Tortugas corals kept in a tank of water with a salinity of 18.28 for 24 hours, all were damaged or killed except *Maeandra areolata*, *Siderastrea radians*, and *Porites astreoides;* but no specimen of 16 species showed any evidence of harm after remaining 48 hours in water of a salinity of 27.87. Apparently corals would not be hurt if the salinity of the ocean were reduced to about 80 per cent of its present salinity. Mayer obtained similar results in his work on the corals of Murray Island, Australia.

Although I did not experiment with concentrated sea water, the studies made by Goldfarb and others on the effect of concentrated and diluted sea water on regeneration in hydroids and in the jelly-fish *Cassiopea* are here pertinent. The combined results of the experiments are in accord with the deductions made by oceanographers and geologists from other data, viz, the ocean is becoming more salt, and it appears that marine organisms are now living in an environment which is considerably below the optimum condition for their existence.

HOW CORALS CATCH THEIR FOOD AND WHAT THEY EAT.

I made no more interesting experiments on corals than those to discover how they catch their food and what they eat. Although nearly all the species abundant in the Tortugas were used in making the experiments, one species, *Maeandra areolata*, was studied more than any other. It was fascinating to bring a colony with the animals composing it entirely retracted, as in plate 22, and induce it to expand as in the colony represented by plate 17. This expansion was instigated by placing the colony in a vessel in a shady (not really dark) place, where it would not be shaken, and then feeding it with a little beef juice through a pipette, or by giving it a small bit of meat, usually crab flesh or fish. The tentacles at the end of the colony to which the food was offered would begin to appear, and the stimulus was transmitted to other members of the colony, until after a short time the surface of the specimen would remind one of a beautiful open flower. This condition of a coral colony seems to signify that it is hungry and is ready to capture food.

Special mechanisms of corals for catching food are greatly developed. They comprise, as follows: (1) The nematocysts, the stinging cells and their coiled threads, which occur in the ectoderm, the outer layer of the soft tissue and its modifications, on the tentacles, the oral disk (between the tentacles and the mouth), the sides of the polyps, and also on the mesenterial filaments. (2) The entire ectodermal surface is ciliate, the cilia in response to certain stimuli beating toward the oral apertures; in response to others, beating toward the periphery. (3) The outer surface secretes mucus in which particles may be embedded, the mucus moving under the influence of the beat of the cilia toward the oral apertures or toward the periphery, according to the nature of the response to the stimulation. (4) The tentacles are active and effective in capturing food. (5) The mesenterial filaments, which in many species of corals can be extruded through the column walls, in some instances capture food.

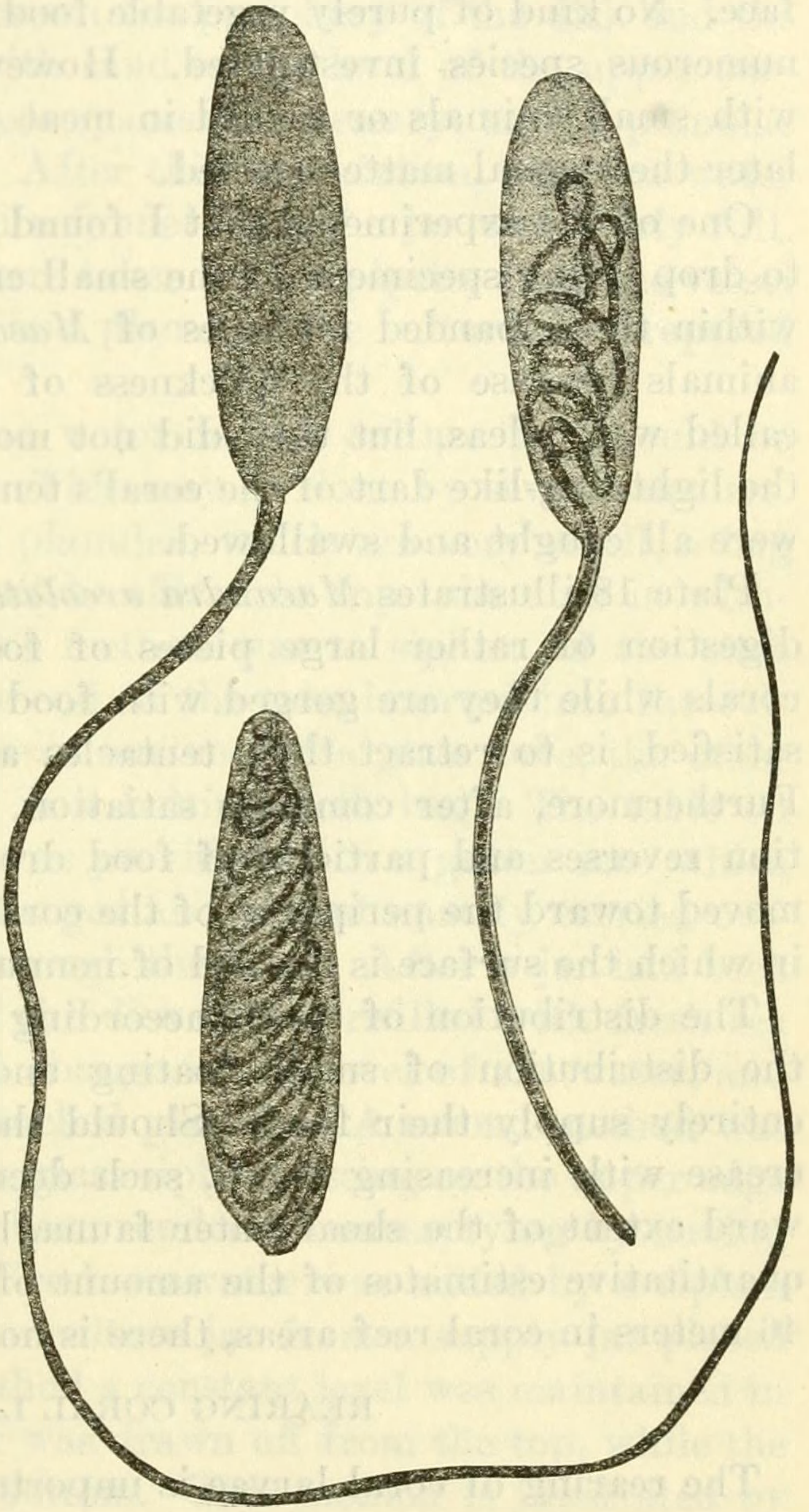


FIG. 4.—NEMATOCYSTS OF MAEANDRA AREOLATA (LINNAEUS), VERY HIGHLY MAGNIFIED. AFTER L. AGASSIZ FROM DRAWINGS BY BURKHARDT AND D. SONREL.

Many different kinds of food were offered corals, but they took only animal food—they are entirely carnivorous. The following experiment was tried many times: A piece of diatom mat was placed on one side of the oral disk and a piece of crab meat on the other. Invariably the crab meat was seized and swallowed; while the diatoms induced no reaction except ultimately to be removed from the surface. No kind of purely vegetable food was taken by any one of the numerous species investigated. However, pieces of plants coated with small animals or soaked in meat juice will be swallowed, and later the vegetal matter ejected.

One of the experiments that I found particularly fascinating was to drop living specimens of the small crustacea, known as copepods, within the expanded tentacles of *Maeandra areolata.* These little animals because of the quickness of their motion are popularly called water fleas, but they did not move swiftly enough to escape the lightning-like dart of the coral's tentacles and nematocysts—they were all caught and swallowed.

Plate 18 illustrates *Maeandra areolata* during the swallowing and digestion of rather large pieces of food. The usual behavior of corals while they are gorged with food and after hunger is entirely satisfied, is to retract their tentacles and other distensible organs. Furthermore, after complete satiation, the direction of ciliary motion reverses and particles of food dropped on the surface will be moved toward the periphery of the coral in a manner similar to that in which the surface is cleaned of nonnutrient particles.

The distribution of corals according to depth is dependent upon the distribution of small floating and swimming animals which entirely supply their food. Should the quantity of such food decrease with increasing depth, such decrease would limit the downward extent of the shoal-water fauna, but as I do not know of any quantitative estimates of the amount of such food above and below 46 meters in coral reef areas, there is no basis for a positive opinion.

REARING CORAL LARVAE.

The rearing of coral larvae is important because only by knowing the duration the free-swimming planulae stage can the possibilities of the distribution of corals by marine currents be understood; and, it is obvious that, in order to ascertain precisely how rapidly corals grow, the life of the same colony should be followed from the time the planula to which it owes its existence first settled. Two of the methods of obtaining and rearing planulae will be briefly described.

Colonies extruding planulae were brought into the laboratory and kept in glass vessels of sufficient size to furnish an adequate supply of water, which should be changed rather frequently. The planulae were removed from the vessels containing the parent colony to a culture jar, on the bottom of which was a terra-cotta disk having a central perforation that fitted over the head of an iron stake.

The disks[1] had a diameter of 8 inches and were placed in jars, the inside diameter of which was about 8¼ inches, and the depth about 8½ inches. After the bottom of a jar had been covered with the cleanest sand obtainable, a disk was placed in the jar, and the central perforation and the space between the periphery of the disk and the sides of the jar were filled with sand to the level of the upper surface of the disk. Filling these spaces is necessary, as the planulae tend to settle in depressions. After this preparation, pure sea water was gently poured in through a funnel until the jar was nearly full. Then the extruded planulae were taken with a pipette from the vessel containing the parent colony and placed in the culture jar prepared for their reception.

To get the best results, the water in the culture jar should be changed at least once a day. This may be done by several devices. In order not to draw off the planulae, which are very small, a bag of fine-mesh bolting cloth must be affixed to any tube used in withdrawing the stale water. One method was to siphon off the stale water with a rubber tube, the end of the tube inserted into the culture jar having been drawn over one end of a glass tube, the other end of which was enveloped in a bolting-cloth bag. The table on which the culture jars stood was provided with a gutter into which the water drawn off was discharged and was ultimately carried outside the building by a pipe through the floor. After a jar had been emptied to within an inch of the disk it was refilled with fresh sea water. This method causes a change in the level of the water, and the pouring stirs up the unattached planulæ. A second method was to withdraw the old water by a glass siphon resting on the upper edge of the jar, the siphon having been rendered nonemptying by having its outer end bent upward. Fresh seawater was added by a siphon extending to the bottom of the culture jar from a supply jar placed at a higher level. By this method a constant level was maintained in the culture jars, the old water was drawn off from the top, while the new water was added at the bottom. This method is illustrated by pl. 19, figure A.

Two other devices were used for changing the water—one of them replenished it without, the other with change of level, but they will not be described here. All four of the methods tried were successful, and the preference between them was not determined. Pure water is necessary and occasional stirring of unattached planulae may be beneficial. It is imperative that the sea water used in these cultures be

---

[1] Vaughan, Carnegie Institution of Washington Year Book No. 9, 1911, pp. 141, 142.

normally pure, that is, not contaminated by refuse or other abnormal impuritites.

It is relatively easy to get large numbers of planulae to attach themselves to disks by using the culture methods above described.

DISTRIBUTION OF CORALS BY MARINE CURRENTS.

It has already been stated that because of its bearing on the possibility of the distribution of coral species by oceanic currents, it is highly important to know the duration of the free-swimming larval stage. Observations were made on four species. The range was from 2 to 23 days. Should an ocean current have a velocity of 3 knots per hour, in 23 days planulae might be carried 1,656 knots; at 2 knots per hour, 1,104 knots; at 1 knot per hour, 552 knots. It is known that every species of shoal water coral in the Bermudas is found in Florida and the West Indies; while not only is the Hawaiian fauna Indo-Pacific in its affinities, but several of the species (at least four) also occur on the east coast of Africa or in the Red Sea, and I seriously doubt any part of the Hawaiian fauna being peculiar to those islands. The clue to the cause of the wide distribution of living coral species is given by the possibly long duration of the free-swimming larval stage. It should be mentioned here that numerous instances of the transport of coral colonies attached to floating pumice or to driftwood are on record, but it seems to me that the transportation of larval corals is more important in the distribution of corals by ocean currents than the transportation of attached colonies.

RATE OF GROWTH OF CORALS.

The growth-rate of corals was studied on colonies developed from planulae that were reared in the laboratory according to methods already described and then planted in the sea (pl. 21), and on colonies from planulae naturally attached but known to have settled in a certain season; on colonies fastened with Portland cement to terra cotta or reinforced concrete disks and then fixed on the heads of iron stakes driven into the sea bottom (pls. 22–25); and on colonies naturally living in the ocean.

Two methods were used for rearing to subsequent stages the larvae that settled in the laboratory culture. One was to fasten the disks bearing the young polyps to the bottom of a floating live car; the other was to plant the disks directly on stakes. Both methods succeeded. Plate 20, figures A and B, illustrate the method of planting in a floating live car; Plate 19, figure B, the apparatus for planting on iron stakes. A long iron bar, with a cap on the lower end fitting the head of the stake, was used for driving the stakes below water level. The disk was made fast by an iron pin through a hole in the head of the stake.

In the Tortugas, colonies that were attached to disks with hydraulic cement were planted (a) off the northwest face of Fort Jefferson moat wall; (b) on the reef off Loggerhead Key. Colonies naturally attached were studied at the following places: (a) In Fort Jefferson moat; (b) on piers of the Fort Jefferson wharf; (c) on the outside of the northwest face of the Jefferson moat wall; (d) on the reef off the northwest face of Loggerhead Key. The different places at which corals were planted and those at which observations on naturally attached colonies were made are illustrated by plate 16, figures A, B, C, and plate 26, figures A, B.

Observations and experiments were made in the Bahamas on the leeward side of the north end of a small island, known as Golding Cay, which is on the east side of Andros Island at the mouth of South Bight. The specimens included (a) those cemented to tiles and planted; (b) those living naturally attached.

The colonies in the Tortugas were measured and photographed once a year; while two years elapsed between the first and second measurements of the colonies in the Bahamas. The measurements and photographic exposures of the colonies attached to disks were made while the colonies were out of the water. It was shown on page 205 of this article that corals may live out of the water a much longer time than is needed for such operations.

The following table gives the size of colonies of *Favia fragum* according to age (pl. 21). The average annual increment is indicated by the number preceded by the + sign below that for the average size. The average most rapid growth is during the first year, after which it declines, but should a specimen not attain an average size during the first year, it may grow rapidly during succeeding years until it catches up to the average. Compare specimens Nos. 1 and 6 of the table.

Size of colonies of Favia fragum—averages according to age.

No.	1 year old.		2 years old.		3 years old.		4 years old.		5 years old.	
	Diameter.	Height.	Diameter.	Height.	Diameter.	Height.	Diameter.	Height.	Diameter.	Height.
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	11	4	27	8	30	11	30.5	11		
2	12.5	4	22.5	7	25	10	26	11		
3	19	6	31	11	33.5	13	34	13		
4	19	5	29	11	32.5	14	33	16		
5	19	4.5	31	11	36	14	41	17		
6	5.5	5	17.5	8	26.5	13	32	16	38	20
7[1]	16	5		10.5		14.5		16		22
8[1]	13	3		9						
9	9	2.5	19	7	20	9	21	11		15
10	10	2.5	17	10	26		29	10	33	13.5
11	8	2.5	11	4						
12					26		31		34.5	
13	9		20.5	8	23	11				
14	13		20	8						
15	18		23.5	9	27.5	12	31	15	39	16
16	11		25	9	27.5	11	32	14	36	16
17	10		16	9						
18	9		11.5	6	17	10				
19	10		16.5	5	19	6				
20	12.5		15		17					
21	18.5		18	5						
22	6.5		15							
23	9		19.5	10	23	11				
24	12		24		27.5	12	26	14		
25	9		21.5	9	25	12	27	15		
26	10		15		19.5		29			
27	16.5		22.5	6	23					
28	12		18	7	22		28.5		28.5	
29	17		23	7	26.5		31		33	18
30	11		13	3						
Average	11.93	4	20.01 (+8.08)	7.9 (+3.90)	25.14 (+5.13)	11.46 (+3.56)	30.13 (+4.99)	13.77 (+2.31)	34.71 (+4.58)	17.21 (+3.44)

---

[1] As Nos. 7 and 8 fused, separate measurements of the diameters became impracticable.

Favia fragum is a species that never attains a large size, between 60 and 75 millimeters being about the usual maximum diameter.

The size of colonies of *Porites astreoides*, according to age is given in the following table:

Size of colonies of Porites astreoides—averages according to age.

No.	1 year old.		2 years old.		3 years old.		4 years old.		5 years old.	
	Diameter.	Height.	Diameter.	Height.	Diameter.	Height.	Diameter.	Height.	Diameter.	Height.
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1	12.25	....	35	12	43.5	20	59.5	39	75	54.4
2	11.75	....	32	....	37	....	41.5	....	54.25	....
3	9	2 or 3	23	6	29	10	46.75	18	54	21
4	18.75	3	38.5	10	53.5	12	89.5	23	99.75	31
5	16.25	....	34.23	....	41	....	54	....	66.75	....
6	10.5	....	31.5	....	38	....	41.75	....	48.5	....
7	16.5	....	31	....	45	....	50.5	....	68.25	....
8	10.75	....	24.5	....	25	10	28	17	35.5	21
9	6.25	....	18.5	....	26.5	7	35.5	13.5	53	21
10	8.5	....	18	....	24.5	5	....	9	41	....
11	7.75	....	18.5	....	26	....	....	....	....	....
12	18.5	....	42	7	52.50	8	62.5	13	75.5	18
13	10.75	....	21	....	35.5	....	51.75	....	65.5	....
14	15.75	....	30	....	39.5	....	44.5	....	55.5	....
15	....	....	....	....	....	....	47	....	64.5	....
Average	12.38	3	28.41 (+16.04)	8.75 (+5.75)	36.89 (+8.48)	10.28 (+1.53)	50.21 (+13.32)	18.92 (+8.64)	61.21 (+11.00)	27.75 (+8.83)

Tables giving the summaries of my work on the growth-rate of the Floridian and Bahaman corals have been published in the papers cited in the footnote.[1] The growth-rate of 25 species was investigated, and a total of some thousands of measurements were made. Of course, as no such mass of data can be presented in this place, a few general statements must suffice.

The size of the colonies of all species of corals seems limited, but some attain large dimensions, 2 to 3 meters or even more in diameter, and nearly as much in height, while other species are adult when a diameter of 35 to 50 millimeters has been reached. The records of *Favia fragum* and *Maeandra areolata* illustrate relatively rapid growth for the first two to four years, after which it decreases. Other species, for instance, *Orbicella annularis* and *Maeandra strigosa*, are not so limited in size. Ramose corals increase in dimensions more rapidly than massive species; while of the former, the growth-rate of species with perforate, loose-textured skeletons is more rapid than that of those with dense skeletons. In general the more massive and the denser the corallum, the slower the growth; while the more ramose and the more porous the skeleton, the more rapid theg rowth.

---

[1] Vaughan, T. W., The geologic significance of the growth-rate of the Floridian and Bahaman shoal-water corals: Washington Acad. Sci. Jour., vol. 5, pp. 591–600, 1915; On Recent Madreporaria of Florida, the Bahamas, and the West Indies, and on collections from Murray Island, Australia: Carnegie Institution of Washington Yearbook No. 14, pp. 220–231, 1916.

Some species of *Acropora* under favorable conditions on an average grow in height from 40 to 45 millimeters per year.

There is no average growth rate for corals generally speaking, because growth-rate varies from species to species and varies for the same species according to local environmental conditions. A colony of a species of reef coral in a lagoon, if protected from sediment, may grow more rapidly than a colony of the same species does on the reef. The limitation of reef corals so largely to the outer edges of platforms, is determined primarily by the freedom of the water from silt and by the more uniform temperature.

In order to estimate the rate at which a reef will grow, the upward growth-rate of the true reef-forming species must be taken. The upward growth-rate of *Orbicella annularis*, the principal builder of the Pleistocene and living reefs in Florida and the West Indies, is from 5 to 7 millimeters per year, according to station. At 6 millimeters per year, it would form a reef 150 feet (=46 meters) thick in 7,620 years; at 7 millimeters per year it would build the same thickness of rock in 6,531 years. *Acropora palmata*, which grows more rapidly might build a similar thickness in 1,800 years. The growth of corals in the Pacific appears to be more rapid and according to Stanley Gardiner they might build a reef 150 feet thick in 1,000 years.

Growth-rate is one of the important factors in the battle between corals and some of their natural enemies. For instance, if corals grow less rapidly than sediment is being deposited on the bottom, although other conditions may be favorable for their life, they will surely be killed by smothering. In the competition between attached and incrusting organisms, growth-rate is one of the most important factors in determining which shall survive. Corals, as my experiments showed, may grow with great rapidity in locations where they cannot survive, or are only poorly represented, because the habitat is suited to other organisms of a more rapid rate of growth. Among these inimical organisms are various marine algae, including the calcareous *Halimeda* and incrusting nulliperes; other such organisms are sponges, tunicates, Bryozoa, and pelecypods.

A study of the growth-rate of corals has an interest not only in understanding the rate at which they may form rock, but also in understanding their struggle for life against enemies, both organic and inorganic.

SUMMARY OF STATEMENTS ON CORALS.

The preceding pages show that in the ocean there are:

1. The deep-sea corals at depths of 180 meters or more, where the light is weak or where there is perpetual darkness, and where the temperature ranges from 1° to 15.6° C., although they thrive best

where the temperature is between 4.5° and 10° C.; these are mostly cup-corals or delicately branching forms. It seems that this fauna lives in shallower water in higher latitudes than it does in the Tropics.

2. Between depths of 46 and 74 meters in the Tropics, there is a moderately distinctive fauna that is more closely related to the shallow-water than to the deep-water fauna.

3. In the shallow waters of the warm parts of the tropical oceans there is another fauna, the one that forms coral reefs, and its local adaptations to the character of motion of the water, sediment, and other factors have been described. The conditions necessary for the vigorous growth of reef-forming corals are as follows: (a) Depth of water, maximum, about 46 meters (25 fathoms); (b) bottom firm or rocky, without silty deposits; (c) water circulating, at times strongly agitated; (d) an abundant supply of small animal plankton; (e) strong light; (f) temperature, annual minimum not below 18° C.; minimum average temperature for the coldest month in the year not lower than about 22° C.; (g) salinity between about 27 and about 38 parts per thousand.

4. According to conservative estimates, reef corals can build a reef 46 meters (150 feet) thick within a period ranging from 1,800 years to 7,500 years; but, in places, a reef of such a thickness might be formed within 1,000 years, according to Gardiner.

THE FORMATION OF CORAL REEFS.

DEFINITION OF THE TERM "CORAL REEF."

The preceding pages are devoted to a general account of corals and the conditions under which they live, and no definition of "coral reef" has as yet been given, although the term has been used. In order to give some idea of a coral reef several illustrations are introduced. Plate 26, figures A, B, represent the reef off the west face of Loggerhead Key, Tortugas, Florida, as exposed at very low tide on June 6, 1910. The heads projecting above the water are *Orbicella annularis*, the principal reef-building coral of the Floridian and West Indian region; the fanshaped objects are the alcyonarian coral, *Gorgonia flabellum;* while the rod or whip like objects are other Alcyonaria that belong mostly to the genus *Plexaura.* Plate 26, figure C, is from an undersea photograph taken at Carysfort Reef, south of Miami, Florida. This illustration shows the beautiful, waving gorgonians, especially the fan coral, and large heads of *Orbicella annularis*, as well as some other stony corals; but it does not show the highly colored fishes that dart in and out among the coral heads and constitute one of the enchanting sights to be seen on coral reefs. Plates 27 and 28 are reproductions of two of Saville-Kent's photographic illustrations of the Great Barrier Reef of Australia. These three plates illustrate true coral reefs, which in my opinion should be defined as follows: Coral reefs are ridges or mounds of limestone, the upper surfaces of which lie, or lay at the time of their formation, near the level of the sea, and are predominantly composed of calcium carbonate secreted by organisms, of which the most important are corals.[1]

The composition of what I consider true coral reefs is very complex. The main framework of the reef is formed by coral heads and stout coral branches, while the interspaces are filled by small corals, and the skeletons of other organisms, some of which in the course of time are more or less broken up by the waves. In many cases it is difficult to decide whether or no to apply the designation "coral reef" to richly coralliferous deposits that are obviously bedded. However, it seems to me that it should be applied wherever corals of reef facies seem sufficiently abundant to have formed appreciable rugosities on the sea bottom, although the deposits are bedded. Reefs predominantly composed of the remains of calcareous algae should be designated "nullipore" or "Lithothamnion reefs." But, where the proportion of these organisms to corals is so nearly the same that only exact computation will decide between the two, such a reef may be designated "coral."

SOME KINDS OF LIMESTONE THAT HAVE BEEN CONFUSED WITH CORAL-REEF ROCK.

To many it may seem superfluous in a definition of coral reefs to say that the remains of corals should be an important constituent of the rock; but the term "coral rock" or "coral-reef rock" has been repeatedly applied to limestone with the making of which corals have had either nothing, or practically nothing, to do. An excellent instance of such a popular, and until recently scientific, misconception is supplied by the Bahama Islands.

According to Alexander Agassiz the Bahamas are composed of wind-blown coral-sand. The sand composing the ridges in the Bahamas, at least those I have seen on New Providence and Andros Islands, has certainly been wind-blown. Plate 30 illustrates an exposure along East Street in Nassau, and plate 29, figure B, represents the face of a small cliff at the south end of Morgan Bluff, Andros Island, both in the Bahamas; while figure A of plate 29 is from a photograph of a section of a sand dune at Cape Henry, Virginia. These illustrations show the essential similarity of the

---

[1] Vaughan, T. W., Physical conditions under which Paleozoic coral reefs were formed: Bull. Geol. Soc. America, vol. 22, p. 238, 1911.

arrangement of the material in the Bahamian ridges and of that in a sand dune at Cape Henry. The sand at Cape Henry is siliceous (quartz) sand; while that composing the hills and ridges in the Bahamas is calcareous, almost pure, more than 99 per cent, carbonate of lime. Limestone composed of grains similar to the grains in the wind-formed hills underlies the surface of the low, flat areas in the Bahamas, but its grains have not been wind-blown. They were formed in the sea and were later uplifted so that they now stand above sea-level. As this kind of limestone has been improperly called coral rock, a short account of the mode of its formation will be given.

A close inspection of a piece of this rock, even with the naked eye, reveals that it is composed of minute balls and ovoid or ellipsoid bodies, from 0.2 to about 1 millimeter in diameter, set into a cementing groundmass. Plate 31, figure A, illustrates the surface of a specimen natural size, and figure B represents a part of the same surface enlarged 10 times. Because the ball-like bodies composing the rock give it an appearance similar to fish roe, it is known as oolite, which means egg rock. Plate 32, figure 1 illustrates a thin slice of a single grain magnified 100 times. It is entirely obvious that these bodies are composed of concentric coats, and that they were formed by some process that caused outer coats to be successively laid down on the inner ones. It was stated in the preceding paragraph that this rock contains more than 99 per cent calcium carbonate, and that the egglike granules originated in the sea. How was the carbonate of lime taken out of the sea?

Recent investigations have very clearly shown that there is in the shallow waters of the tropical and subtropical parts of the ocean as much carbonate of lime in solution as it is possible for the water to hold—in other words, the water is saturated with carbonate of lime. It is therefore clear that any agency that will reduce the capacity of such water already saturated to hold calcium carbonate in solution will cause that substance to be precipitated. The principal solvent of calcium carbonate in sea water is carbon dioxide (CO_2), popularly known as carbonic-acid gas, and the reduction of the amount of it in the sea water will produce precipitation. Raising the temperature of the water, whether naturally or artificially, reduces its capacity to hold CO_2, and agitation, if there is too little CO_2 in the air, will hasten the process. Evaporation, leading to a greater concentration of salts in the water, will also cause precipitation of calcium carbonate.

Besides the inorganic agencies mentioned, there are organic agencies that cause the precipitation of calcium carbonate in the sea. It has been known for a long time that the addition of a strong alkali, such as ammonia, to sea water will produce precipitation of carbonate of lime. There are several kinds of bacteria that cause the formation of ammonia in the ocean. One of these kinds is known as denitrifying bacteria, because they break up nitrate salts in the sea, converting nitrates into nitrites and these into ammonia, and they are to a considerable degree responsible for the limited development of green plants in tropical seas, as they rob such plants of an important part of their food. G. H. Drew found as many as 160,000,000 of these bacteria in 1 cubic centimeter of mud off the west side of Andros Island, Bahamas, opposite the mouth of South Bight. A figure (reproduced from one by Kellerman) is here given of this very minute organism, which is known as *Pseudomonas calcis* (Drew) Kellerman. Any other bacteria that will evolve ammonia and green plants by taking CO_2 from the water will also cause the precipitation of calcium carbonate. In such areas as the shoal waters on the lee sides of the islands and in the lagoons in the Bahamas, where all of the agencies mentioned are cooperating to bring about the precipitation of calcium carbonate, it is not at present possible to estimate how much of the effect is attributable to each.

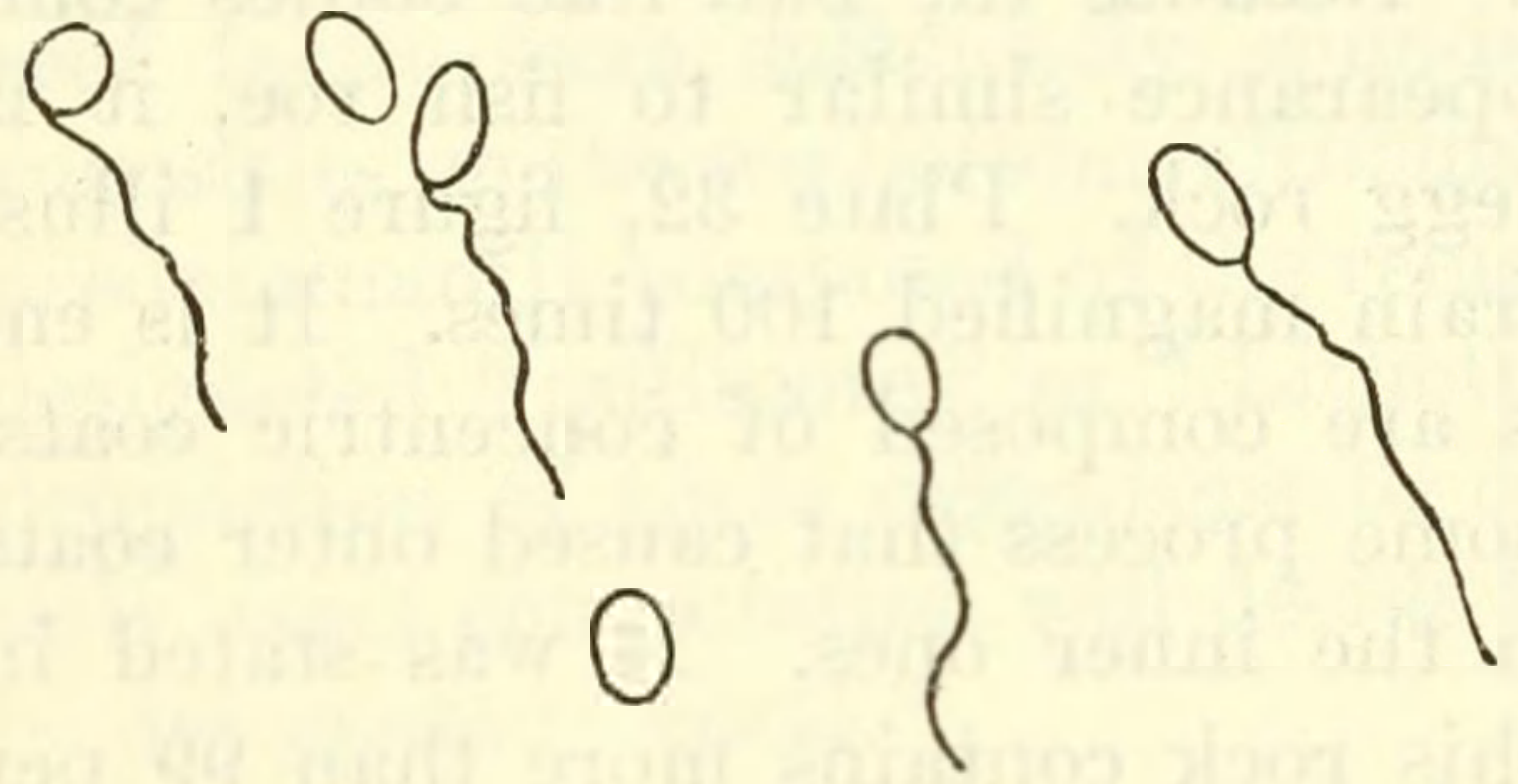


FIG. 5.—*Pseudomonas calcis* (DREW) KELLERMAN. GREATLY ENLARGED. AFTER KELLERMAN.

The material when first precipitated is very finely divided, and may form very minute needles or small balls of the mineral known as aragonite. On plate 32, figure 3 illustrates some of the aragonite needles, magnified 840 times, and figure 2 illustrates some balls taken from the mud, both out of the same sample, from the west side of Andros Island, Bahamas.

Oolite grains of calcium carbonate may be produced artificially, either by means of cultures of bacteria that evolve ammonia or by adding ammonia to sea water. An illustration of a thin section of an oolite grain from Great Salt Lake is given on plate 32, figure 4; the figures on plate 33 illustrate artificially formed grains. As the very fine concentric banding of the Bahamian oolite grains has not yet been reproduced in the laboratory, there are still some features of these grains that need more investigation.

Some investigators of the origin of oolite grains have contended that they are formed by filamentous algae, because borings apparently made by such organisms were found in the grains. Algae of this kind bore into nearly all carbonate of lime structures exposed to their attacks; they even bore into coral skeletons up to the limits of the soft animal tissues. On plate 34, figure 1 illustrates some of these algae obtained by decalcifying a specimen of the coral *Orbicella cavernosa;* figure 2 shows the algae in place in the skeleton of *Orbicella annularis;* while plate 32, figure 1, represents an oolite grain in which there are no algae, but I am confident I could have found an oolite grain with algae in it.

Some of the oolite of the Bahamas remains as it was bedded in the sea, except that it has risen or fallen with the movements of the crust of the earth, while other rock has been broken up and has supplied grains to be heaped into dunes by the winds.

Although the Bahamas have been called coral islands, they are not coral islands, for they are mostly composed of oolite formed from calcium carbonate organically or inorganically precipitated in the ocean, some of which has been broken up and blown about by the wind. There are coral reefs in the Bahamas, and they are exceedingly dangerous to navigation, but they occupy an area probably between only one three-thousandth and one six-thousandth as large as that underlain by the oolitic limestone.

Oolitic limestone similar to that so widespread in the Bahamas also occurs in southern Florida, where the area underlain by it is many times greater than that occupied by coral-reef rock; and the Bermudas, popularly thought to be "coral islands," according to Verrill, are mostly composed of shell sand and *not coral sand.* Besides these two kinds of limestone, rock predominantly composed of the tests of Foraminifera and Bryozoa should be definitely excluded from the category of "coral rock." The study of the formation and classification of limestones is fascinating, and I should like to pay much more attention to it than is practicable in the present brief review of a large subject.

I also regret being obliged to pass over, almost without mention, other organisms than stony corals that contribute material incorporated in reefs. There are the discoid *Orbitolites* and flat-coiled *Orbiculina*, Foraminifera so abundant in Florida and the West Indies, the stellate *Tinoporus baculatus* of Australia and other species that live on the Pacific reefs, and *Polytrema mineaceum*, ubiquitous on coral reefs as blood red, reticulated incrustations on dead corals and shells. Alcyonaria are important contributors to bottom deposits in places, although, in my opinion, no quantitative evaluation of their work has yet been accomplished; and echinoids add their tests and spines to the remains of the members of the other groups. Coralline algae vie with stony corals in relative importance, in some places one group, in other places the other holding first rank as reef-builder, and at least in many places in the Pacific form incrustations just landward of the sea face of barriers. An account of the charms and dangers or discomforts of reefs must be abbreviated practically to its suppression. I will only say beware of the long, waving, pointed spines of the sea urchin, *Diadema setosum* (now called *Centrechinus setosus*); look warily into crevices, and step carefully into pools, otherwise sore feet, legs, arms, and hands for days or weeks to come may be the penalty!

GEOGRAPHIC DISTRIBUTION OF CORAL REEFS.

Having given a definition of "coral reef" and having eliminated from the category of coral reef and coral rock, limestones whose formation is independent of the activities of corals, a few words will be devoted to stating where coral reefs occur. They are found in those parts of the ocean where the conditions summarized on page 215 of this article prevail. As the proper conditions of depth, salinity, and purity of water, intensity of light, and character of bottom, are widespread in the ocean, the temperature factor is critical in restricting coral reefs to certain areas in tropical and subtropical seas. Coral reefs thrive only where the average temperature of the coldest month of the year does not fall below about 21° C. (70° F.), and where the usual temperature is between 25° and 30° C. (77° to 86° F.).[1] A well-known oceanographic fact is that the waters along the western shores of continents are colder than those on the eastern sides. The great living coral reefs are therefore in the tropical western Pacific Ocean, around the tropical islands of the mid-Pacific, in the Indian Ocean and the Red Sea, and in the tropical and subtropical western Atlantic Ocean. Reef corals are weakly developed on the Pacific side of Central America and Mexico and on the Atlantic coast of Africa.

Some features of the Atlantic (Caribbean and Floridian) reefs will now be compared with those of the Indo-pacific reefs. There are at present two great biogeographic divisions of reef-coral faunas: one is the Atlantic, the other is the Indo-Pacific, separated from each other by the land area of Central America. In their ecologic relations the reef corals of the two regions are identical, but there are important systematic differences, and the Pacific corals are more luxuriant in growth and more numerous in species than the Atlantic. That Pacific corals appear to grow more rapidly than those in the Gulf of Mexico and the West Indies was pointed out on page 214 of this article. The number of species on a section of an Indo-Pacific reef usually ranges between about 55 and something over 70. Von Marenzeller records 71 species from the Red Sea; Bedot lists 74 species and 5 varieties from Amboina, but I believe 4 of his specific names are synonyms, leaving 70 valid species. I have identified 63 species in Mayer's collection from Murray Island, Australia, and 51

---

[1] For detailed information on this subject see as follows: Vaughan, T. W., Temperature of the Florida coral reef tract: Carnegie Inst. Washington Pub. 213, pp. 319–339, 1917; and Mayer, A. G., in his "Ecology of the Murray Island coral reef," ibid., pp. 1–48, pls. 1–19, gives the temperature records for the Murray Island reef for the period while he was there.

species in Wood Jones's collection from Cocos-Keeling Islands, but it is known that a few more species occur in the latter group of islands. I collected at the Tortugas, Florida, about 32 species, but this does not represent all the species in the Floridian reef fauna, and about 26 species at Cocoanut Point, Andros Island, Bahamas, but additional species were collected on the reefs near the mouth of South Bight, and other species are known to occur in the Bahamas. The total number of Bahamian shoal-water species is about 35. Therefore, on a segment of a rich reef in the Indo-Pacific there are about twice as many, or a few more than twice as many, species as there are on a similar segment of a West Indian or Floridian reef. It would require too much space to discuss the systematic differences between Indo-Pacific and Atlantic faunas here, but it may be stated that the following are the names of some of the Indo-Pacific genera not known living in the Atlantic, viz: *Pocillopora**, *Seriatopora*, *Stylophora**, *Euphyllia**, *Cyphastrea*, *Leptastrea*, *Galaxea**, *Antillea**, *Favites**, *Trachyphyllia*, *Hydnophora**, *Leptoria**, *Symphyllia*, *Fungia*, *Herpetolitha*, *Polyphyllia*, *Halomitra*, *Podobacia*, *Pachyseris*, *Pavona**, *Leptoseris**, *Haloseris**, *Coeloseris*, *Psammocora*, *Diploastrea**, *Astreopora**, *Turbinaria*, *Montipora*, and *Goniopora**, but those whose names are marked by an asterisk (*) occur in geologic formations of Oligocene age in the southern United States, the West Indies, and Central America, and some of them range upward into the Miocene. This list might be greatly increased, but it will impress the reader that many genera now living in the Indo-Pacific region, but absent in the living Atlantic fauna, are represented in the Tertiary geologic formations on the Atlantic side of the North American Continent. Of the Atlantic genera not known to be living in the Indo-Pacific region there are *Stephanocoenia*, *Eusmilia*, *Meandrina*, *Dendrogyra*, and *Manicina*, and some other genera are probably not represented there, while the species of other genera that are represented in both the Atlantic and the Indo-Pacific are not closely related.

That the Indo-Pacific and Atlantic faunas were not always so distinct as they now are has been indicated in the foregoing paragraph. Geologic investigations have revealed that during later Eocene, all or most of Oligocene, and a part of early Miocene time, the two oceans were connected across Central America, and that the same faunas occurred in both oceans. In places the older Tertiary faunas in the West Indies contained as many species as are at present found on an Indo-Pacific reef. For instance, about 69 species are reported from the Oligocene of the island of Antigua, where I personally collected 60 species. In middle and later Miocene time the Atlantic and Pacific became separated by a land bridge from South to North America, and by Pliocene time the corals of distinctive Indo-Pacific facies had become extinct on the Atlantic side, so that the Pliocene coral fauna of Florida is purely Atlantic in its affinities. After the differentiation of the Atlantic from the Indo-Pacific fauna it seems that there was a short connection somewhere that permitted the Atlantic fauna to extend on the Pacific side of America up to the head of the Gulf of California.

THEORIES OF THE FORMATION OF CORAL REEFS.

Three kinds of coral reefs are generally recognized, viz: (1) fringing or shore reefs which occur along the shore; (2) barrier reefs which occur at variable distances offshore and have lagoons from 1 or 2 to as much as 30 or even 40 fathoms in depth between them and the shore line; (3) atolls, which are ringlike and inclose lagoons above whose surface no land masses of importance protrude.

As the literature on coral reefs is so enormous that a detailed review of it in this paper is impossible, coral reef theories will be here classified into three general categories, with a subordinate division of the third.

1. The first theory is that of Darwin and Dana. According to these authors corals first form a fringing reef along the shore of the gently sloping bottom of a subsiding land area; the reef grows upward at such a rate that its top remains near the surface of the water and through retreat of the shore it is converted into a barrier. Continued subsidence, where the inclosed land area is an island, may result in the production of an atoll circumscribing a lagoon without any land mass projecting above the water level. But the Darwinian hypothesis involves more than mere subsidence and the conversion of a fringing into a barrier reef, for it also attempts to account for extensive submarine platforms by assuming that they have been built upon *sloping* basements through agencies dependent on the presence of reefs.

The accompanying two figures (p. 223) are reproductions of Darwin's original illustrations; while the third (p. 224) is J. B. Jukes's diagrammatic cross section of the Great Barrier Reef of Australia.

2. The next general theory of coral reef formation was originated by Carl Semper,[1] who, in 1863, after studies in the Pelew Islands and noticing evidence of uplift there, announced the opinion that atolls could be formed in areas of stability, or even uplift, by the solution of the interior of limestone masses, and that erosion by currents and wave cutting could develop channels behind fringing reefs, and in that way transform a fringing into a barrier reef.

---

[1] Semper, Carl, Reisebericht: Zeitschr. für wiss. Zool., vol. 13, pp. 563–569, 1863.

Murray[1] in 1880 published the following summary of his opinions on the formation of coral reefs:

> That when coral plantations build up from submarine banks they assume an atoll form, owing to the more abundant supply of food to the outer margin, and the removal of dead coral rock from the interior portion by currents and by the action of the carbonic-acid gas dissolved in sea water.
>
> That the barrier reefs have been built out from the shore on a foundation of volcanic débris or on a talus of coral blocks, coral sediment, and pelagic shells, and the lagoon channel is formed in the same way as a lagoon.

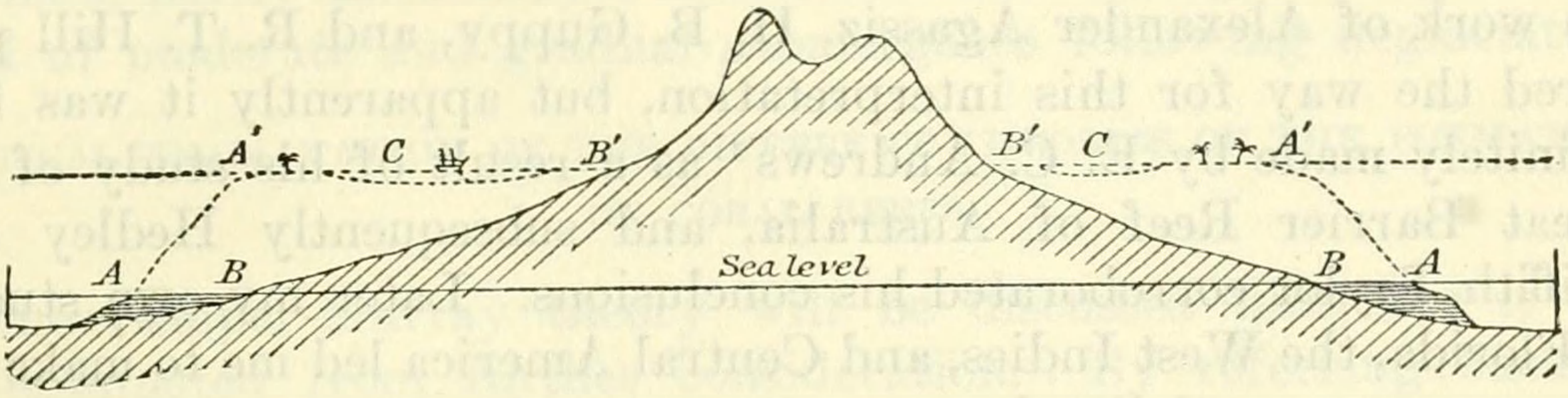


Fig. 6.—Copy of Darwin's figure illustrating conversion of a fringing into a barrier reef, according to his hypothesis. *AA*. Outer edge of the reef at the level of the sea. *BB*. Shores of the island. *A'A'*. Outer edge of the reef, after its upward growth during a period of subsidence. *CC*. The lagoon-channel between the reef and the shores of the now encircled land. *B'B'*. The shores of the encircled land.

N. B.—In this and the following cut the subsidence of the land could only be represented by an apparent rise in the level of the sea.

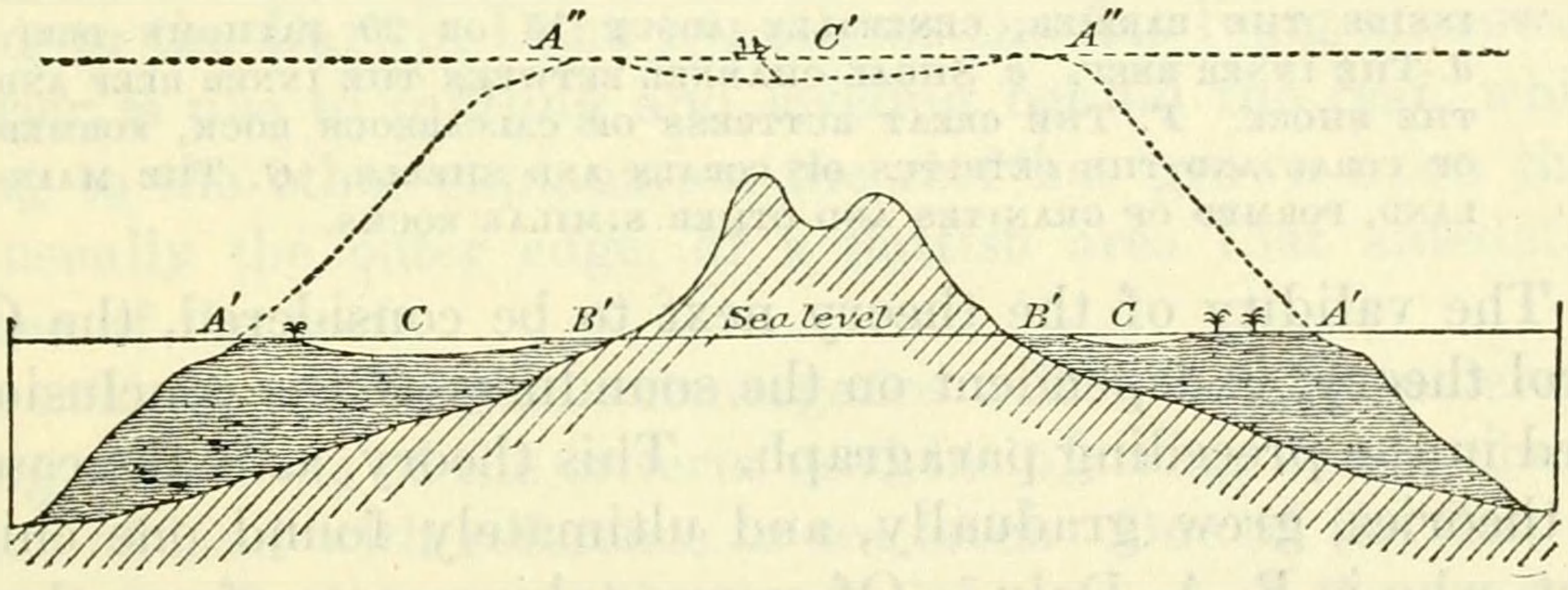


Fig. 7.—Copy of Darwin's figure illustrating conversion of a barrier reef into an atoll, according to his hypothesis. *A'A'*. Outer edges of the barrier reef at the level of the sea. The cocoanut trees represent coral islets formed on the reef. *CC*. The lagoon channel. *B'B'*. The shores of the island, generally formed of low alluvial land and of coral detritus from the lagoon channel. *A''A''*. The outer edges of the reef, now forming an atoll. *C'*. The lagoon of the newly formed atoll. According to the scale, the depth of the lagoon and of the lagoon channel is exaggerated.

> That it is not necessary to call in subsidence to explain any of the characteristic features of barrier reefs or atolls and that all these features would exist alike in areas of slow elevation, of rest, or of slow subsidence.

Alexander Agassiz and Stanley Gardiner were in essential accord with the opinions of Semper and Murray.

---

[1] Murray, John, On the structure and origin of coral reefs and islands: Roy. Soc. Edinburgh Proc., vol. 10, 1879–1880, pp. 505–518, 1880.

3. The third theory can not be referred to any one man, as it has gradually grown out of the work of many men. Briefly stated it is that offshore reefs have formed on antecedent flattish basements or platforms, during or after submergence, in areas where the ecologic conditions are favorable for the life of reef-building corals. Some of the work of Alexander Agassiz, H. B. Guppy, and R. T. Hill prepared the way for this interpretation, but apparently it was first definitely made by E. C. Andrews[1] as a result of his study of the Great Barrier Reef of Australia, and subsequently Hedley and Griffith Taylor corroborated his conclusions. Later my own studies in Florida, the West Indies, and Central America led me to make for those areas essentially the same interpretation as that of Andrews and Hedley and Griffith Taylor for the Australian Great Barrier.

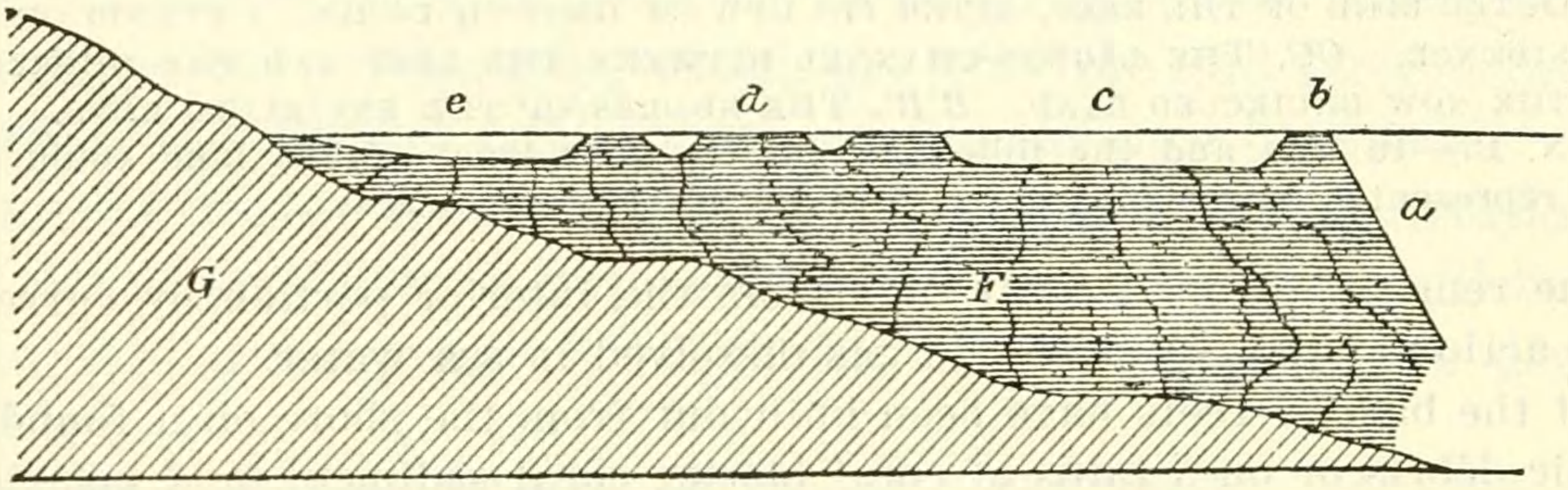


FIG. 8.—REPRODUCTION OF J. B. JUKES'S SECTION ACROSS THE GREAT BARRIER REEF OF AUSTRALIA. *a*. SEA OUTSIDE THE BARRIER, GENERALLY UNFATHOMABLE. *b*. THE ACTUAL BARRIER. *c*. CLEAR CHANNEL INSIDE THE BARRIER, GENERALLY ABOUT 15 OR 20 FATHOMS DEEP. *d*. THE INNER REEF. *e*. SHOAL CHANNEL BETWEEN THE INNER REEF AND THE SHORE. *F*. THE GREAT BUTTRESS OF CALCAREOUS ROCK, FORMED OF CORAL AND THE DETRITUS OF CORALS AND SHELLS. *G*. THE MAINLAND, FORMED OF GRANITES AND OTHER SIMILAR ROCKS.

3a. The validity of the theory next to be considered, the Glacial Control theory, is dependent on the soundness of the conclusions expressed in the preceding paragraph. This theory, as is the case with most theories, grew gradually, and ultimately found one chief exponent, who is R. A. Daly.[2] Of course taking water from the ocean to form the continental glaciers of Pleistocene time would lower the level of the surface of the sea during that time to an amount equal to the quantity of water abstracted from the ocean, if there were no crustal movements, such as down-bending due to the weight of the ice caps in high latitudes, that would counteract the effects produced by removal of water from the ocean to form the great ice caps. During Pleistocene time, because of the cold climate of that time, the rate of formation of coral reefs was probably reduced, and, as the protection they afforded shores was thereby lessened, the waves of the sea would then cut extensive submarine plains. With the return of warmer

---

[1] Preliminary note on the geology of the Queensland coast with reference to the geography of the Queensland and N. S. Wales plateau: Linn. Soc. New South Wales, pt. 2, pp. 146–185, 1902.

[2] The Glacial-Control theory of coral reefs: Amer. Acad. Arts and Sci. Proc., vol. 51, pp. 157–248, 1915.

climatic conditions the great ice caps melted, and the water, thus released, flowed back to the sea, raising its level by an amount equal to the quantity of water returned to it. The warmer waters were favorable for the growth of reef corals, and coral reefs grew luxuriantly on flats, partly formed by Pleistocene wave-cutting, during the period of moderate and gradual submergence following deglaciation.

CRITICAL EXAMINATION OF THE DIFFERENT THEORIES OF THE FORMATION OF CORAL REEFS.

The Semper-Murray theory will be discussed first, for it can be eliminated from further consideration. By referring back to page 217 of this article, it will be seen that present evidence is convincing that neither a lagoon channel nor the lagoon of an atoll can be formed by the solvent effect of sea water in coral reef areas, and as lagoons in general are areas where the deposition of sediment predominates over its removal, they must be explained by an inclosing and not by an excavating process. However, in small areas local destruction may predominate over construction, but such localized destruction will not explain the phenomena presented by lagoons.

Both of the other two explanations are in agreement as regards the part played by submergence in the formation of offshore coral reefs, which include those of the barrier kind, but differ in that according to the Darwin-Dana hypothesis the flat lying shoreward of a barrier is due to infilling and leveling behind the reef, while according to the other explanation the reef has grown upon the surface, usually the outer edge, of a flattish area that antedates the presence of the reef.

The evidence bearing on submergence will be briefly reviewed, beginning with some of the criteria used in inferring such a change in position of land with reference to sea level. One of the first recognized kinds of evidence indicating submergence of the land is the presence of arms of the sea extending into the land area and occupying the lower parts of valleys to be accounted for only by stream erosion operating at altitudes above present sea level. Plate 35, figures D, C, illustrates submerged lower courses of valleys in the islands of Antigua and St. Thomas, West Indies; text figure 9 illustrates a part of the shore of Antigua, where it is deeply indented by arms of the sea that as a result of submergence of the land extend up valleys eroded when the land stood higher above the sea level than it does at the present time. Figure B, of plate 35, illustrates a view looking toward the head of Santiago Harbor, Cuba, and figure A of the same plate is a view looking seaward through the harbor mouth. Text figure 10 illustrates a cross section of Habana Harbor, showing that within the harbor there is a filled channel, which must have been cut when the land was at least 100 feet higher with reference to sea level than at present. The Cuban harbors are pouch-shaped drainage basins into which the sea has been admitted by submergence of the land. Plate 36 illustrates the basin of Yumuri River and the gorge through which it flows into the sea near Matanzas, Cuba. A slight lowering of the land would convert this basin into a pouch-shaped harbor. There are living coral reefs off the shores of Antigua, St. Thomas, and Cuba, and they have evidently grown upward since the submergence of the former shore lines of those islands. Shore-line phenomena such as these occur around many of the West Indian Islands, along the coasts of Nicaragua and Honduras in Central America and along that of Brazil. Instances of similar phenomena may be seen in New Caledonia, the Society, Fiji, and other islands of the Pacific, and along the Queensland coast, landward of the Great Barrier Reef of Australia.

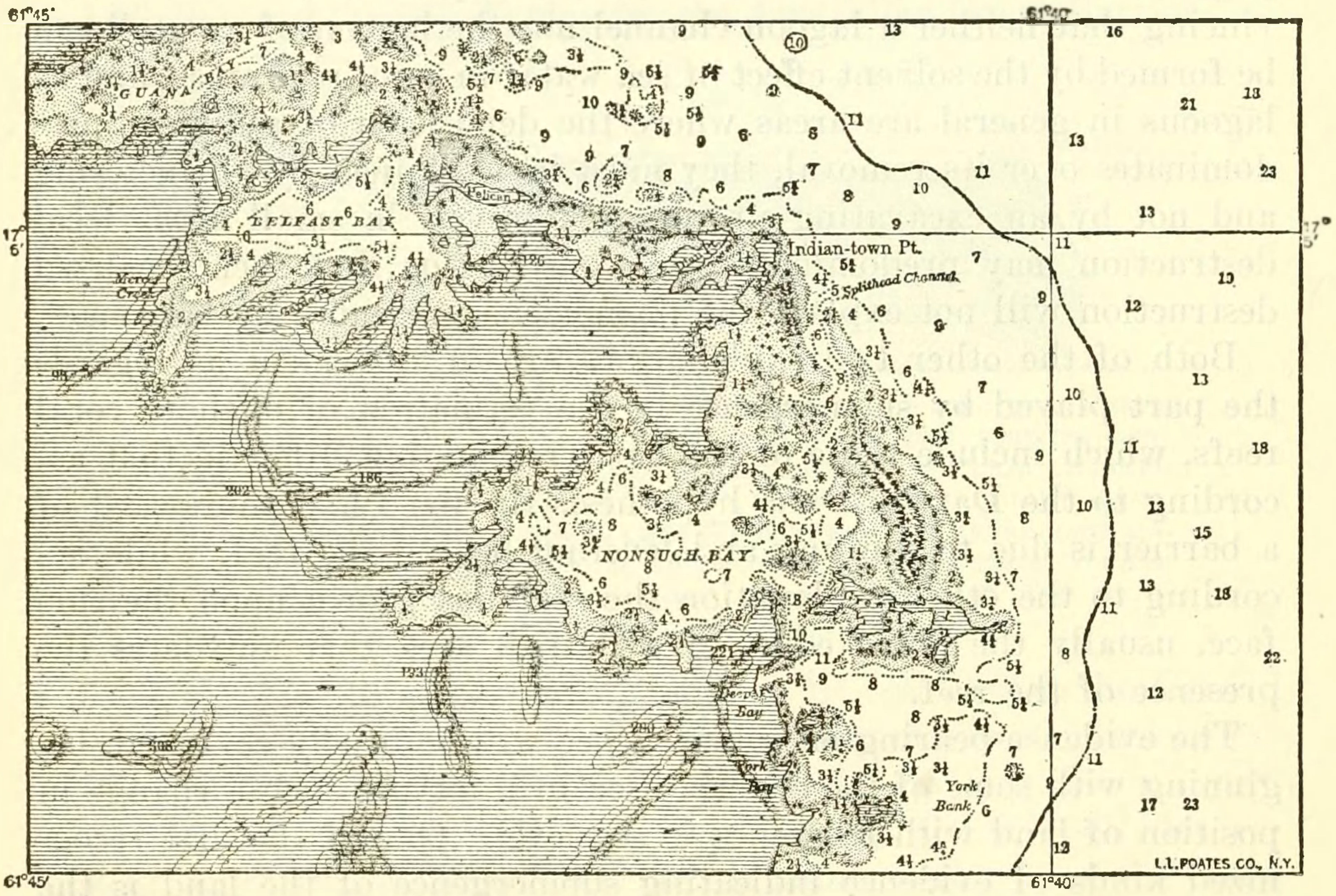


FIG. 9.—CHART OF PART OF EAST COAST OF ANTIGUA. FROM U. S. HYDROGRAPHIC CHART No. 1004.

Where the surface of the land is underlain by limestone, rain water that falls on the earth, instead of eroding stream ways and valleys, in making its way back to the ocean may produce caves and solution-wells by dissolving the limestone because of the carbonic-acid gas it contains. In many areas, such as the Bermudas, the Bahamas, and in places in southern Florida, caverns and solution-wells are found below sea level. Text figure 11 (p. 228), a cross section from the shore of

Andros Island, Bahamas, across the barrier reef, shows the relation of some solution-wells there to the outer reef. The flat between the reef and the shore has certainly been submerged since the formation of the wells.

FIG. 10.—PLAN AND CROSS SECTION OF FILLED CHANNEL IN HABANA HARBOR. AFTER HAYES, VAUGHAN, AND SPENCER.

Another kind of evidence is the presence undersea of steeply sloping areas of bottom between flat plain surfaces, thereby indicating the submergence of an escarpment or steep slope formed by marginal cutting of the sea, at a time while the land stood high enough for the shore to have been at the escarpment front. (See p. 236 of this article for additional consideration of this criterion.)

The presence below sea level of deposits of peat composed of the remains of land plants is still another kind of evidence. Submerged peat deposits of this kind occur in St. John Harbor, Antigua, and near Key West, Florida.

There are other kinds of evidence, but the four mentioned are sufficient for present purposes. Nearly all of the important living offshore reefs of the world have now been investigated with reference to evidence of submergence, and it has been found that practically all, if not actually all, have formed after an episode of submergence.

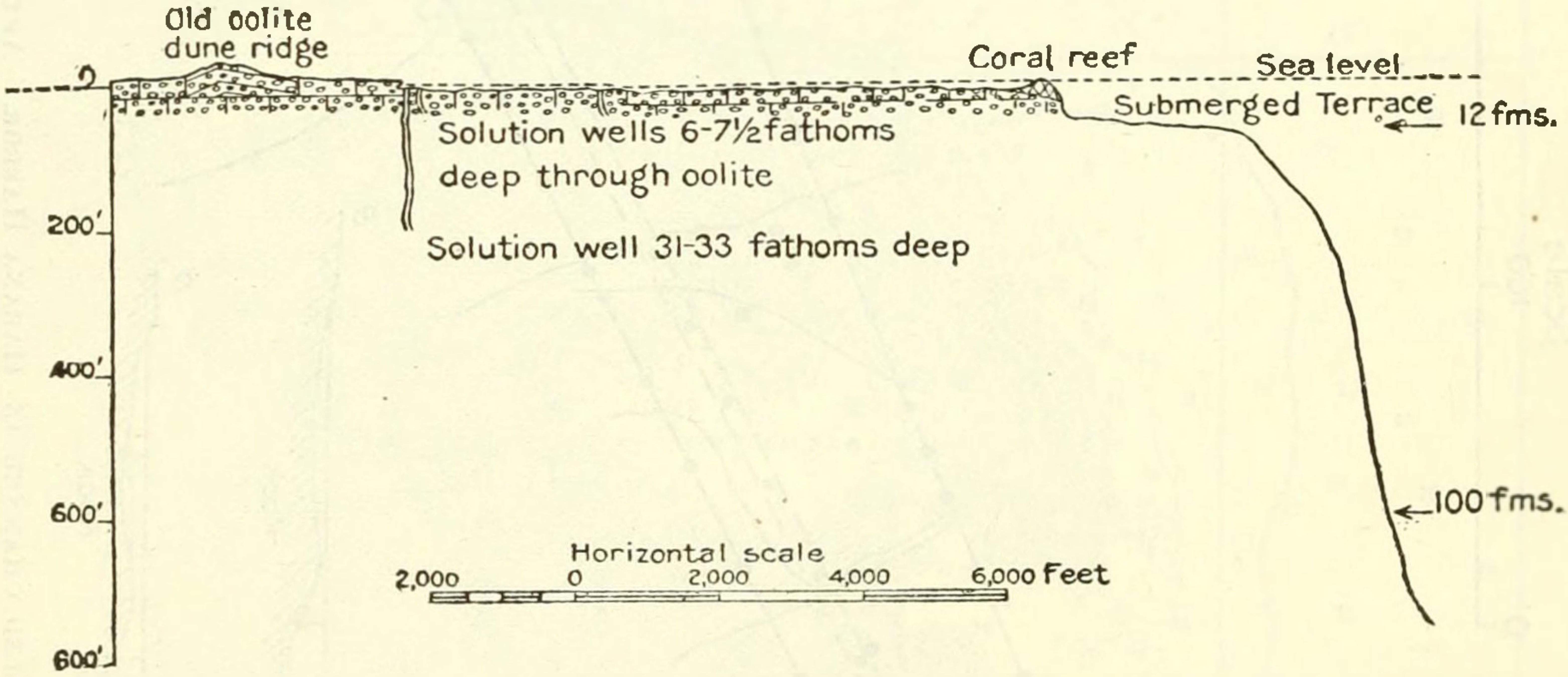


FIG. 11.—DIAGRAMMATIC SECTION ACROSS THE BARRIER REEF, ANDROS ISLAND, BAHAMAS.

In the study of fossil reefs the principal criterion for inferring whether they were formed during the submergence of their basements is the nature of the contact between the fossil reef and the immediately underlying geologic formation. If the underlying formation has an uneven upper surface and if pebbles derived from it are incorporated in the overlying reef, the deduction is considered warranted that the basement stood above sea level long enough for it to have been eroded by atmospheric agencies and that it was then brought below sea level before the reef occurring above it began to form. Contacts of the kind indicated are called unconformities. For a number of years I have been studying not only the corals in the fossil reefs of the West Indies and the southern United States, as may be seen by referring back to pages 221, 222 of this paper, but also the geologic relations of the reefs, including the nature of their basal contacts, and the results are given in the following tables:

Stratigraphic relations of West Indian and Canal Zone Eocene and Oligocene reef corals and coral reefs.

Geologic age.	Locality.	Basal contact.
Upper Oligocene.	Canal Zone (Emperador limestone).	Unconformable on Culebra formation.
	Anguilla.	Unconformable on igneous rock or on sandstone and conglomerate.
Middle Oligocene.	Antigua.	Do.
	Porto Rico (Pepino formation).	Do.
	Cuba (Guantanamo).	Do.
Upper Eocene.	St. Bartholomew.	Do.

Stratigraphic distribution of coral reefs and reef corals in the southeastern United States from Oligocene to Recent time, and their relation to changing sea level.

Geologic series.	Geologic formations, members, and unconformities.	Distribution of reef corals and coral reefs.	Change in relation of basement to sea level.
Recent.		Coral reefs.	Submergence.
	Erosion unconformity.		
Pleistocene.	Key Largo limestone.	Do.	Subsidence.
	Erosion unconformity.		
Pliocene.	Caloosahatchee marl.	Reef corals.	Do.
	Erosion unconformity.		
Miocene.	Choctawhatchee marl.	No reefs, a few corals.	Do.
	Erosion unconformity.		
	Alum Bluff formation. Shoal River marl.	A few corals; slight development of reefs in central and northern peninsular Florida.	Do.
	Oak Grove sand.		
	Chipola marl.	A few corals; 1 species of reef facies.	
Oligocene.	Chattahoochee formation. Upper.	Coral reefs, Tampa, Florida, etc.	Do.
	Lower.	Coral reefs, Bainbridge, Georgia.	Do.
	Erosion unconformity.		
Eocene.	Ocala limestone.	No coral reefs.	Do.

It appears unnecessary to present more evidence on this subject. The result of the examination of the fossil reefs is the same as that obtained from the study of the living reefs—which is that the important offshore reefs have formed during or after submergence. The contacts at the bases of fringing reefs are usually those of unconformity, indicating that the land stood higher and was lowered before the formation of reefs of this kind, but at least many of the fringing reefs were formed during periods of intermittent emergence following submergence.

Have the flats above which offshore reefs rise, either as patches or as barriers, been formed by infilling and leveling behind the reefs, that is. are they dependent on the presence of the reefs, according to the postulates of the Darwin-Dana hypothesis; or are the flats in origin independent of the existence of the reefs and are the reefs merely superposed on flattish areas that antedate their presence?

There are at least three criteria that are applicable in deciding between these two interpretations. The first of these is the relation of the width and depth of the flat, or platform, to the presence or absence of barrier reefs. If the flat is dependent on the presence of the reef, where a break in the reef occurs there should be a landward projecting reentrant in which the seabottom is deeper than behind the reef. The second criterion consists in the position of the barrier on the surface of the flat. If the flat is due to infilling behind the reef, the reef should stand on its outer edge, not back from the edge with the flat projecting seaward beyond the reef. The third criterion concerns the composition and geologic history of the flat landward of the reef. In many places it is possible to ascertain the nature of the rock forming the sea floor between a barrier and the shore. Such a floor, if formed by agencies associated with the presence of the reef, will not exhibit geologic phenomena that in age antedate the reef; but, on the other hand, if the floor can be shown to be composed of rock older than the reef, or to have had any kind of geologic history antecedent to the presence of the reef, it is demonstrated that the reef is merely growing on the surface of a flat whose formation is independent of the reef development.

The Great Barrier Reef of Australia is definite in its testimony. Text figure 12 presents cross sections south of the reef limits and across the reef tract. Profiles 1, 2, and 3, which are south of the southern end of the reef, show the continuity of the platform southward beyond the end of the reef; while profiles 4 and 5 show the platform projecting some miles beyond the reef. At its northern end the reef appears usually to stand on the seaward edge of the platform or shelf. The continuity of barrier platforms irrespective of the presence or absence of reefs is general off the shores of large land areas. Plate 38 is from a photograph of a model of the Gulf of Mexico and the Carribbean Sea. There are offshore reefs on the Floridian Plateau, and on both Campeche and Mosquito banks, but a person would indeed be bold to contend that these features of the earth's crust are due to infilling behind reefs, especially when some additional facts presented in the next paragraphs are considered.

The geologic succession of the reef-coral faunas of Georgia and Florida is given in the table on page 229. The geographic extent and composition of the Ocala limestone, of late Eocene age, which forms the basement of the Floridian Plateau, have been ascertained with considerable exactness. Its surface outcrop has been mapped in Georgia and Florida, and well borings have revealed its presence under younger formations in west Florida at Panama City, and in peninsular Florida at Tampa, Key West, Key Vaca, and Palm Beach. The limestone is largely composed of the remains of myriads of *Nummulites* and orbitoidal Foraminifera, many Bryozoa, and some mollusks and echinoids, with which there seems to be an undetermined proportion of chemically precipitated calcium carbonate and some terrigenous material. Corals are everywhere rare and as a rule are absent. The organisms occurring in the formation are characteristic of tropical shoal water, 50 fathoms or less in depth; and, as the 100-fathom curve delimits the submerged border of the Coastal Plain, it is evident that the Floridian Plateau has been a part of the Coastal Plain and has had essentially its present outline since late Eocene time, *before the formation of the oldest Chattahoochee reef*, which was therefore superposed on a subsiding platform not produced by corals. The geologic history of the Floridian Plateau shows that each successive development of Tertiary reefs was on an antecedent platform which was formed by agencies not dependent on the presence of coral reefs, and in all instances the volume of coral as compared with material from other sources is

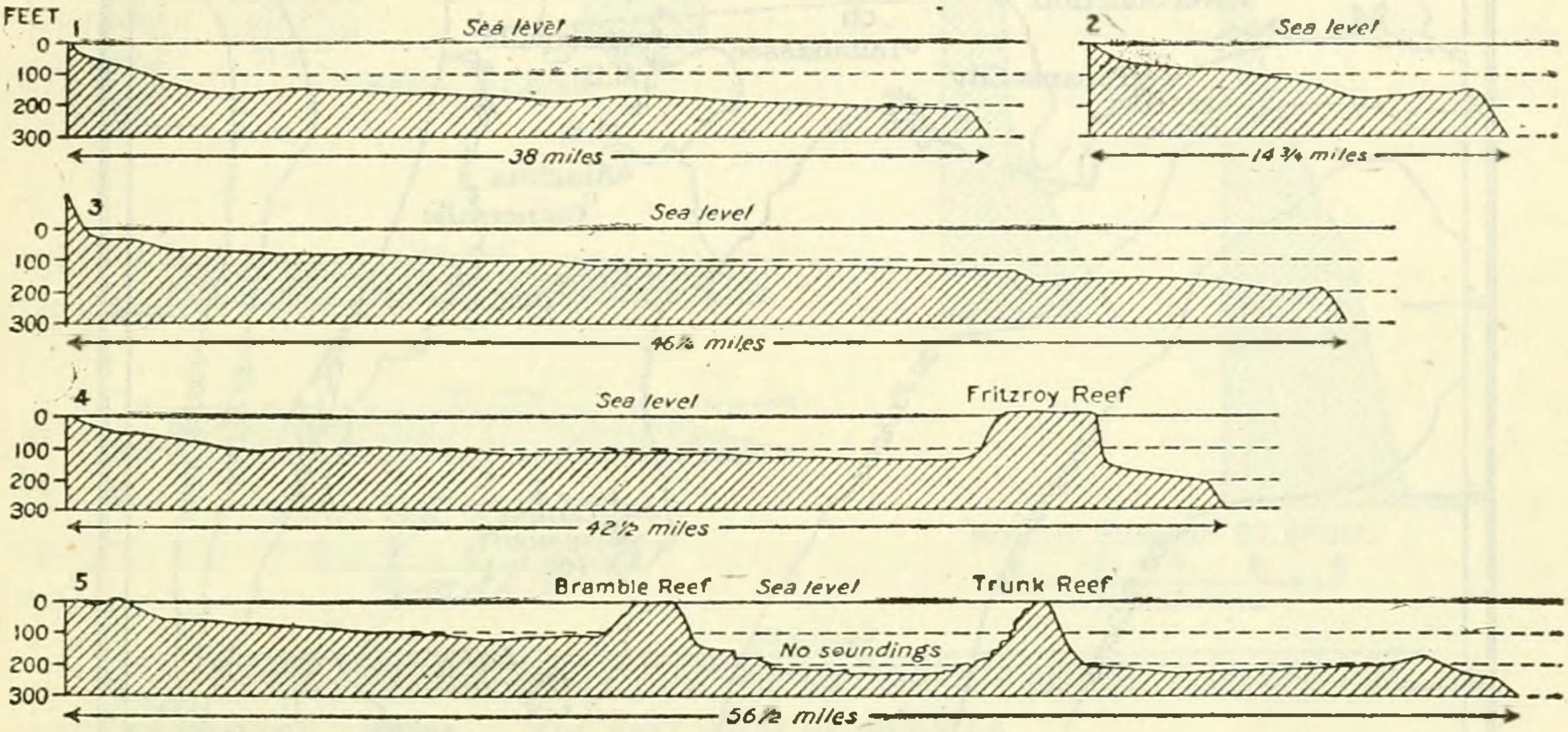


Fig. 12.—Profiles across continental shelf, east side of Australia. The latitude at the intersection of each profile with the shore line is followed by the statement of the direction of the profile from the shore.

South of the southern end of the Great Barrier Reef.

1. From shore east of Leading Hill, S. Lat. 25° 26′ 15″, South 82° East.
2. From base of Sandy Cape, S. Lat. 24° 53′ 40″, North 68° East.
3. From Toowong Hill, S. Lat. 24° 22′ 4″, North 45° East, passing between Lady Elliot and Lady Musgrove islands.

Across the Great Barrier Reef.

4. From Rodd Peninsula, S. Lat. 24° 0′ 0″, North 50° East.
5. From Georges Point, Hinchinbrook Island, S. Lat. 18° 25′ 40″, North 72° 32′ East.

of minor and usually of negligible importance. The accompanying map shows the location of the Oligocene and Miocene reefs and reef corals of Florida and Georgia with reference to the plateau surface.

The evidence of these fossil reefs is the same as that of the living Australian, Floridian, and Central American reefs. But this is not all. There are off the eastern shores of North America three banks at such a depth that coral reefs might grow on them were they within the proper climatic zone. These banks are Georges Bank off Nantucket, the banks off the coast of Nova Scotia, and the Grand Banks of Newfoundland. Such banks are not confined to the coral reef zone.

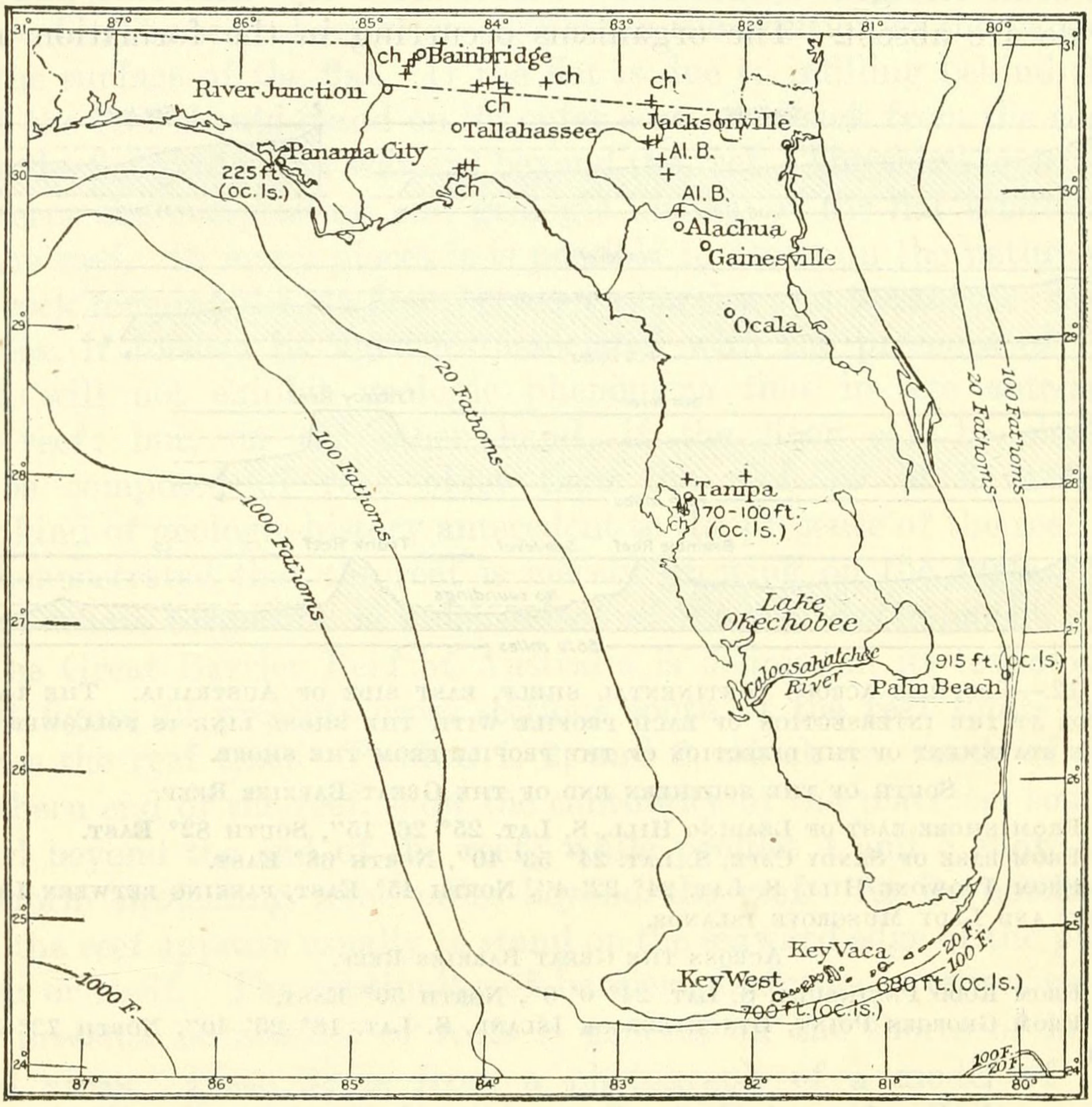


Fig. 13.—Florida, Ocala limestone plateau with superposed Oligocene and Miocene coral reefs and reef corals. oc. ls.=Ocala limestone; the figures are for the depths of its upper surface below sea level. Ch.=Chattahoochee and Tampa Oligocene formations. Al. B.=Alum Bluff Miocene formation.

Text figure 11, page 228, of this article shows solution wells through the oolite between the shore and the barrier reef off the east side of Andros Island, Bahamas. The flat between the reef and the shore must have existed before the present reef formed in order that those holes, now submerged, might be made in it. In the West Indies in general the living reefs are growing on antecedent platforms that have been submerged in geologically Recent time. There are continuous platforms and discontinuous reefs in New Caledonia, the Fiji Islands, and Tahiti, and such relations, which are certainly usual, if not entirely general, are *not* in accord with the Darwin-Dana hypothesis. Information on the small islands of the Society group, Murea, Huaheine, Raiatea, Bora-Bora, etc., is inadequate for a definite statement, and there is controversy as to whether the reefs are growing on previously formed flats or whether the flats are due to infilling behind the reefs.

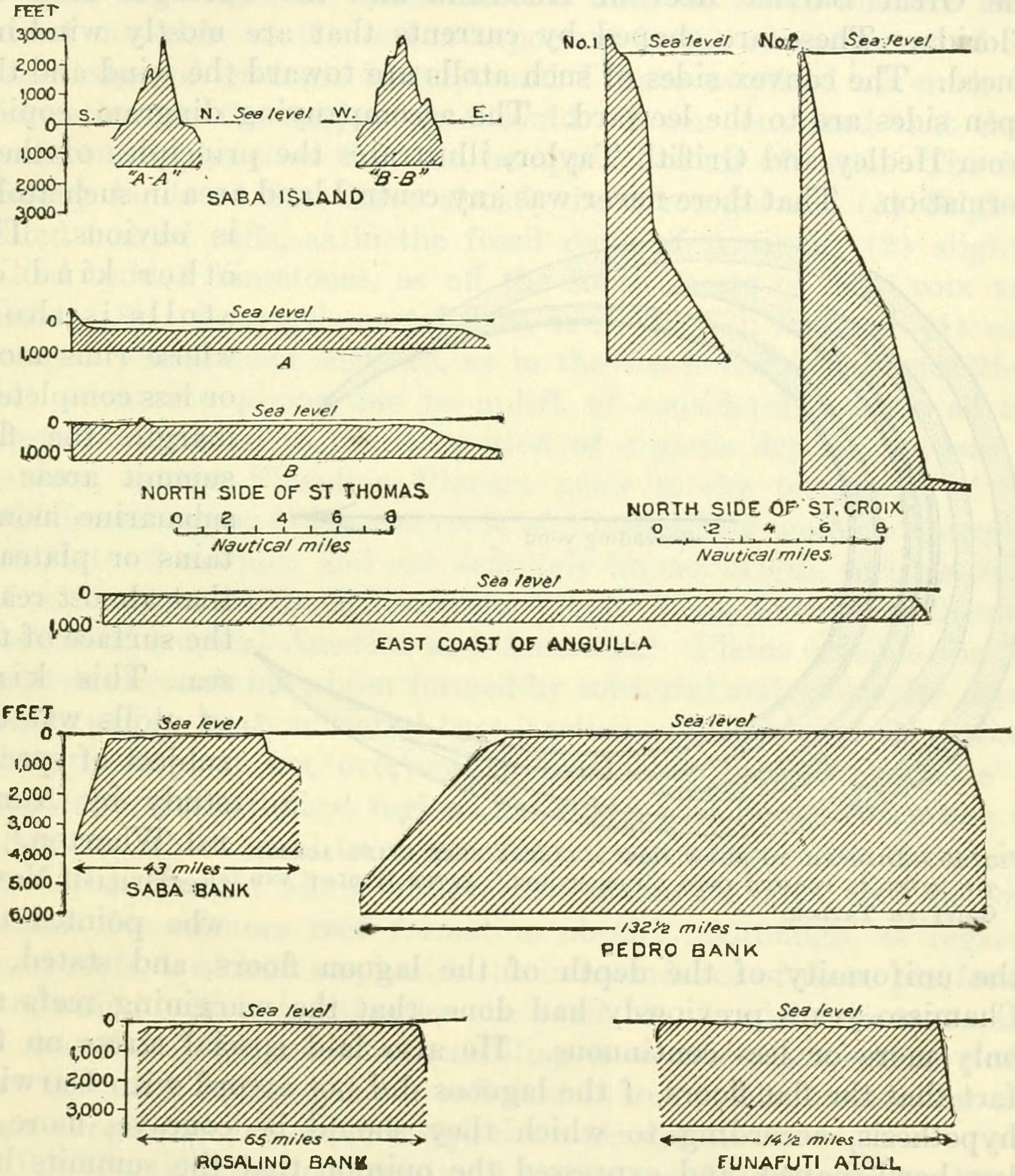


FIG. 14.—TYPES OF WEST INDIAN SUBLITTORAL PROFILES AND PROFILE OF FUNAFUTI ATOLL.

West Indian Islands sublittoral profiles are interesting in this connection, and are represented by text figure 14. There are no offshore reefs where no platforms have been developed, as off the young volcanic island Saba, and the steep shore along the north side of St. Croix. The presence of a flat seems necessary to initiate vigorous coral growth.

Only a few paragraphs will be devoted to atolls, of which there are two kinds. Those of the first kind are ring-shaped segments of long reefs that rise above shallow platforms, such as the atolls of the Great Barrier Reef of Australia and the Tortugas atoll of Florida. These are shaped by currents that are mostly wind-induced. The convex sides of such atolls are toward the wind and the open sides are to the leeward. The accompanying diagram, copied from Hedley and Griffith Taylor, illustrates the principles of their formation. That there never was any central land area in such atolls is obvious. The other kind of atolls is those whose rims more or less completely margin the flat summit areas of submarine mountains or plateaus that almost reach the surface of the sea. This kind of atolls was the subject of special study by Admiral Wharton,[1] of the British Navy, who pointed out the uniformity of the depth of the lagoon floors, and stated, as Chamisso years previously had done, that the margining reefs are only more or less continuous. He also laid special stress on the fact that the flat floors of the lagoons did not accord with Darwin's hypothesis, according to which they should be concave, more or less bowl-shaped, and expressed the opinion that the summits had been leveled by marine erosion previous to the formation of the atoll rims. It appears to me that the most plausible explanation of atolls is that they have formed on flat summit areas during moderate submergence.

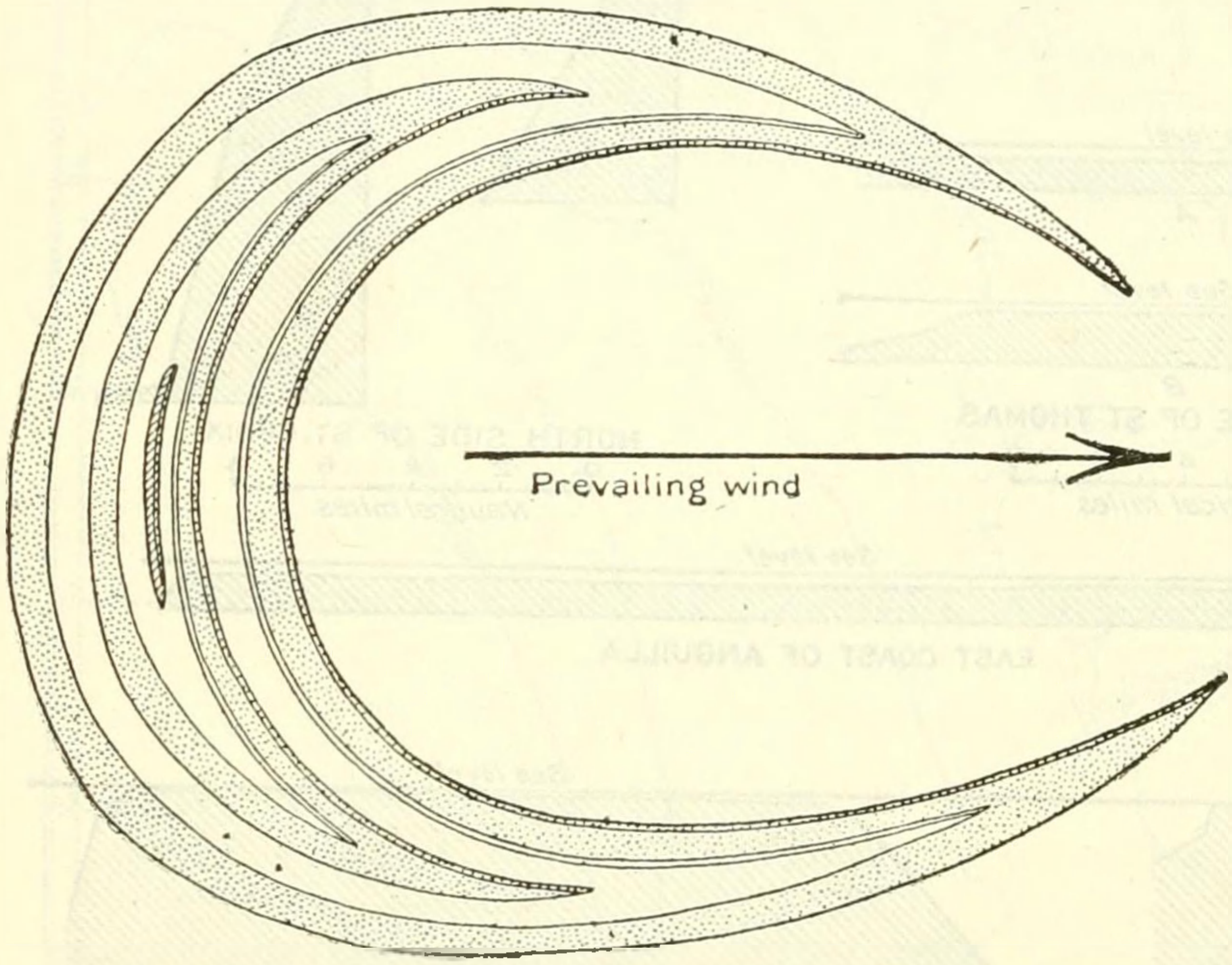


FIG. 15.—DIAGRAM TO SHOW HOW A LINEAR REEF LYING ACROSS THE WIND IS FORMED INTO A HORSESHOE. AFTER HEDLEY AND GRIFFITH TAYLOR.

In reply to a criticism of my interpretation of the relations of offshore reefs to the platforms above which they stand because I have not attempted to explain the origin of the platforms,[2] I may say that

---

[1] Wharton, W. J. L., Foundations of coral atolls: Nature, vol. 65, pp. 390–393, 1897.

[2] Davis, W. M., The origin of coral reefs: Nat. Acad. Sci. Proc., vol. 1, pp. 146–152. March, 1915.

the recognition of the fact that books, papers, inkstands, etc., are on the top of a desk does not require knowledge of the process of manufacture of the desk or even of the material out of which it is made; and that one geologic formation overlies another may be ascertained without having complete knowledge of the geologic history of either the overlying or the underlying formation.

That the origin of the submarine flats on which offshore reefs stand should be understood is important in the advancement of our knowledge of geologic history, and I have acquired as much information on the subject as I could. I am convinced that there is no one explanation that can be applied to all of them. The following kinds of flats have already been recognized: (1) Slightly tilted bedded tuffs, as in the fossil reefs of Antigua; (2) slightly tilted bedded limestones, as off the south coasts of St. Croix and Cuba; (3) submerged coastal flats, as in the Fiji Islands; (4) submerged peneplained surfaces, as in the fossil reefs of Porto Rico; (5) submarine plains due to uplift of considerable areas of the ocean bottom and to the deposition of organic deposits on such a surface, as the Floridian Plateau prior to the formation of the middle and upper Oligocene reefs of Florida and southern Georgia; (6) flats of complex and not definitely known origin, such as those of the Antigua-Barbuda Bank, the Virgin Bank, and the continental shelves of tropical America and Australia.[1] Plains suitable for the growth of corals have been formed by subaerial and submarine deposition, and by both subaerial base-leveling and submarine planation. Nearly every, if not every, plain-producing process operative in tropical and subtropical regions has taken part in the formation of plains on which coral have grown or are growing where the plains have been brought below sea level and where the other ecologic conditions for offshore reef formation obtain. Although, as regards coral reefs, I wish to emphasize the independence of those platforms concerning which information is available, I wish also to make it clear that I recognize that in-filling does take place behind reefs, but that such in-filing is not sufficient in amount to account for the flats above the surfaces of which the reefs stand.

The Glacial Control theory will now be considered in more detail. If this theory is true the following conditions should now prevail:

---

[1] Professor Davis, in an article entitled "The Great Barrier Reef of Australia," published in the Amer. Jour. Sci., 4th ser., vol. 44, pp. 339–350, November, 1917, proposes the hypothesis that the platform on which the living Great Barrier Reef is growing resulted from in-filling behind a barrier until a "mature reef-plain," according to his terminology, was formed. Although this is an interesting hypothesis, it is at present not possible to procure decisive information on the processes whereby the Australian continental shelf was produced.

(a) There should be evidence of geologically Recent submergence of most of the shore lines of the earth; (b) the average amount of the submergence should be equal to the amount of lowering of the ocean level during Pleistocene glaciation: (c) the position of the shore line during Pleistocene glaciation should be indicated by scarps separating flats, and the amount of submergence indicated by their present position below sea level should agree with the amount of the raising of ocean level due to deglaciation; (d) the rate of growth corals should be such that since the disappearance of the continental ice sheets coral reefs could grow to a thickness equal to the amount sea level was raised as a result of deglaciation; (e) living barrier coral reefs and atoll reefs should be superposed on antecedent basement flats or platforms. It should here be stated that the fact that there has been local differential crustal movements does not at all invalidate the importance of the Glacial Control theory in its application to the explanation of modern coral reef development.

In the foregoing discussion it has been shown that within coral-reef regions there has been geologically Recent submergence. The shore lines of the earth can not be reviewed in this place, but it may be said that the available evidence indicates that the sea has recently, geologically speaking, overflowed the seaward margins of the land. According to estimates by W. J. Humphreys[1] and by Daly the maximum amount of the lowering of sea level because of the abstraction of water from the ocean to form the continental ice sheets was of the order of magnitude of 67 meters (about 36 fathoms). Daly has made elaborate compilations of the depths of lagoons, lagoon channels, and drowned valleys, in the coral reef areas of the Pacific and Indian Oceans; and the lowering of sea level, between 55 and slightly more than 37 meters, indicated by the compilations agrees with the computations about as closely as should be expected. I obtained similar results in the West Indies. The accompanying text figure 16 indicated a raising of sea level in excess of 37 meters (20 fathoms), on the basis of interpreting the steeper slope at a depth below 20 fathoms as a marginal sea-cut scarp that has been submerged. A similar steeply sloping facet is shown in the profile of the Australian platform, text figure 12. The statement on the growth-rate of corals shows that any known living coral reef could have grown to its estimated thickness since the disappearance of the continental ice sheets, calculated to have been between 10,000 and 30,000 years ago; and finally, so far as definite information has been procured, living offshore coral reefs are superposed on basement platforms that have been recently submerged. I am entirely convinced that glacial control is one of the most important factors in bringing about the

---

[1] Changes of sea level due to changes of ocean volume: Washington Acad. Sci. Jour., vol. 5, pp. 445–446, 1915.

great development of coral reefs at the present time. However, I am not in agreement with Daly in attributing so much work to marine abrasion while the level of the sea was lowered during Pleistocene time. It seems to me that most of the platforms are of pre-Pleistocene age, and were wave-cut and remodeled around their edges during Pleistocene time; but this is a subject that needs much more investigation.

It should be stated that the raising of ocean level because of deglaciation will not explain the formation of all coral reefs, for in places, as in some of the Fiji Islands, according to W. G. Foye,[1] the submergence of the reef basements is due to the tilting of previously flat-lying areas, on the submerged part of which reefs have formed after the tilting. In other areas there is clear evidence of tilting and warping as in the Bahamas and Florida. General submergence because of deglaciation is concomitant with local crustal deformation. How the submergence produced is, as regards corals, unimportant, provided there be gradual submergence of moderate amount.

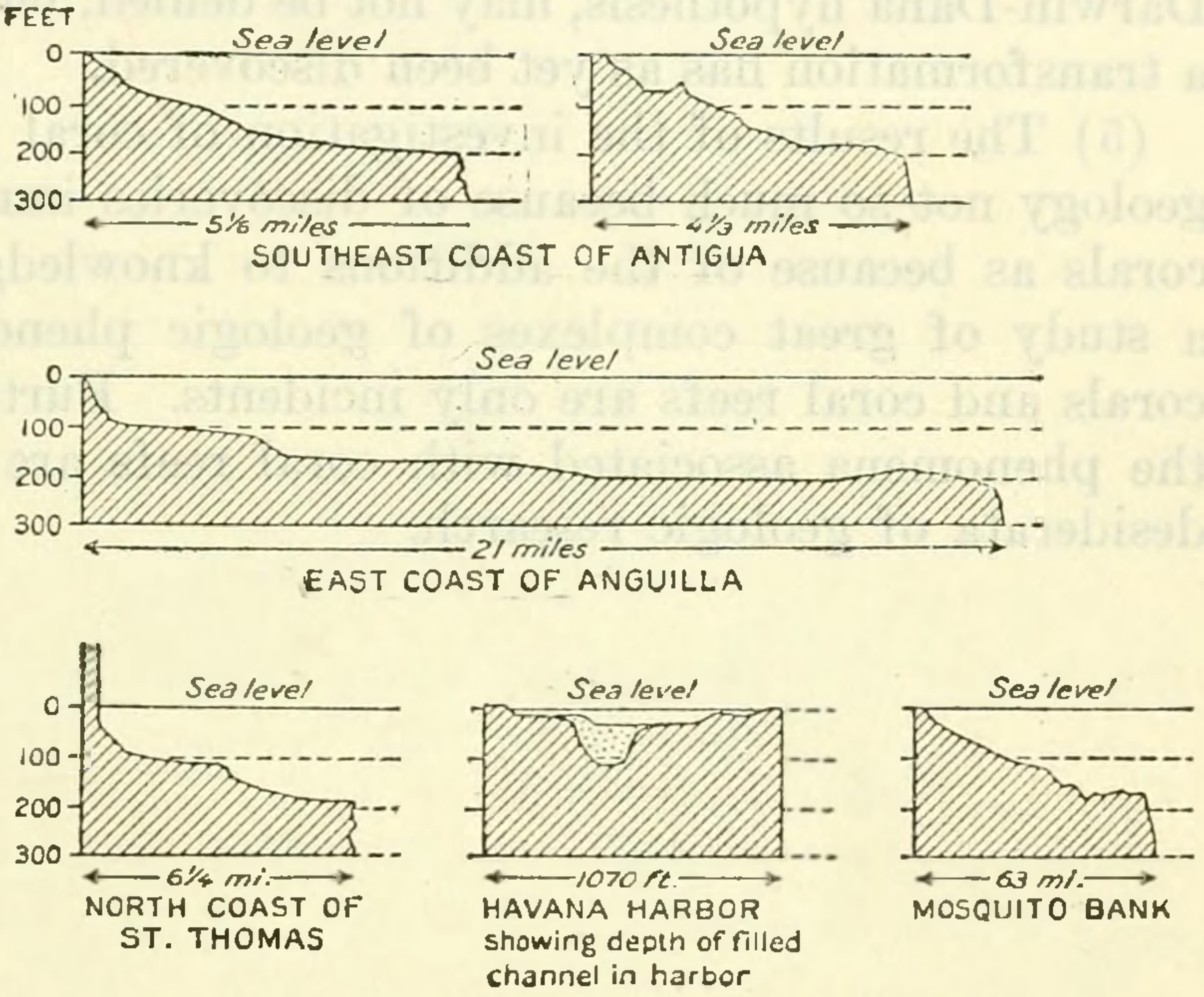


FIG. 16.—SUBMARINE PROFILES OFF WEST INDIAN ISLANDS AND ACROSS MOSQUITO BANK.

CONCLUSIONS.

The following are my conclusions on the formation of coral reefs:

(1) Fringing reefs seem uniformly to have uncomformable basal contacts; they may form after submergence that is not followed by uplift or they may form during intermittent uplift that follows submergence—that is, they may form during either emergence or submergence.

(2) Offshore coral reefs, barriers and atolls, form on antecedent flattish basements during and after submergence in areas where the general ecologic conditions suitable for reef-coral growth prevail, as stated on page 215. This generalization applies to fossil as well as to living reefs.

---

[1] The geology of the Fiji Islands: Acad. Nat. Sci. Proc., vol. 3, pp. 305–310, April, 1917.

(3) Recent rise of sea level because of deglaciation has made conditions favorable for coral reef formation over enormous areas, and it is one of the important factors in causing the great development of coral reefs at the present time. But in some areas, as in the Fijis, the flats on which the reefs are growing are coastal flats that have been brought below sea level by tilting, as described by Andrews and Foye.

(4) The theoretic possibility of the progressive change of a fringing reef into a barrier and later into an atoll, according to the Darwin-Dana hypothesis, may not be denied, but no instance of such a transformation has as yet been discovered.

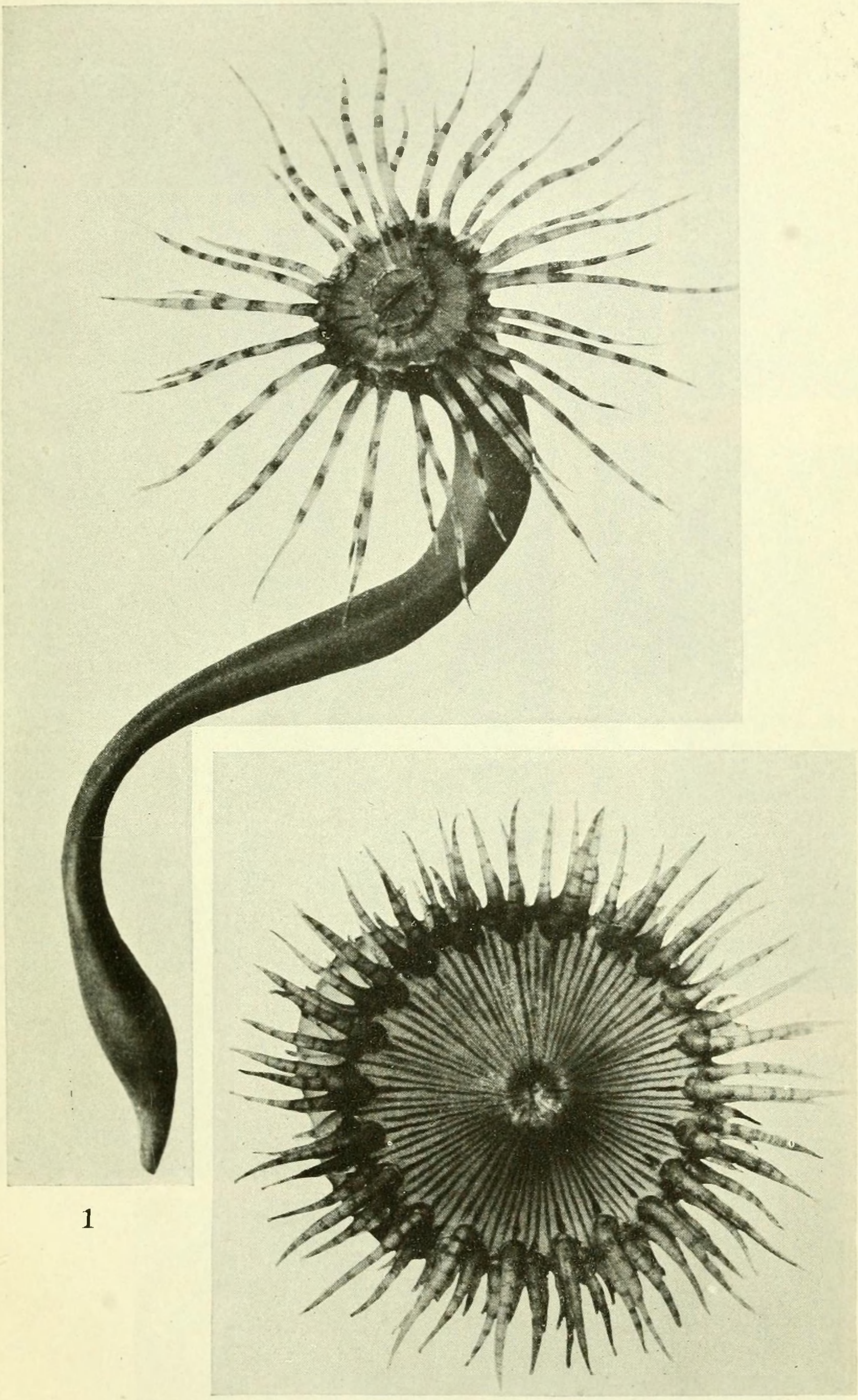
(5) The results of the investigation of coral reefs are valuable to geology not so much because of discoveries immediately concerning corals as because of the additions to knowledge obtained through a study of great complexes of geologic phenomena among which corals and coral reefs are only incidents. Further investigations of the phenomena associated with coral reefs are among the pressing desiderata of geologic research.

EXPLANATIONS OF PLATES.

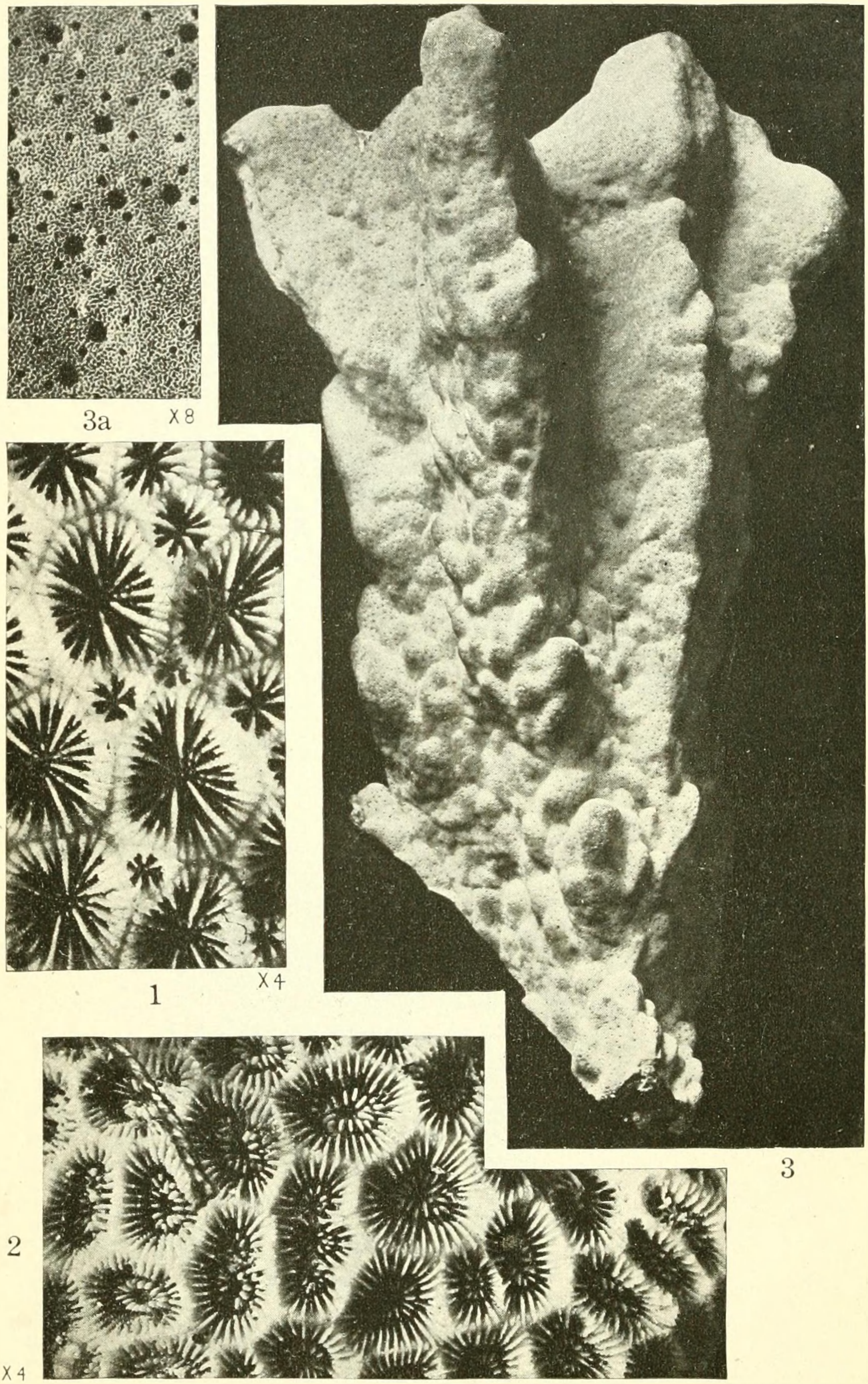
Plate 1.

Illustrations from photographs, natural size, of two Blaschka models of sea-anemones.

Fig. 1. *Cerianthus lloydi* Gosse.
2. *Heliactis bellis* (Ellis and Solander).



BLASCHKA GLASS MODELS OF SEA ANEMONES.



1. LEPTASTREA PURPUREA (DANA). 2. GONIASTREA PECTINATA (EHRENBERG).
3, 3A. MILLEPORA TRUNCATA (DANA).

PLATE 2.

FIG. 1. *Leptastrea purpurea* (Dana). Calices, × 4, to show the formation of new calices by budding between the older ones.

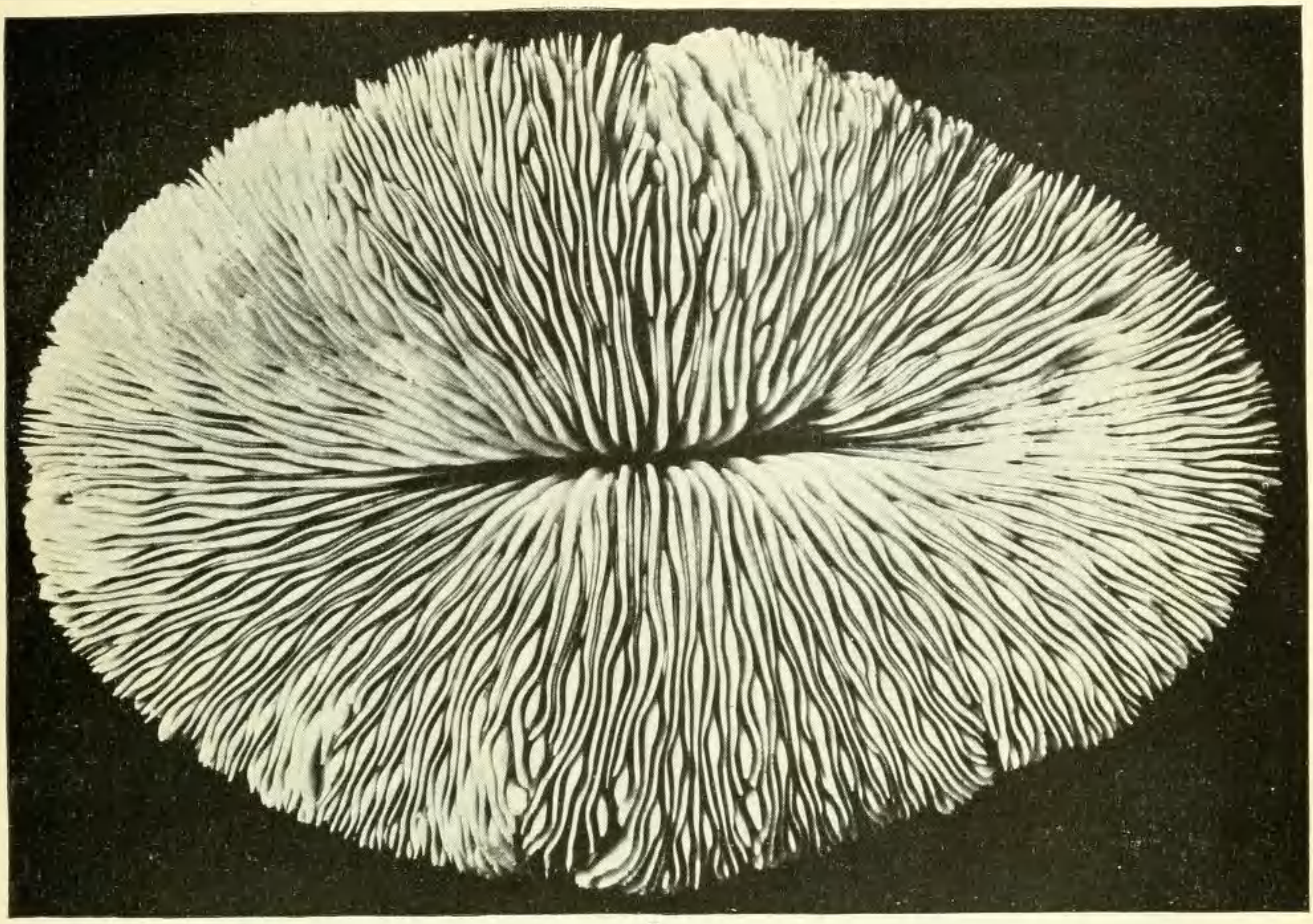
2. *Goniastrea pectinata* (Ehrenberg). Calices, × 4, to show the formation of new calices by the division of the older ones.

3, 3*a*. *Millepora truncata* Dana. Fig. 3, the skeleton, natural size; fig. 3*a*, part of the surface, × 8, to show the larger gastropores and smaller dactylopores.

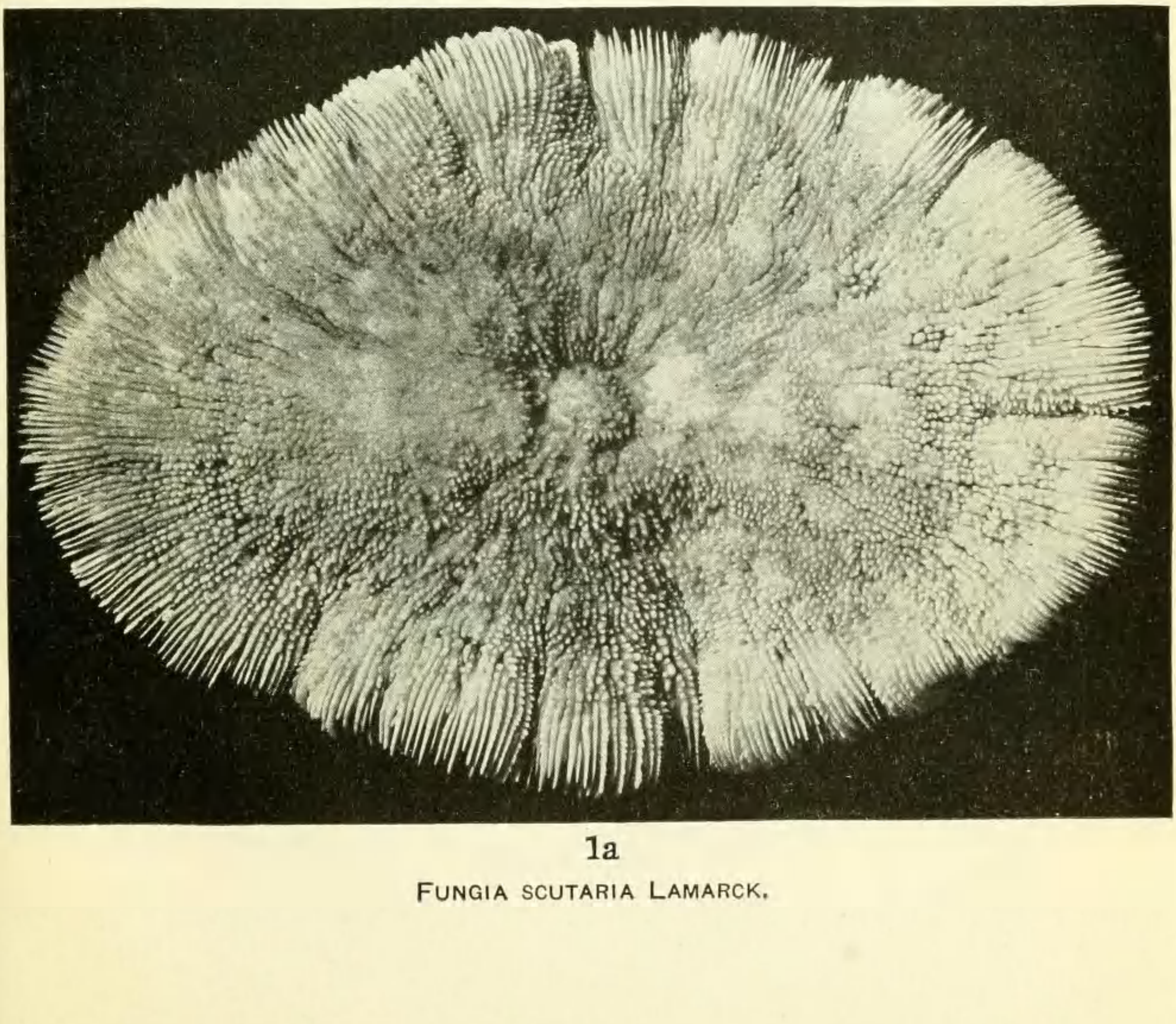
PLATE 3.

Fungia scutaria Lamarck.

FIG. 1. Upper surface; fig. 1*a*, lower surface, both natural size.
242

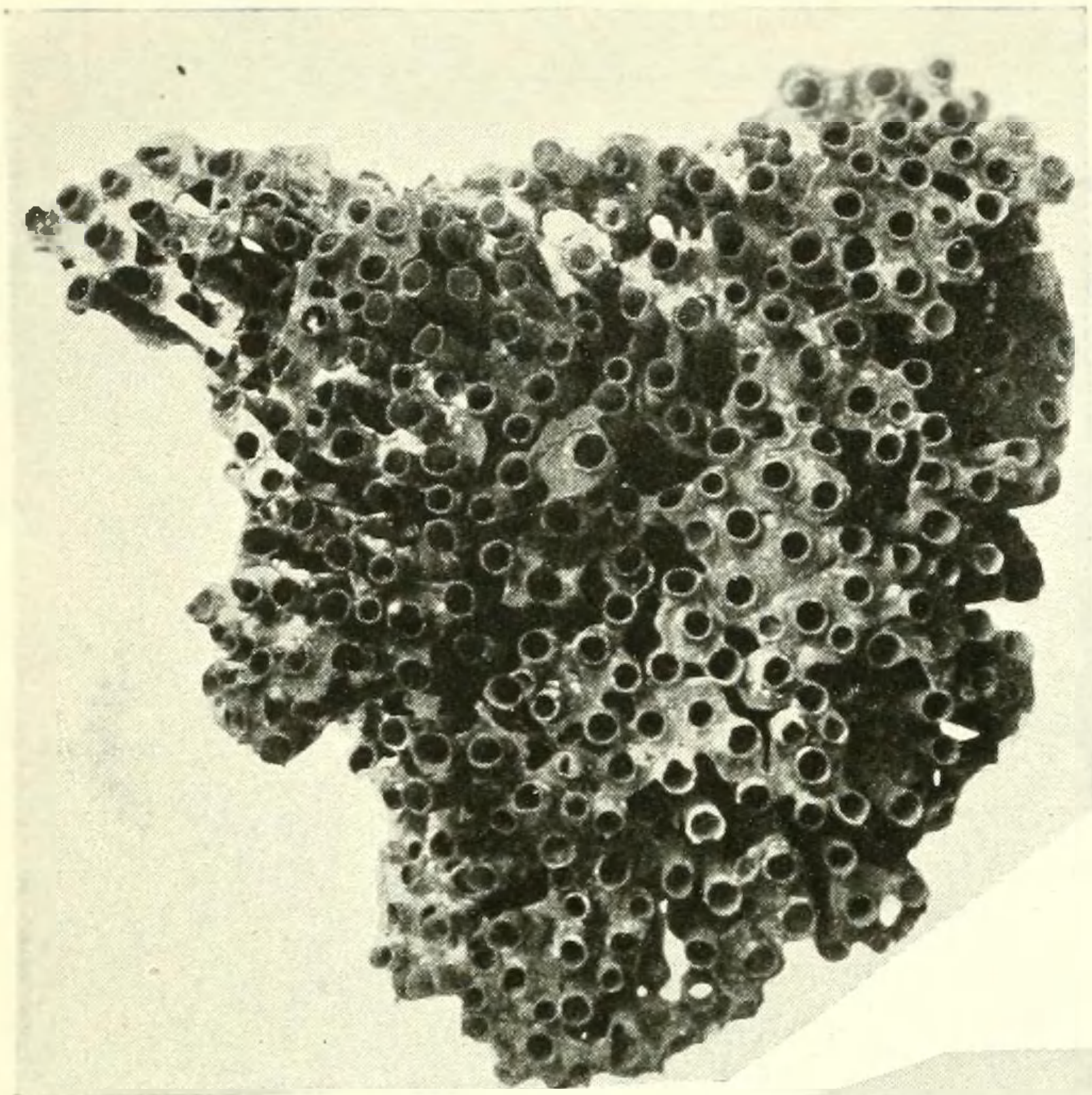


1

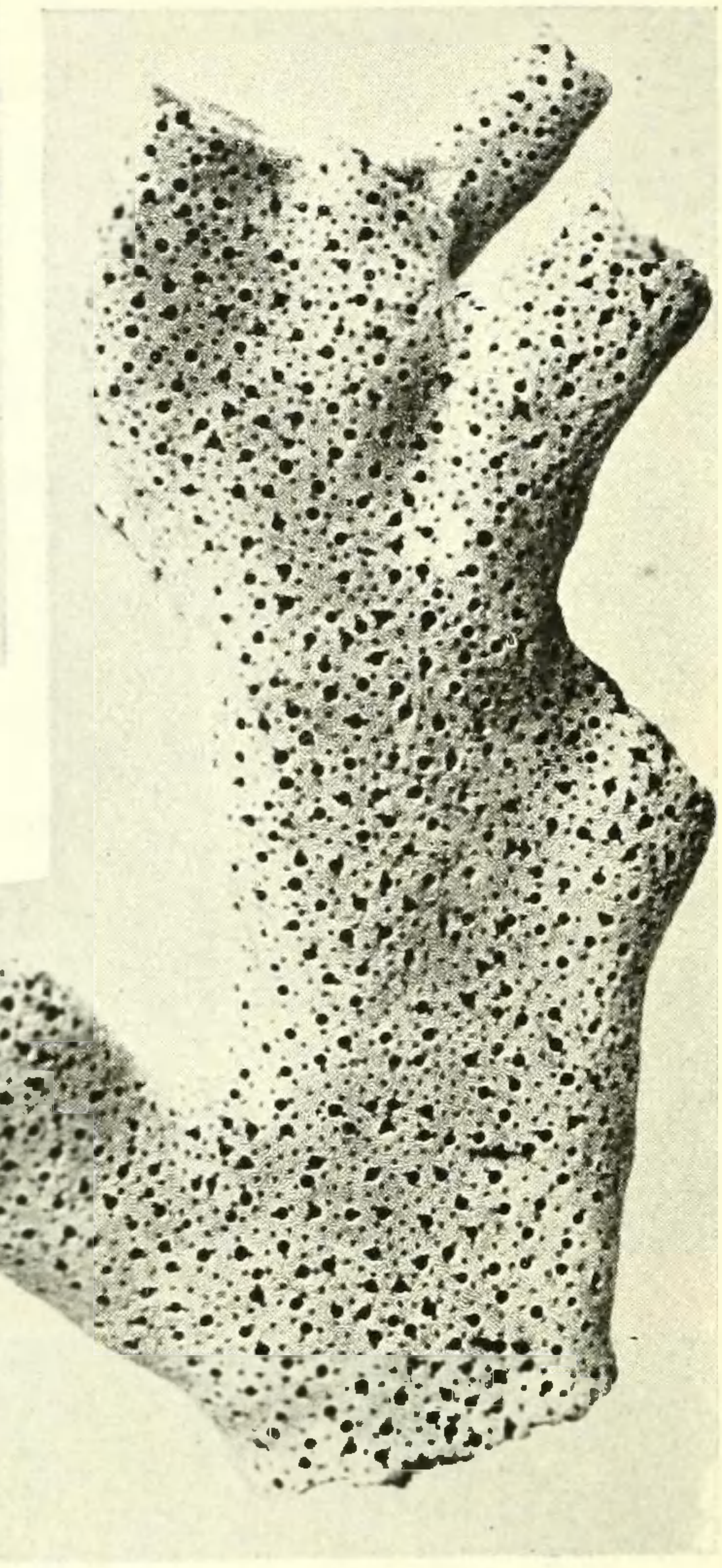


1a

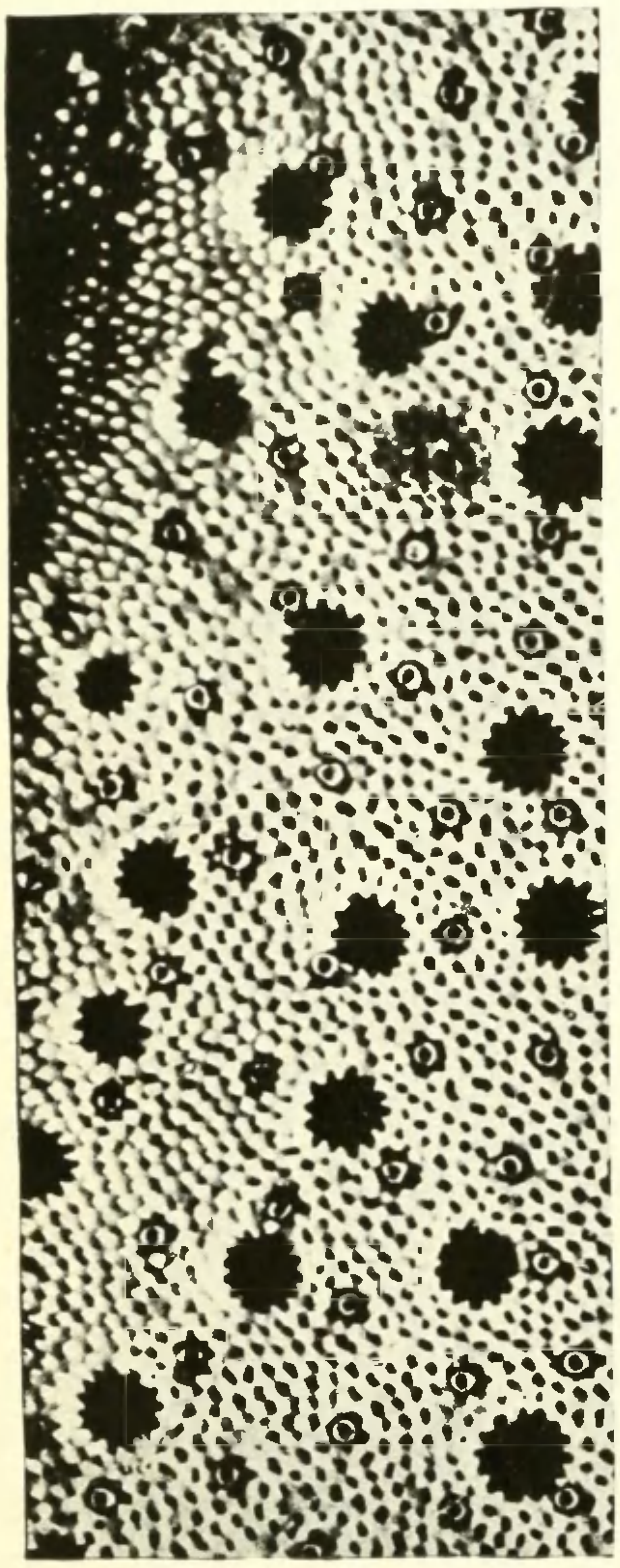
FUNGIA SCUTARIA LAMARCK.



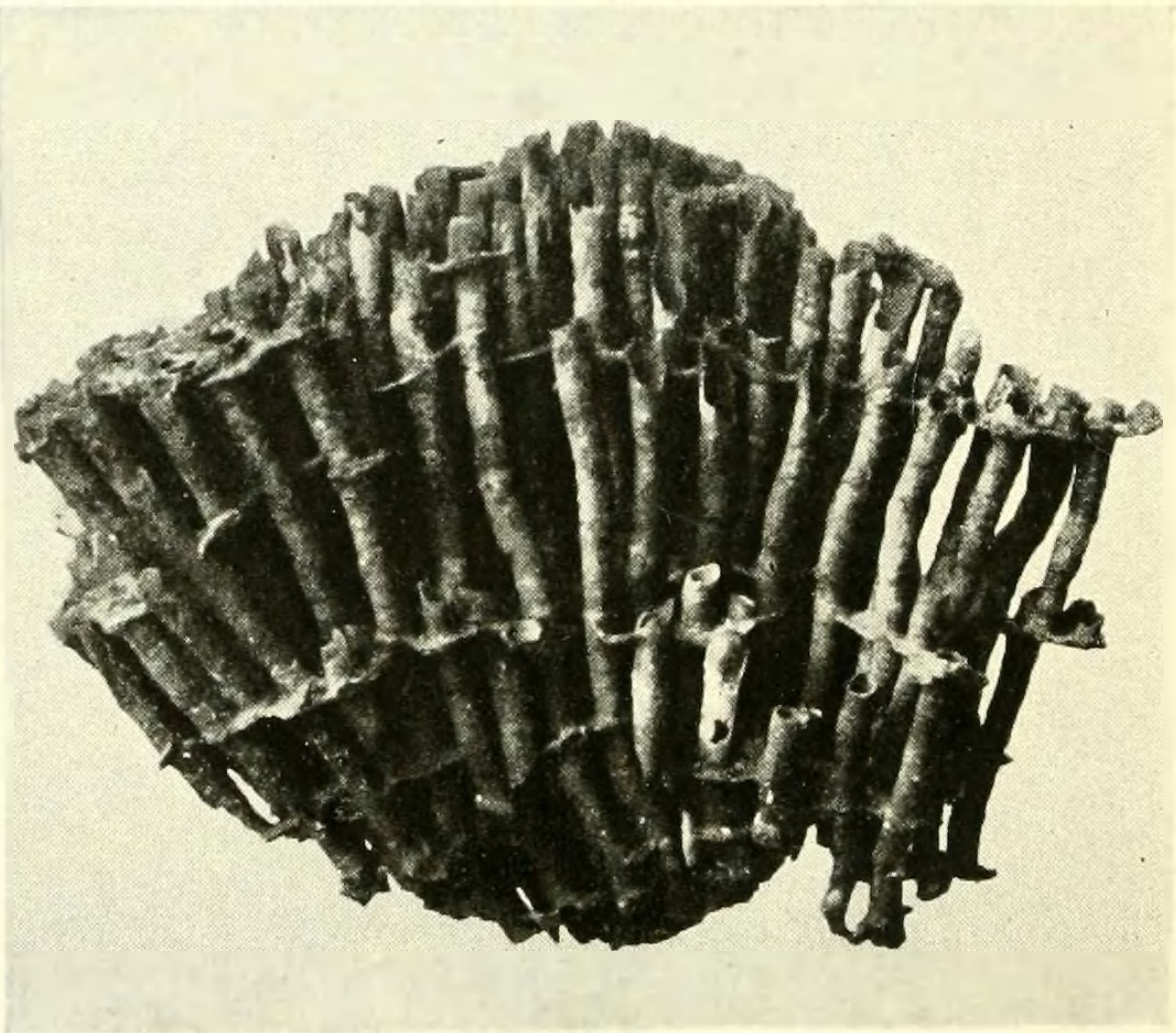
1



2



2a X6



1a

1, 1A. ORGAN-PIPE CORAL, TUBIPORA SP. 2, 2A. BLUE CORAL, HELIOPORA CAERULEA (PALLAS).

PLATE 4.

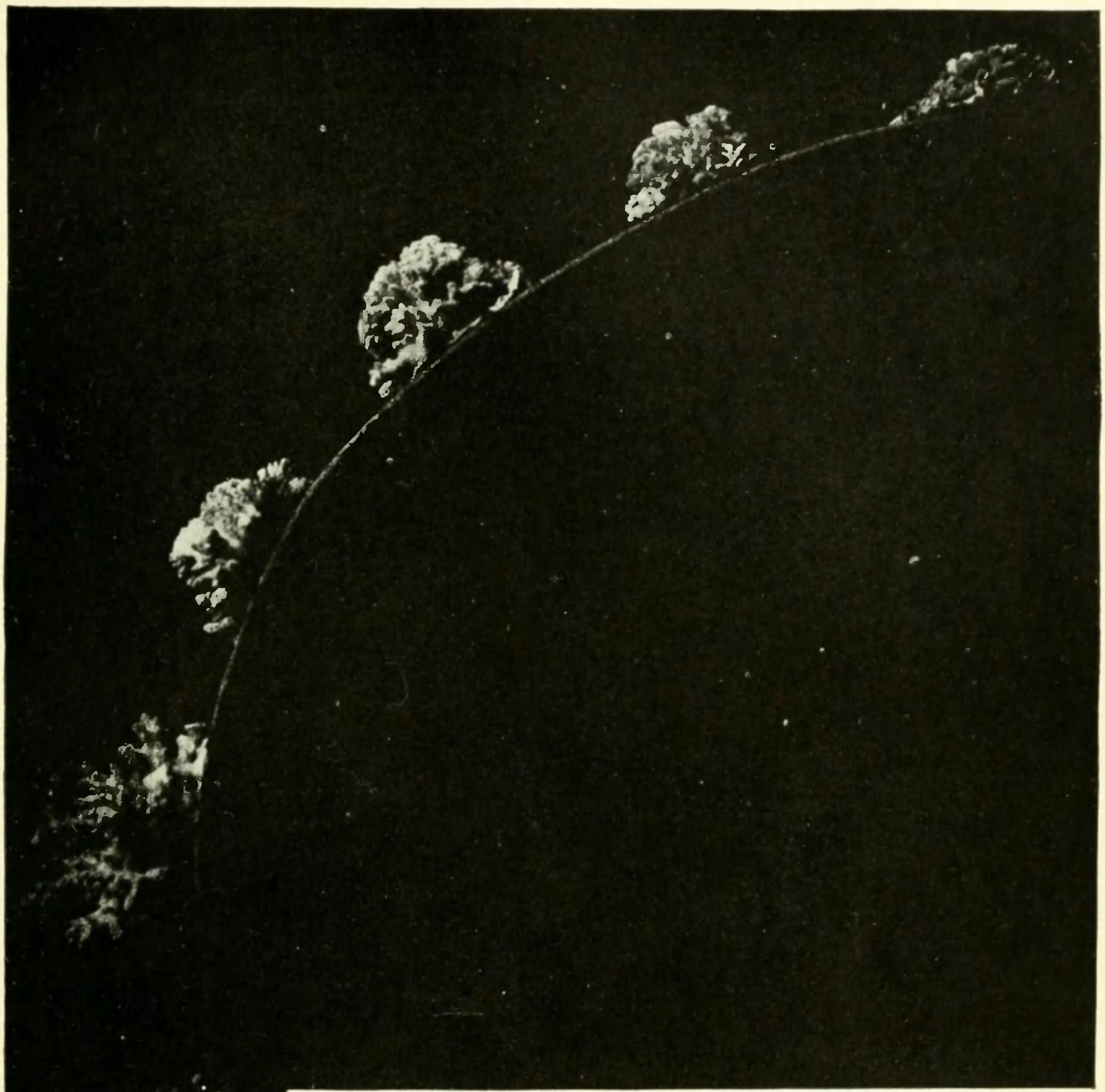
FIGS. 1, 1*a*. Organ-pipe coral, *Tubipora* sp. Fig. 1, upper surface; fig. 1*a*, side view, both natural size.

2, 2*a*. Blue coral, *Heliopora coerulea* (Pallas). Fig. 2, corallum, natural size; fig. 2*a*, surface, × 6.

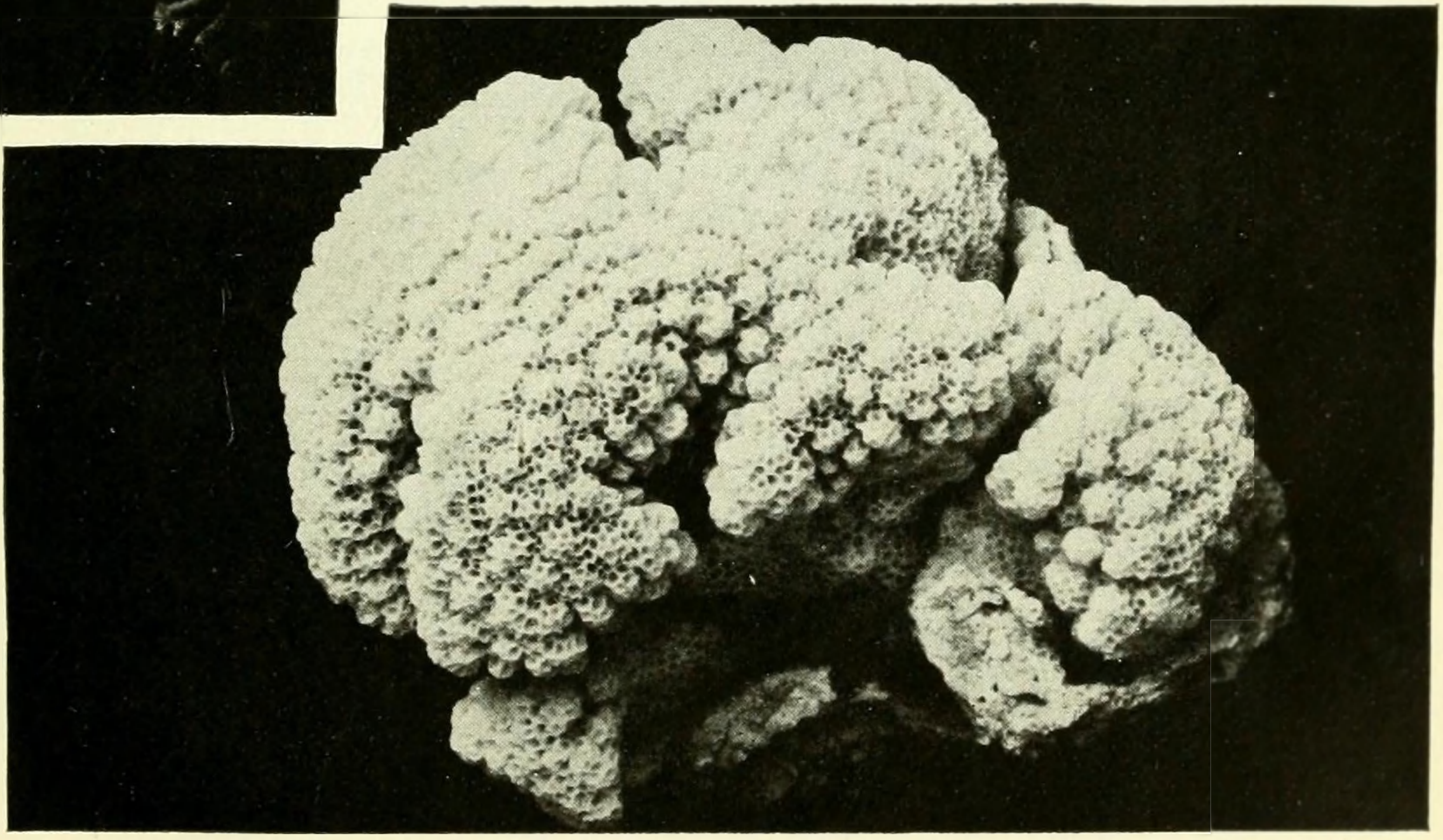
PLATE 5.

FIG. 1. Specimen of *Pocillopora bulbosa* Ehrenberg, as attached to a log in Cocos-Keeling Islands. From a photograph kindly supplied by Dr. F. Wood Jones.

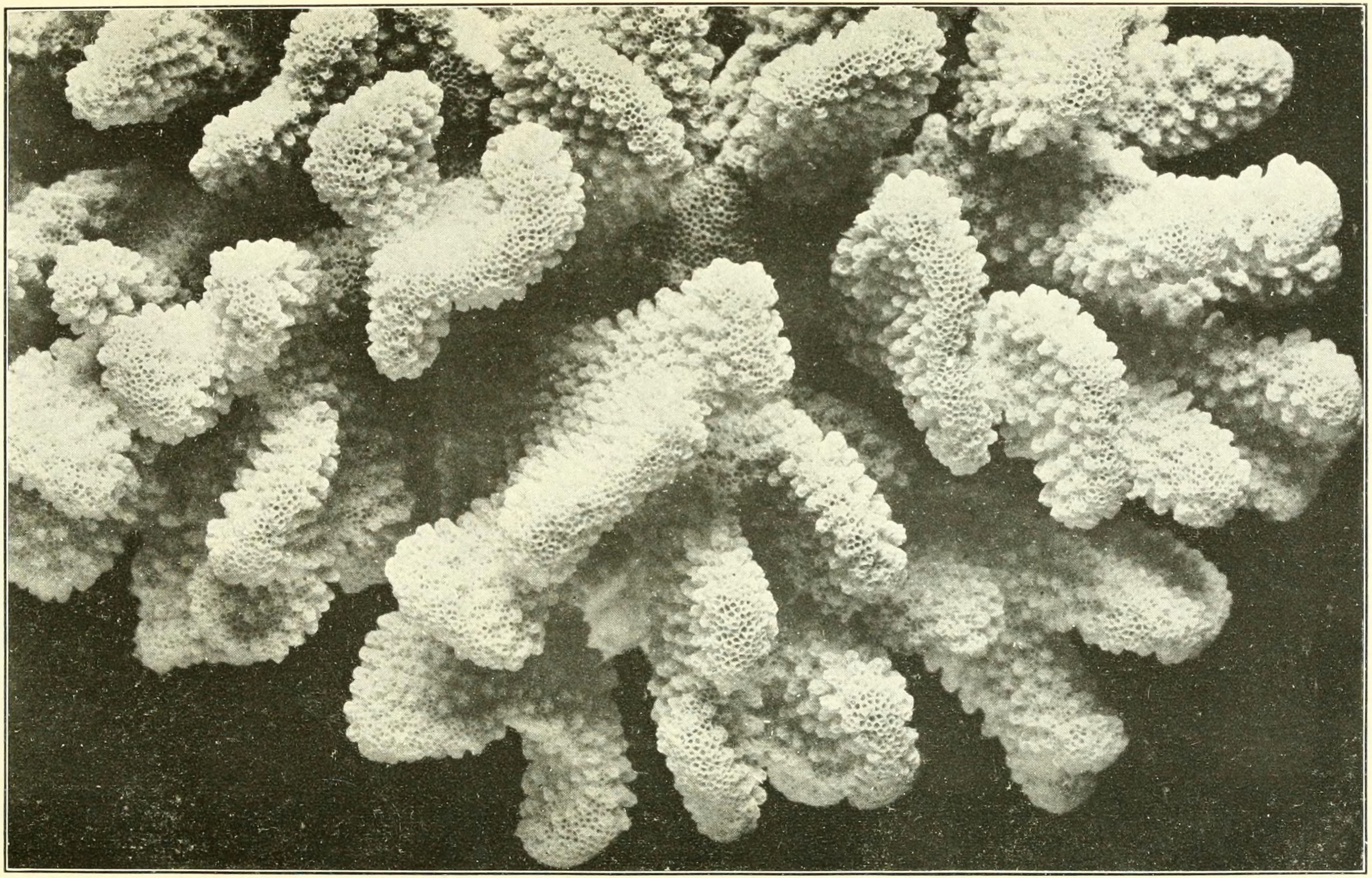
2. *Pocillopora elegans* Dana, natural size. A specimen from the outer barrier, Cocos-Keeling Islands. The rough water facies of the species.



1



1. POCILLOPORA BULBOSA (EHRENBERG). 2. POCILLOPORA ELEGANS (DANA.)



POCILLOPORA ELEGANS (DANA).

PLATE 6.

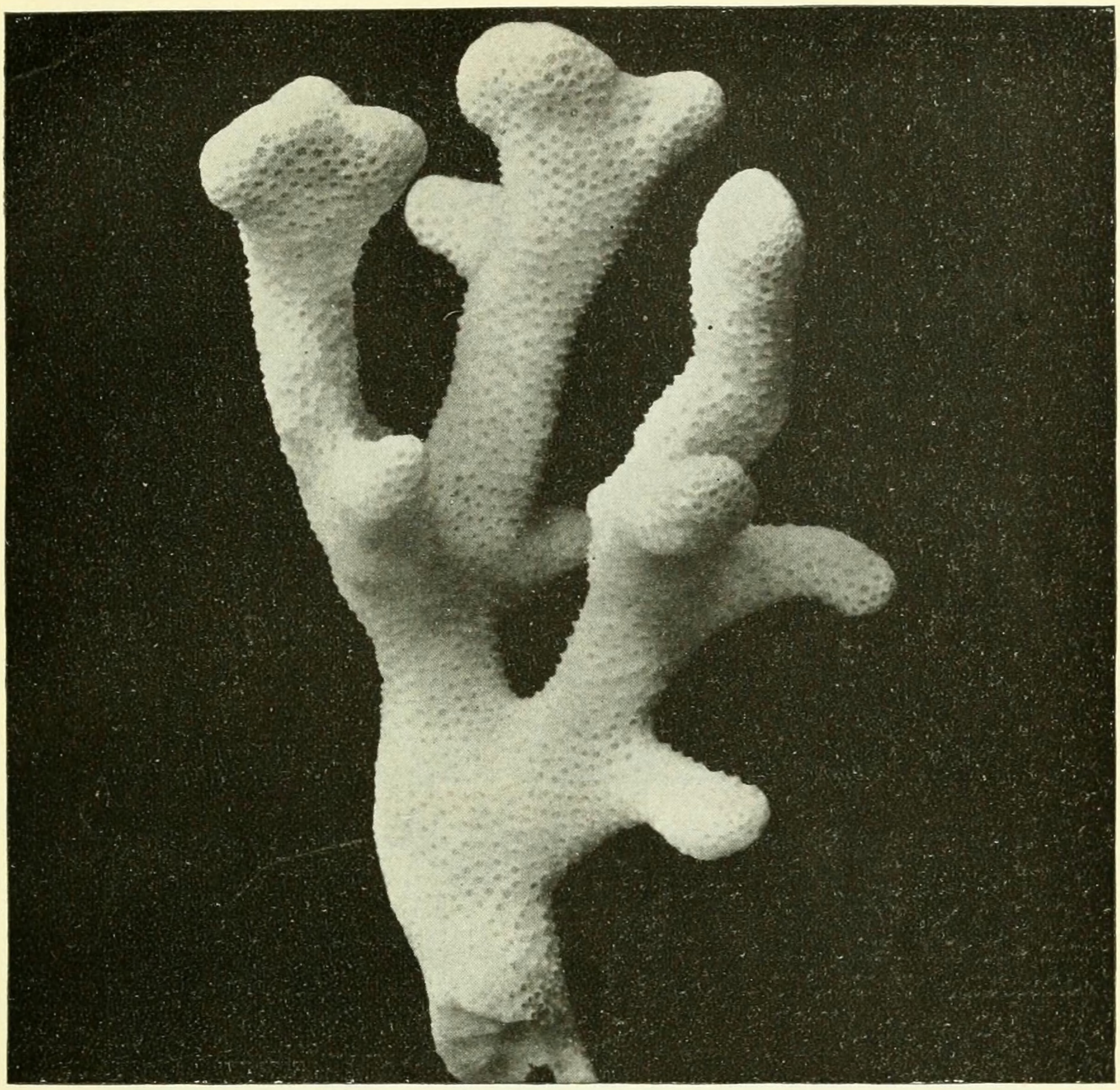
Pocillopora elegans Dana.

A part, natural size, of Dana's type from the Fiji Islands. This is the same as the quieter-water facies of the species found in Cocos-Keeling Islands.

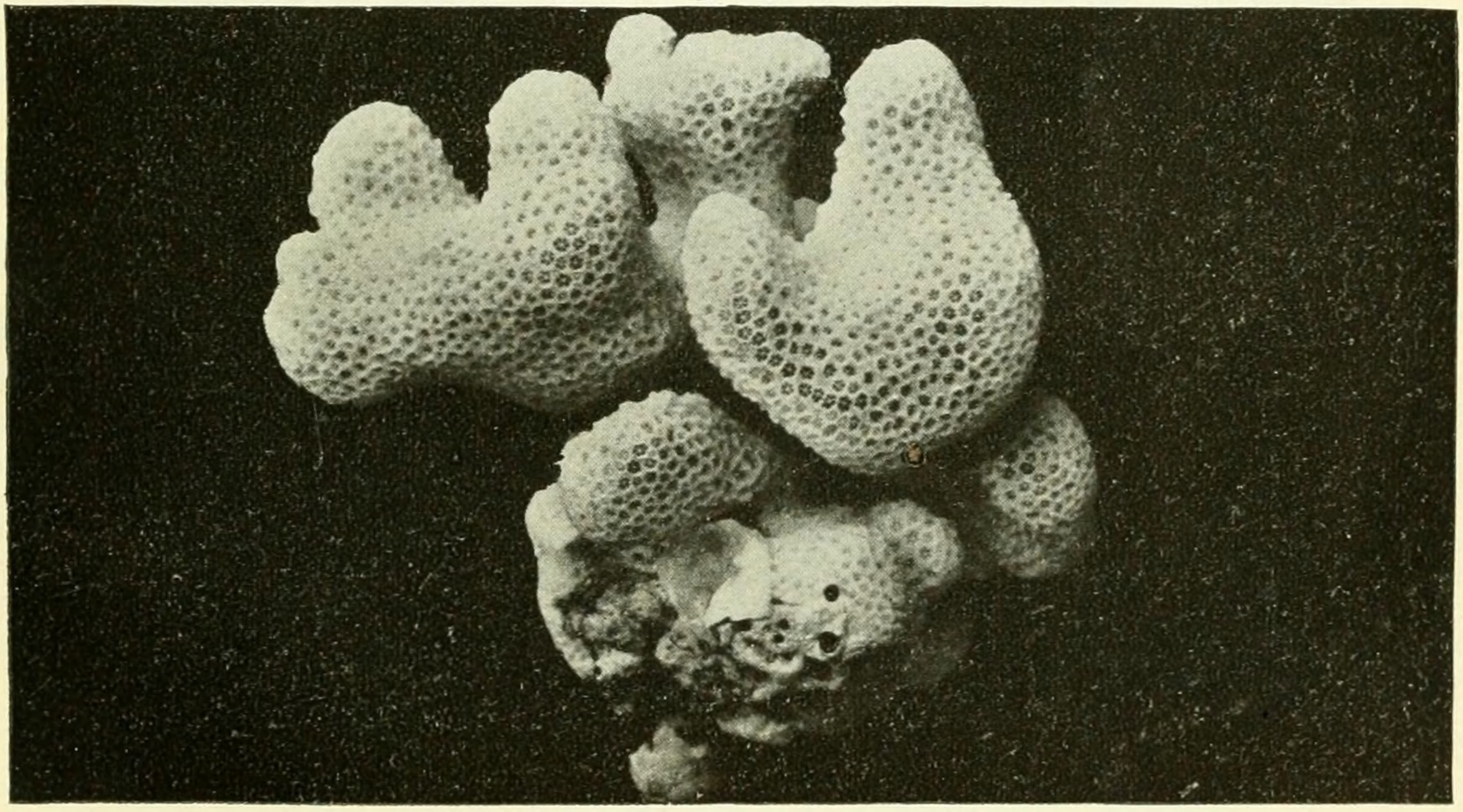
PLATE 7.

Stylophora pistillata (Esper), from Murray Island, Australia.

FIG. 1. From quiet, rather deep water, depth 18 fathoms.
2. From the exposed seaweed edge of the reef.
Both figures natural size.

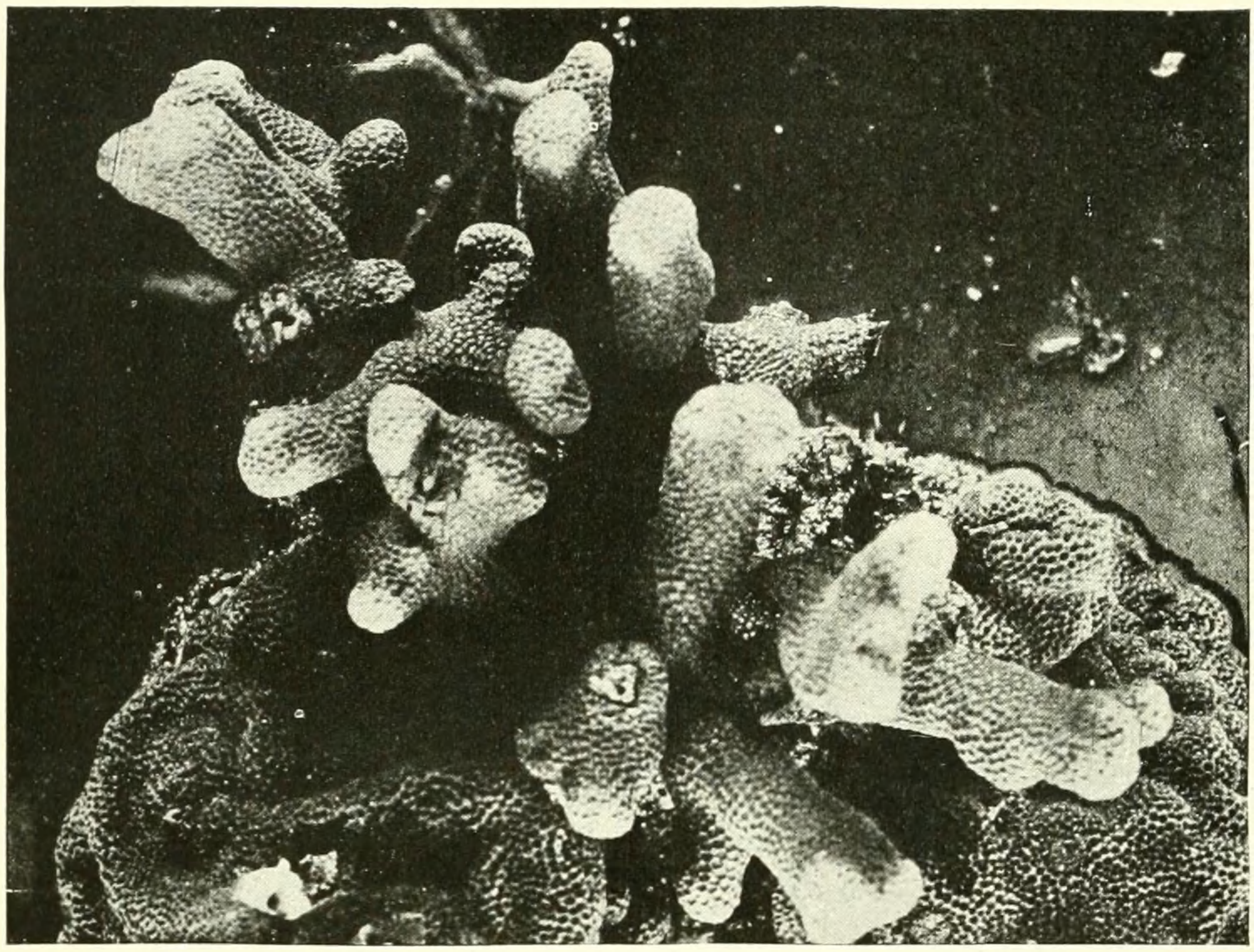


1

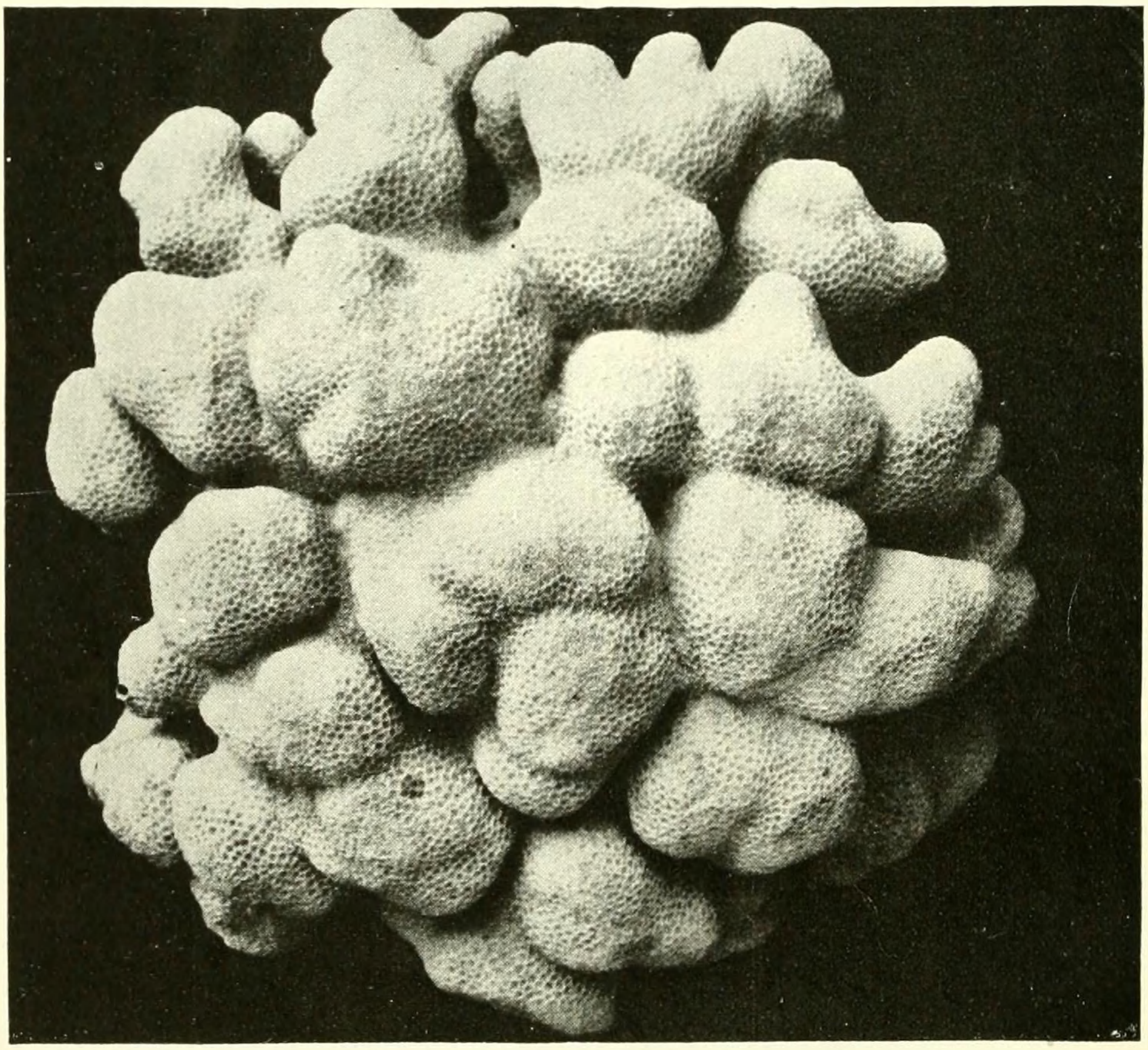


2

STYLOPHORA PISTILLATA (ESPER).



1



2

PORITES PORITES (PALLAS).

PLATE 8.

Porites porites (Pallas), from Tortugas, Florida.

FIG. 1. Quiet water, lagoon facies.
2. Exposed reef facies.
Figure about one-half natural size.

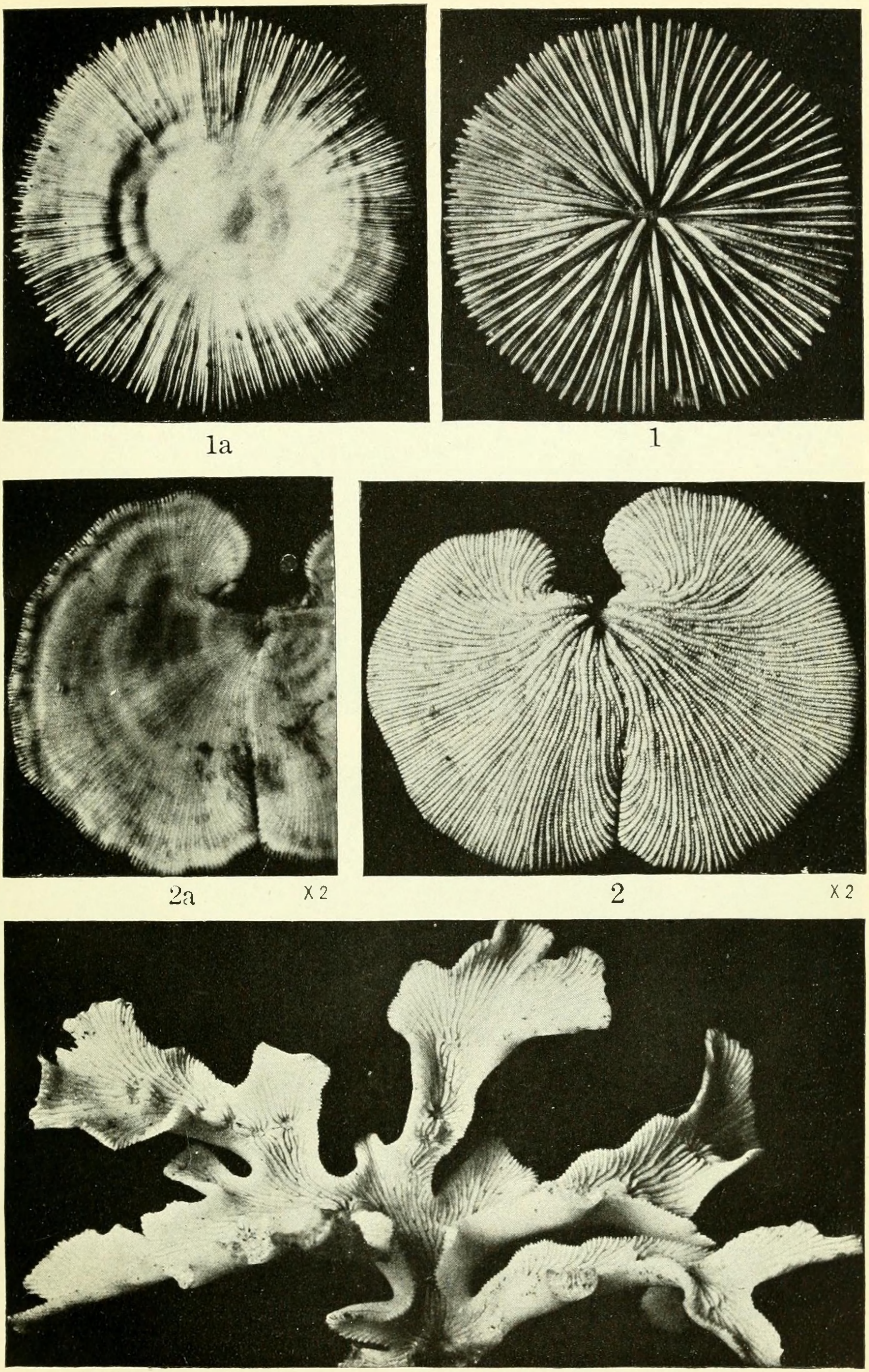
PLATE 9.

Hawaiian corals obtained between 25 and 40 fathoms (46 and 74 meters) in depth.

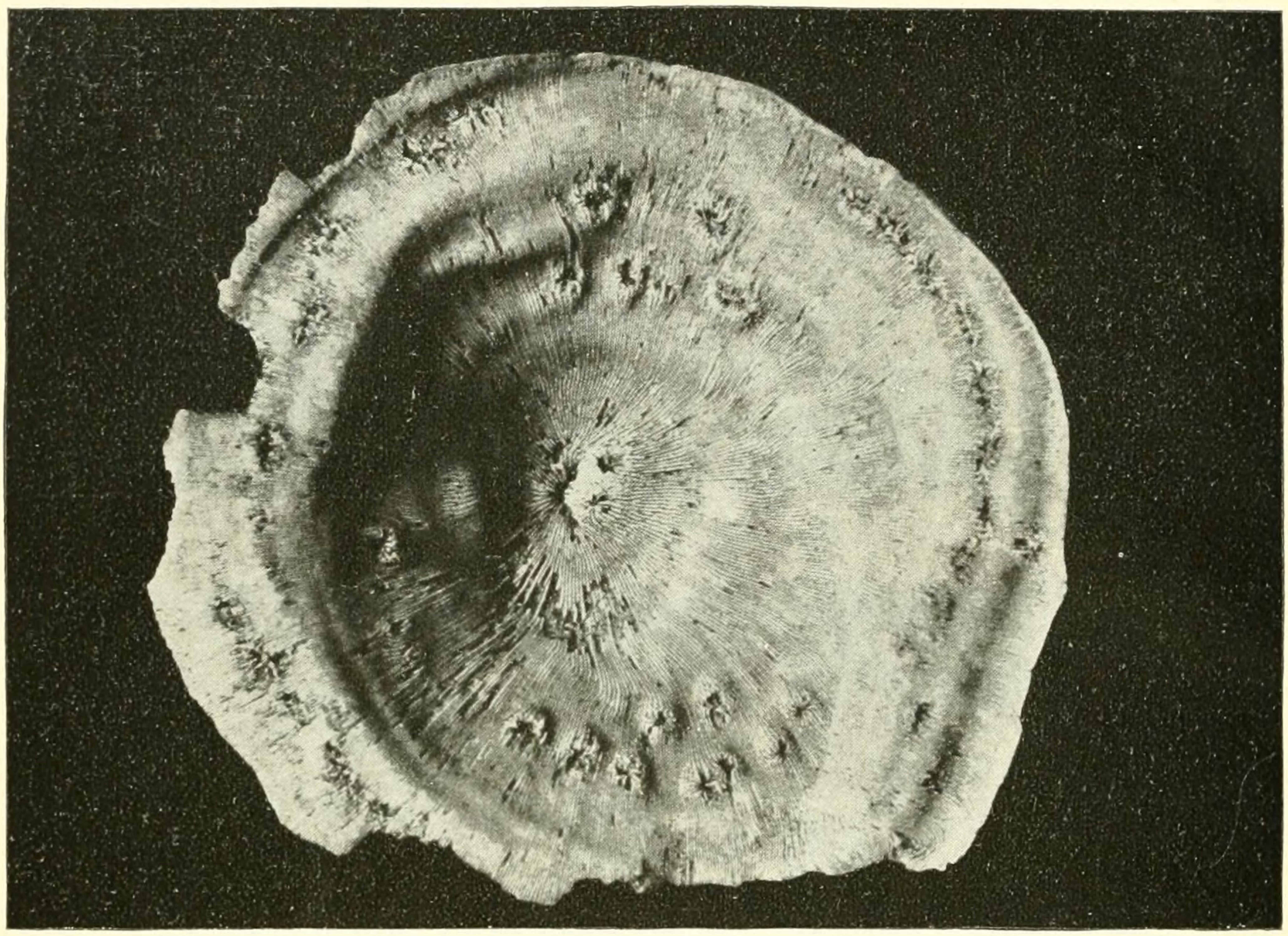
FIGS. 1, 1*a*. *Fungia patella* (Ellis and Solander), two views, natural size, of the same specimen. Fig. 1, upper surface; fig. 1*a*, lower surface.

2, 2*a*. *Fungia* (*Diaseris*) *fragilis* (Alcock), two views, about twice natural size, of the same specimen. Fig. 2, upper surface; fig. 2*a*, lower surface.

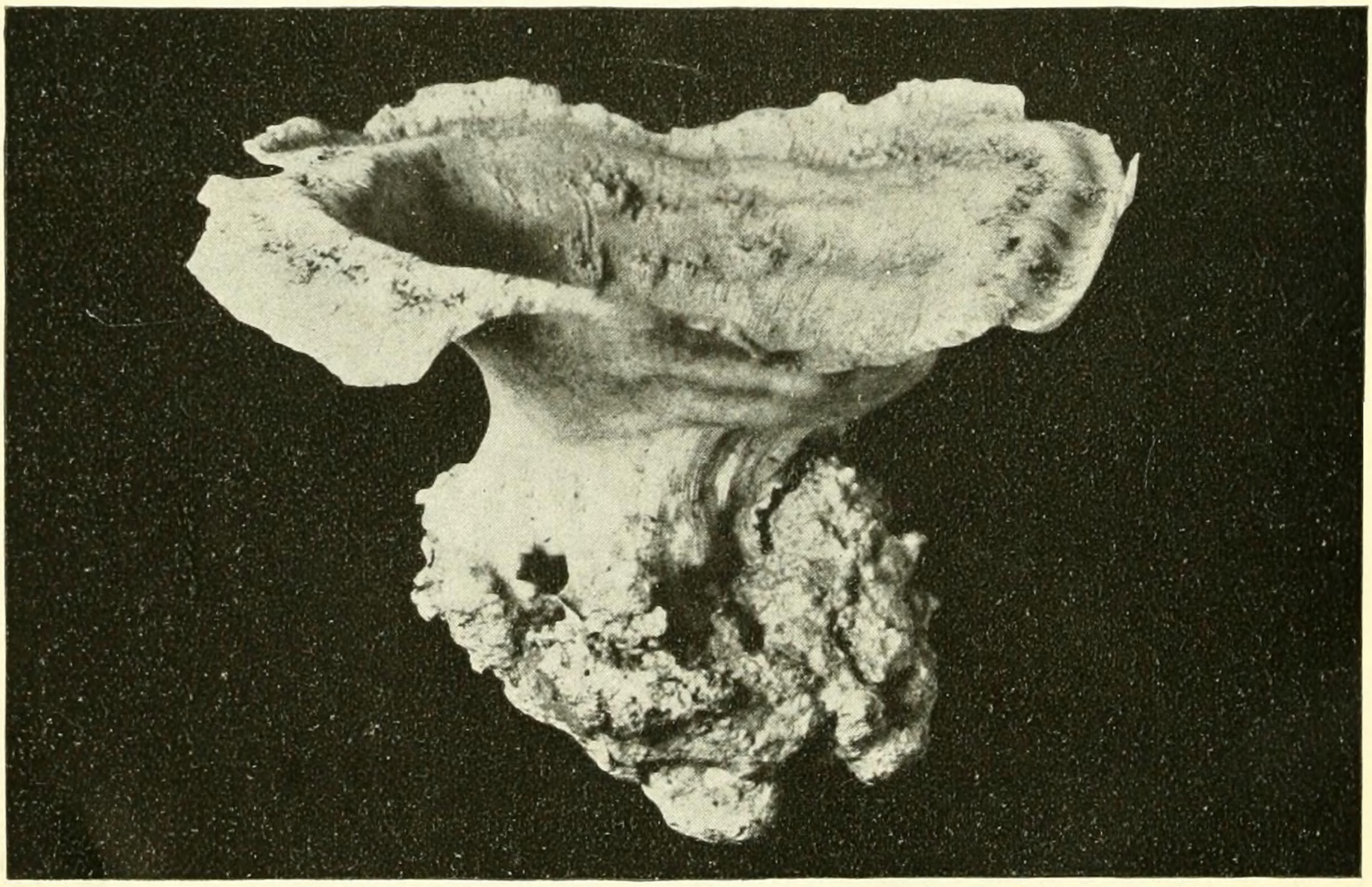
3. *Leptoseris digitata* Vaughan, × 2.



Hawaiian Corals Obtained Between 25 and 40 Fathoms (46 and 74 Meters) in Depth.



1



1a

HAWAIIAN CORALS OBTAINED BETWEEN 25 AND 40 FATHOMS (46 AND 74 METERS) IN DEPTH.

PLATE 10.

Hawaiian corals obtained between 25 and 40 fathoms (46 and 74 meters) in depth.

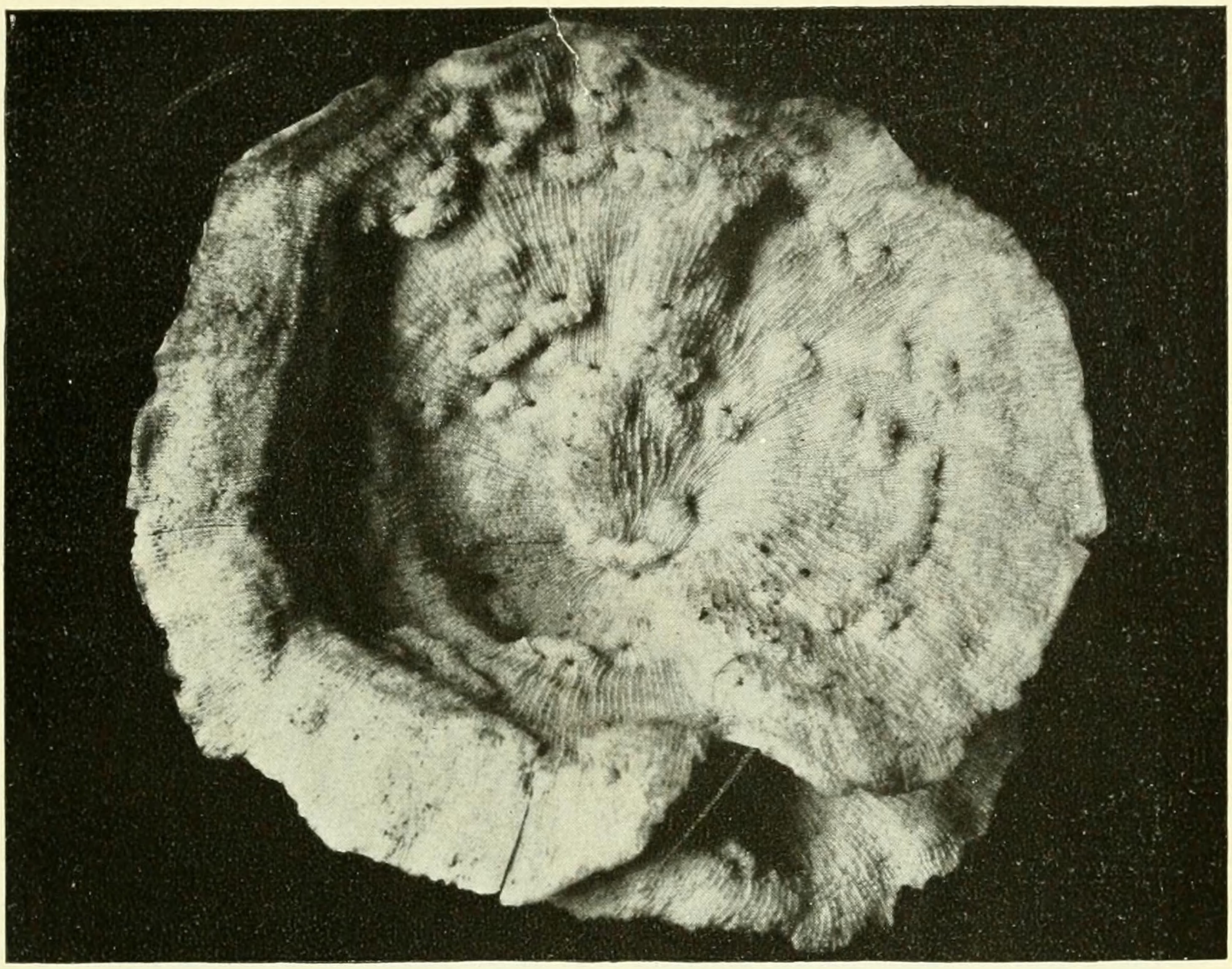
Leptoseris hawaiiensis Vaughan.

FIG. 1. Upper surface; fig. 1*a*, side view, each natural size.

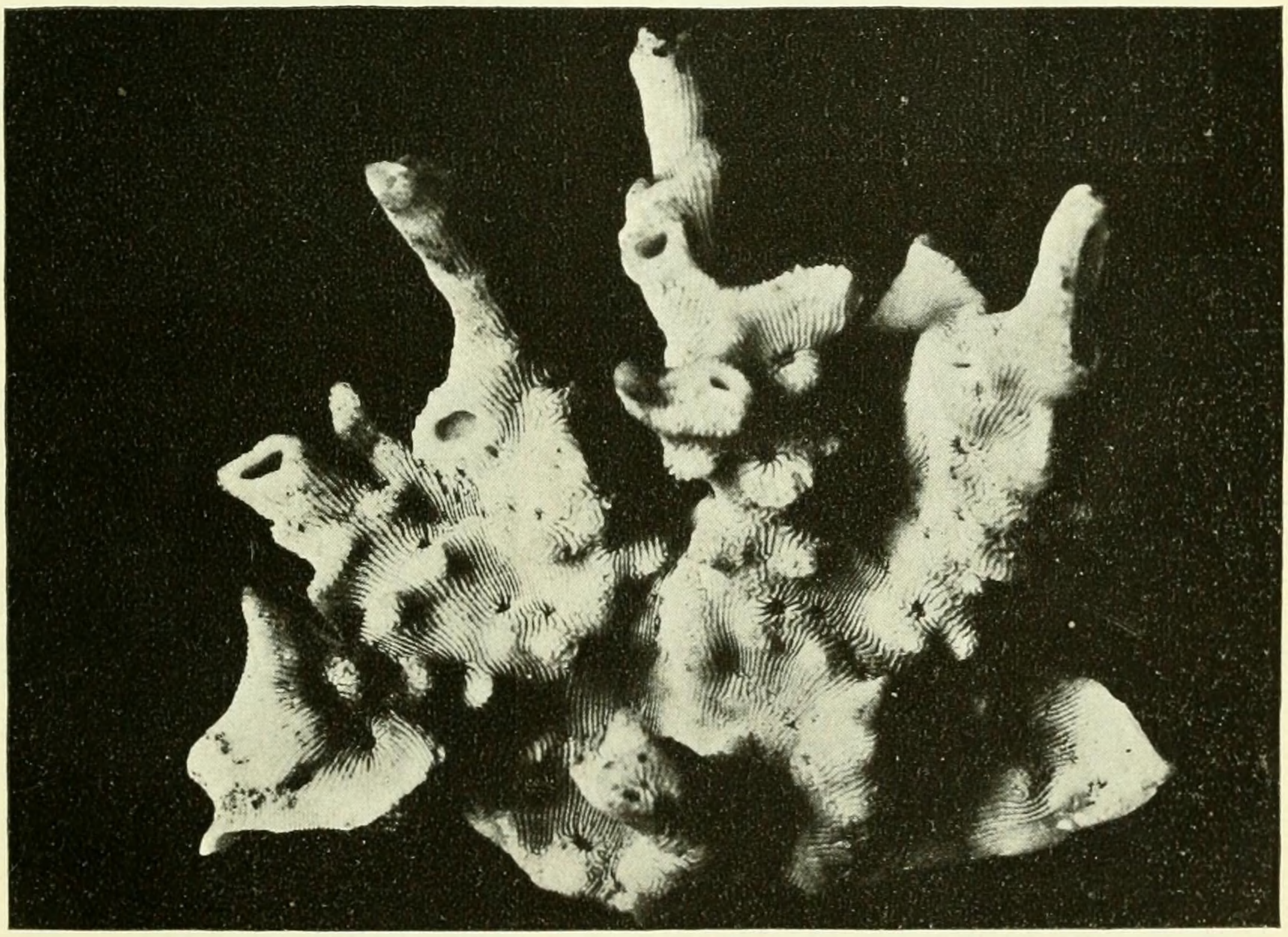
PLATE 11.

Hawaiian corals obtained between 25 and 40 fathoms (46 and 74 meters) in depth.

FIG. 1. *Leptoseris scabra* Vaughan. Upper surface, natural size.
2. *Leptoseris tubulifera* Vaughan. General view, × 2.



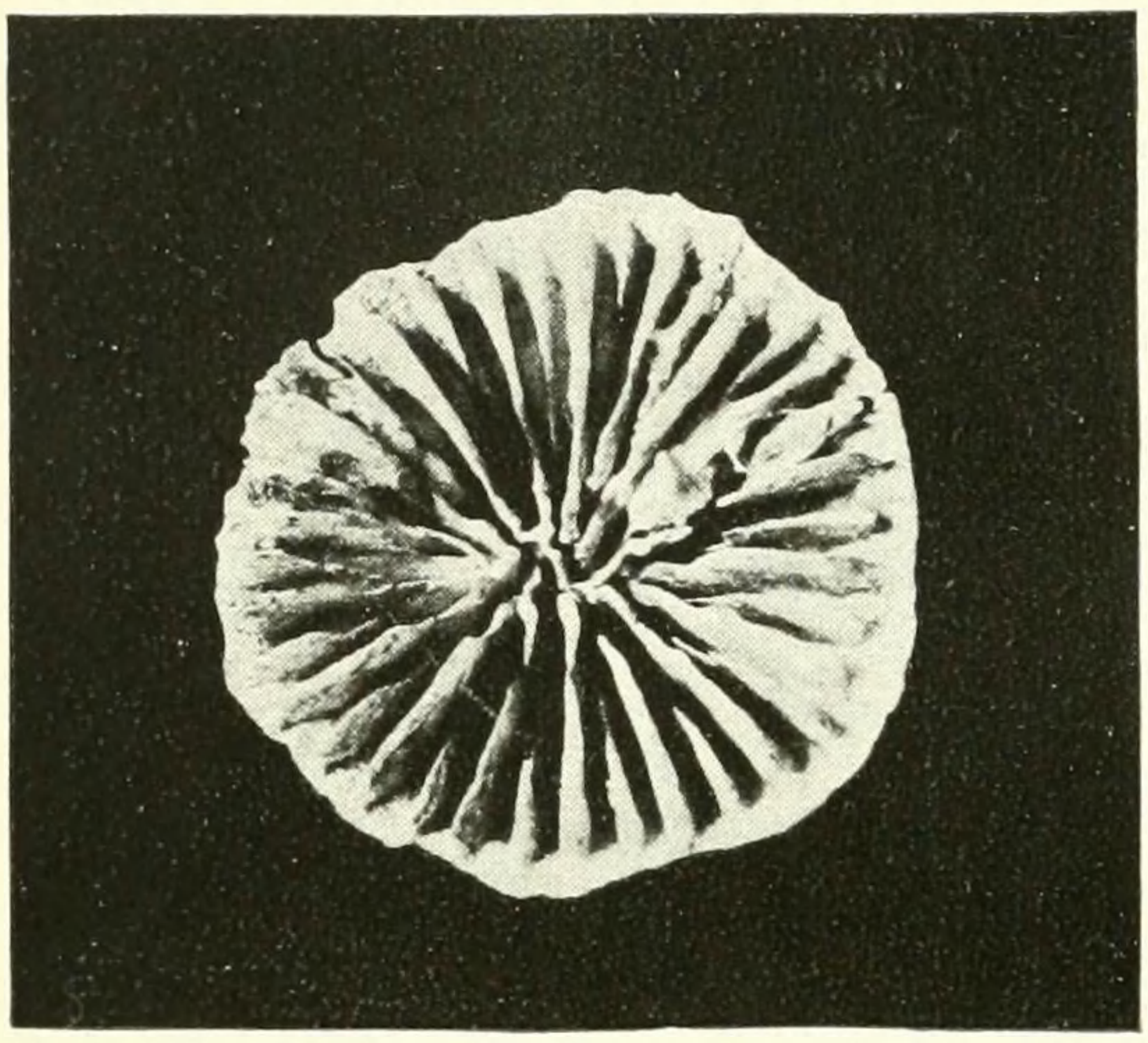
1



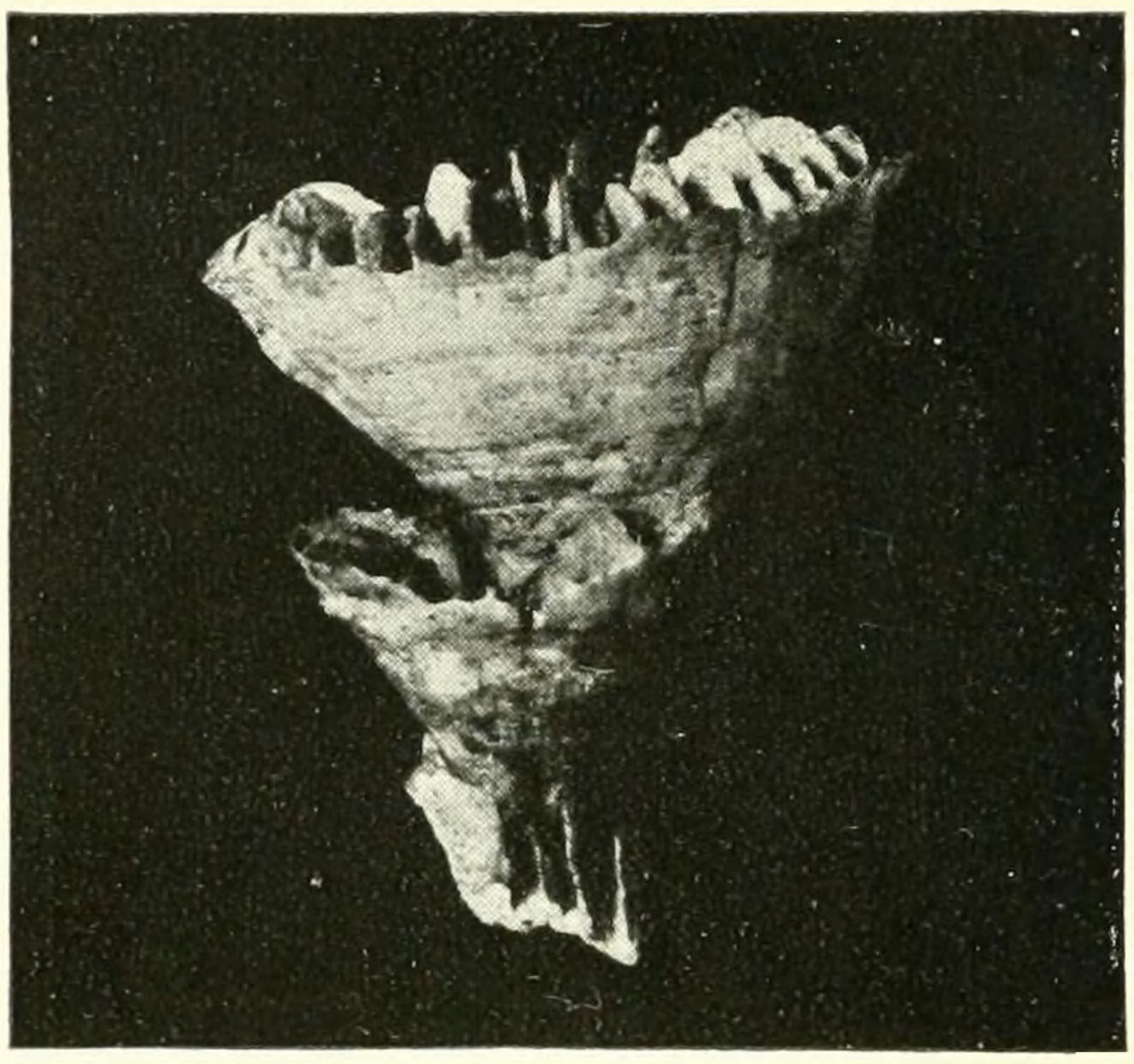
2

X 2

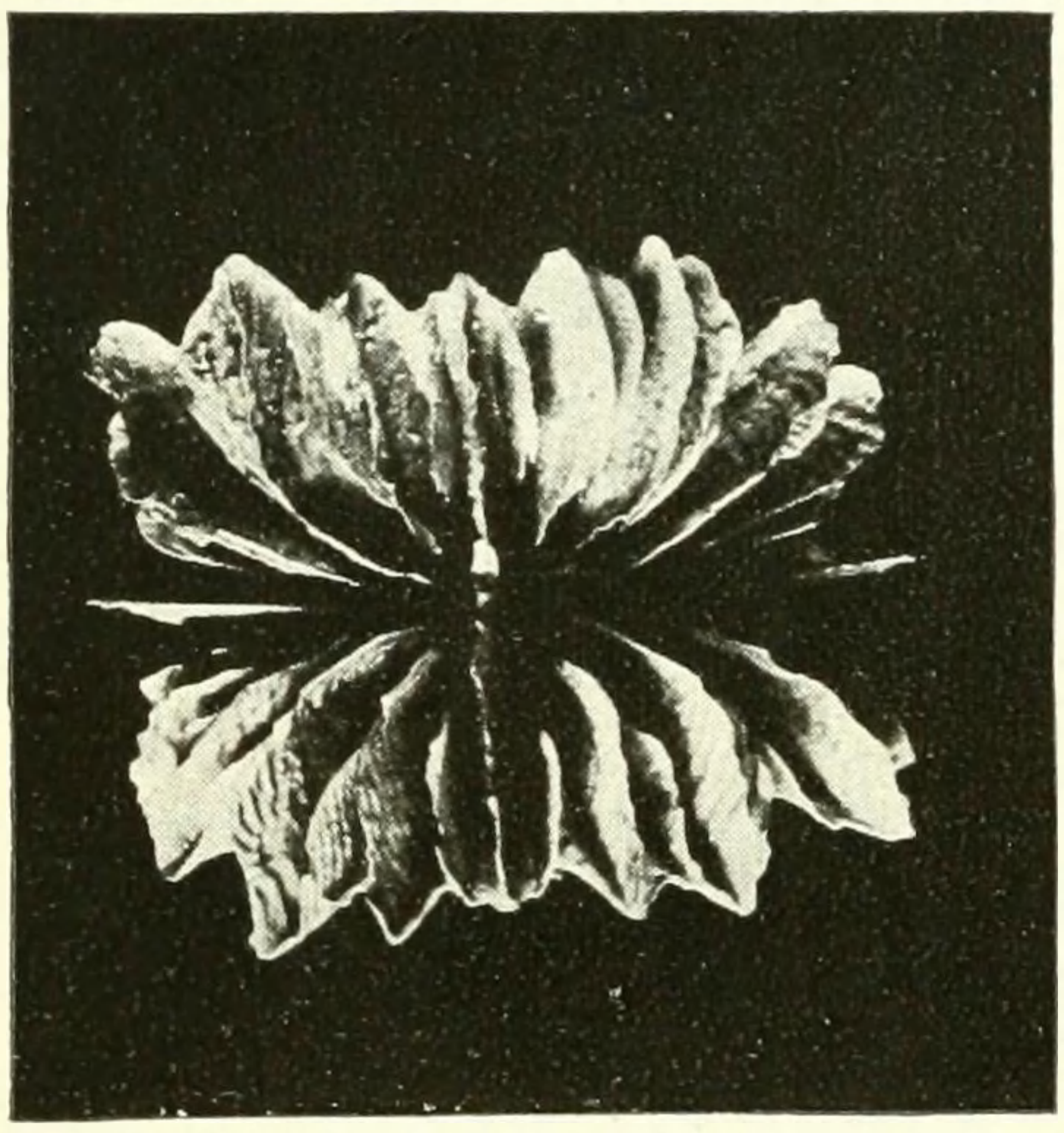
HAWAIIAN CORALS OBTAINED BETWEEN 25 AND 40 FATHOMS (46 AND 74 METERS) IN DEPTH.



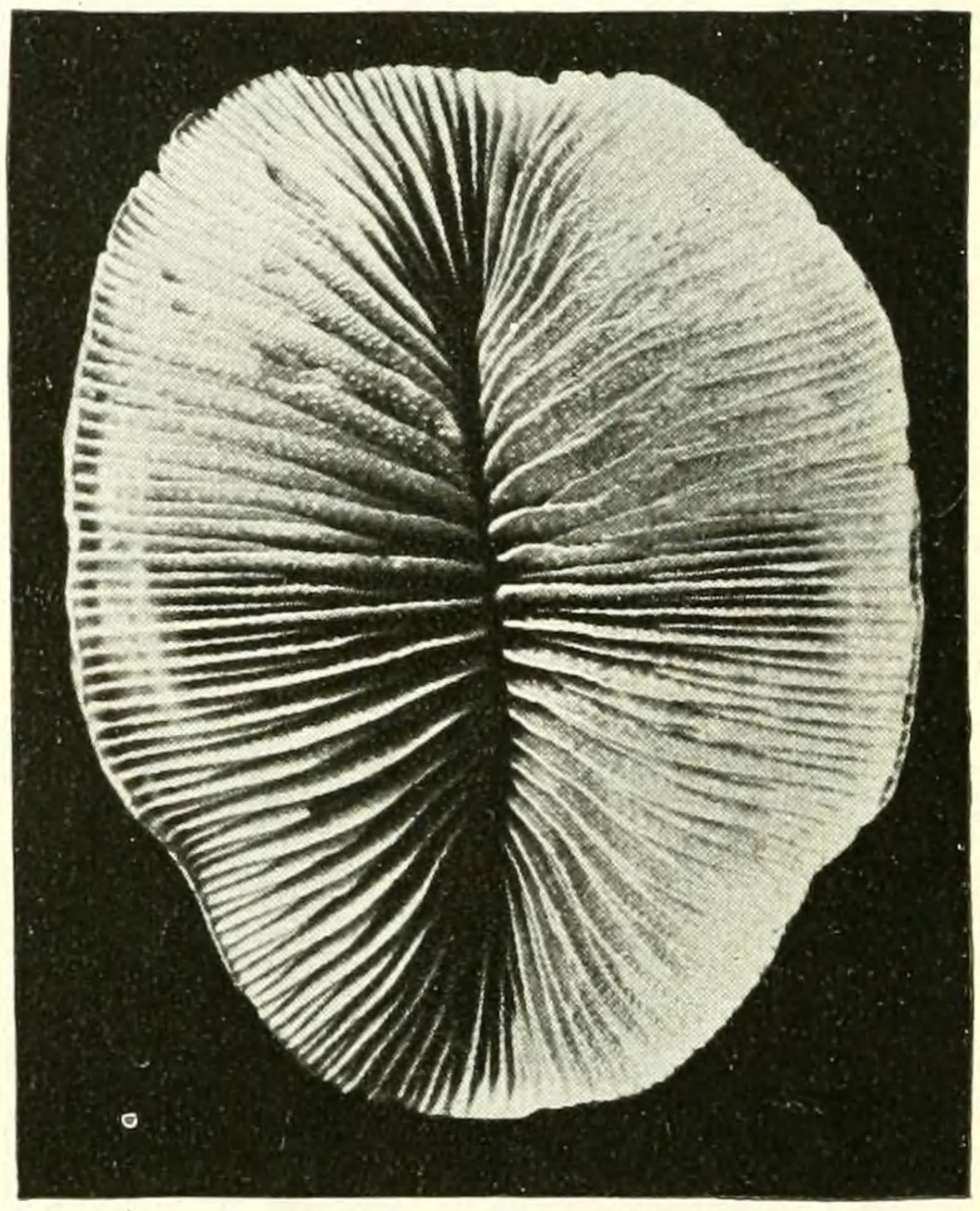
1a X 2



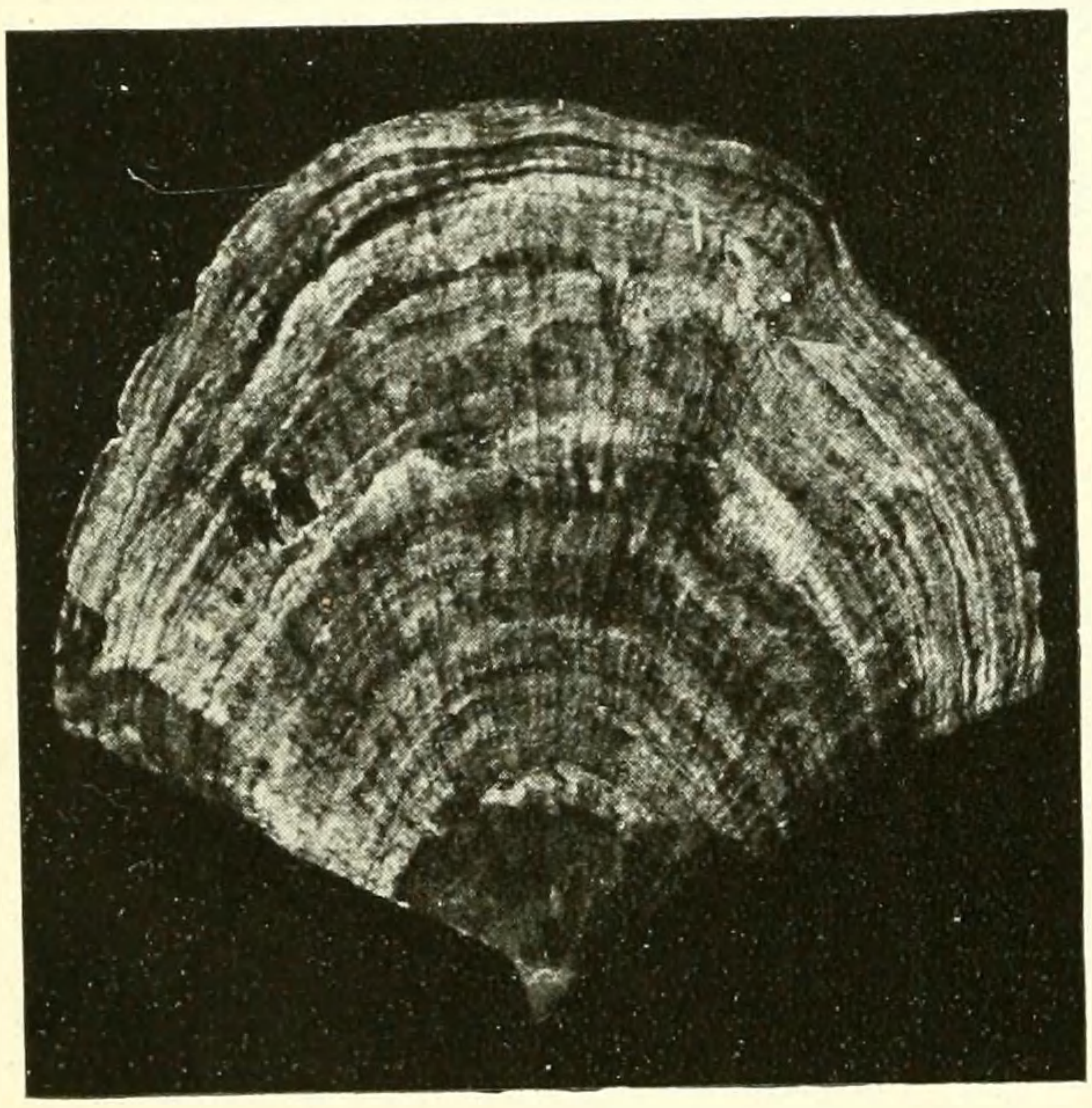
1 X 2



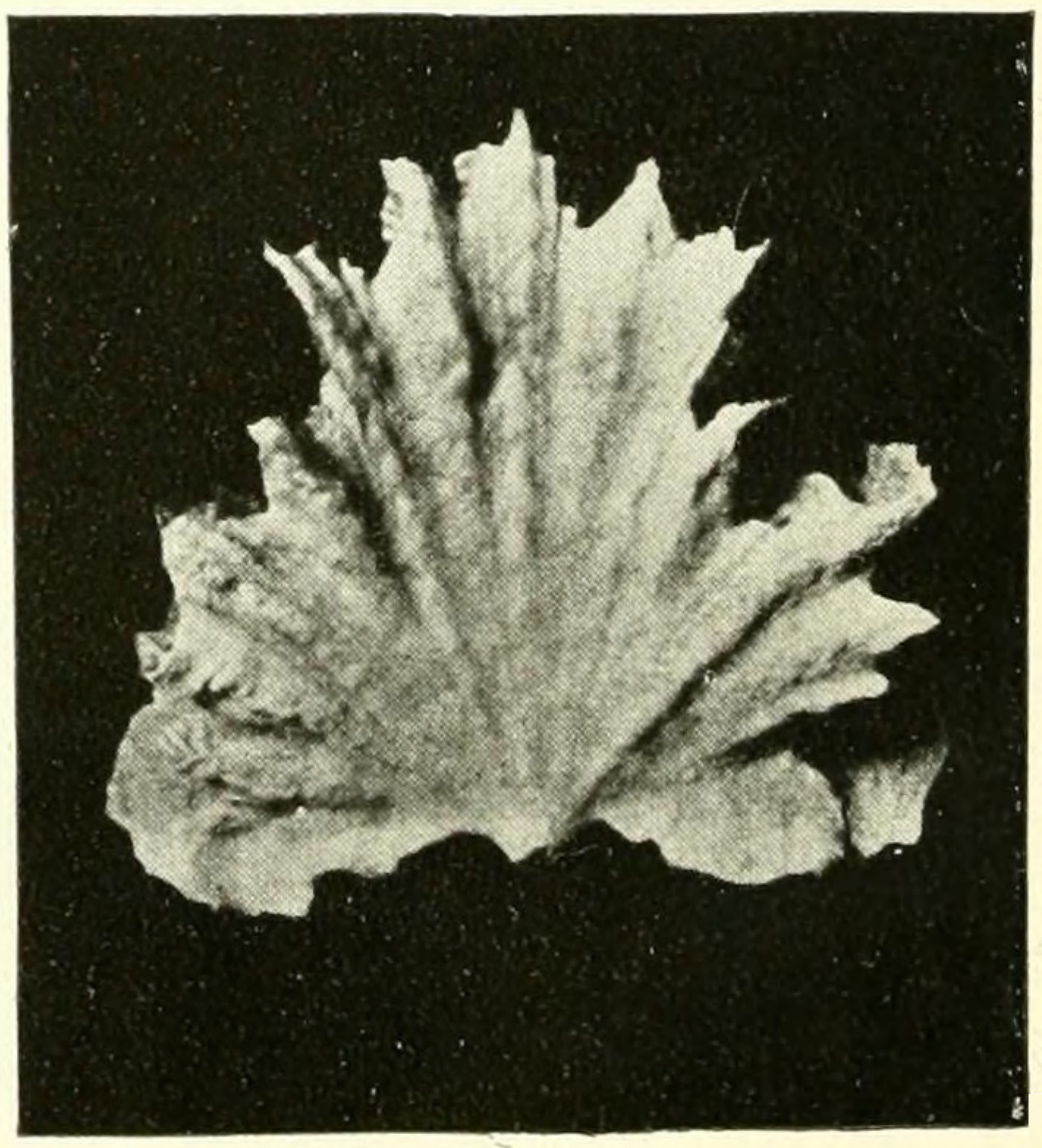
3a



2a



2



3

HAWAIIAN DEEP-SEA CORALS.

PLATE 12.

Hawaiian deep-sea corals.

FIGS. 1, 1*a*. *Gardineria hawaiiensis* Vaughan. Fig. 1, side view; fig. 1*a*, calice, of the same specimen, each × 2.

2, 2*a*. *Flabellum paripavoninum* Alcock. Fig. 2, side view; fig. 2*a*, calice of the same specimen, both natural size.

3, 3*a*. *Flabellum deludens* von Marenzeller. Fig. 3, side view; fig. 3*a*, calice of the same specimen, both natural size.

Plate 13.

Hawaiian deep-sea corals.

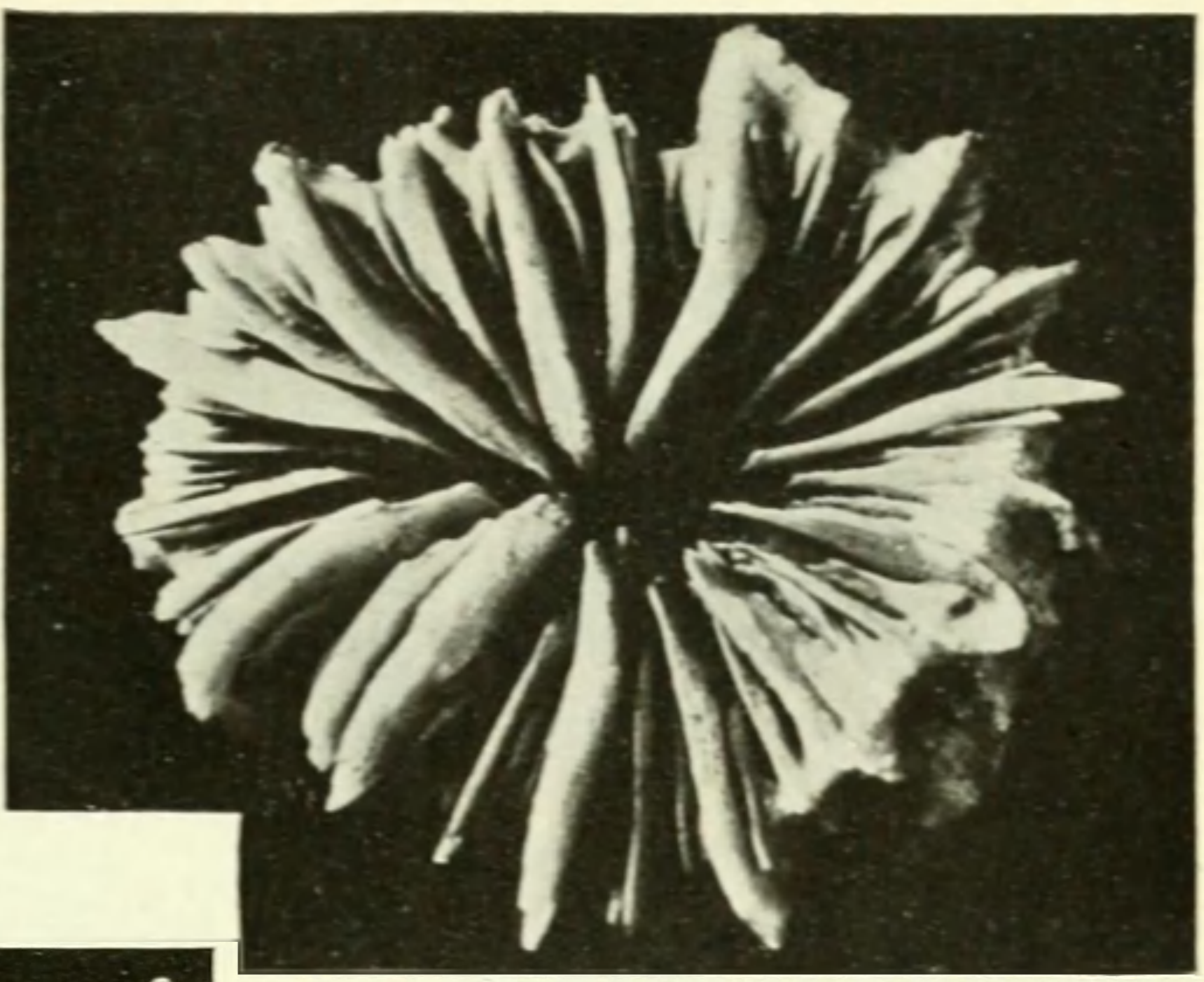
Figs. 1, 1*a*. *Desmophyllum cristagalli* Milne Edwards and Haime. Fig. 1, side view, natural size; fig. 1*a*, calice, × 2, of the same specimen.

2, 2*a*. *Cyathoceras diomedeae* Vaughan. Fig. 2, side view, natural size; fig. 2*a*, calice, × about 2, of the same specimen.

3, 3*a*. *Caryophyllia alcocki* Vaughan. Fig. 3, side view, natural size; fig. —.

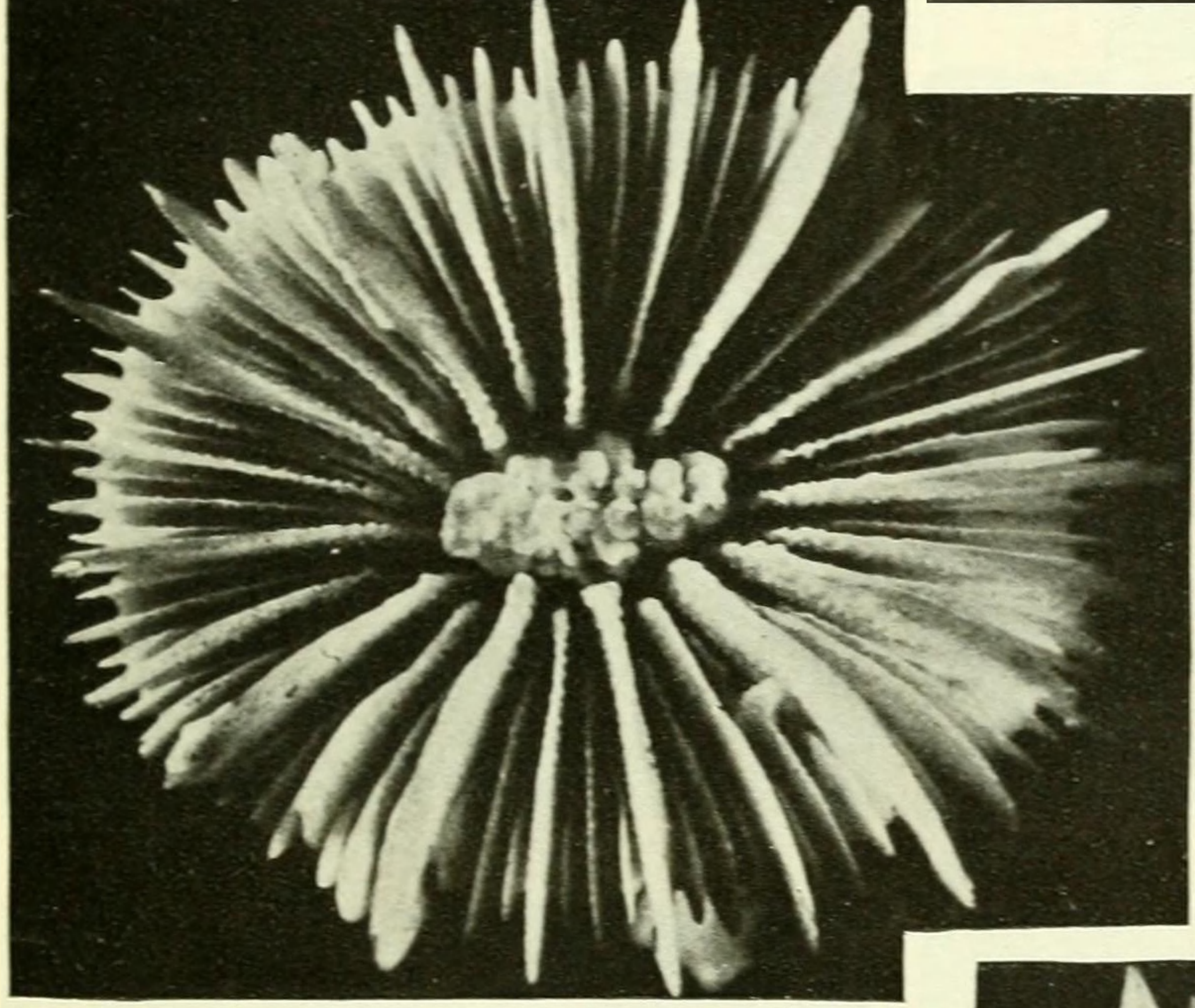
3*a*, calice, × 2 1/2, of the same specimen.

1



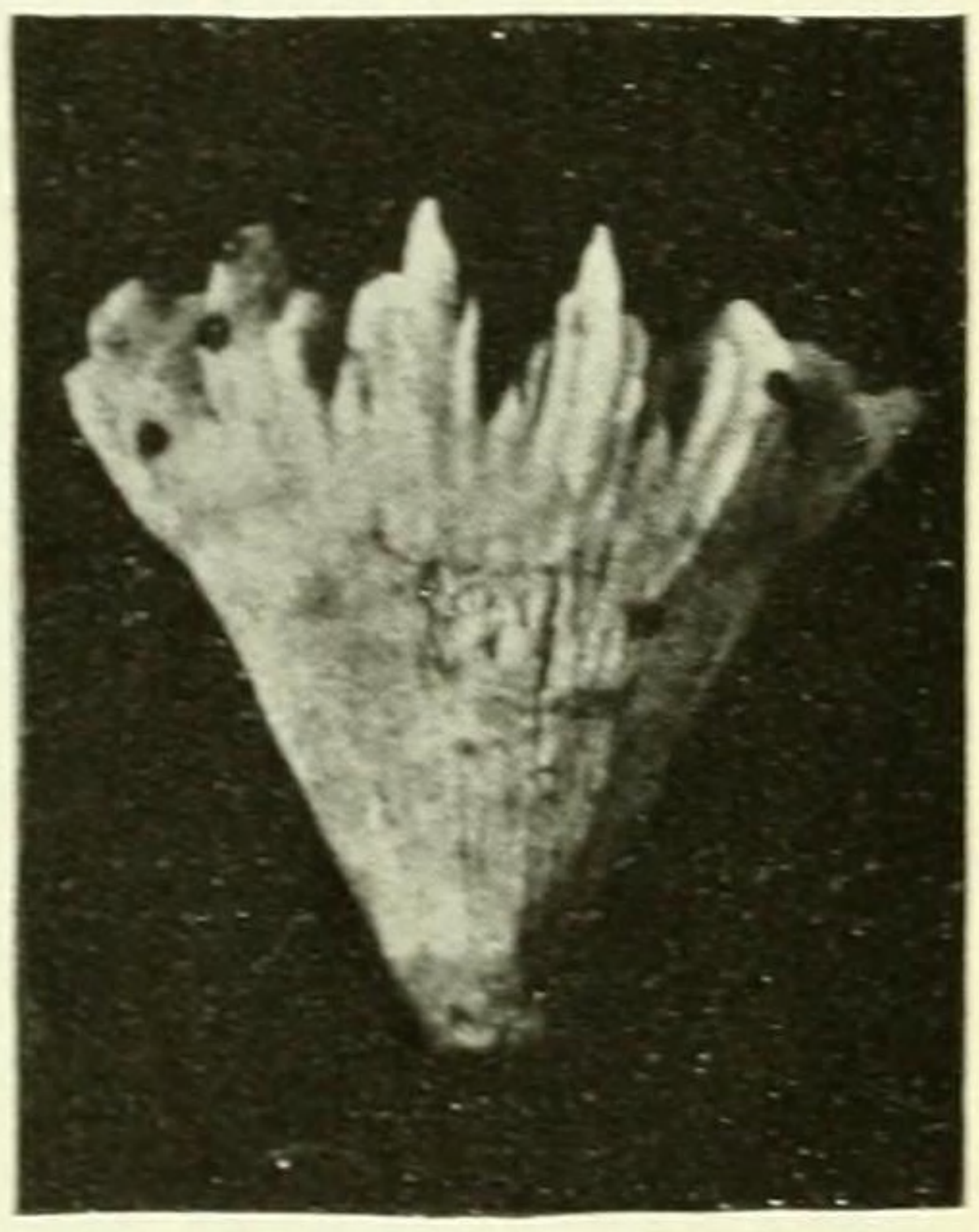
1a

X 2

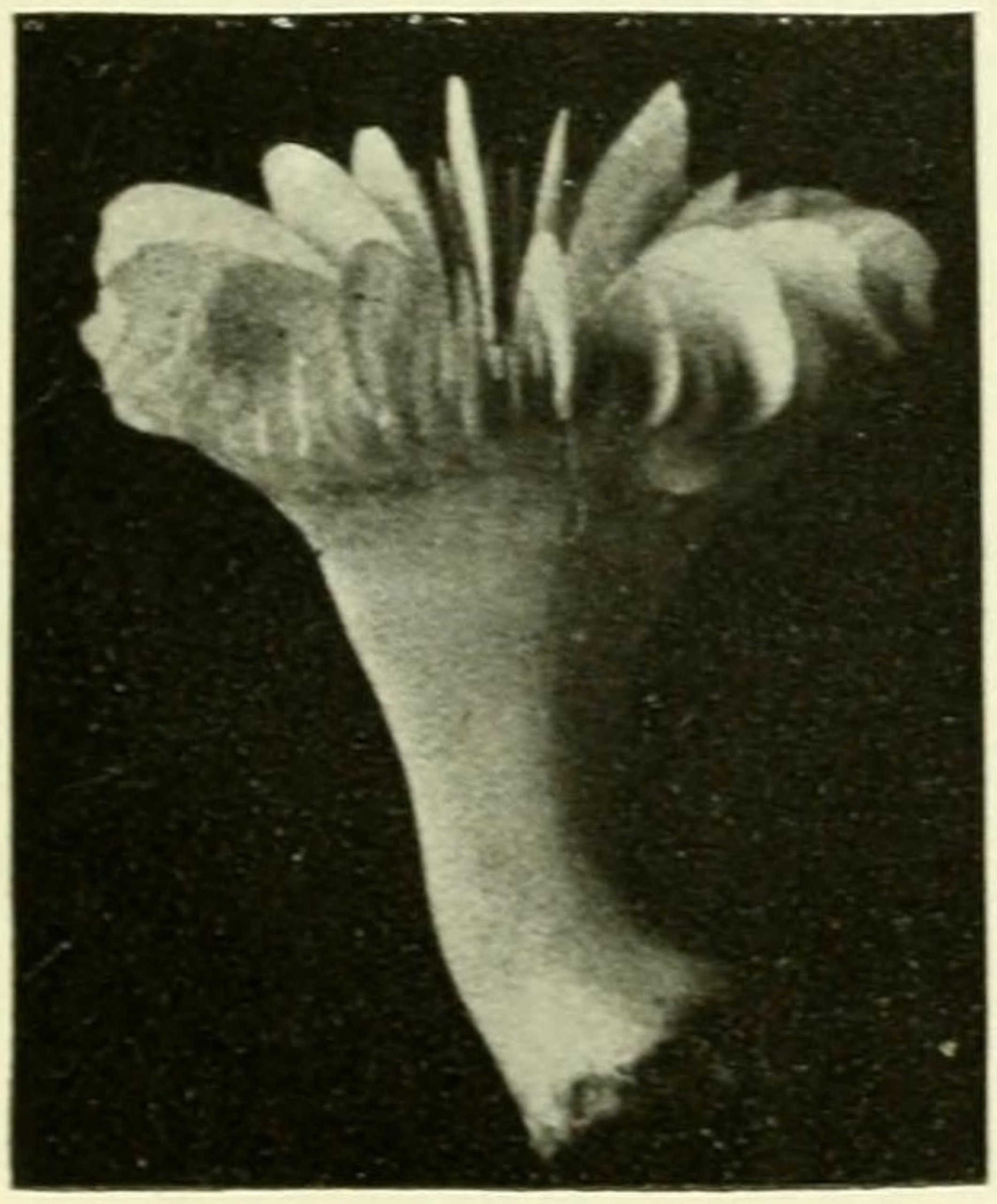


X 2

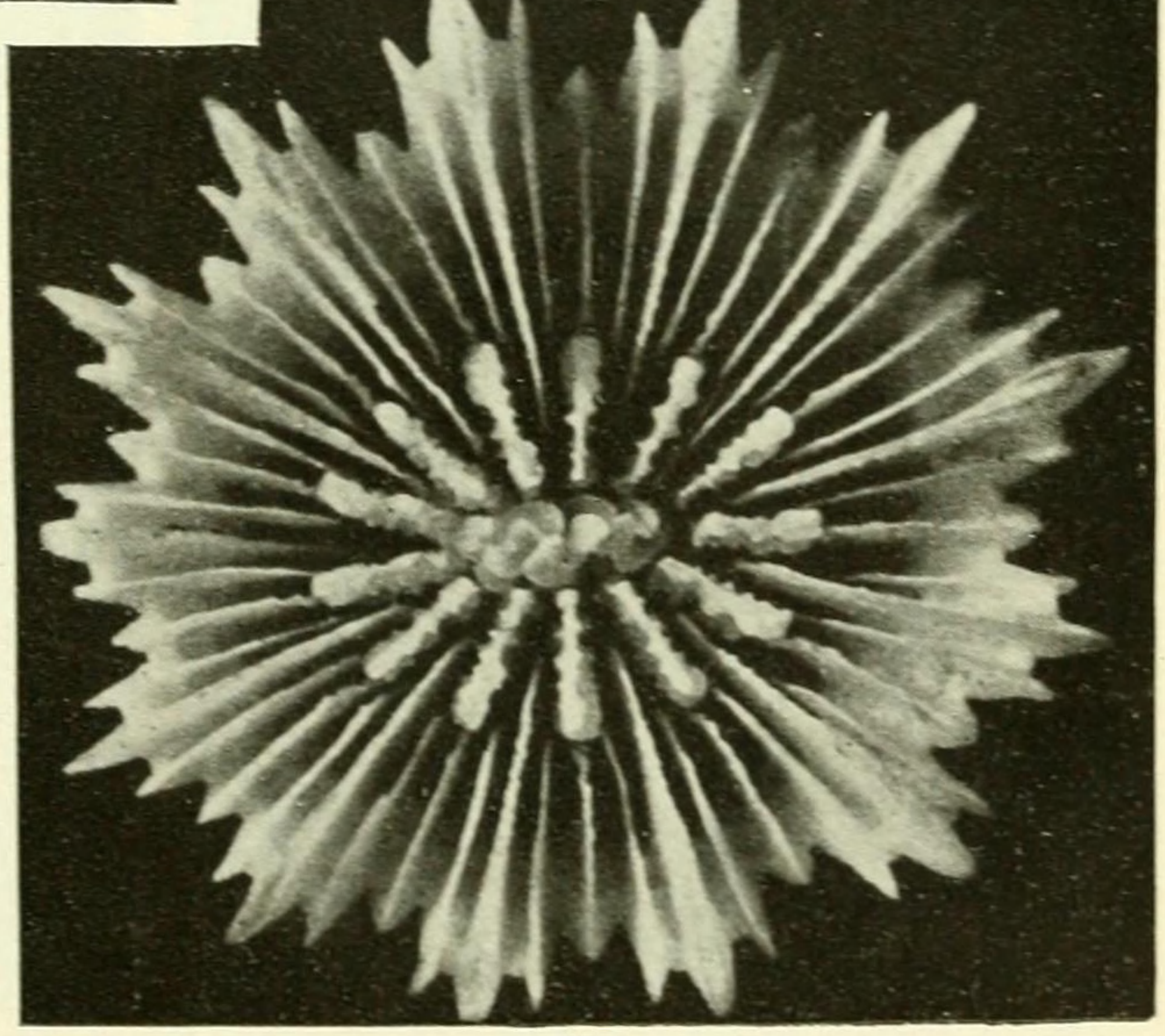
2a



3



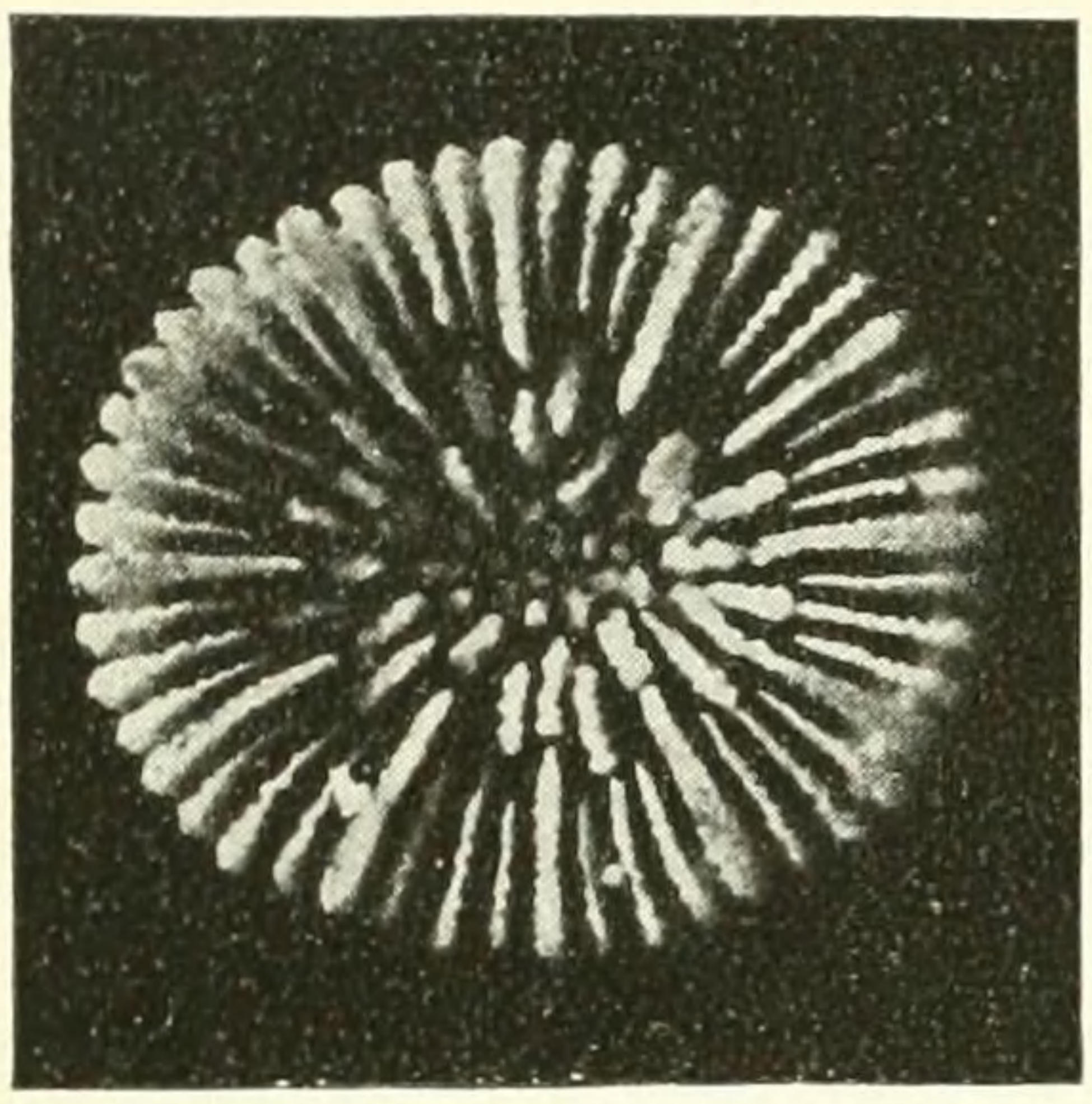
2



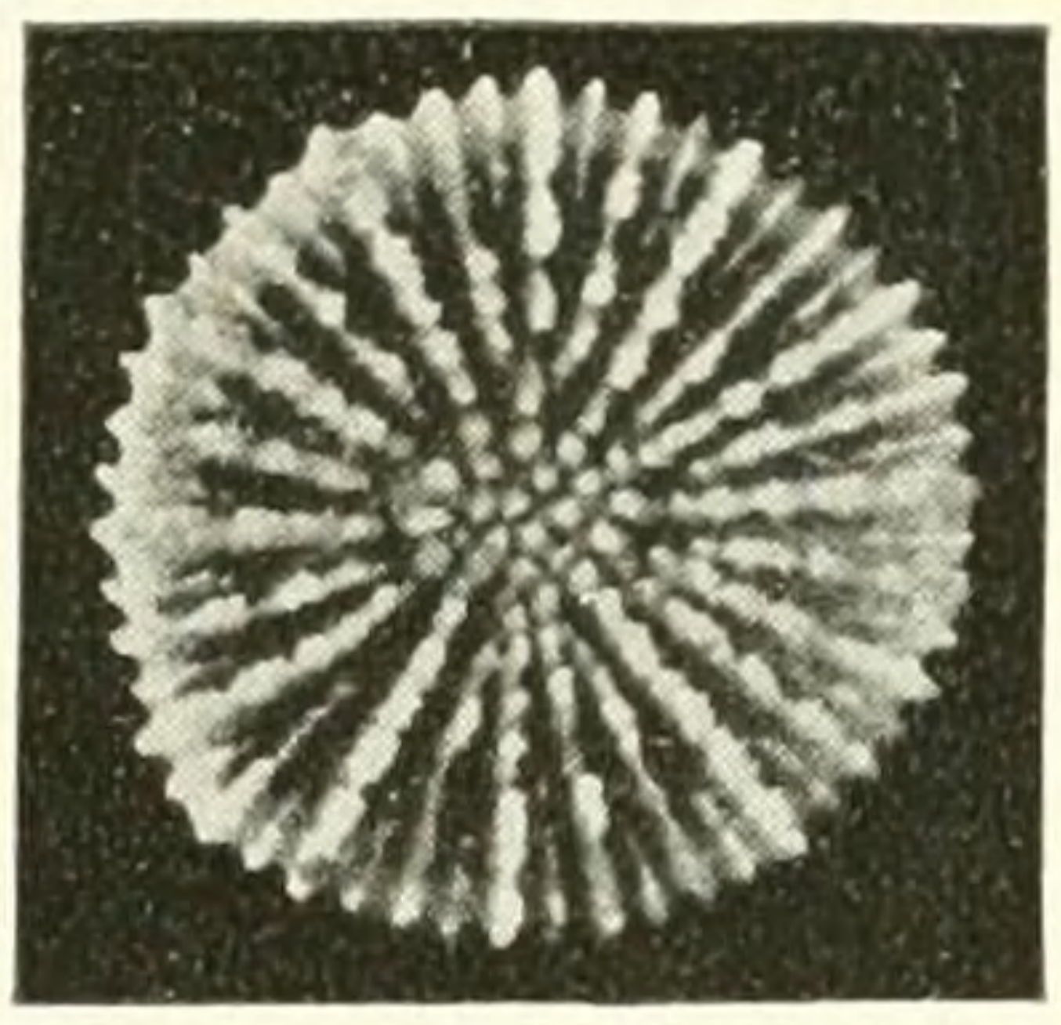
3a

X 2½

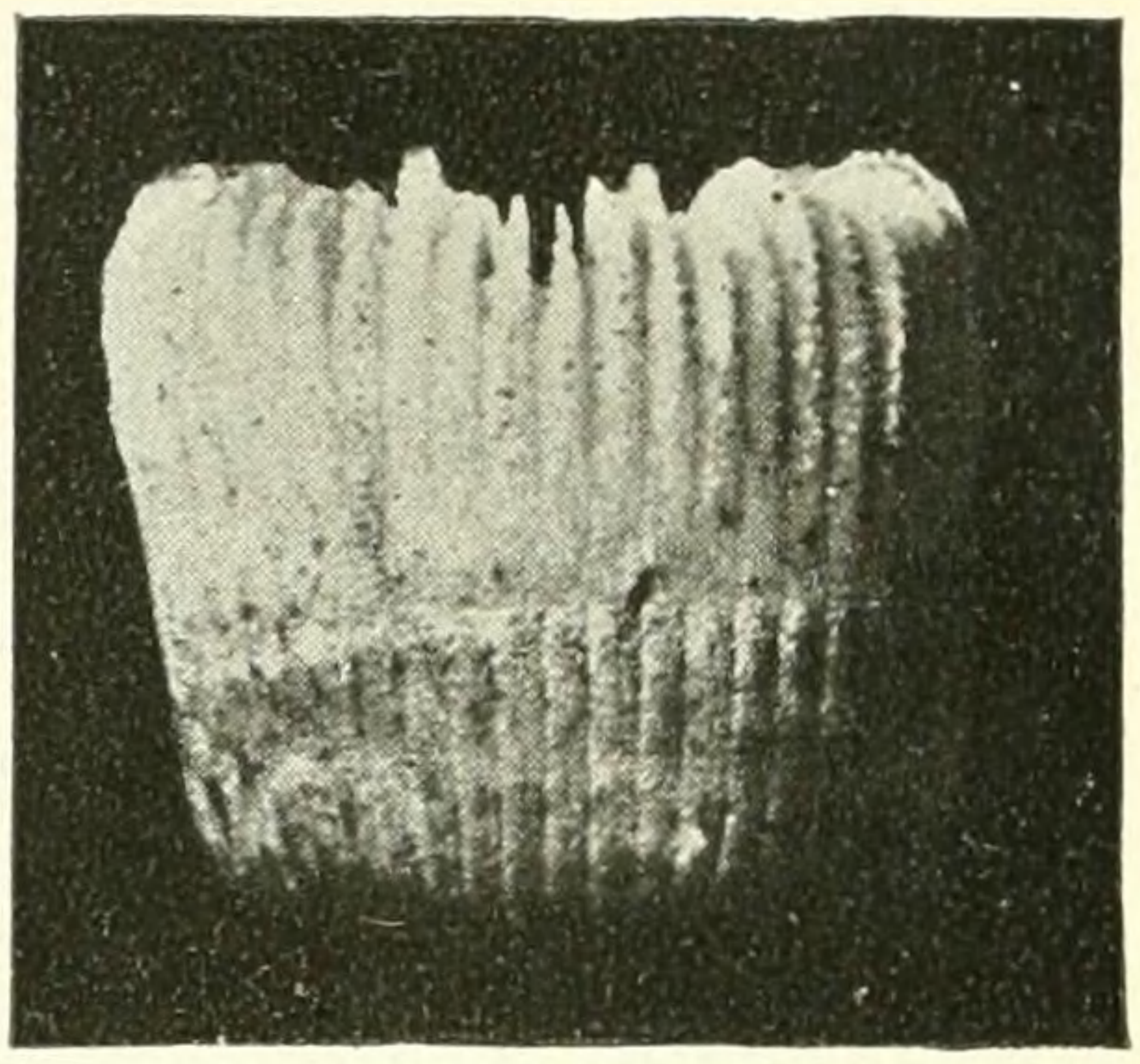
HAWAIIAN DEEP-SEA CORALS.



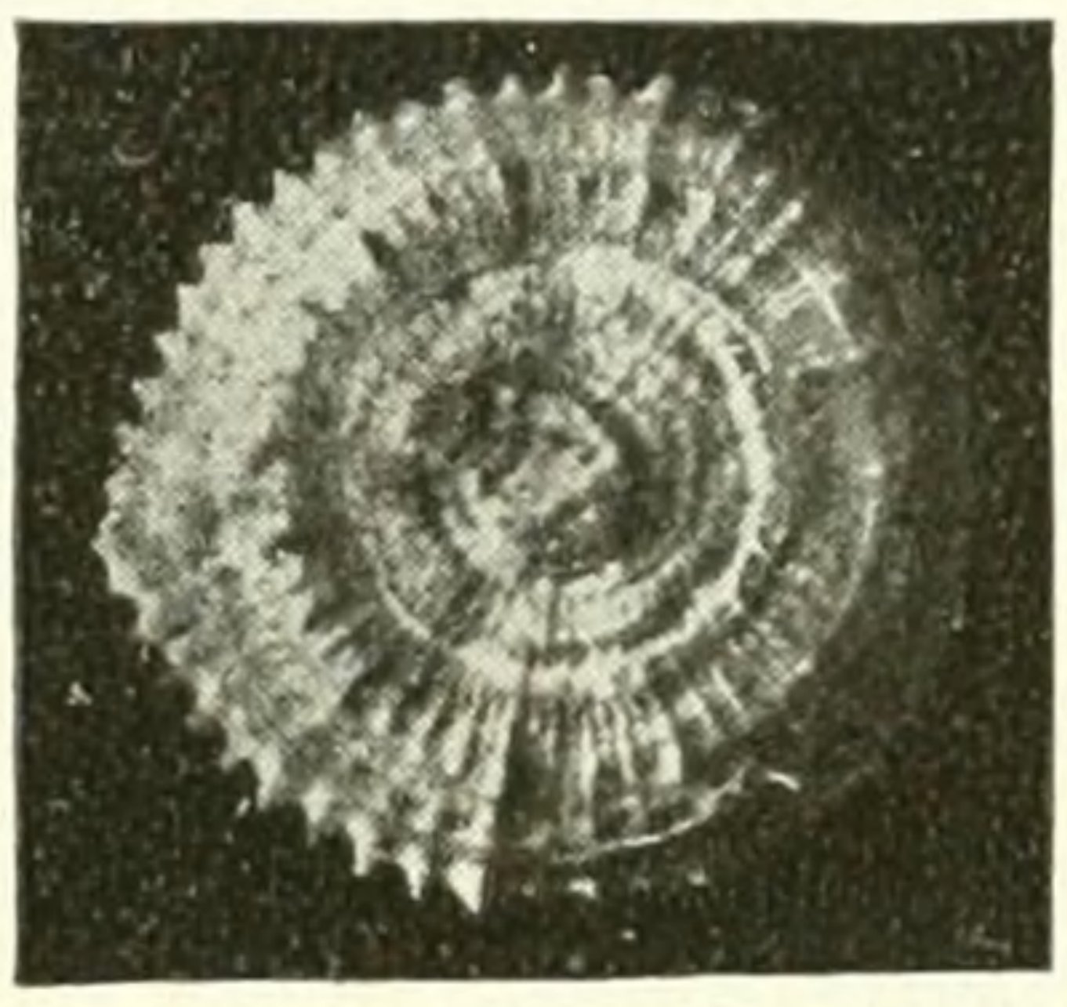
1 X 2



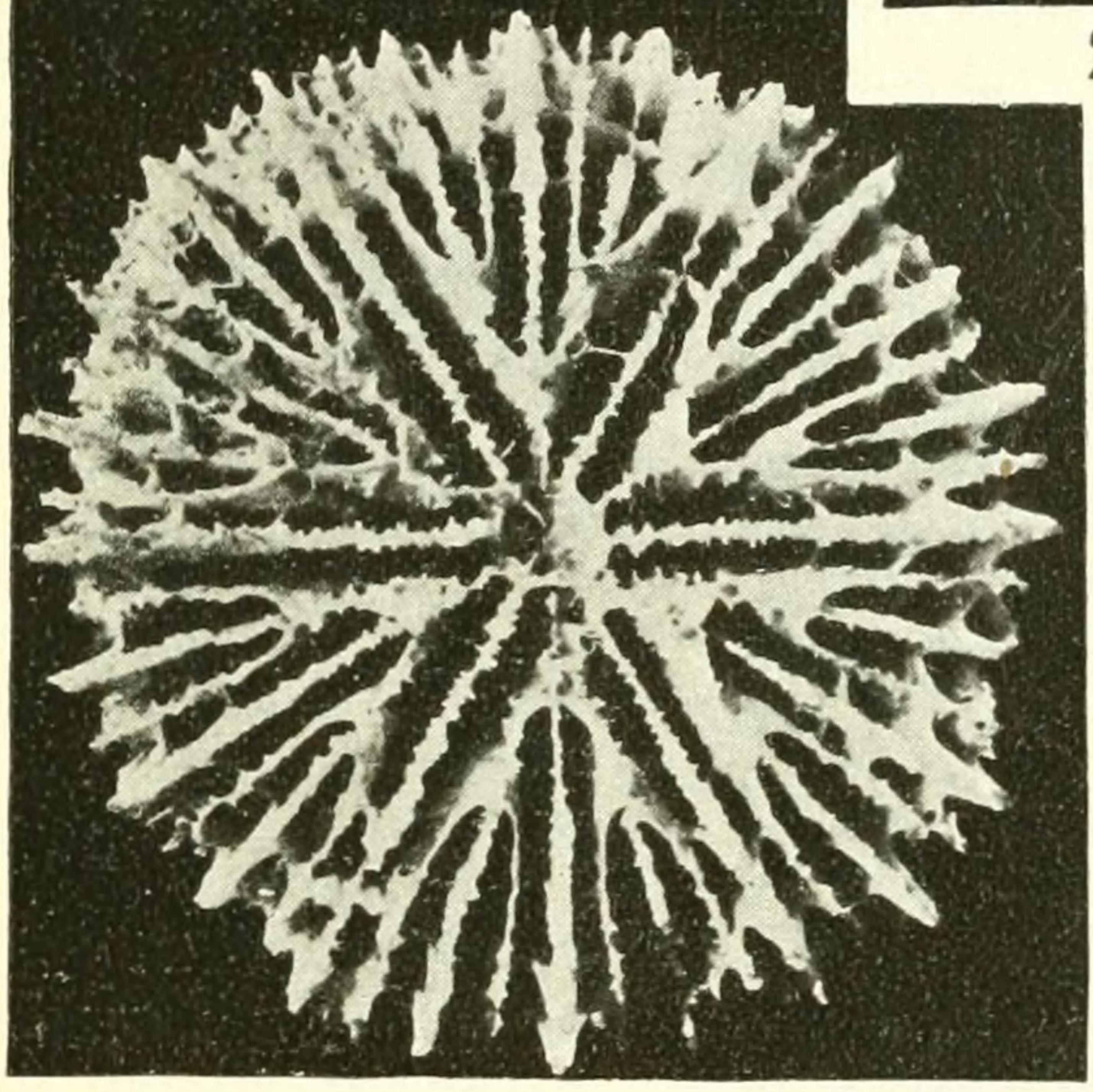
2 X 2



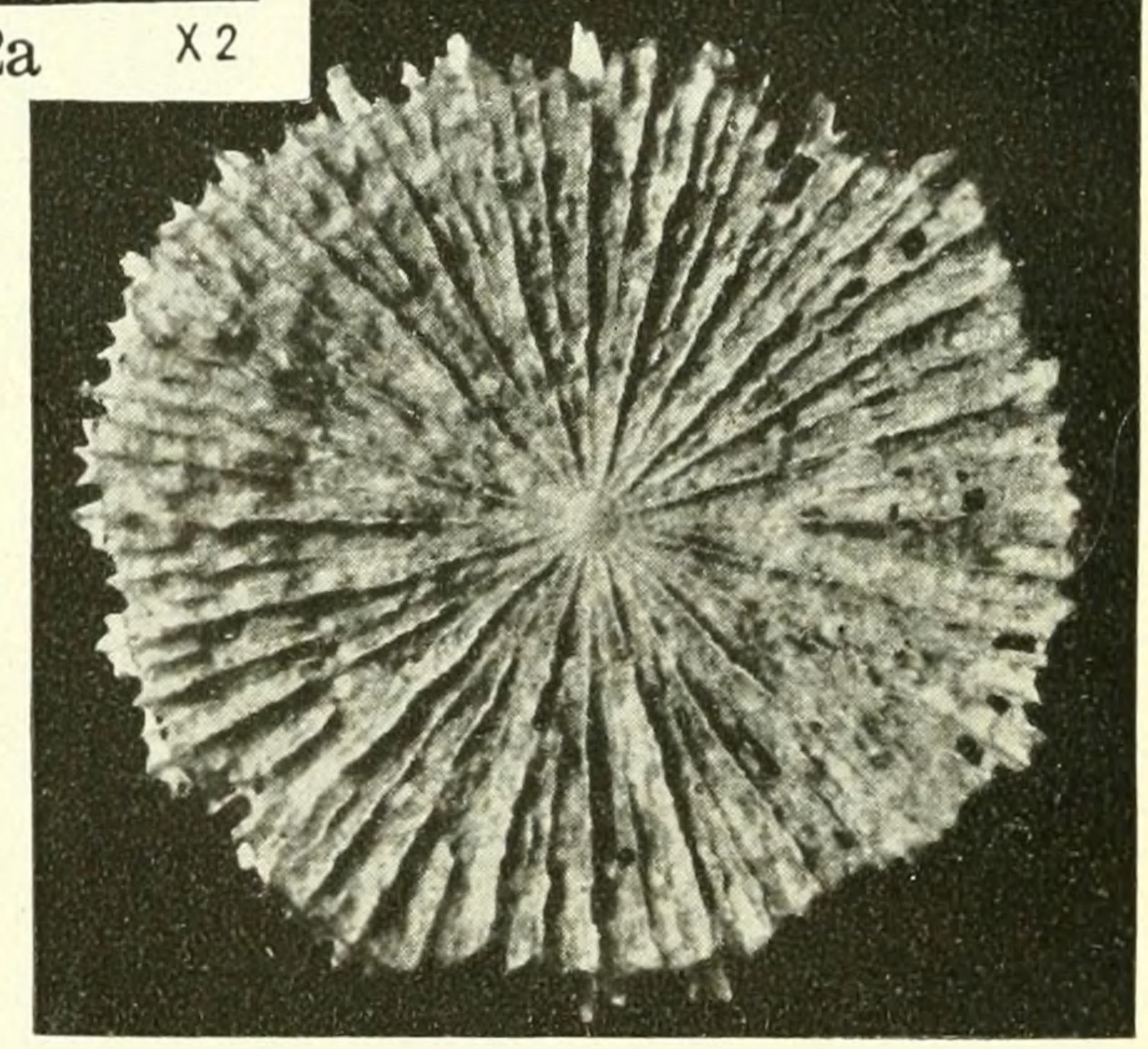
1a X 2



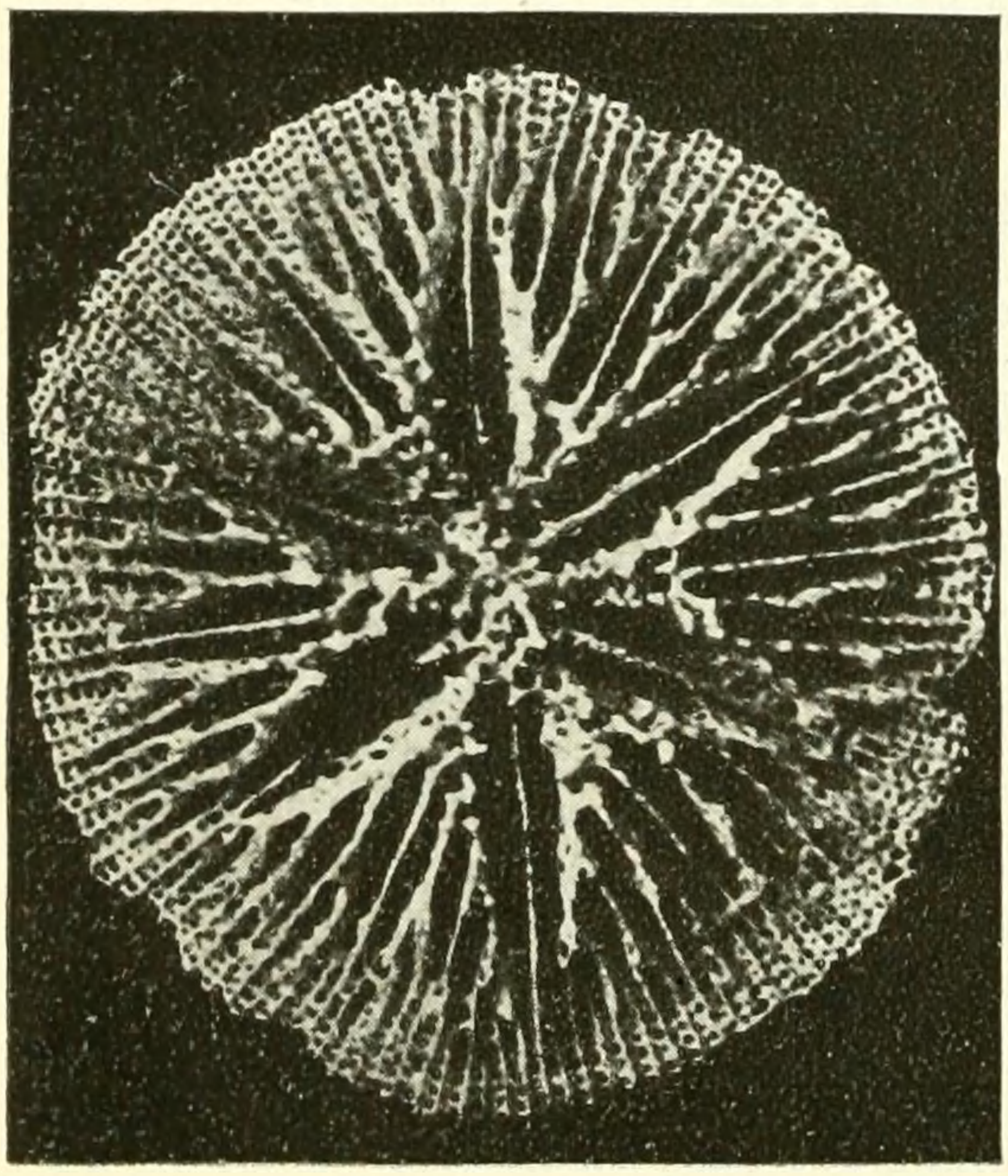
2a X 2



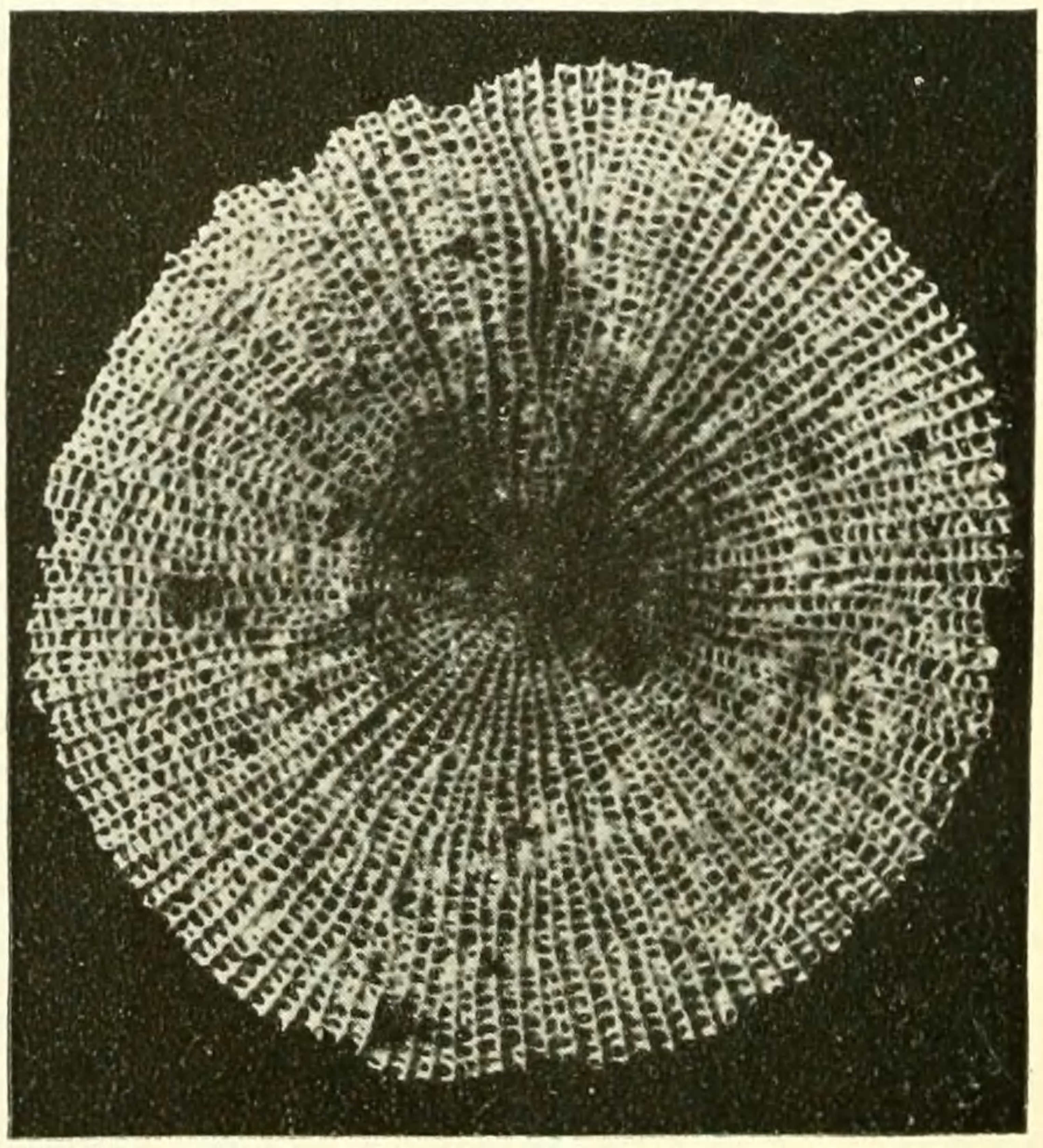
3 X 2



3a X 2



4 X 2



4a X 2

HAWAIIAN DEEP-SEA CORALS.

PLATE 14.

Hawaiian deep-sea corals.

FIGS. 1, 1*a*. *Paracyathus gardineri* Vaughan. Fig. 1, calice; fig. 1*a*, side view, of the same specimen, both × about 2.

2, 2*a*. *Anthemiphyllia pacifica* Vaughan. Fig. 2, calice; fig. 2*a*, base, of the same specimen, both × 2.

3, 3*a*. *Bathyactis hawaiiensis* Vaughan. Fig. 3, calice; fig. 3*a*, base, of the same specimen, both × 2.

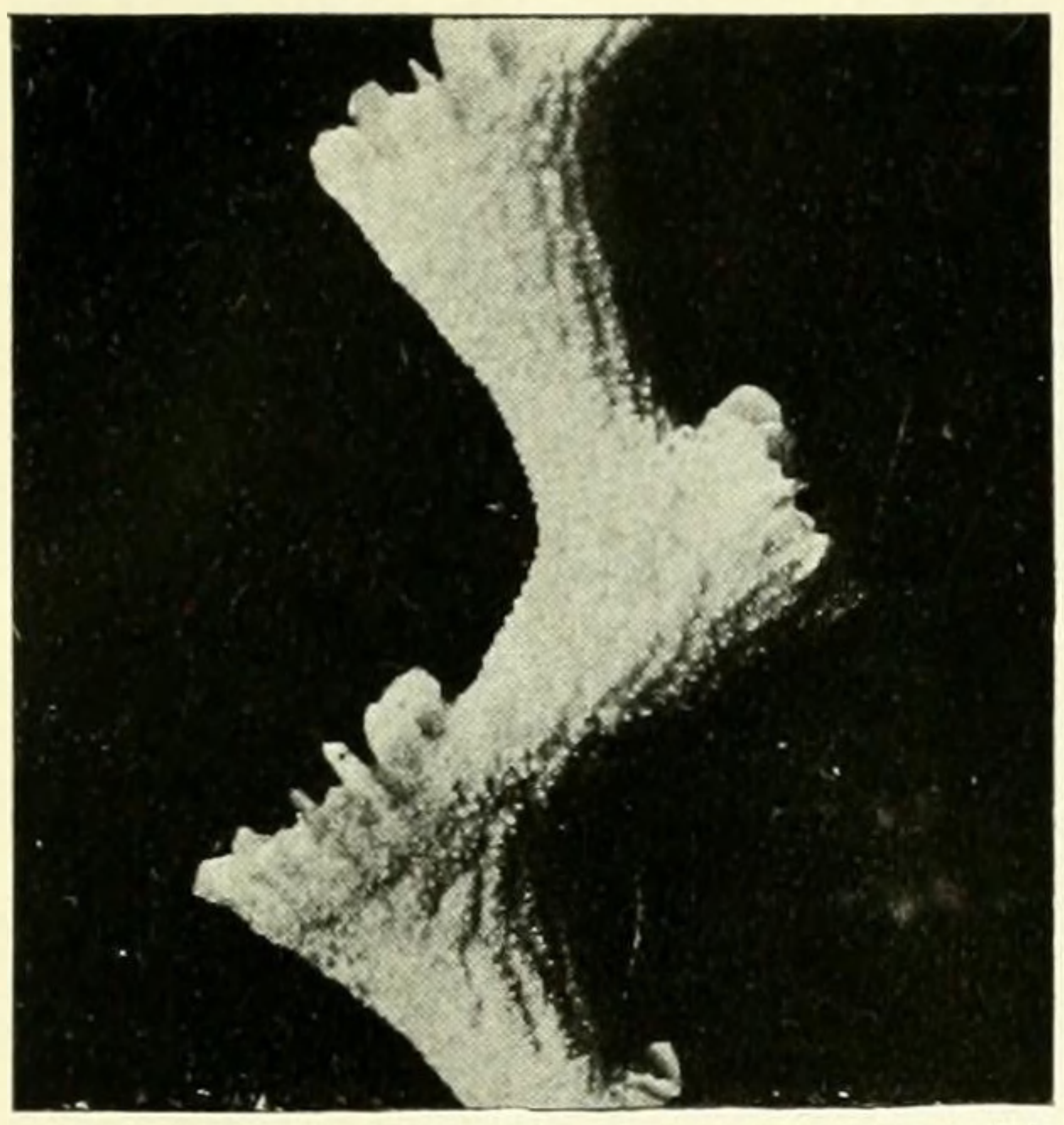
4, 4*a*. *Stephanophyllia formosissima* Mosely. Fig. 4, calice; fig. 4*a*, base, of the same specimen, both × 2.

PLATE 15.

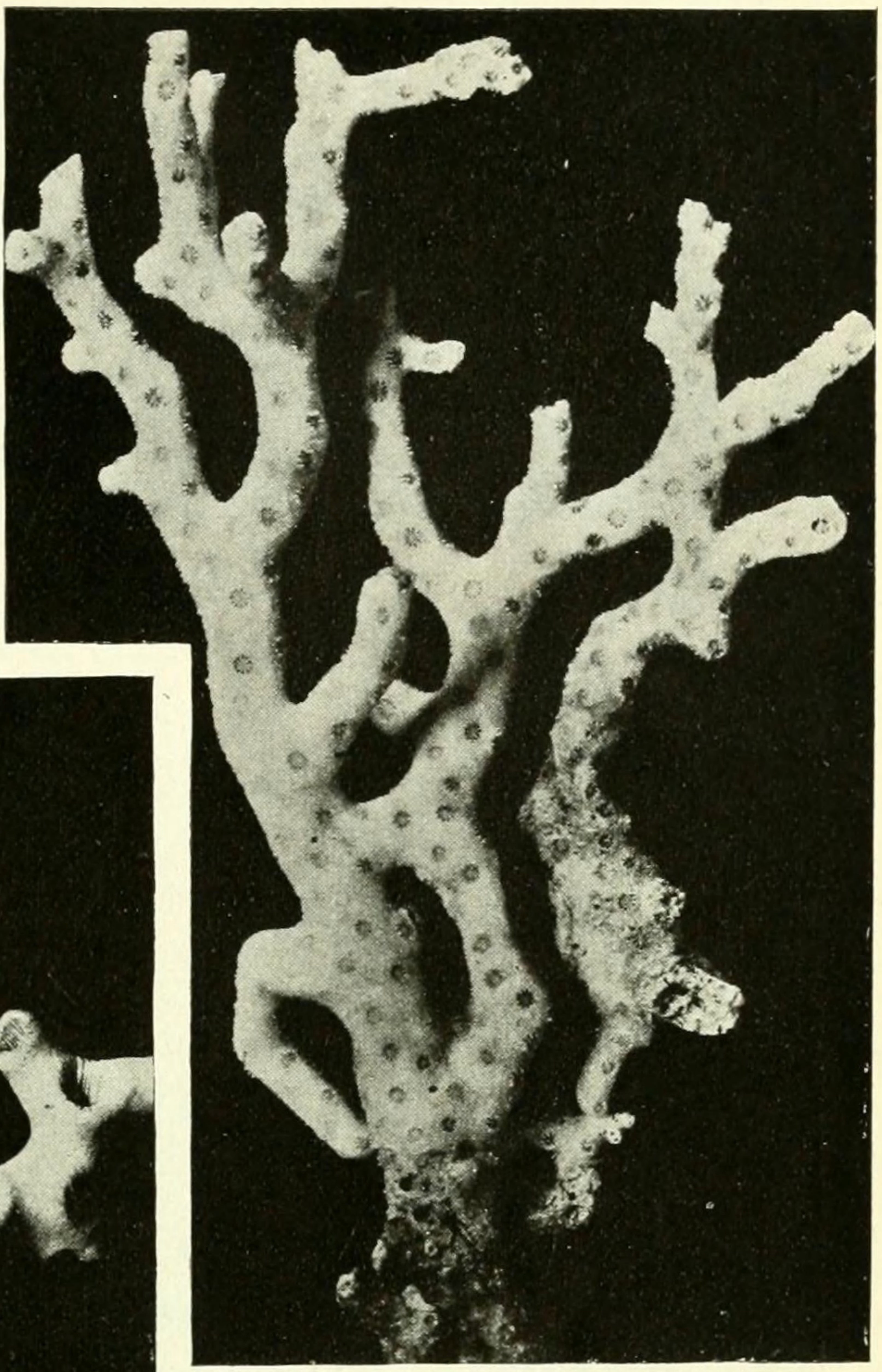
Hawaiian deep-sea corals.

FIGS. 1, 1*a*. *Madrepora kauaiensis* Vaughan. Fig. 1, corrallum, natural size; fig. 1*a*, part of a branch, × 4½, of the same specimen.

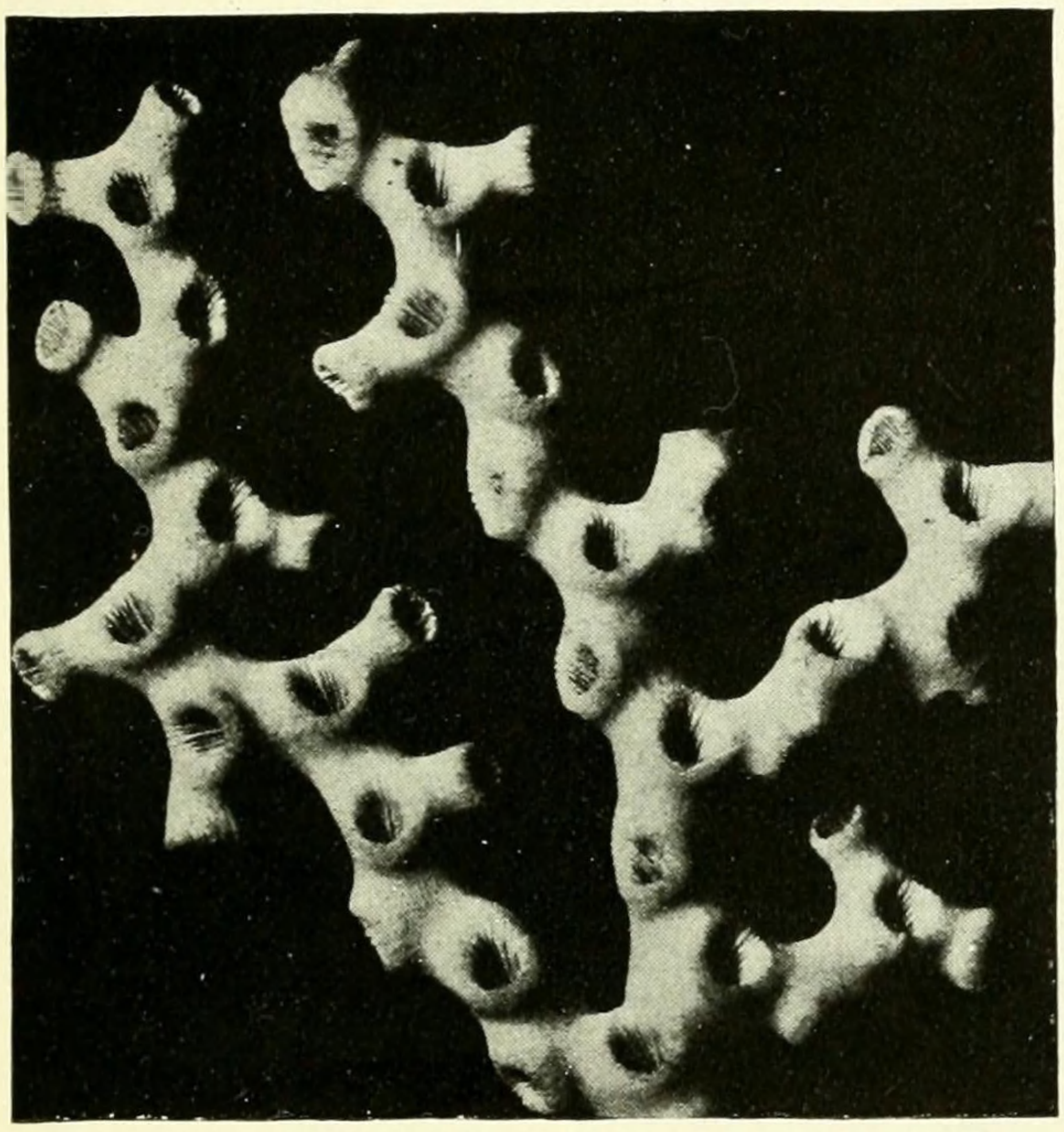
2. *Madracis kauaiensis* Vaughan, corallum, natural size.
3. *Anisopsammia amphelioides* (Alcock), part of a corallum, natural size.



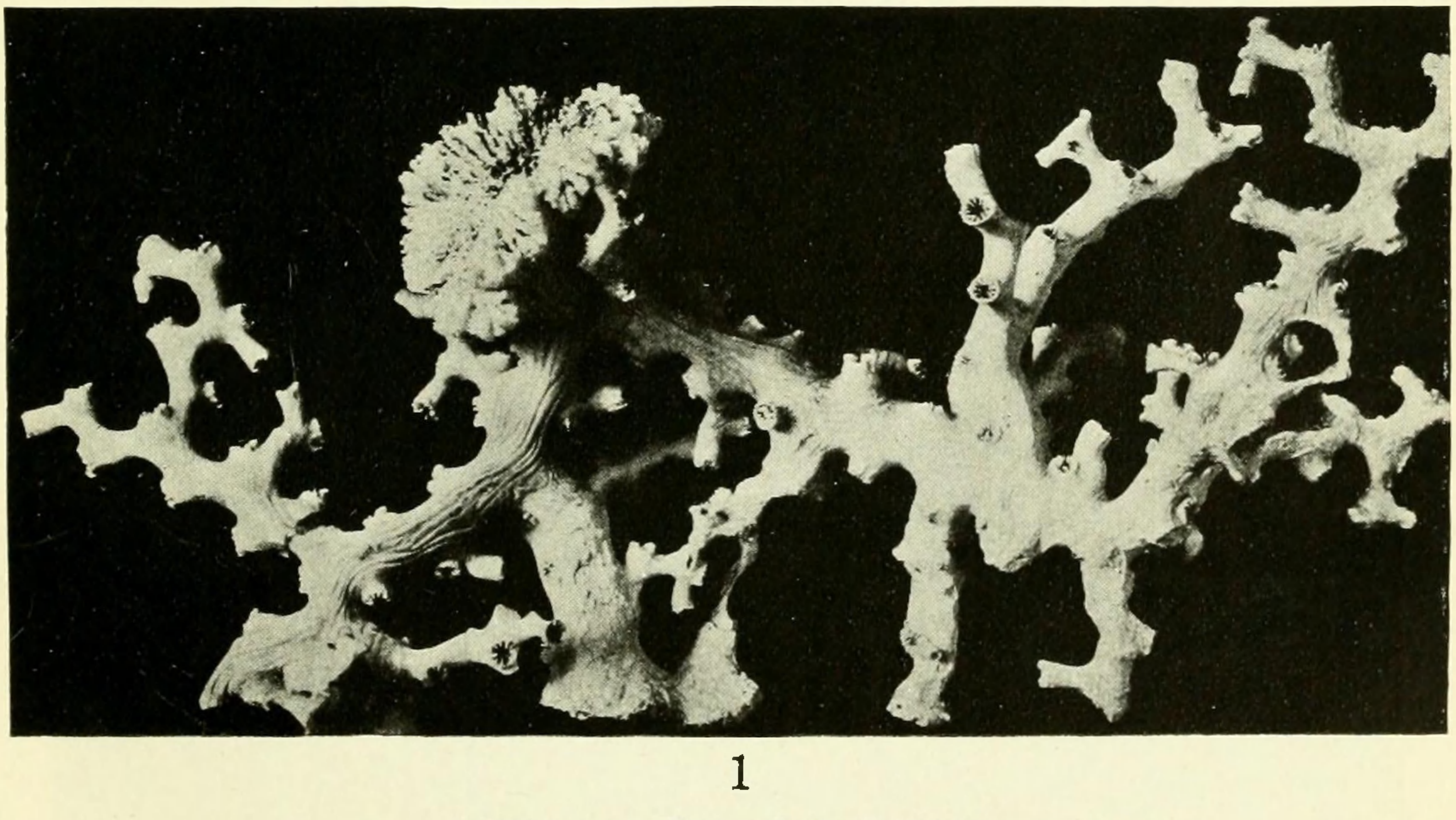
1a X4½



2

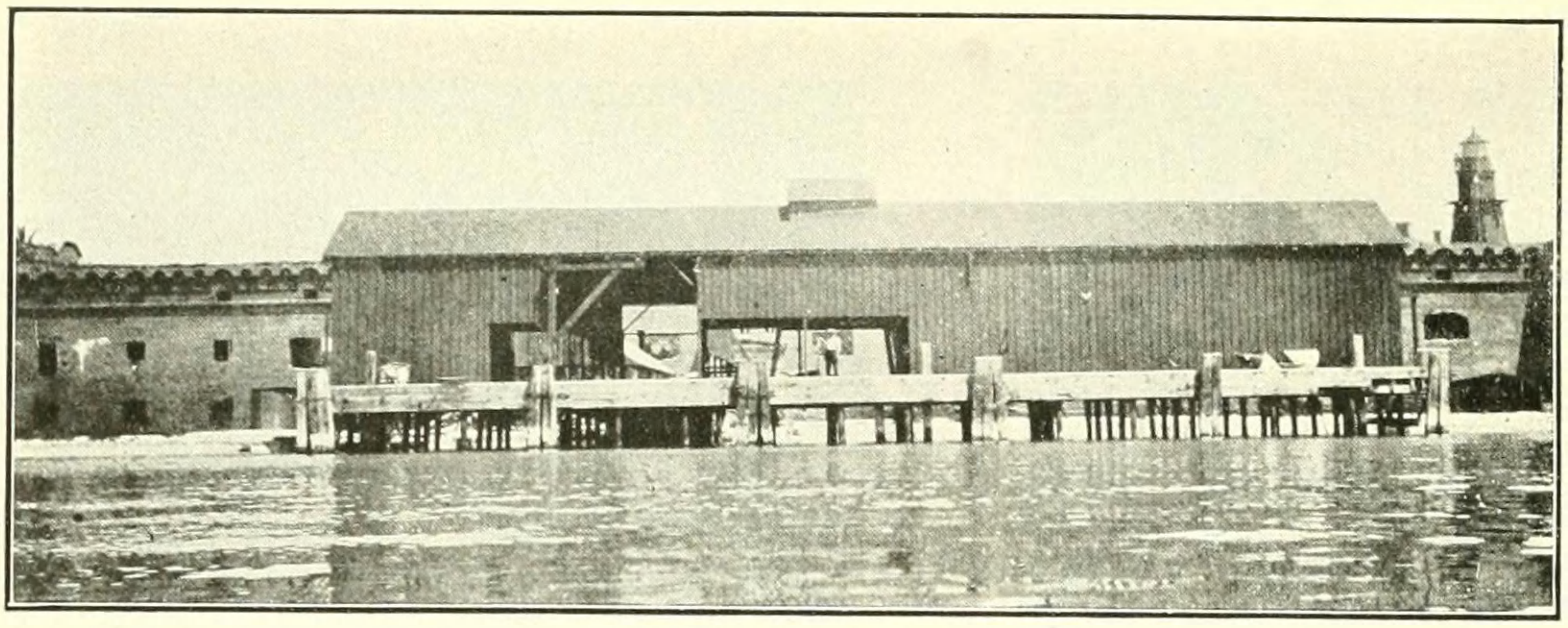


3

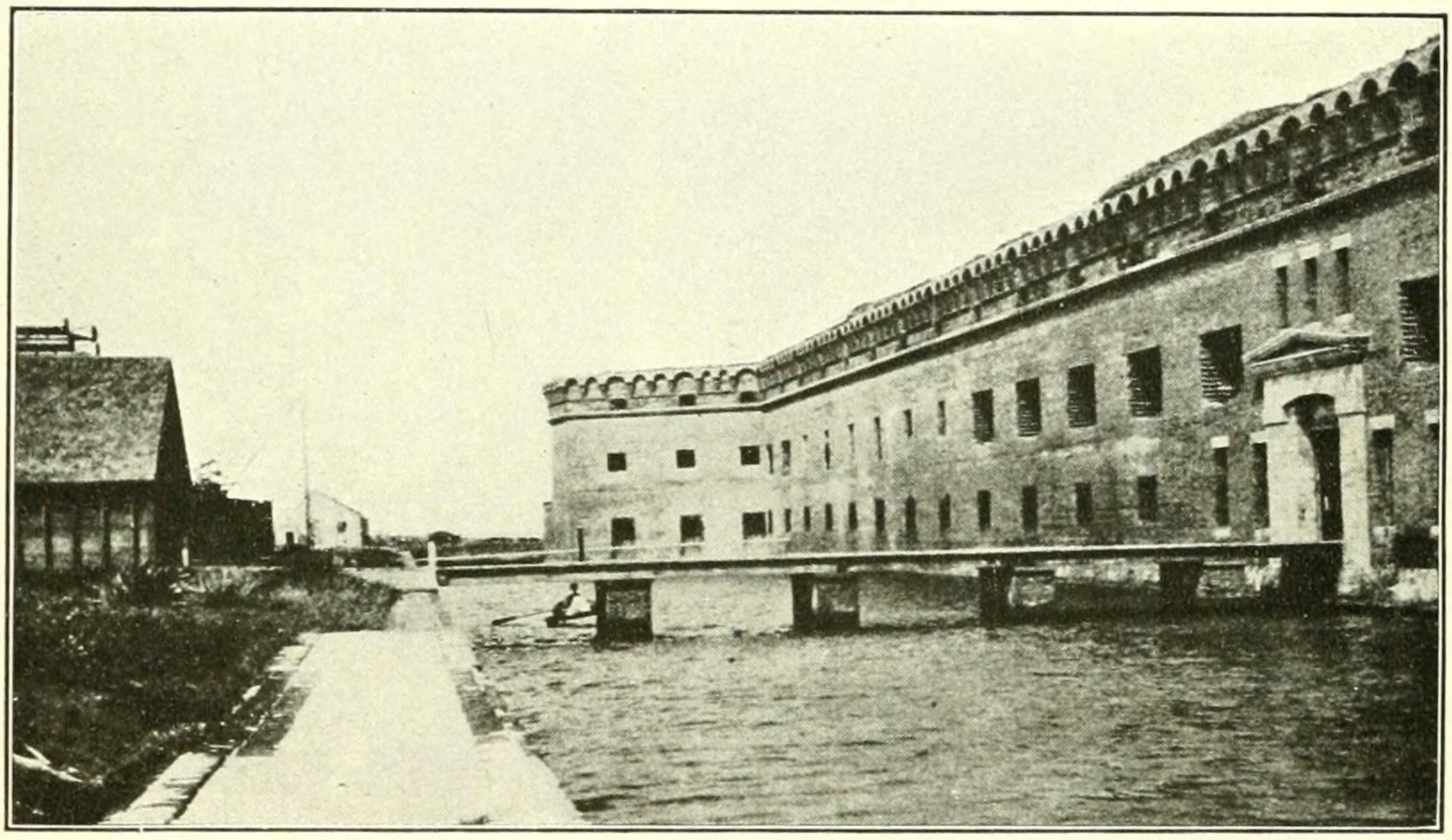


1

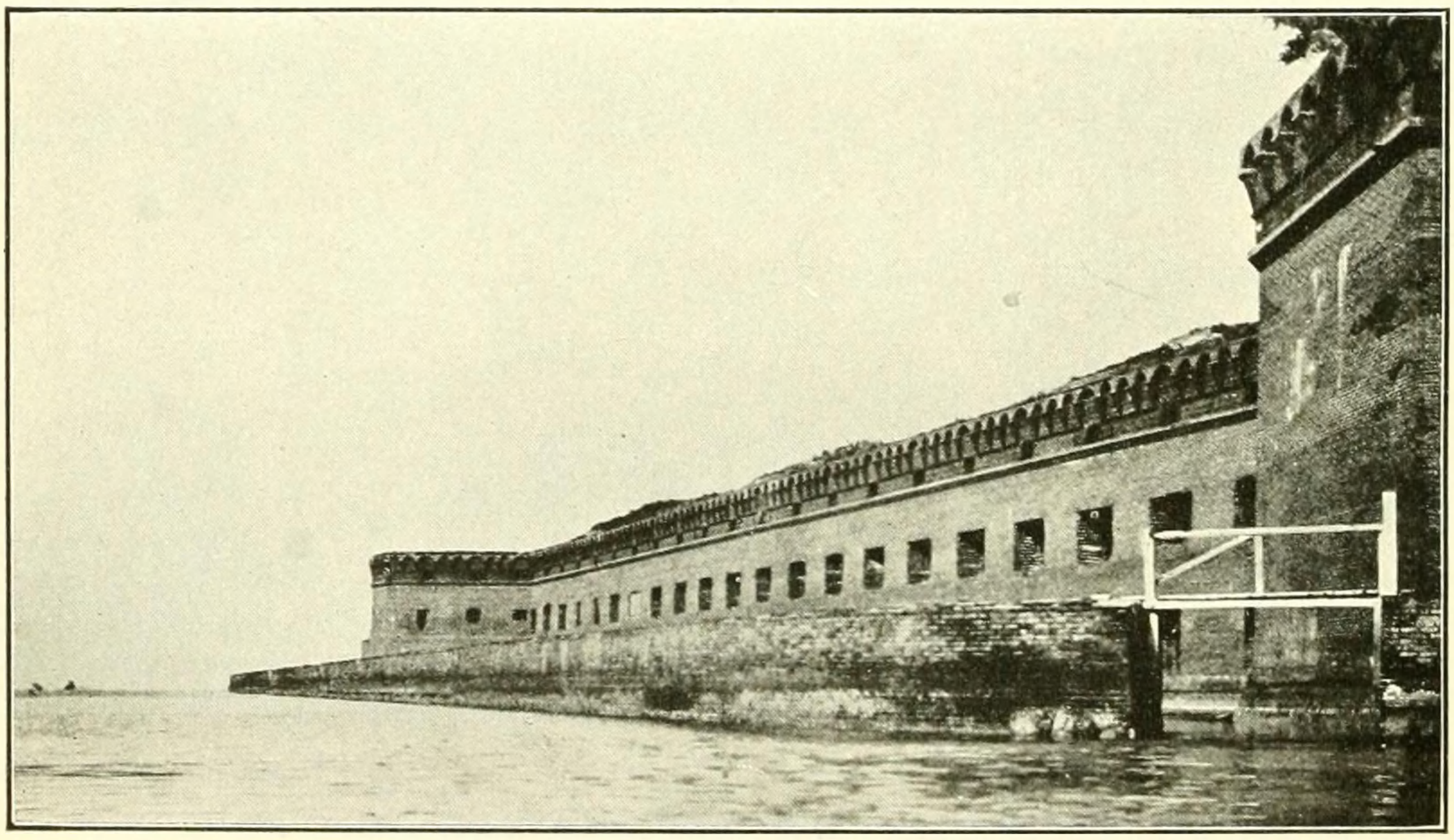
HAWAIIAN DEEP-SEA CORALS.



A.



B.



C.

VIEWS AT FORT JEFFERSON, TORTUGAS, FLA.

Plate 16.

Fort Jefferson, Tortugas, Florida.

Fig. A. Wharf. Many corals are growing on the peripheral piers.

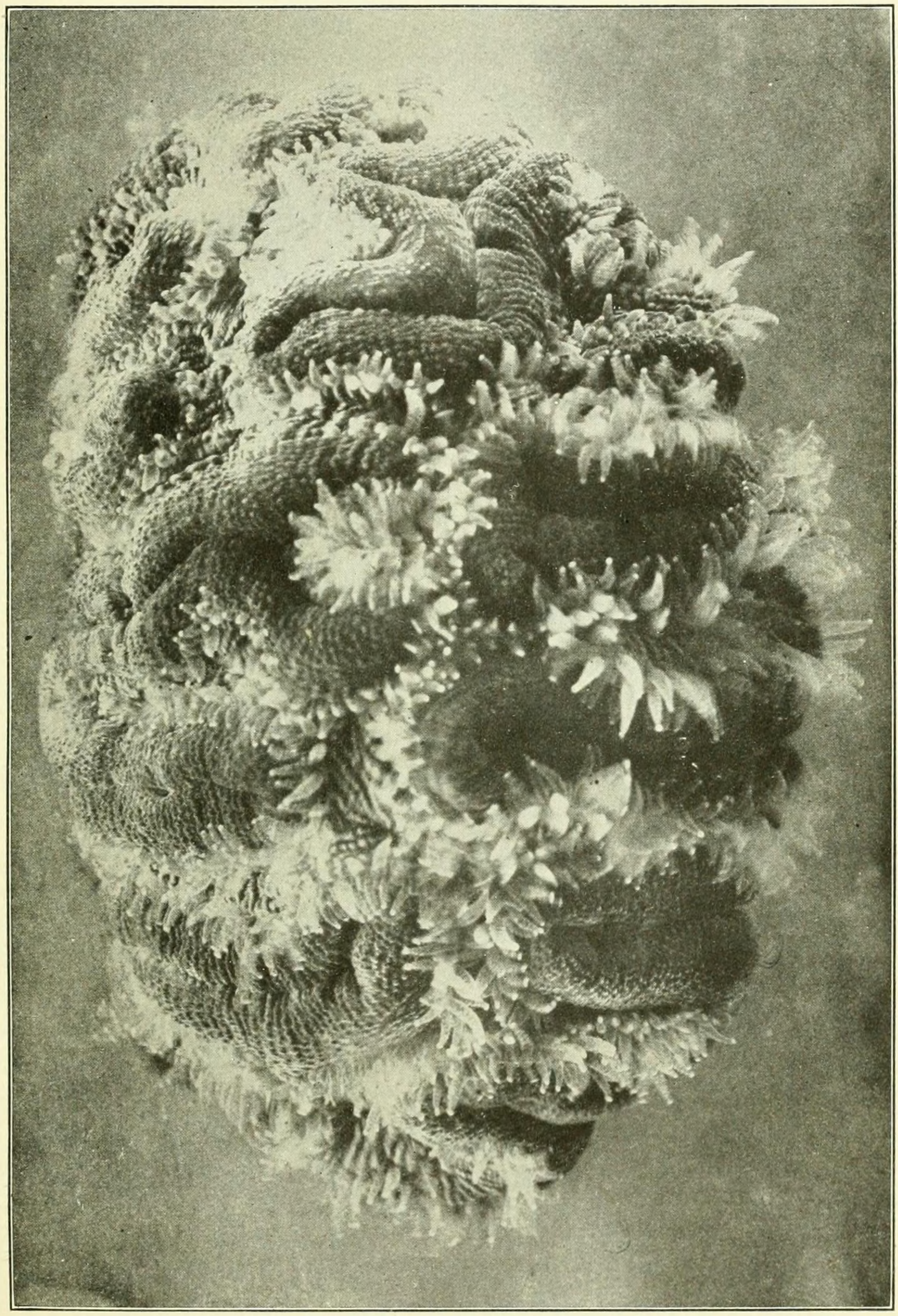
B. The moat and sallyport. Corals of lagoon facies live in the moat.

C. Outside of the moat wall and the flood-gate, the northwest side of the fort. Many corals were planted near the wall, north of the flood-gate.

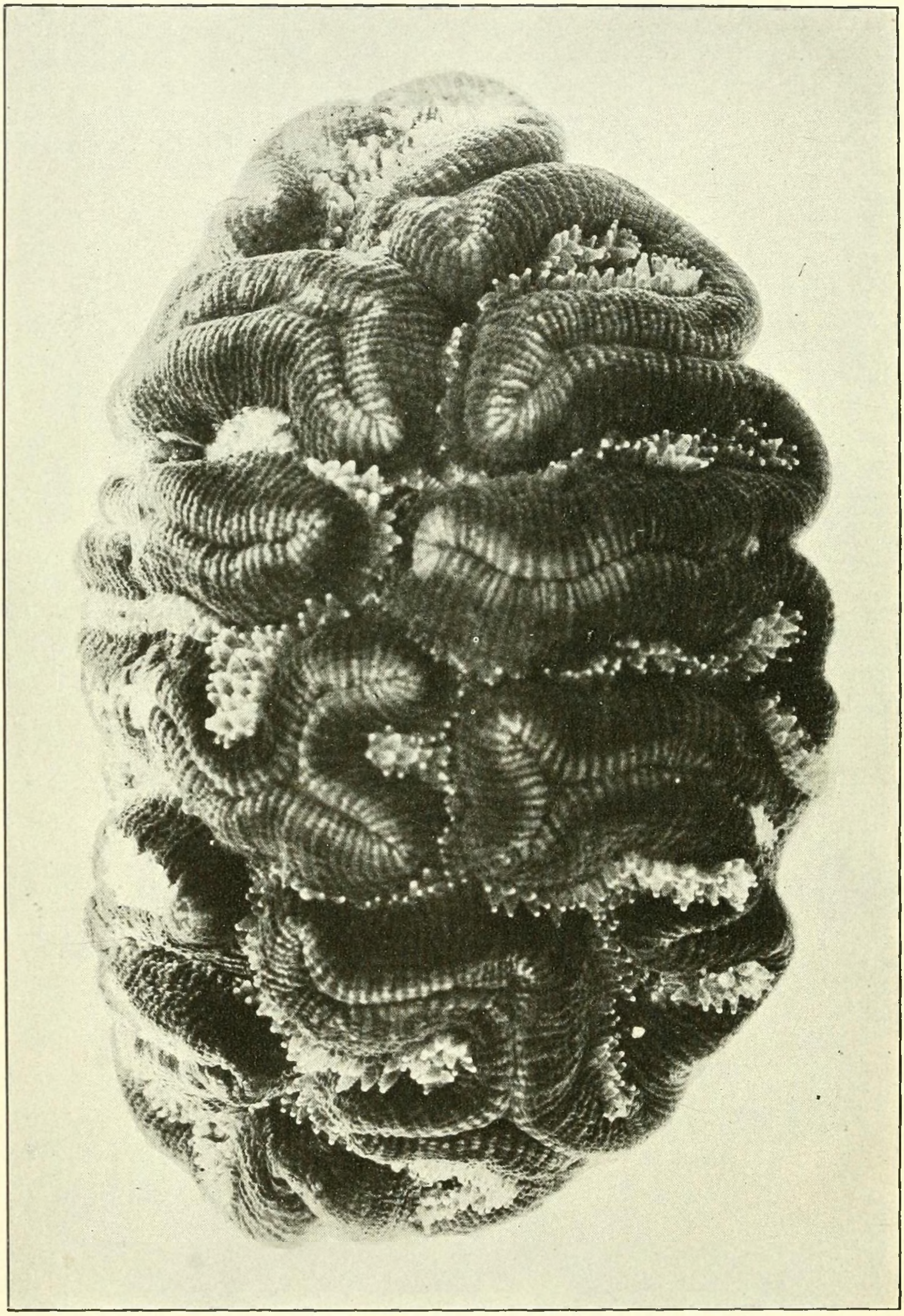
PLATE 17.

Maeandra areolata (Linnaeus).

The tentacles are fully distended, following stimulation by a small amount of food. The figure is about 1.4 natural size.



MAEANDRA AREOLATA (LINNAEUS), WITH ITS TENTACLES FULLY DISTENDED.



MAEANDRA AREOLATA (LINNAEUS), WITH THE POLYPS PARTIALLY CONTRACTED.

PLATE 18.

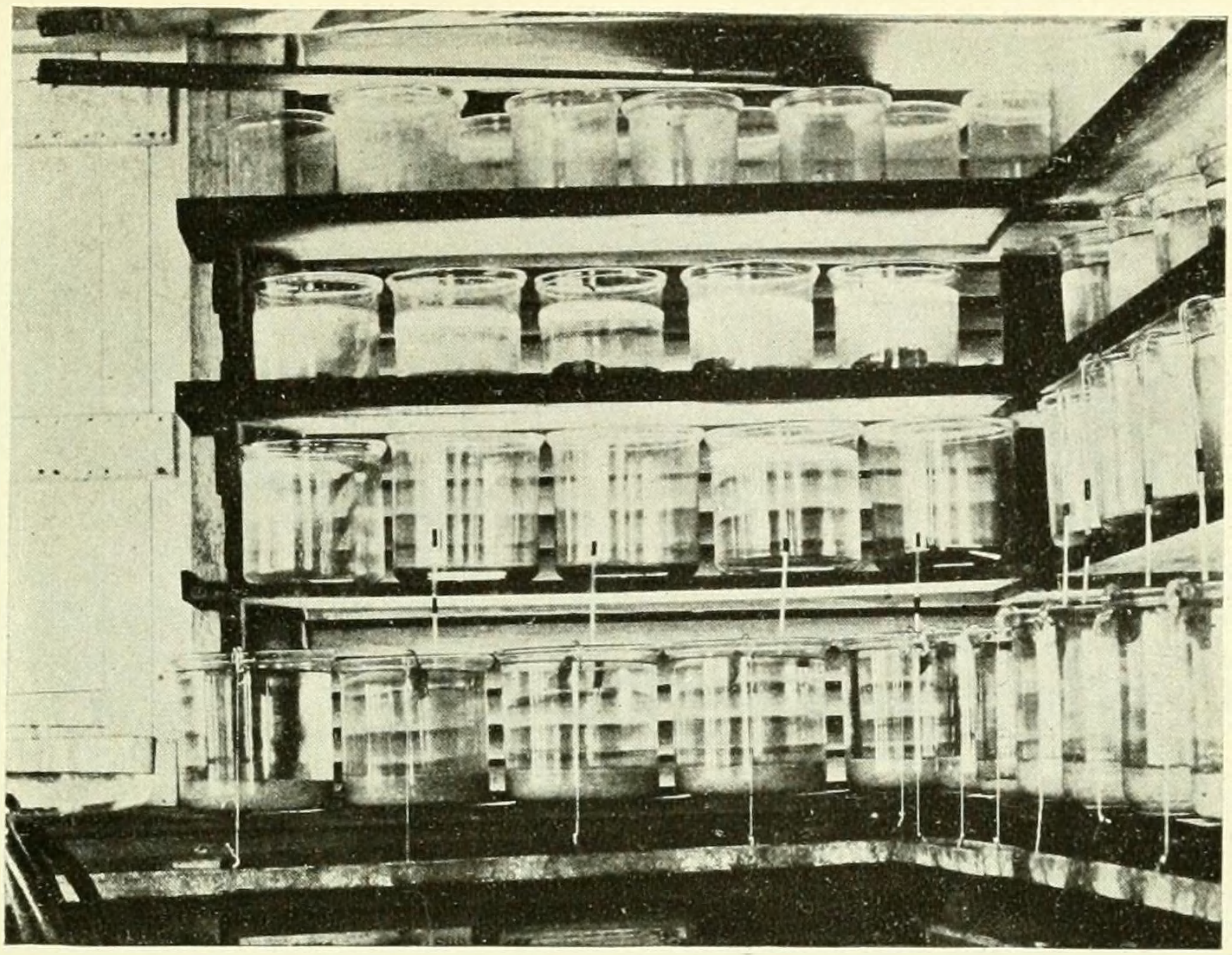
Maeandra areolata (Linnaeus).

The same colony represented by plate 17, as it appeared during the digestion of food. The figure is about 1.4 natural size.

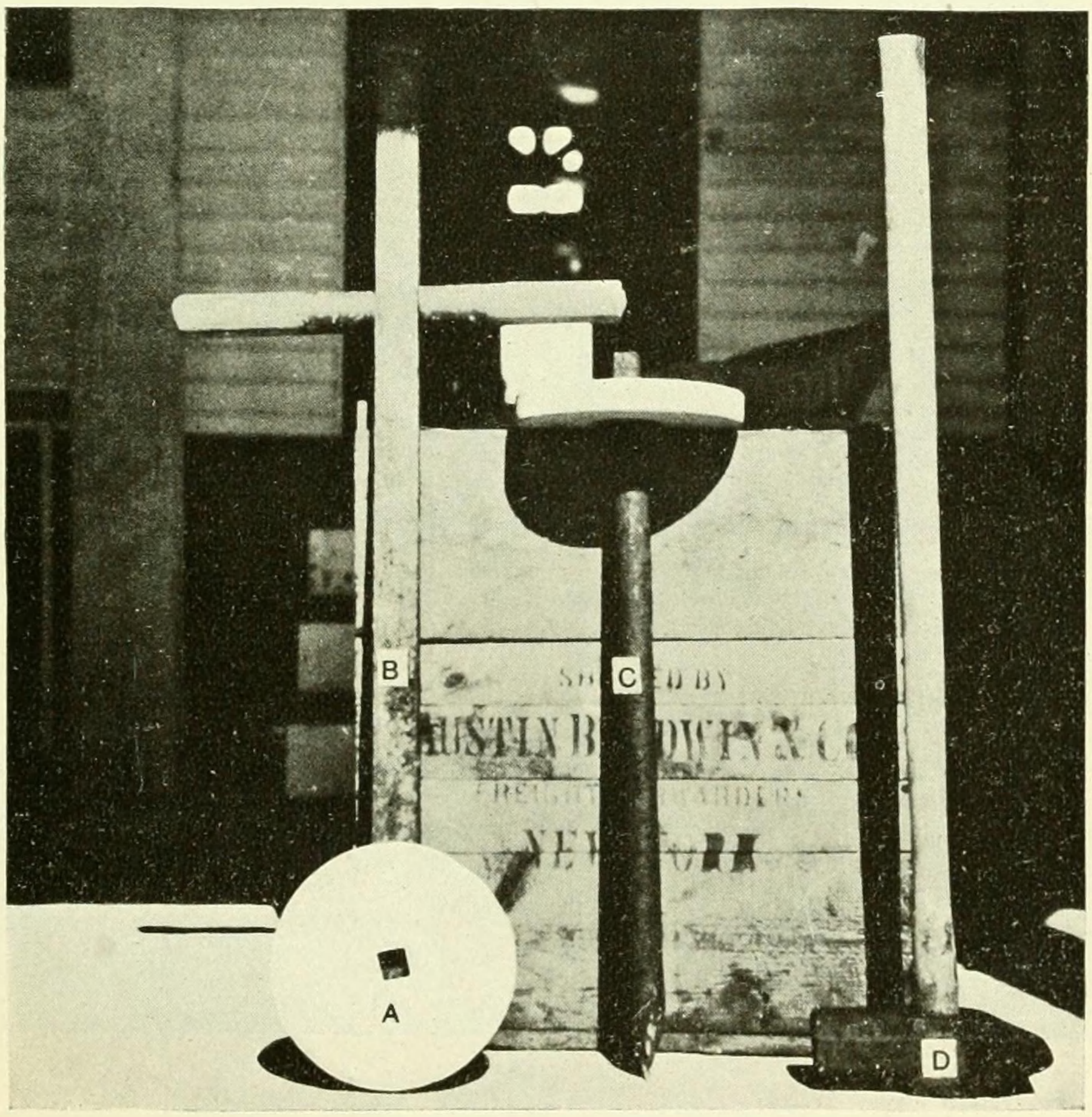
PLATE 19.

FIG. A. Aquarium at the laboratory, Tortugas, Florida. The jars on the lowest shelf contained coral planulae that were being reared; the jars on the next higher shelf contained clean seawater that was siphoned to the jars below; the jars on the top shelf contained coral colonies from which the planulae for the rearing experiments were obtained.

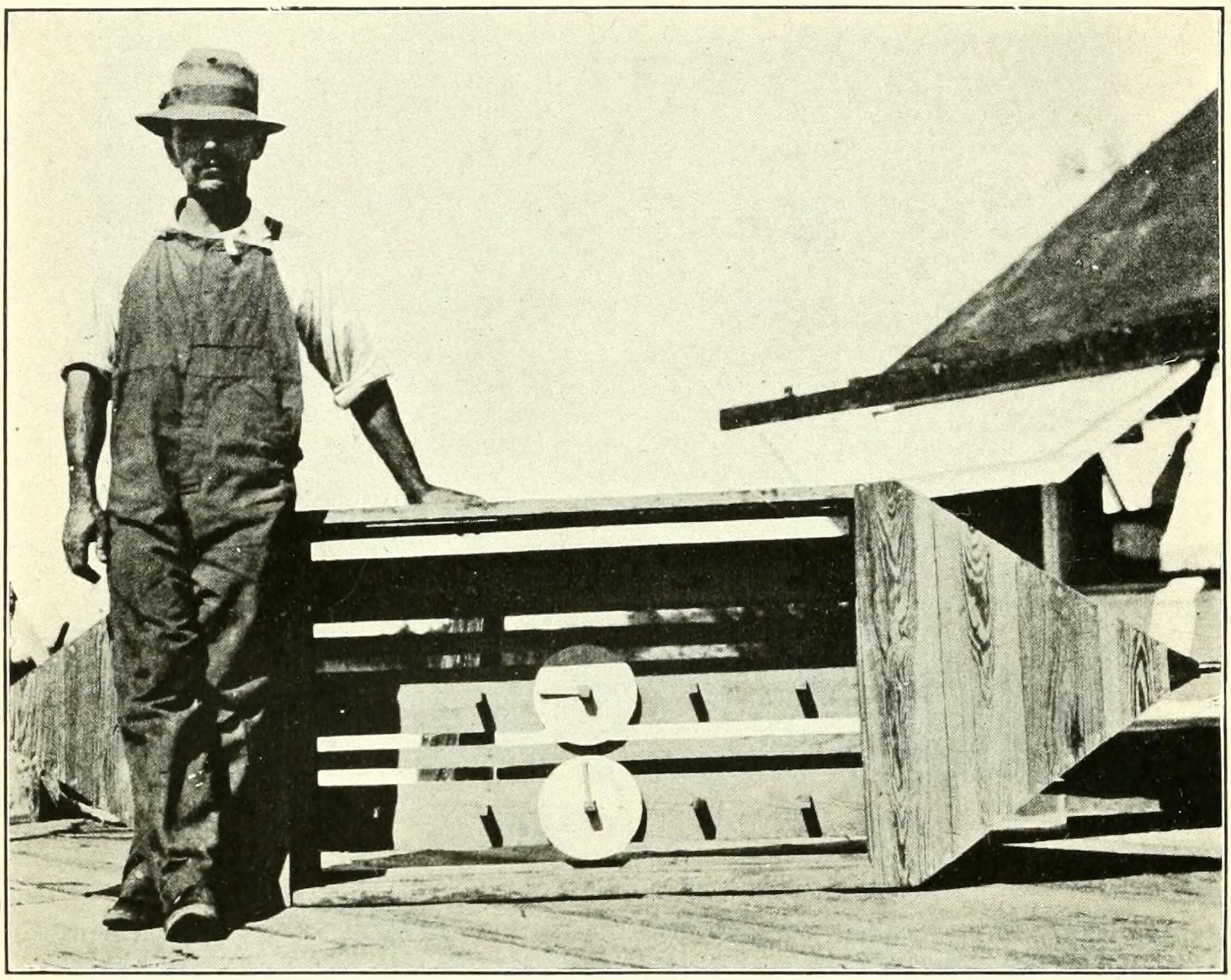
B. Apparatus for planting corals. A, terra-cotta disc (8 inches in diameter), to which corals were attached; B, iron bar, the lower end a cap that fits over the heads of the iron stakes; C, iron stake with a terra-cotta disc in place on its head; D, sledge hammer.



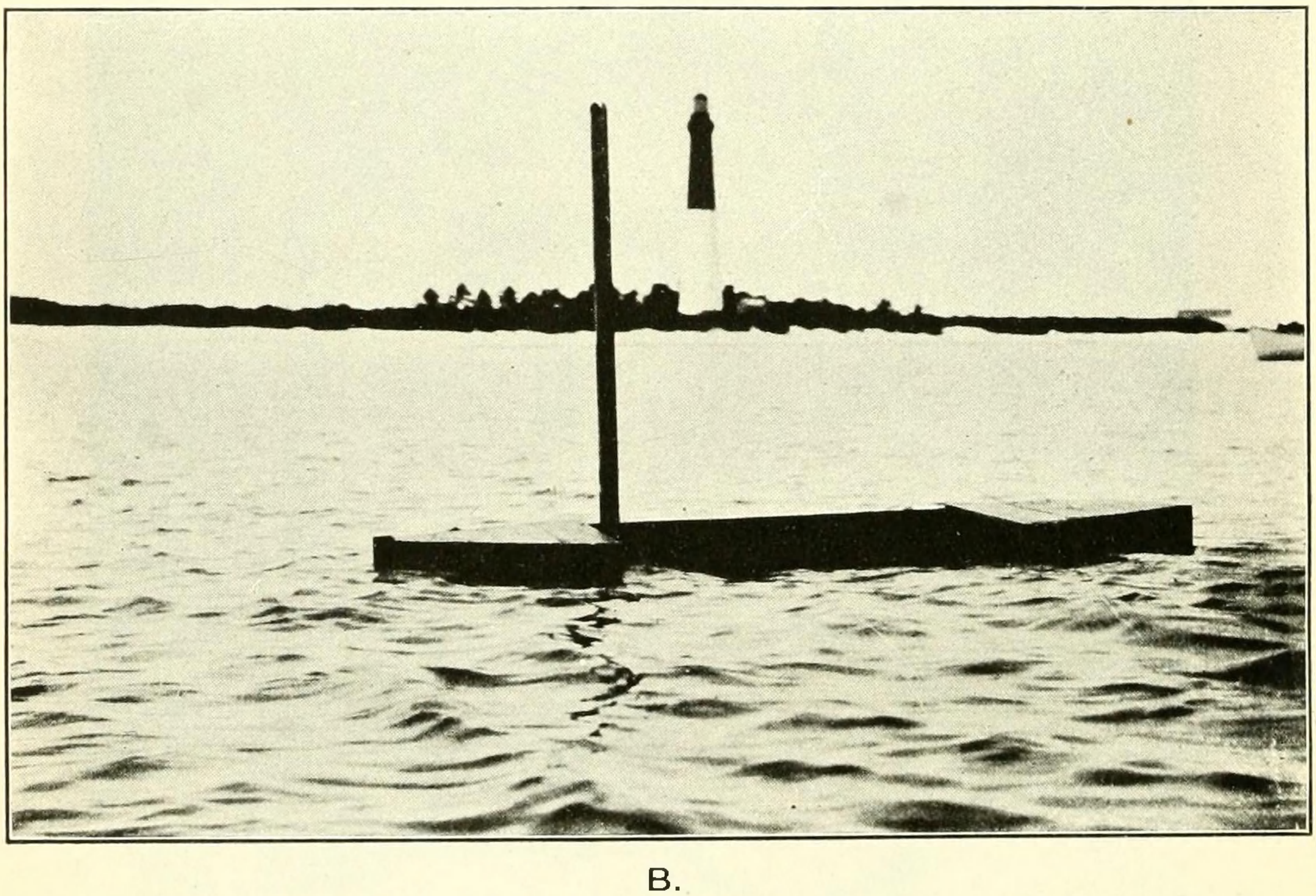
A. AQUARIUM AT THE LABORATORY, TORTUGAS, FLA.



B. APPARATUS FOR PLANTING CORALS.



A.



B.

LIVE CAR IN WHICH CORALS WERE PLANTED.

PLATE 20.

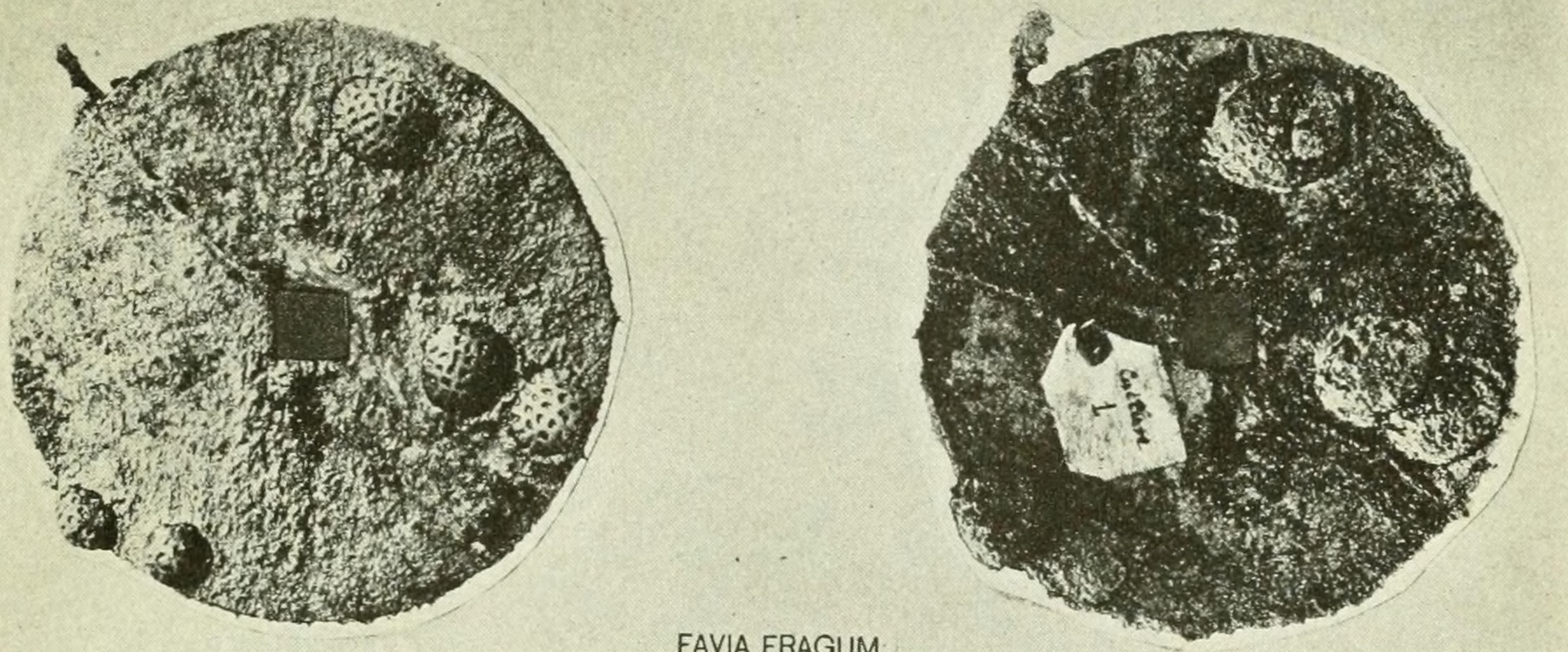
FIG. A. Live car with terra-cotta discs fastened to its bottom.

B. The same live car in the water after corals had been planted on its bottom.

Plate 21.

Corals reared from planulae.

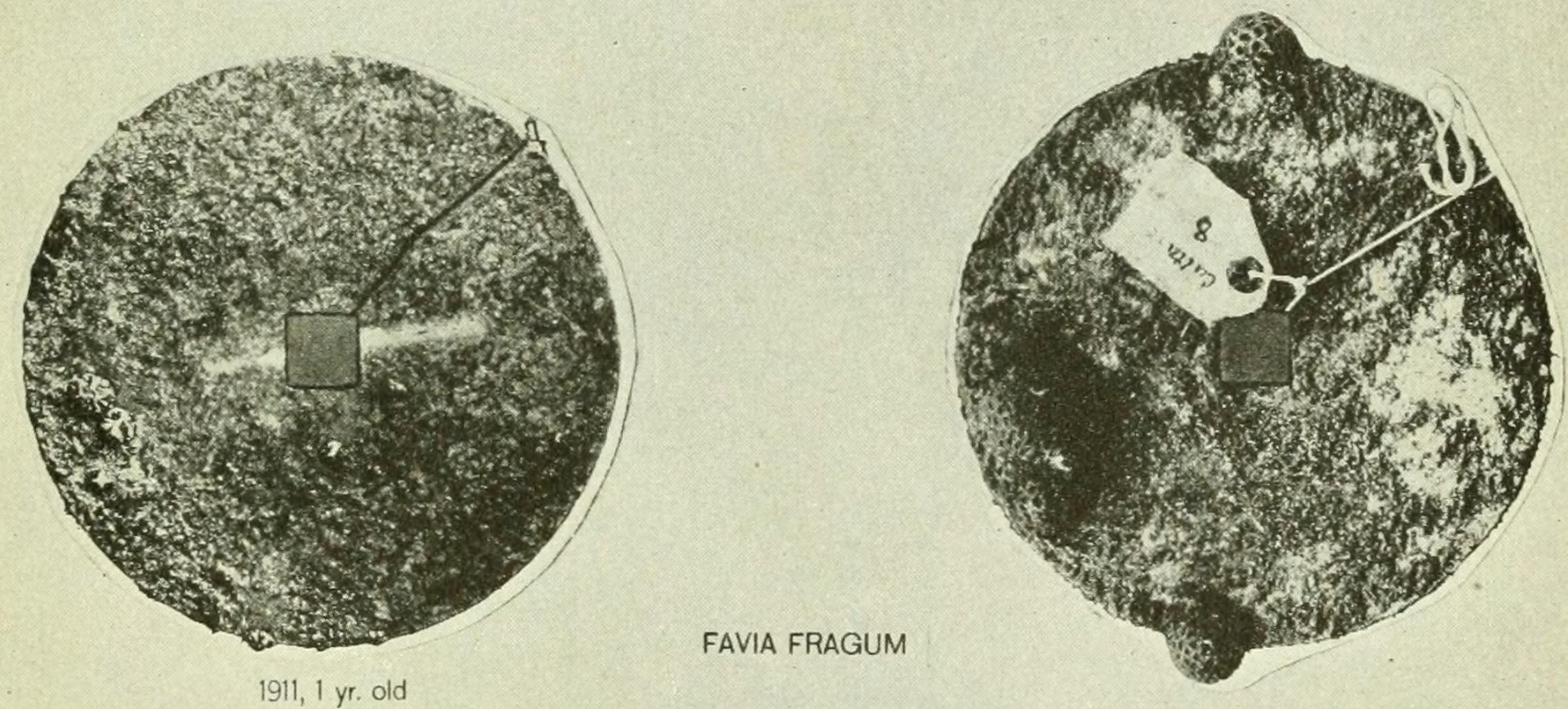
Top row, *Favia fragum* (Esper), 2 years old and 4 years old.
Middle row, *Favia fragum* (Esper), 1 year old and 4 years old.
Bottom, *Porites astreoides* Lamarck, 1 year old and 4 years old.
Diameter of the discs, 8 inches.



1912, 2 yrs. old

FAVIA FRAGUM

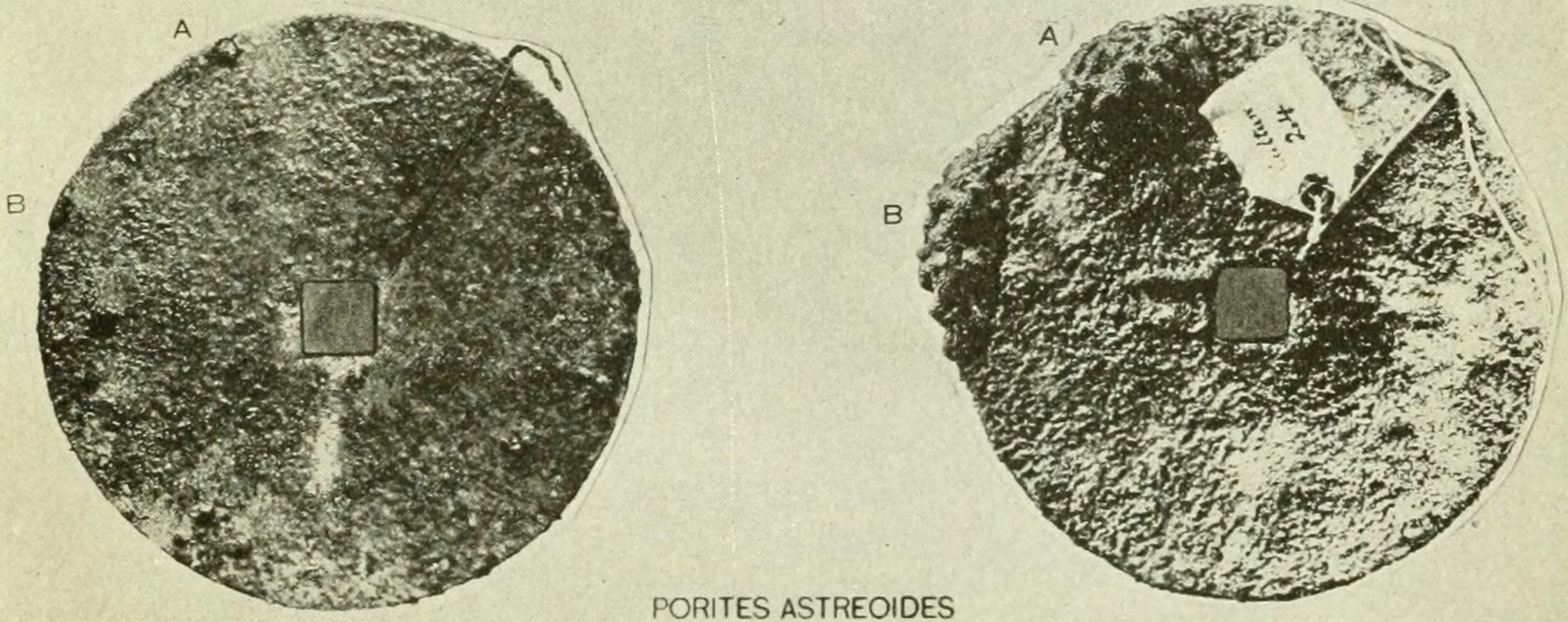
1914, 4 yrs. old



1911, 1 yr. old

FAVIA FRAGUM

1914, 4 yrs. old

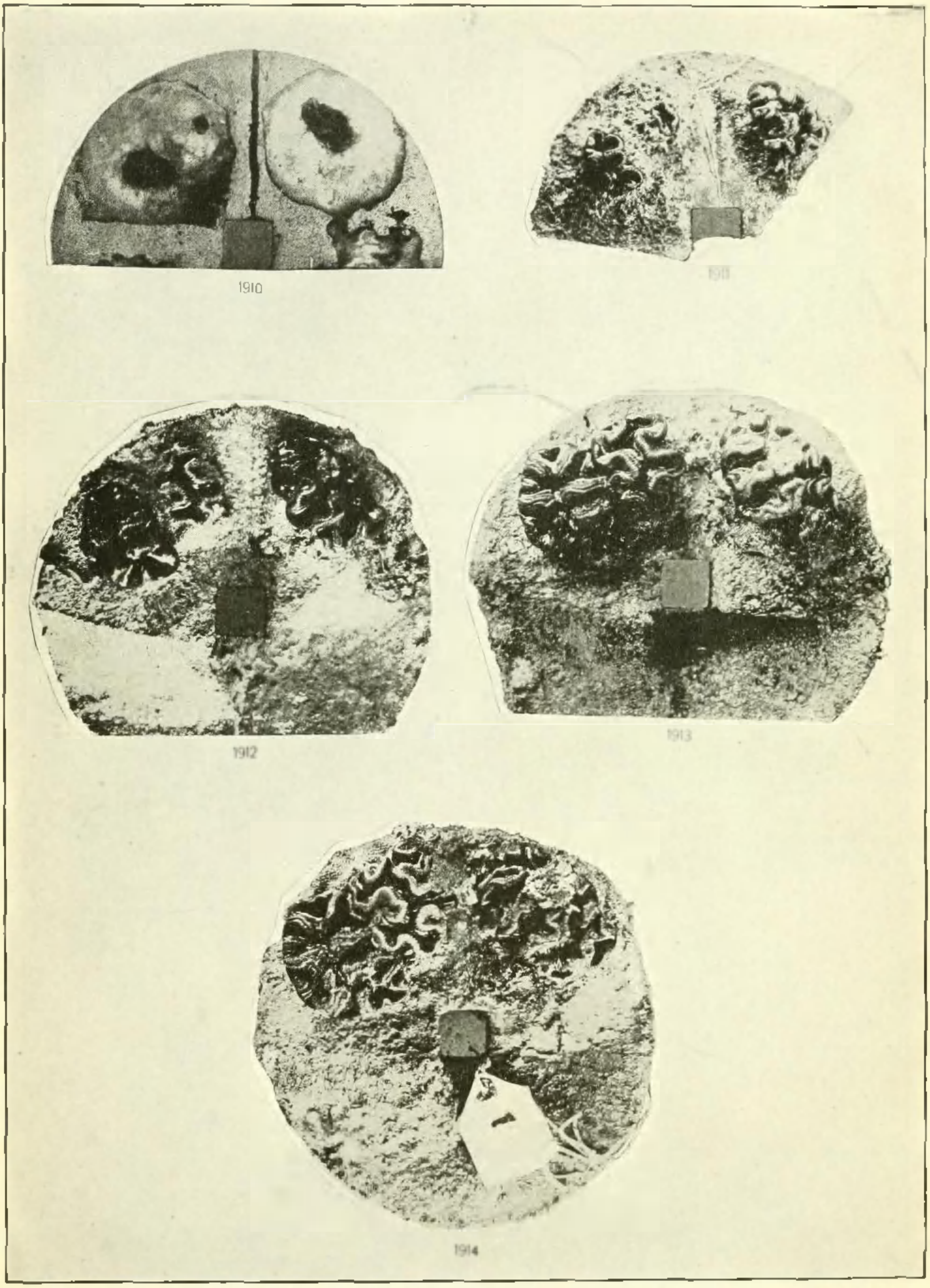


1911, 1 yr. old

PORITES ASTREOIDES

1914, 4 yrs. old

CORALS REARED FROM PLANULAE.



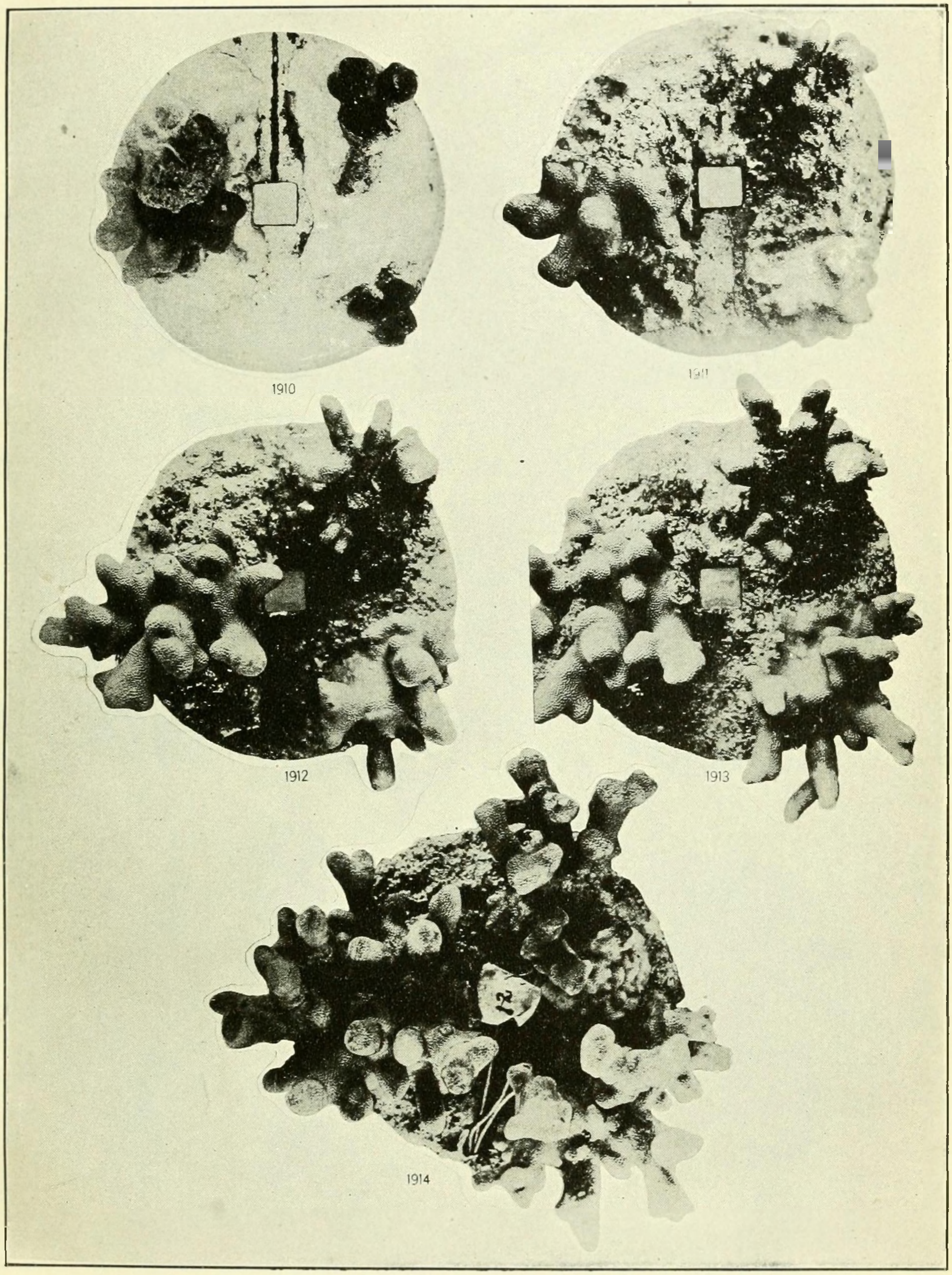
MAEANDRA AREOLATA (LINNAEUS), SHOWING GROWTH BETWEEN 1910 AND 1914.

Plate 22.

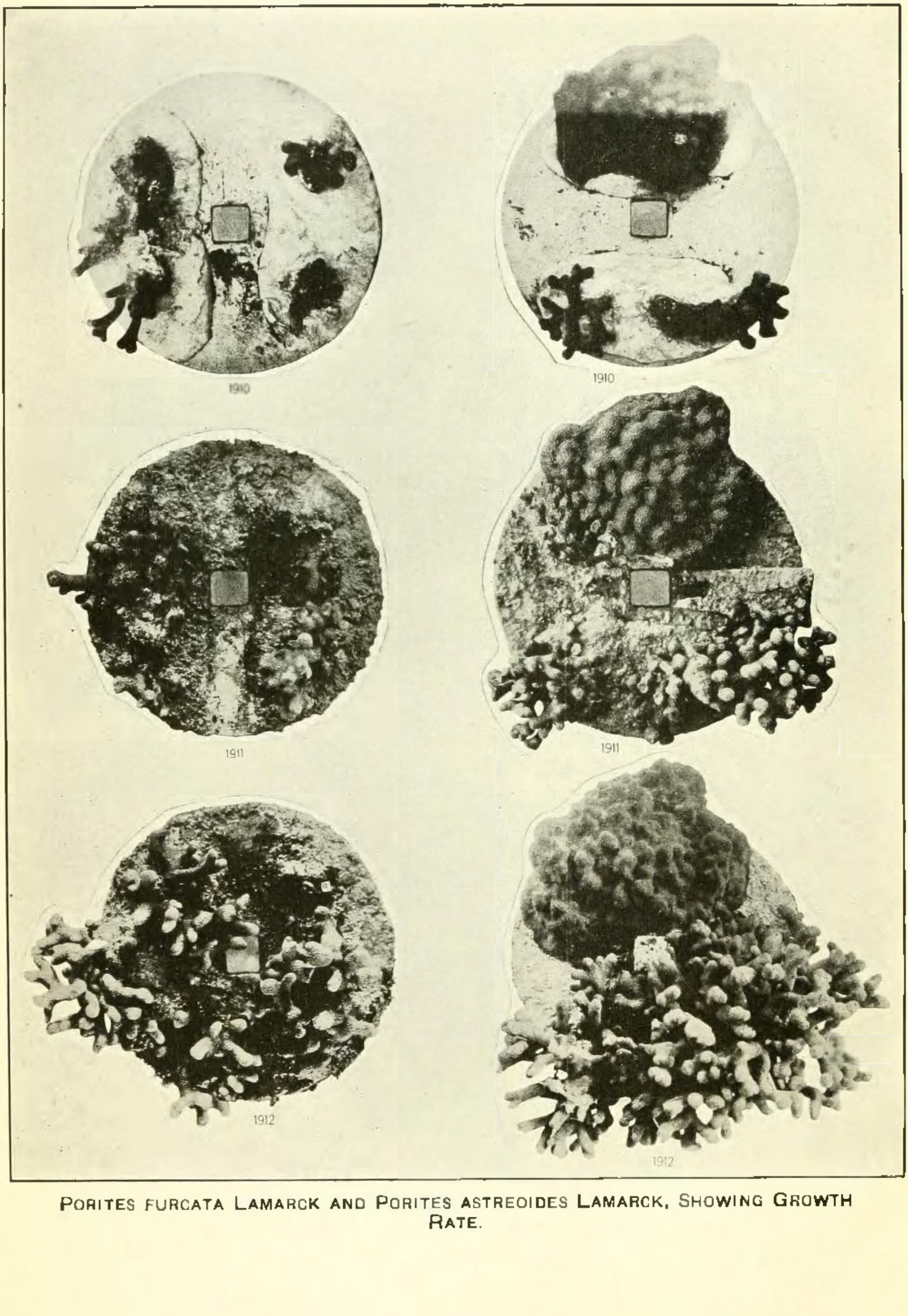
Growth rate of *Maeandra areolata* (Linnaeus) between 1910 and 1914. Diameter of the disc, 8 inches.

PLATE 23.

Growth rate of *Porites porites* (Pallas) between 1910 and 1914. Diameter of the disc, 8 inches.



PORITES PORITES (PALLAS), SHOWING GROWTH RATE BETWEEN 1910 AND 1914.



Porites furcata Lamarck and Porites astreoides Lamarck, Showing Growth Rate.

PLATE 24.

Growth rate of *Porites furcata* Lamarck, the tier on the left and the lower specimens on the disc of the tier on the right; and *Porites astreoides* Lamarck, the upper specimen of the right-hand tier. Diameter of the disc, 8 inches.

PLATE 25.

Growth rate of *Acropora muricata* (Linnaeus) between 1911 and 1914. Diameter of the disc, 8 inches.