A LITHOTHAMNION BANK AT BONAIRE (NETHERLANDS ANTILLES)

by

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"In the formation of future strata of the earth's crust..... Lithothamnion species.... become of essential importance." (F. R. KJELLMAN in "The Algae of the Arctic Sea", 1883, p. 96; slightly modified).

Survey of the literature

The part certain lime-secreting marine algae play in the building of coral reefs and in the formation of banks was discussed chiefly at the end of the last and in the beginnig of this century.

At that time it was already known that extensive parts of the sublittoral zone of the Arctic sea were covered by a luxuriant growth of *Lithothamnion* species. Kjellman states in 1883 (p. 96) that along the northern coast of Norway *Lithothamnion soriferum* "covers large spaces of the bottom in great masses", and that off the shores of Spitsbergen and Nova Zembla in 10 to 20 fathoms of water *Lithothamnion glaciale* "covers the bottom in deep layers for several miles, and altogether determines the general aspect of the vegetation wherever it occurs", whereas *Lithothamnion norvegicum* is said to form banks on the coasts of Iceland and of Greenland. Rosenvinge (1893, p. 772) reports that *Lithothamnion ungeri* forms banks on the coast of Iceland and of Greenland.

Foslie in his article on the Lithothamnia of the Maldives and Laccadives (1903, p. 462) records that "north of the Polar circle on the coast of Norway banks have been met with, which cover the bottom for several miles, and plants appear in immense masses frequently representing only one species" and "in the Trondhjem Fjord, rather large banks are to be found which may be composed of a solitary species such as *Lithothamnion norvegicum,* or other and that they in fact may be almost laid dry at lowest springs."

And Foslie adds (l. c. p. 463): "Further it may be remarked, that in several places along the Norwegian coast rather large quantities of dead Lithothamnia have been brought up by excavators in harbours, where living specimens are no more to be found."

In the south of Norway *Lithothamnion calcareum* becomes prominent and Gran (1893) already describes an association composed largely of this species occurring in Kristianiafjord.

Farther to the south, for instance on the west coast of Ireland, Foslie

(l. c. p. 463) states: "I have also seen great masses of partly dead, partly living, specimens."

From these quotations one could get the impression that banks formed by these lime-secreting red algae occur in the temperate and polar regions only. However, as early as 1894 it was already known that fossilized Lithothamnia are found in the subtropics in ancient limestones and that these algae are "rock-building organisms" (Seward, 1894). Seward quotes Walther who detected a tertiary "Nulliporen Kalk" near Syracuse. Many parts of that formation appeared to contain well-preserved specimens of Lithothamnion, whereas other parts were quite structureless. However all kinds of transitional stages could be observed. And the author adds that "a similar instance of structureless lime-stone is described from the Lias of Todten Gebirges".

And, in the tropics (West Indies) fossilized *Lithothamnion limestones* were already known in 1901. K. Martin, who visited Curaçao in 1888 detected in this island *Lithothamnion* limestones from the Cretaceous. He says (p. 162): "Auf der Insel Curaçao stehen unfern der Nordküste, bei Savonet, an Rudisten (Radiolites Lam.) reiche Kalksteine an. Diese enthalten aber neben einzelnen Korallen auch in grosser Zahl Lithothamnien, welche die Rudisten bisweilen geradezu ersetzen und stellenweise gesteinsbildend auftreten".

Moreover, Seward (l. c.) summarizes the results of J. Walther's studies of a Lithothamnion bank in the Bay of Naples about 30 m below the surface of the water. According to the opinion of Walther these banks are formed in this way that by action of the percolating water the Lithothamnion structure is gradually obliterated and the calcareous mass becomes a structureless limestone.

As far as I am aware, the first indication of the existence of flat banks with living Lithothamnium species in the tropics was given by Wyville Thomson in 1877, in writing of the dredges made by the "Challenger", in April 1873, on the Challenger Bank, southwest of the Bermudas. The author writes (p. 360): "The bank, which seems to be about five miles across, consists mainly of rounded pebbles, of the substance of the Bermudas 'Serpuline reef'." And in their report on the deep-sea deposits Murray and Renard (1891, p. 50—51) state "that the bank is covered with corals, *Serpula* and calcareous pebbles". And near Tahiti the "Challenger" came across a bank, which had probably been formed by a single species (Foslie, 1903, p. 461).

Dickie (1876) reports: "A calcareous alga in rounded masses forming the bottom in 10 fathoms off Great Island (Santa Cruz Major), Zambonga. The dredge came up filled with these masses."

Alex. Agassiz (1888a) found immense masses of nullipores covering the Pourtales Plateau off the southern coast of Florida in depths of from ninety to three hundred fathoms.

J. Stanley Gardiner, in 1898, in describing the reefs of Funafuti, Roturna and Fiji emphasized the very important part *Lithothamnion* species play in the formation of coral reefs. He states: "The reef (of

Funafuti) seems to have been mainly formed by the growth of nullipores, which are now building up masses outside the rim and adding them on the reef, causing its extension seawards." (p. 446).

And again, in 1903 Gardiner remarks (p. 462): "This Nullipore (*Lithophyllum craspedium*), Finckh — one of the members of the expedition to Funafuti atoll — says, is actually the reef-former at Onoatoa (Gilbert Islands). He saw no live corals here, but everywhere on the lagoon and ocean-face immense masses of this particular nullipore."

Gardiner's own notes on the distribution of calcareous algae on the banks he observed are cited by Foslie (1903) who examined the collection of Lithothamnia made during the expedition of Stanley Gardiner to the Maldives and Laccadives in 1899—1900. Foslie (p. 463) quotes the following: "Rounded nodules like marbles or eggs (*Lithophyllum reinboldi?*) are invariably from deep passages into the lagoons of atolls or interiors of banks. They lie together with similarly shaped masses of Polytrema and Polyzoa (each usually with a nucleus of dead coral). Presumably all these are rolled over and over with the currents".

Moreover, Foslie stresses the fact that this collection contains the first records of Lithothamnia ever made in the great area between the Red Sea and the East Indies.

Gardiner himself says (1903, p. 462): "While Lithothamnion is an important builder of submerged shoals in the tropics down to about 60 fathoms, Lithophyllum is the chief genus in the seaward growth of the reef edge". And he adds: "On the Brazilian coast too they are described as the chief consolidators of sand and builders of reef from 18° South to the fresh waters of the Amazone mouth". And again: "On Funafuti atoll there were numerous Halimeda clumps on the lagoon sand flat and parts of the surfaces of the lagoon shoals."

In the meanwhile, during the expedition of the "Siboga" in the Netherlands East Indian waters (1899—1900) extensive banks with living Lithothamnia were found in different parts of the archipelago, as was reported by Mrs. Weber—Van Bosse (1901, p. 126; 1904, p. 4): "Near the coast of Haingsisi, an island near the S.W. point of Timor, the Siboga anchored twice ......; the second time good luck favoured us, it was springtide, the water sank very low and we could observe that the whole reef ...... consisted chiefly of *Lithothamnion erubescens* f. *haingsisiana* Fosl. It was remarkable that the branching knolls remained quite dry during several hours of the day, exposed to the glare of the tropical sun, and that this seemed not to injure them ......

This Lithothamnion-bank struck me, because it is such an unique sight to see the ground, as far as the eye can reach, covered by the pretty beautifully pink coloured knolls, which are heaped up so close together that, while walking, one crushes them continually, making a peculiar noise as broken China. We encountered, however, other and perhaps more instructive Lithothamnion-banks during our voyage."

"Near the Key-islands such an enormous number of *Lithothamnion australe* f. *tualensis* Fosl. occurred that this again was to be named a Lithothamnion-bank."

In the West Indies J. Murray (1880) was the first scientist who mentioned the occurrence of Lithothamnion banks with certainty. In reporting the results of the "Challenger" expedition Murray stated that the calcareous seaweeds and their broken down fragments were dominant elements in three out of four analysed samples of the so-called "coral" sand or mud from Bermuda.

Bigelow (1095) in his studies on the shoal-water deposits of the Bermuda banks made a series of dredgings on the Challenger Bank, about 9 miles from Bermuda. Here a number of "calcareous pebbles" were dredged which proved to be a species of Lithothamnion. These were growing at a depth of 30.5 fathoms, a depth too great for most of the corals. (p. 587, 88): "These pebbles ranged from two to six inches in diameter. Neither sand nor mud was brought up by us; in fact, no deposits whatever except these calcareous masses. Such spherical nullipore masses occur very commonly in shoal water, either as concretions about some core, or as independent stalked growths, which eventually become detached and free to roll about. Such forms have been taken in great numbers off Eastport, Me., in a few feet of water, and also in many other localities where they are well within the sphere of wave action, and probably owe their spherical form to the fact that they are frequently rolled over and over."

This observation and various other data (cf. below) lead to the conclusion that the lime-secreting algae occur in greater depths than is the case with corals.

Howe (1912, p. 841) for instance states that lime-secreting seaweeds are much less dependent on high temperature and flourish in greater depths than corals.

Cotton in his Clare Island Survey (1912, pp. 70—72) says that between the outer islands of Clew Bay areas of *Lithothamnion calcareum* ("coral banks") are common. "They are found on a soft but firm bottom, consisting usually of stones and shells on sand, though occasionally Lithothamnion may be dredged where there is a thin layer of mud. The usual depth in which the banks occur is 1—5 fathoms." And of other Lithothamnion Banks in Ireland and Great Britain this author mentions that it was of interest to find that the Clew Bay association agreed exactly in its composition with that which had been described for Roundstone. The latter district is the original station for *Lithothamnion fasciculatum.*" And again: "In the British Islands a fine bed of *Lithothamnion calcareum* in 14 fathoms was once dredged off Fowey in Cornwall. Moreover, according to Cotton, *Lithothamnion calcareum* is also frequent in France. It is abundant in Normandy and in Brittany as far south as Croissic.

Mrs. Lemoine (1911) states that *Lithothamnion calcareum* is known from Denmark, Portugal, Naples, Morocco, and Algeria. As to the occurrence of banks she adds (p. 641): "Sur les côtes de France ...... les Lithothamniées ne constituent pas, à proprement parler des bancs, mais des sortes de gisements, et, en divers points, en particulier à Saint-Vaast, il semble que ces amas soient susceptibles d'une certaine mobilité sous l'influence des courants." And again: "Dans la Méditerranée, ces algues forment sur les rochers des revêtements plus développés que dans l'Océan Atlantique, constituant ce que l'on á appelé les trottoirs. On a signalé, de plus, dans le golfe de Naples, de véritables bancs sous-marins formés par diverses espèces de Lithothamniées et tout à fait comparables aux accumulations fossiles."

However, such a "trottoir" is not the same as a Lithothamnion bank as may be concluded too from the description (1937, p. 196 and plates 5—9) given by Feldmann. "Les algues calcaires ...... y constituent des massifs souvent très développés formant un encorbeillement le long de la côte et désignés sous le nom de "trottoir". A la surface supérieure du trottoir on rencontre souvent: *Lithophyllum incrustans* et *L.*(?) *notarisii*."

These trottoirs are comparable with the exposed outer edges of a reef which are most effective in protecting it against the force of the surf, as is also the case with the tube building annelids. As Gardiner (1903, p. 462) already pointed out, the seaward growth is forwarded especially by the genus Lithophyllum, since (Setchell 1928, p. 119) "both light conditions and water in motion exist here in most favorable intensities for the growth of both active and passive symbionts."

In the tropics we have to distinguish between Corallinaceae playing a very important rôle in the formation of "coral" reefs and those forming independent banks. Now Setchell, in a series of papers (1928—1930), well emphasized the significance of the "nullipores" in the cementation and consequently in the building of reefs, however, he did not mention the banks.

As far as I am aware, the occurrence of a Lithothamnion species in the Netherlands Antillean waters has only been mentioned once (Taylor, 1942). Numerous small specimens of *Lithothamnion occidentale* mixed with coarse sand were dredged from 48 meters off Aruba Island by the Allan Hancock Expedition in 1939.

Whereas so little is known about the formation of Lithothamnion banks the following account of a newly detected bank near the island of Bonaire in the Caribbean Sea may be of some interest.

The Lithothamnion Bank in front of Plaja Sourebon

Flying from Jamaica to Trinidad the Netherlands Antillean Leeward Islands Aruba, Curaçao and Bonaire respectively are to be seen.

They are wholly or partly (65—70 %) covered with carapaces of quaterny calcareous limestone encircling the older formation i. c. diabases, porphyrites, lavas and tuffs. The limestones sometimes show a seaward dip. The dipping carapaces of Aruba are for the greater part eroded away by subaerial erosion. Curaçao and Bonaire have relatively more left. In the following islandgroups, belonging to Venezuela — Las Aves and Los Roques — the carapaces are still lying below sea level and are still growing.

As to the island of Bonaire (fig. 1), at the southeast side of the island a very large shallow lagoon (4 × 3 km) occurs, called "*Lac*" (fig. 2). This lagoon is bordered by a dense mangrove forest with a surface of about 1,5 sq. km, especially developed in the northern and northwestern part. This is probably the largest mangrove forest of the Leeward Islands.

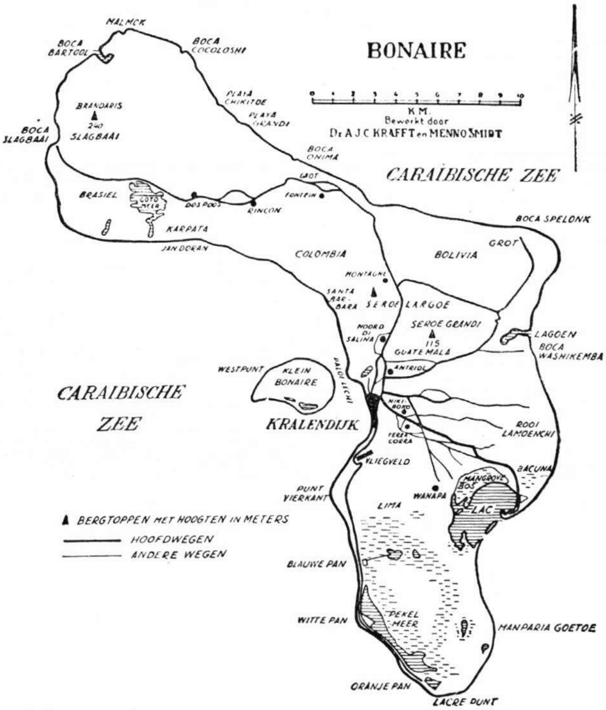

Fig. 1. The Island of Bonaire, Netherlands Antilles, with the lagoon of Lac.

Fig. 2. Aerial view of Lac.

It mainly consists of *Rhizophora mangle* and to a lesser degree of *Avicennia nitida*.

The vegetation in the northern part of the lagoon consists principally of sea grass (*Thalassium testudinum, Cymodocea manatorum*). Apparently this habitat offers unique shelters for *Strombus gigas*, which is the main topic for the fishermen there. In the other parts of the lagoon scattered patches occur of *Halimeda tridens, Padina vickersiae, Dictyota dichotoma, Dictyota ciliolata, Hypnea musciformis* and, near the entrance *Halimeda opuntia*. Gigantic heaps of the empty shells of the above mentioned gasteropod are to be found along the northern entrance to the bay.

Moreover, a number of sea turtles (mainly *Chelone mydas* and *Eretmochelys imbricata*) are captured in Lac in specially constructed nets.

The water in the lagoon is constantly renewed by the movements of the tides. It may freely enter over a broad interrupted bar, running NE—SW, mainly consisting of coral debris which has been thrown up in the entrance by waves and wind and cemented together by crustaceous algae. The northern part of this bar has an altitude of about 3 meters above sea level and is separated from the lower southern part by a channel of 8 m depth, through which fisherboats may enter the bay.

By the action of the rather heavy surf and other influences (solution?) the coral fragments just after the bar gradually become obliterated, and the mass has changed into a structureless, very hard limestone, thus forming a flat bank or plateau (figs. 3, 4). I hardly dare to use the term "solution", as Mayor (1924, p. 28) already remarks that "the solution of calcium carbonate in tropical sea water is so slight as to be negligible, but the question remained open as to whether in regions of shallow flats, where the seawater is often diluted by rains or by streams, limestones might not be dissolved."

This limestone plateau not only occurs in the entrance to the bay, but it extends half a kilometer north and northwestward. Therefore it is mainly situated in the more quiet southern part of the lagoon.

At the western side of the lagoon a 6 m broad and 1 km long beach of chalksand is formed, named "Plaja Sourebon". Walking along the floodline of this beach (April 17th, 1955), I came across an innumerable large number of warty balls which proved to be Lithothamnion knolls. As they were cast ashore I looked for more specimens in the seawater in front of the beach. At this place where the lagoon is from 30 to 60 cm deep, the whole bottom appears to be covered by these globulous and more or less sausage-shaped calcareous red to pink coloured seaweeds. It was impossible to do a step forward without cracking some of the warty balls.

All specimens collected appeared to belong to the same species, most probably being *Lithothamnion erubescens* Foslie (cf. Weber—Van Bosse and Foslie, 1904, p. 31, pl. 3).[1]) The globulous ones being 2—7 cm in

[1]) Professor Wm. R. Taylor, Ann. Arbor, Mich., U.S.A., was so kind to identify some of the Sourebon specimens. His preliminary conclusion without having made microtome sections, is: "I would consider that your alga is probably *Goniolithon spectabile* Foslie, so far as one can tell by superficies. It also has some resemblance to *Lithothamnium invertum* Foslie, similar to *L. erubescens*."

diameter, showing more or less compressed coralloid protuberances well developed at one side, whereas the opposite side often shows a more or les flat spot with a much paler colour. While several balls were not at all attached to the bottom, other ones appeared to be situated on a kind of stalk.

Some ecologicol notes

Very little is known about the different factors which influence the growth of aegagropilous specimens of Lithothamnion and the formation of banks.

As the banks are found all over the world the genus Lithothamnion

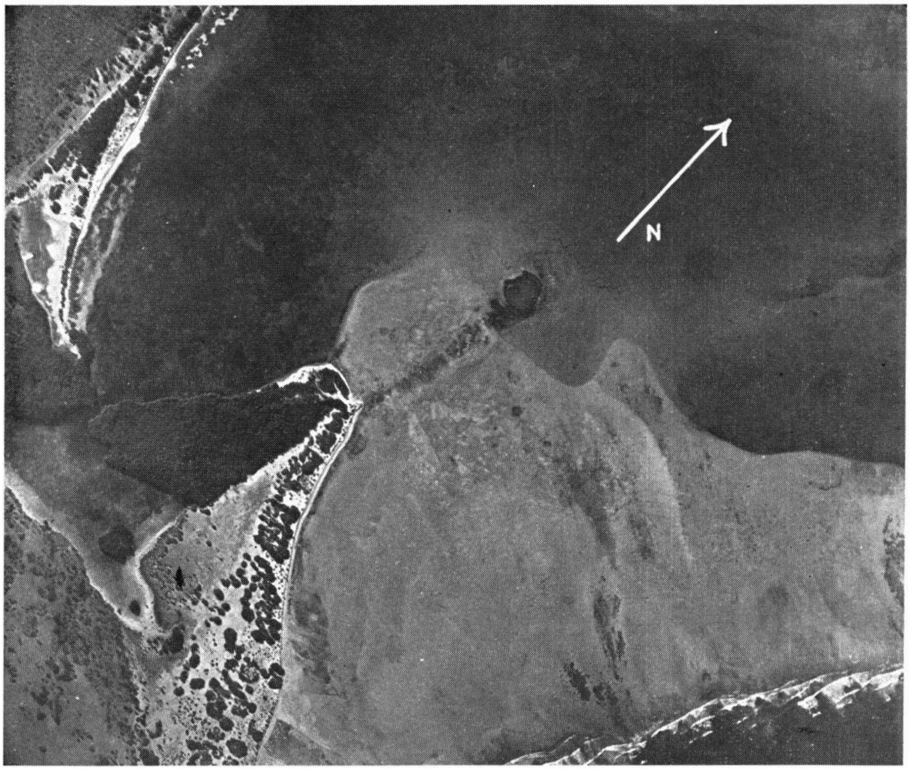

Fig. 3. Aerial view of the Lithothamnion bank in front of Plaja Sourebon.

has wide ranges of tolerance for the various external circumstances. This was already remarked by Foslie (1903, p. 461), stating that: "These algae in general are not dependent on physical or chemical conditions, apart from requiring, like other algae, at least a fairly hard bottom, and besides as a rule a partly exposed habitat over which the tides are running more or les rapidly."

At Sourebon too both a **h a r d b o t t o m** and **r u n n i n g s e a - w a t e r** are present and that is why the knolls become irregularly spherically shaped; due to the tidal currents they are rolled to and fro the hard limestone bank.

Though the tidal amplitude at Sourebon is very small, only 30—50 cm,

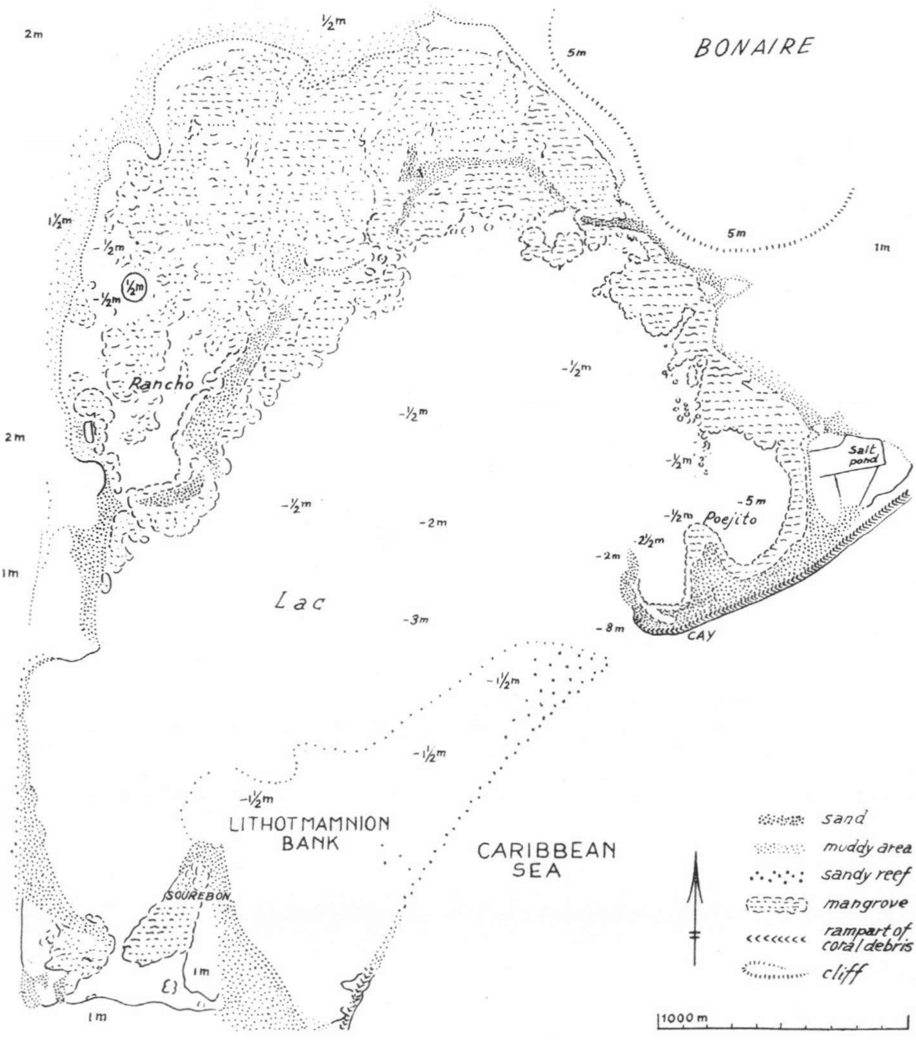

Fig. 4. Lithothamnion bank in front of Sourebon.

the tidal currents in Lac are fairly strong, so strong that it is hardly possible to enter the lagoon with a boat except at neaptide.

The small tidal amplitude and the shallowness of the bank suggest the possibility that the Sourebon bank may become dry at a very low springtide, as was observed by Mrs. Weber—Van Bosse at the Haingsisi bank near Timor (1901, pl. 18—19).

Indeed, the occurrences of the Lithothamnion balls is principally governed by the structure of the bottom and the fastness of the tidal currents, whereas the other environmental relations as will be seen below, are practically unknown.

The vertical distribution of live species of Lithothamnion is governed as is the case in all plants, by the quantity and quality of the light that is received. This was already remarked by Gardiner in discussing the building up by the algae of the "coral"island Funafuti (1898, p. 501): "The chief building organism is Lithothamnion, the bathymetrical zone of which must be limited to a lage degree by the extent to which light can penetrate seawater". And Setchell, pointing out that coral reefs are biological formations, controlled and moulded into zonal form by its plant symbionts, states (1928, p. 120): "The light conditions in clear tropical waters allow red algae of the Nullipore type to flourish down to two thousand feet or below." From the review of the literature in the first part of the present paper, the exactness of these considerations with regard to the distribution of the species of Lithothamnion may be seen. Whereas, according to Vaughan (1911), the greatest depth at which the reef-building corals work effectively amounts 25 fathoms, and only occasionally 40 fathoms, the nullipores are found in a living condition at depths of from 250 to 350 fathoms (Agassiz, 1888a). However, for the occurrence of the aegagropilous Lithothamnion species a rather strong tidal current is necessary at such depths at the same time. As to the depth to which the action of waves extends Admiral Wharton (1897) says that this may be indicated by the change of slope generally taking place off shore below a depth of eighty to one hundred fathoms; and, further, that the existence of banks in the open sea at a depth of from thirty to forty fathoms may show the limit of depth to which oceanic waves may cut down a land mass on which they act.

With regard to the temperature the Lithothamnion species endure a wide variation in temperature. They are, locally at least, abundant between 90°56′ north latitude (Kjellman, 1883) and 73°30′ south latitude (Foslie, 1907; cf. also Skottsberg, 1941).

The specimens of *Lithothamnion erubescens* collected at Sourebon are mostly free and only now and then attached to the bottom.

The less warty underside of some of the specimens may be an indication that this side was attached to one of the various objects that lie scattered over the bank, and that a specimen starts growth as a crust. Occasionally stalked specimens are sometimes formed, and if the encrusting bases of a number of specimens cover some parts of a limestone ledge rising from the bottom, a row of stalked warty balls develop. Later on these holds may become detached and the warty knolls are set free. Then the specimens are regularly turned by the currents and consequently a more or less spherical form results. However, at last they can no longer be moved, being too heavy and too much provided with outstanding warts. Then the cementing process gets a chance, for lying motionless side by side they are cemented together by the activity of the encrusting algae. In this way a solid lime-

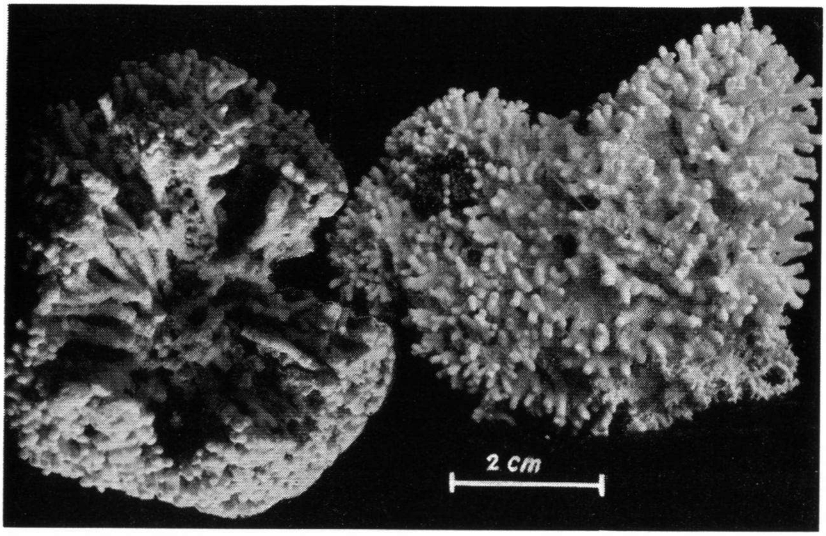

Fig. 5. *Goniolithon spectabile* Foslie. Bonaire, Lac, Plaja Sourebon Specimen washed ashore. Leg. J. S. Zaneveld, 17-4-1955.

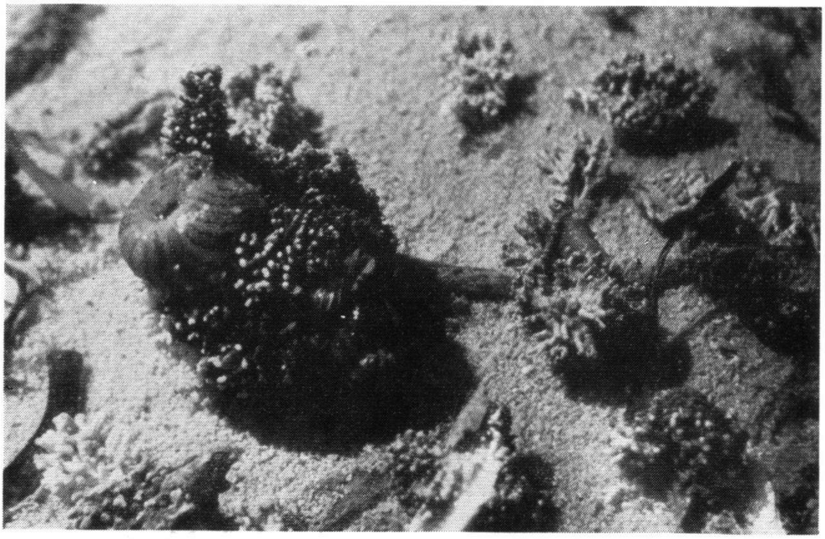

Fig. 6. *Lithothamnion erubescens* Foslie. An old specimen with a sea-anemone.

stone may be formed in a proportionally short time. Several kinds of lime-boring algae, molluscs, etc. may attack the older construction and the holes thus shaped are filled with percolating water, consequently converting these parts in a structureless mass.

In this way Bigelow (1905) explained the formation of the Challenger Bank near the Bermudas and rather thick layers may be built in this manner as is learned from the borings at Funafuti atoll. The main boring in that atoll was driven to a depth of 1114½ feet and the cores studied by Hinde (cf. Bonney, 1904, p. 186) showed that "Nullipores" were more or less abundant, whereas Halimeda was only locally abundant from 28 to 1096 feet.

Very little is known about the r a t e o f g r o w t h of coral species, however, nearly nothing is known about that of Lithothamnion species and about the factors by which their growth is stimulated. Howe remarks (1912, p. 842) that at least certain species of Lithothamnion must grow faster than certain coral species do, as they often cover living corals. And Finckh (1904) observed in Funafuti a vertical growth of a cluster of the calcareous chlorophyte Halimeda, which in six weeks attained a height and thickness of three inches, however, it was growing through a hole in a board.

In the barrier reef of Tahiti, Setchell (1929, p. 281) noted "the increase of the curved edge of the pavement nullipore association as somewhere between one-third and one-fifth mm per year. A 50 meter pavement of living nullipore, such as exists there, if the growth has been uniform and at a recurved edge, would have taken 150.000 to 250.000 years. Horizontally the nullipore expands at about the rate of 2 inches (see Funafuti Report p. 81) or about 5 cm per year." According to all these figures the growth-rate of Lithothamnion species may perhaps be much faster than any thus far measured in corals.

That coralline algae are capable of building limestones of great thickness especially *outside* the belt of vigorous coral growth as Bigelow (1905, p. 591) suggests is in contradistinction to the cretaceous limestones found in the tropics in between the real coral girdle, i. a. in the West Indies at Curaçao (Martin, 1901) and in the East Indies at Java (Martin, 1911).

These observations and the newly detected bank at Bonaire once again indicate that the Lithothamnion species play a very important part in the formation of the appearance of the earth's crust.

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