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THE TAXONOMY AND DISTRIBUTION OF THE MELOESIOID
ALGAE FOUND ON RONGELAP ATOLL, MARSHALL
ISLANDS

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INTRODUCTION

Atoll research has gained attention during the last decade or so, stimulated by World War II events and the activities in the Pacific Proving Grounds. Many hypotheses--some mere speculations--have been proposed in attempts to formulate explanations of atoll phenomena. A limiting factor to the resolving of atoll problems appears to be the lack or narrow disciplinary limits of the factual information available to, or used by, those workers formulating the hypotheses. The information must necessarily include not only oceanographic, physical and geological aspects, but the biological phenomenon as well, for atoll-reefs in the Pacific and Indian Oceans are biogenic. However in the attempt to interpret atoll phenomena, a study of the literature indicates that very little, if any, empirical biological data have been utilized. Certainly this is due, in part, to the limited amount of information on the roles of organisms in atoll structure and development. Especially limited is information on the coralline algae. These algae provide not only much of the skeletal foundation for reef development but also may provide much of the detrital material which affects the physiographic character of an atoll.

The lack of information available on the coralline algae is, in the writer's opinion, a major interposing factor in atoll research. The gathering of information on the coralline algae is, thus, considered to be of major importance, yet their taxonomy is, at best, only poorly known. This fundamental lack hampers and possibly discourages morphological, physiological and ecological studies on the corallines, for in all phases of botanical science recognition of the specific entities of the pertinent

flora is essential.

This study was conducted with the purpose of contributing to the taxonomic and distributional knowledge on the reef-building coralline algae, namely, the members of the Melobesioideae. This red algal sub-family of the family Corallinaceae, order Cryptonemiales, seems to include all the algae that have a direct role in atoll formation.

Because it seemed best to confine the study to a definite locale, I chose Rongelap Atoll, Marshall Islands, where I had the opportunity of spending the month of August, 1959, making extensive algal collections. There is little published on the algae of Rongelap. Taylor's "Plants of Bikini and Other Northern Marshall Islands" (1950) is the only available taxonomic reference for the reef-building algae. To my knowledge there is as yet no publication that deals more than incidentally with the distribution or the ecology of the coralline algae anywhere.

Rongelap Atoll (Fig. 1), which is located 11 degrees, 20 minutes North and 166 degrees, 50 minutes East, can be roughly sectored into eastern, western, northern and southern sections. The sides facing north and east and the sides facing south and west are, respectively, the windward and leeward areas of the atoll. The reef is interrupted by nine channels, seven of which are located at the southern and eastern rims. The broadest part of the atoll (up to 1200 m) is along the northern rim and the narrowest (ca. 300 m) is along the southern rim. Most of the islets are on the southern and eastern reef flats.

The reef flat is covered by one or a very few meter of water at high tide. At low tide, the reef flat is exposed for the most part and there is little movement of water over the reef. Especially conspicuous at low

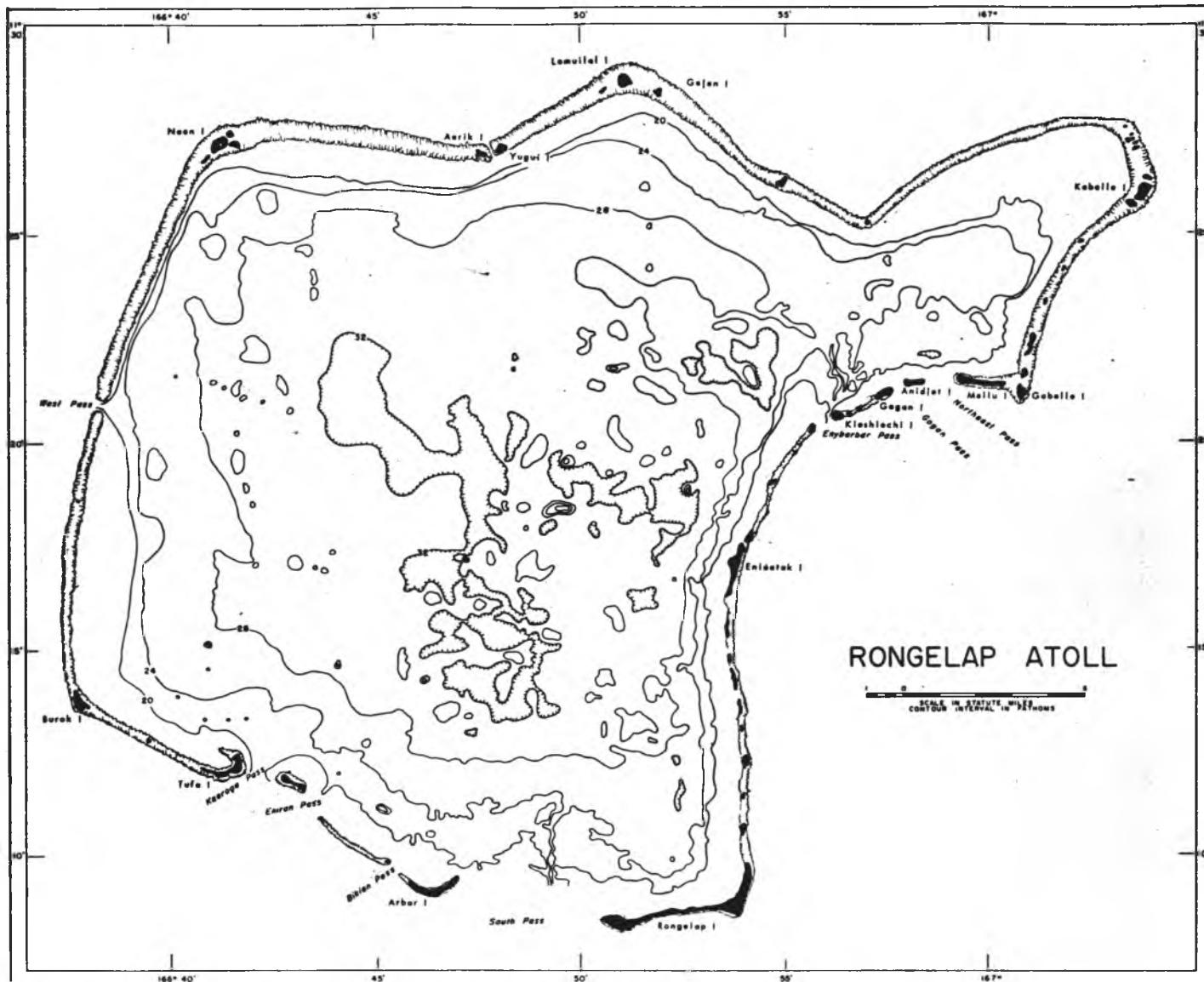


FIG. 1. Outline map of Rongelap Atoll provided through the courtesy of the University of Washington, Laboratory of Radiation Biology, Seattle, Washington.

tide is the melobesioid algal growth that forms a ridge along the windward reef seaward edges. On the seaward margins of a leeward reef a ridge is not apparent. The melobesiods found on the reef flat, especially those growing along the seaward margins, are the organisms believed to play the dominant role in atoll development and morphology.

Only two genera of reef-building corallines, Porolithon and Neogonio-
lithon, were found on Rongelap. Other atolls, as discussed below, also seem to have only species of these two genera on their reef flats. Indeed other coralline algae are found upon occasion but, like the coelenterate corals, play a minor role. Although this paper includes information pertinent to the Malobesioideae in general, it concerns mainly these two genera.

MICROTECHNIQUE

The structure of a coralline alga is such that diagnostic characteristics are often microscopic anatomical details. Thus, microtechnique procedures are required.

For taxonomic studies, dried material is found to be adequate. The principle problems concern finding and recognizing the tetrasporangial conceptacles, since their character is used in separating the genera into groups (Tribes). However, non-fixed specimens kept dry for eight years have tetrasporangial conceptacles in which the zonate tetraspores are still distinguishable.

For histological studies, a portion of the living specimen to be sectioned is killed and fixed in a solution of 10% formalin in seawater. Acidified killing and fixing solutions are not used because the cell structure tends to deteriorate in such solutions.

The dried or fixed material is decalcified in a 10% hydrochloric acid in seawater solution. The length of acid treatment depends on the size of the material to be sectioned. The acid-seawater solution is replaced with fresh solution at 24-hour intervals until carbon dioxide bubbles are no longer emitted from the specimen.

After decalcification is completed, the material is run through a graded series of ethyl and tertiary butyl alcohol changes for dehydration. The specimens are imbedded in paraffin and microtomed into serial sections 7-10 microns thick. The sections are mounted and stained, using tannic acid as a mordant, in ferric chloride and safranin-O. This staining technique is found to be superior to other techniques for coralline algal

material, because of its simplicity and the clarity with which the diagnostic characteristics are displayed in the microsections.

A HISTORY OF THE DEVELOPMENT OF PRESENT DAY
KNOWLEDGE OF THE MELOBESIOIDEAE

As with many other limestone-secreting algae, the first described members of the Melobesioidae were thought to be animals and were classified as such. They were often referred to as zoophytes or lithophytes (e.g., Pallas, 1766; Linnaeus, 1767; Ellis & Solander, 1786; and Lamouroux, 1812) and were included in various genera, such as Millepora, Melobesia, Cellepora, Coralium and Gleba. Among these, the epithet Melobesia, authored and described as a zoophyte by Lamouroux (1812: 186), is the only melobesioid generic epithet retained in its original application.

It was Gunnerus (1768: 21) who recognized a group of coralline "animals" as being distinct from other "polypers" by the absence of pores, and established the genus Apora. Later, Lamarck (1801: 374) erected the genus Nullipora to include those forms with "aucuns pores apparens." According to Foslie (1895: 152), Apora and Nullipora are both to be included in the circumscription of a group of algae for which there has come to be used a later name, Lithothamnium. Foslie saw no reason to change the name of the genus Lithothamnium, and the present author agrees, for as Foslie said (1898c: 7) of Lithothamnium, it ". . . has been accepted and applied for about 60 years."

The epithets Lithothamnium and Lithophyllum were created by Philippi (1837: 387) in a paper titled "Beweis, dass die Nulliporen Planzen sind." From the literature, it appears that this is the first publication stating definitely that the organisms in question should be removed from the zoological concept. The separation of the two groups of coralline algae,

Lithothamnium and Lithophyllum, was based on gross external morphology. Lithothamnium was characterized by a crustose thallus with cylindrical or compressed branches, and Lithophyllum was characterized by a flat foliose thallus.

Following Philippi's work, other genera were described by various authors, many of whom proposed schemes of classification. These are reviewed by Printz (1929) and Ishijima (1954) among others. The genera were separated according to gross external characteristics just as Lithothamnium and Lithophyllum were first distinguished. One of the schemes of classification was the following, proposed by Areschoug (1852: 508 & 509), and it is outlined here by naming the systematic units as he arranged them from order to genus.

Order Corallinaceae

Tribe Malobesiace

Hapalidium
Malobesia
Subgenus Lithophyllum
Lithothamnion (sic)
Mastophora

Tribe Corallinace (verae)

Amphiroa
Cheilosporum
Arthrocardia
Jania
Corallina

Except for some minor changes in rank, this organizational scheme is utilized today by most algologists.

Two of the early workers who made detailed anatomical studies on members of the Corallinaceae were Rosanoff (1866) and Solms-Laubach (1881). The former is credited by Suneson (1937: 88 & 89) and Kylin (1956: 202)

with having provided the foundation of our anatomical knowledge of the melobesioids. Solms-Laubach (1881: 50-64, Pls. 1-3) probably contributed the most in making manifest the reproductive characteristics of the group. He was probably the first to recognize, and interpret correctly, the three kinds of conceptacles one may find in a red coralline thallus, tetrasporic, carpogonial or spermatangial.

Subsequently, the anatomical and reproductive characteristics of the corallines came to be better known and were utilized (see e.g., Hauck, 1885: 259-281) in describing the family and the species. This knowledge was merely added onto the list of characteristics of the different species without being used as systematic criteria.

Rothpletz (1891: 310), after studying both living and fossil specimens, distinguished three groups according to the formation of the tetrasporic organs. For the first two groups he used the generic epithets Archaeolithothamnium and Lithothamnium; both were characterized as having spores developing singly and not contained in conceptacles. Archaeolithothamnium was distinguished from Lithothamnium by the lack of protuberant sori. Rothpletz misinterpreted spore formation of his Lithothamnium group, as being non-conceptacular, for the spores, while produced singly, are in conceptacles. The third group, for which the generic epithet, Lithothamniscum, was proposed, was characterized as having spores produced in groups with each group in a conceptacle.

Archaeolithothamnium is an accepted genus today. Most of its members are fossils and are found in deposits beginning with the Lower Cretaceous. Lithothamnium and Lithothamniscum correspond, respectively, to Lithothamnium Philippi and Lithophyllum Philippi. The former is found in deposits

beginning with the Cretaceous and the latter in deposits beginning in the Eocene; both are well represented in the present day flora. Actually, Rothpletz laid the groundwork upon which phylogenetic relationships between the generic groups could be established. These relationships are discussed below.

After Rothpletz came Michael Foslie and Franz Heydrich, contemporaries, who intermittently published systems of classification which differed not only from each other's, but also from their own previous systems.

Heydrich (1897b) began with a system based on the vegetative character; however, he established (1897b: 66) a new genus, Sporolithon, based on the development of the sporangia. Later, he published (1897c) a classification scheme which laid emphasis on sporangial development. Finally, he proposed (1900) a system which utilized development of the cystocarps as a basis.

Foslie (1895), at first, used essentially gross morphological characteristics as a basis for classification. Later, he proposed (1898a, 1898b) a system based on sporangial and conceptacular development, which he revised (1900c) with a detailed consideration of the cystocarp. Finally, Foslie gradually revised (1904, 1905, 1909) his system with a consideration of both vegetative and reproductive characteristics.

Much of our classification today is dominated by the works of Foslie and Heydrich. Foslie, especially, named and described many species and established a number of genera.

Lemoine (1911) made extensive studies on the vegetative anatomy of the melobesioids, and this information has been found useful by the paleontologists in identifying their fossilized forms. The results of her detailed anatomical treatments of the various species provided a precis

of what is believed necessary today in circumscribing melobesicoid species. Publications by Lemoine represent almost a half-century of taxonomic study on, especially, the European melobesicoids; her most recent paper was published in 1952.

Suneson (1937, 1943) has contributed much to our knowledge concerning the nature of the pre- and post-fertilization stages of reproduction.

GENERAL CHARACTERISTICS OF THE MELOBESIOIDEAE

The members of the Corallinaceae have a pseudoparenchymatous thallus, which, except for some parasitic forms, is strongly calcified. The calcification may be localised or it may occur throughout the thallus. In the former case the thallus is an erect branched system with uncalcified flexible joints; these are not of concern to this thesis. The latter condition, which is characteristic of the subfamily Melobesioideae, is expressed in various shapes and forms. Such thalli may be composed, for the most part, of prostrate filaments forming a thin crust 1-2 cells thick, or they may be composed of prostrate filaments (hypothallar portion) that are erect in their distal (perithallar) portions forming structures that are thick and solid bearing simple excrescences or structures that are elaborately branched.

The life cycle of this family is hypothetical, but if a life cycle similar to other Cryptonemiales can be assumed, then an alternation of isomorphic generations would be the situation here. On this assumption a thallus is either of the asexual (diploid) generation or of the sexual (haploid) generation. Asexual thalli develop sporangia, which after meiosis should produce tetraspores. These tetraspores should then give rise to sexual thalli. Such thalli bear spermatangia and carpogonia.

The reproductive organs characteristically are in conceptacles that either are sunken into the thallus or protrude from it. The tetraspores are transversely divided (zonate) and, depending on the genus, are released through a common pore or through several pores in the roof of the conceptacle. The sexual conceptacles have only one pore. The

spermatangia are produced on short filaments that may arise only from the bottom or from the entire inner surface of a conceptacle. Whole spermatangia are released. The carpogonial branches usually develop only on the central part of the conceptacle floor and are basically three-celled. The lowermost cell is the auxiliary cell. The uppermost cell is the carpogonium, the trichogyne of which may come to protrude through the ostiole. An auxiliary cell may subtend two carpogonial systems, but usually in such cases one carpogonium is abortive.

After fertilization, the carpogonium fuses with the auxiliary cell by a short connecting filament. The other auxiliary cells in the conceptacle then become fused, perhaps first by connecting filaments, to one another and soon form a single multinucleate fusion-cell. Gomimoblast initials develop from the upper surface of the fusion-cell, commonly from near its margins, and carposporangia form terminally.

**REMARKS ON SYSTEMATICS AND A CHECKLIST
OF THE MELOBESIOID GENERA**

With the scant information available it would appear presumptuous to attempt to formulate a natural system of classification. The usually recognized genera are arranged below in what are believed to be natural groups depicting phylogenetic relationships. This arrangement is offered with the understanding that as data on the structure, life history and ecology of these organisms become better known, the true relationships will become more apparent. It is expected that succeeding systems could well be improvements over the one presented here. Needless to say, we can only progress as pertinent information becomes available.

The presence or absence of conceptacles and the number of pores in the roof of the tetrasporic conceptacles have been recognized as being useful diagnostic tools. For example, Satchell (1943: 134) divided the Corallinaceae into five subfamilies, three of which were distinguished according to features of the tetrasporangial conceptacles. Mason (1953: 316 & 333) treating only the melobesiod corallines (except for the Archaeolithothamnium-forms which she did not consider) distinguished among them two tribes: Lithothamniace, the members of which have conceptacles opening by more than one pore, and Lithophylleae, the members of which have conceptacles opening by only one pore.

Kylin (1956: 200ff) in his key separated three groups of melobesiod genera: a Sporolithon group (= the Archaeolithothamnium-group below), whose members were characterized by the absence of tetrasporangial conceptacles; a Lithothamnium group, whose members were characterized by tetrasporangial conceptacles having more than one pore; and a Lithophyllum

group, the members of which were characterized by having tetrasporangial conceptacles opening by a single pore.

To demonstrate the plausibility that the generic groupings as outlined by Kylin are "natural," I consider in the schema below what I believe to be the ontogeny of the development of the tetrasporangium in each group.

The Archaeolithothamnium-group:

The tetraspore initials are produced singly and are more or less aggregated in sori. No tetrasporangial conceptacles are formed. The imbedded tetrasporangium subtends the uppermost cell or cells of the tetrasporangial filament. These cells disintegrate later leaving an opening through which the spores are released.

One genus:

Archaeolithothamnium Rothpletz, 1891: 310 (= Sporolithon Heydrich, 1897b: 66).

The Lithothamnium-group:

The tetraspore initials are imbedded in the thallus. They develop singly but are closely aggregated in sori that become conceptacular in nature late in their ontogeny. The conceptacle is a result of the breakdown of the vegetative cells that lie between the sporangia. The upper cells of the intervening vegetative filaments do not disintegrate, but instead form the roof of the conceptacle. The numerous pores in the conceptacle roof each represent the residual area of the uppermost cell or cells of a tetrasporangial filament.

The genera:

Lithothamnium Philippi, 1837: 387 (= ? Clathromorphum Foslie, 1898a: 4).

Melobesia Lamouroux, 1812: 186.

Mesophyllum Lemoine, 1928: 251.

Chaetolithon Foslie, 1898b: 7.

Phymatolithon Foslie, 1898a: 4.

Polyporolithon Mason, 1953: 316.

The Lithophyllum-group:

The tetraspore initials develop early and are superficial on the thallus. They develop in groups without intervening vegetative filaments. All the cells of a potential sporangial group enlarge to a certain stage when most of them abort; these cells are homologous to the vegetative filaments found within the sori proper of the Lithothamnium-group. The uppermost cells of the abortive sporangial filaments become hair-like and drawn out, producing an upended funnel-like effect. The conceptacle appears to be the result of the formation of the sporangia in a group. The surrounding vegetative cells continue to divide and enlarge, and the resulting tissue completely encloses the sporangia except for the region occupied by the above mentioned hair-like cells. The result is a single-pored conceptacle.

The genera:

Porolithon Foslie, 1909: 57.

Dermatolithon Foslie, 1898b: 11 (= ? Goniolithon Foslie, 1898a: 5, partim).

Lithophyllum Philippi, 1837: 387.

Neogoniolithon Satchell & Mason, 1943: 89 (= Goniolithon Foslie, 1901: 14; Goniolithon Foslie, 1898a: 5, partim).

Hydrolithon Foslie, 1909: 55.

Fosliella Howe, 1920: 587.

Heteroderma Foslie, 1909: 56.

Choreonema Schmitz, 1889: 21.

Schmitziella Bornet & Batters, in Batters, 1892: 186.

Crodelia Haydrich, 1911: 12 (= ? Pseudolithophyllum Lemoine, 1913: 45).

Tenarea Bory, 1832: 207.

Metamastophora Satchell, 1943: 130.

Mastophora Decaisne, 1842: 359.

Litholenis Foslie, 1905: 5.

Lithoporella Foslie, 1909: 58.

On this basis, together with some consideration of their geological histories discussed above, a monophyletic origin, with the Archaeolithothamnium-group representing the most primitive condition and the Lithophyllum-group representing the most advanced or specialized condition, seems to be indicated.

**DIAGNOSTIC KEY TO THE GENERA NEOGONIOLITHON
AND POROLITHON**

Only two genera, Neogoniolithon and Porolithon, are distinguished in the collections made at Rongelap. Hence, the following key has been formulated to distinguish these genera from other members of the Corallinaceae and to separate them from one another.

1. Calcification localized; thallus an erect branched system with non-calcified flexible joints (subfamily Corallinoidae Mason, 1953) (not treated here)

1. Calcification continuous; thallus crustose, or if branched, without non-calcified joints (subfamily Malobascioidae Mason, 1953) 2

 2. Tetrasporangia occurring in indefinite sori that are not conceptacular in nature (the Archaeolithothamnium-group)
 (not treated here)

 2. Tetrasporangia occurring in conceptacles 3

3. Tetrasporangial conceptacles with more than one pore (the Lithothamnium-group) (not treated here)

3. Tetrasporangial conceptacles with only one pore (the Lithophyllum-group) 4

 4. Thallus with megacells, polystromatic throughout 5

 4. Thallus without megacells, polystromatic; or, if megacells present, thallus mainly monostromatic . . (not treated here)

5. Megacells occurring singly or in vertical rows
 Naegoniolithon

5. Megacells in horizontal lenticular groups Porolithon

TAXONOMY

Neogoniolithon Setchell & Mason, Proc. Nat. Acad. Sci. 29: 89, 1943.

Goniolithon Foslie, Kgl. Norske Vidensk. Selsk. Skr. 1900, No. 6, p. 14, 1901. Goniolithon partim, Kgl. Norske Vidensk. Selsk. Skr. 1898, No. 2, p. 5, 1898.

Thallus crustose or fruticulose, surface texture porcelaneous; when fruticulose ultimate branches with horizontal striations; filaments differentiated into hypothallium and perithallium, each tissue consisting of several cell layers; lateral fusion between adjacent cells present in both tissues; megacells solitary or in uniseriate vertical rows; tetrasporangial conceptacles perforated by one pore; sexual conceptacles unknown.

Lectotype: N. fosliei (Heydrich) Setchell & Mason, 1943.

Geographical range: northern and southern temperate to tropical waters.

One species recognized at Rongelap: N. frutescens (Foslie) Setchell & Mason, 1943.

The epithet Neogoniolithon was proposed by Setchell & Mason (1943) for a segment of Goniolithon not considered to be within the original author's restricted concept of Goniolithon. Foslie first published Goniolithon in 1898, for which name-genus relationship Setchell & Mason (1943) and I accept as the type, Lithophyllum papillosum Zanardini. Later, in 1901, Foslie applied Goniolithon to a differently circumscribed genus

using G. frutescens as the type. This new generic entity excluded L. papillosum. Setchell & Mason, preferring to continue the prior application of the name yet recognise the second generic entity, selected a new name for this second entity. They chose (1943: 89), for the new name, two lectotypes, Lithothamnium fosliei Heydrich (1897b: 58) and Goniolithon frutescens Foslie (1900b: 9), to represent, respectively, the crustose species and the fruticulose species. One nomenclatural type being sufficient for one genus, L. fosliei is maintained here as the lectotype following Setchell & Mason's (1943: 88) stated choice.

One of the distinguishing features of the members of Neogoniolithon is the presence of large cells, the megacells, that are either arranged uniserially in vertical rows or dispersed singly throughout the perithallar tissue (Fig. 5). Among other melobesioids, it is similar in anatomical structure to the Lithophyllum species in that the filaments of the medullary and basal hypothallium are coaxial and that the tetrasporangial conceptacles open by only one pore.

The taxonomic criteria in the paragraph above, which are essentially those Setchell & Mason (1943: 89) and Johnson (1954: 21, 1957: 231) used to distinguish the genus, require microscopic examination of sectioned material. It appears possible, however, to distinguish members of Neogoniolithon from other melobesioids on the basis of two external morphological characteristics. These are (1) the presence of conspicuous superficial striations that more or less encircle the apical portions of the branched forms (Figs. 2 & 3), and (2) the porcelaneous or glazed character of the thallus, whether it is fruticulose or crustose. These generic features, which would be useful in making field determinations, are based

on observations made on specimens collected by Dr. F. R. Fosberg from Ujae, Bikar, Taka and Likiep atolls, Marshall Islands, as well as those collected by myself from Rongelap.

Under the dissecting scope (Fig. 3) the superficial striations, which can be seen without the aid of a lens (Fig. 2), appear to be growth zones. In photographs of N. frutescens specimens collected from Saipan, Marianna Islands (Johnson, 1957: Pl. 59, Fig. 4), and from several atolls in the Indian and Pacific Oceans (Printz, 1929: Pl. 48), the striations on the ultimate branches are obvious. Photographs of the Atlantic and Caribbean fruticulose species N. spectabile (Foslie) Setchell & Mason, N. strictum (Foslie) Setchell & Mason and Goniolithon acropetum Foslie & Howe (yet to be transferred to Neogoniolithon) in Printz, 1929: Pls. 49, 50 & 51, rather clearly depict the horizontal striations on the ultimate branches.

Upon microscopic examination of sectioned material, the striations appear (Fig. 4) to be merely outgrowths of perithallial tissue. As Figure 4 shows, differentiation of hypothallial tissue is not very apparent in the upper portion of a branch, at least where the perithallial outgrowths are present. It may well be that the apical, or the actively growing portion of a branch includes the outgrowths of tissue and that apical growth is incremented. In N. frutescens, an "elongated apex" would explain the presence of branches that taper toward the tips and the restriction of the ridges to the upper extremities of the branches.

The porcelaneous nature is more apparent under the dissecting scope. Especially near the tips, the surface is usually smooth and appears as though glazed. This has been found to be the case not only with the

N. frutescens specimens, but with the crustose Neogoniolithon specimens in Dr. Posberg's collection as well.

While it may appear to be hazardous to imply that these two gross morphological characteristics are applicable to the genus as a whole since other workers do not mention them, the evidence seems to support their inclusion as generic characteristics. Their addition as generic morphological features appears to be a tangible one--subject to confirmation by examination of the type specimen.

Neogoniolithon frutescens (Foslie) Satchell & Mason, Proc. Nat. Acad. Sci.

29: 91, 1943.

Goniolithon frutescens Foslie, Kgl. Norske Vidensk. Selsk. Skr. 1900,

No. 1, p. 9, 1900.

Thallus fruticulose, often up to 8 cm wide and 4 cm high; branching dichotomous to monopodial; ultimate branches 1.0-2.5 mm wide, terete or complanate, tapering, marked by superficial striations, apex truncate; ultimate branches sometimes flabellate, up to 15 mm wide; hypothallar cells elongate, perithallar cells irregular in shape; megasells infrequent commonly individually dispersed; cavity of tetrasporangial conceptacles 216-315 μ wide, 130-144 μ high; conceptacular roof usually protruding, composed of 6-7 cell layers.

Type locality: Funafuti Atoll, Ellice Islands.

Geographical range: tropical waters of the Pacific and Indian Oceans.

The two growth forms recognized at Rongelap may be separated by use of the following key:

1. Ultimate branches terete or complanate (Fig. 2A)
 forma frutescens

1. Ultimate branches flabellate (Fig. 2B)
 forma flabelliformis (Foslie) comb. nov.

Specimens examined:¹ f. frutescens--646.² middle of seaward reef flat

¹All specimens examined were those collected at Rongelap Atoll.

²All collection numbers referred to in the text are the author's.

opposite Naen; 681 & 689, seven meters in from ridge at seaward reef margin opposite Gogan.

f. flabelliformis--682 & 684, seven meters in from ridge at seaward reef margin opposite Gogan.

In accordance with Article 26 of the 1956 edition of the International Code of Botanical Nomenclature, forma typica Foslie (1900b: 9) is changed to forma frutescens, because it is accepted as including the nomenclatural type of the species. Thus, the form should now be referred to as M. frutescens (Foslie) Satchell & Mason forma frutescens. The epithet forma flabelliformis Foslie (1900b: 9) of Goniolithon frutescens is here transferred to M. frutescens to form a new combination.

M. frutescens is a Pacific and Indian Ocean species and, as far as I know, the only fruticulose member of the genus described from these areas.

In a longisection of a branch (Fig. 4), the filaments of both the medullary hypothallium and the perithallium are loosely packed and, indeed, hardly to be distinguished from one another. The hypothallium is broad in relation to the perithallium. In fixed material, the intracellular spaces of the perithallial cells are darkly stained, while in the hypothallial cells only the walls are stained. Lateral fusion (Fig. 5) occurs between cells in both tissues, but it is more common in the perithallial tissue.

While it is customary to include cell dimensions in diagnostic discussions, I have excluded them above because they are superfluous in circumscribing the species. The following are micron measurements of

four typical hypothallar cells and four typical perithallar cells taken from one longisection of a branch.

Hypothallar Cells		Perithallar Cells	
Length	Width	Length	Width
22.4	9.8	7.0	9.8
22.4	8.4	7.3	8.4
19.6	14.0	10.5	10.0
26.2	16.8	18.2	7.7

As the measurements indicate, the hypothallar cells are elongate, but the perithallar cells, as Figure 5 also shows, have variable shapes, which may be rectangular, square, flattened or round.

As illustrated in Figures 6 & 7, the tetrasporangial conceptacles have protruding roofs with tubular ostioles. At times, however, the ostiole may be subconical. The tetraspores seem to develop only from the conceptacle floor (Figs. 6 & 8). Figure 8 depicts an abnormal development of a conceptacle, the cavity of which was 780 u wide.

As in the case of the vegetative cells, the shape and size of the tetrasporangial conceptacles are variable. The dimensions, in microns, of the cavities of four conceptacles measured were as follows.

Width	Height
216	130
245	144
315	133
320	118

These micron measurements are smaller than those given by other workers for the same species.

Foslie (1900b: 10) Taylor (1950: 123) Johnson (1957: 231)

Width--500-600
Height--none given

Width--300-680
Height--170-250

Width--350-450
Height--none given

Obviously any presumed reliability of conceptacle or cell dimensions for delimiting the species, or even genera, would require more monographic work.

Here and there outgrowths of new thalli are formed from the older branches of this species. As shown in Figures 9, 10 & 11, a section of perithallar filaments growing from the side of a branch has initiated the formation of a crust that completely encircles the branch. This crustose stage, with its prostrate hypothallar and upright perithallar filaments, may represent the basal crust from which the characteristic branches of this species are formed. One such branch, as indicated (Fig. 11) by the presence of medullary hypothallar tissue, was seen in section to have developed from such a crust.

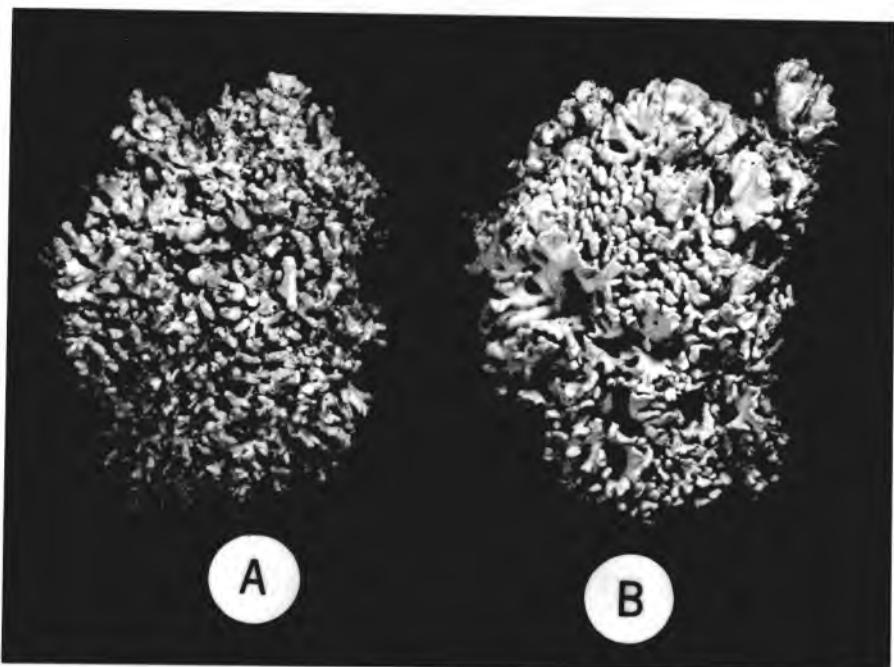


FIG. 2. *N. frutescens*. Two growth forms: A, forma frutescens; B, forma flabelliformis.
1 mm = 1.5 mm.



FIG. 3. *N. frutescens*. Branch tips showing the characteristic horizontal striations.
6 mm = 1 mm.

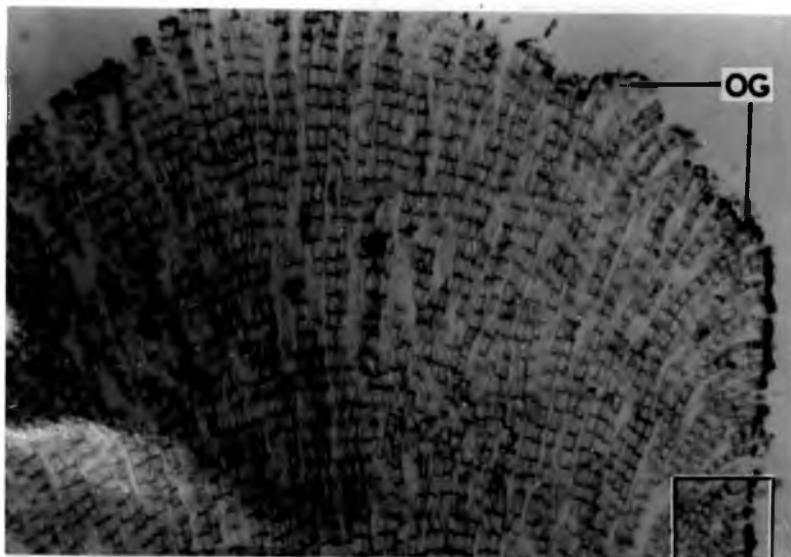


FIG. 4. *M. frutescens*. Longisection of
branch tip: OG, perithallial outgrowths.
1 cm = 130 u.

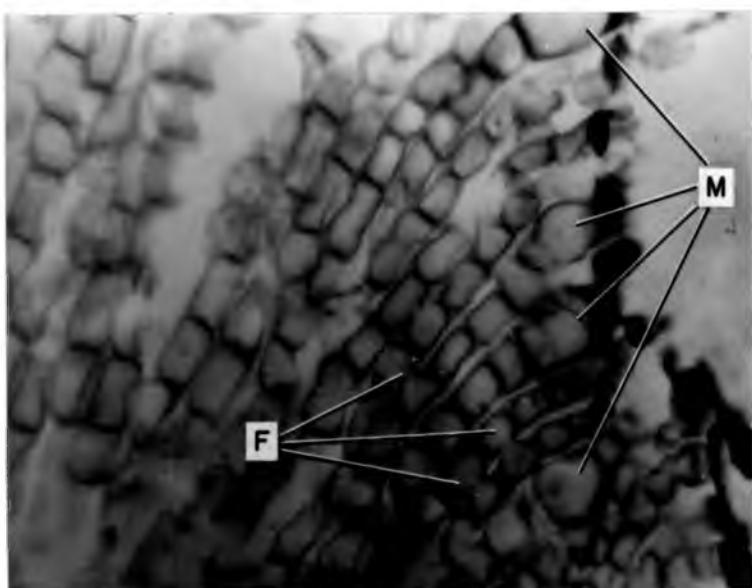


FIG. 5. *M. frutescens*. Perithallial portion.
An enlargement of the boxed section in Fig.
4: M, megacells; F, fused cells.
1 cm = 26 u.

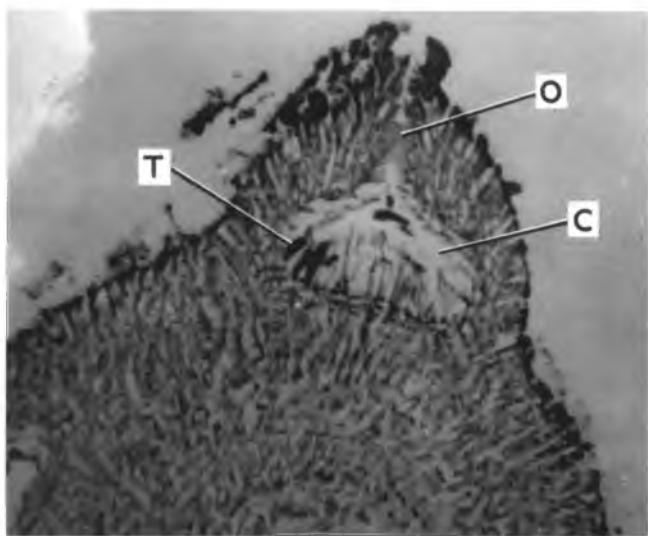


FIG. 6. *N. frutescens*. Cross section of a tetrasporangial conceptacle: T, tetraspore; O, ostiole; C, cavity.
1 cm = 100 u.

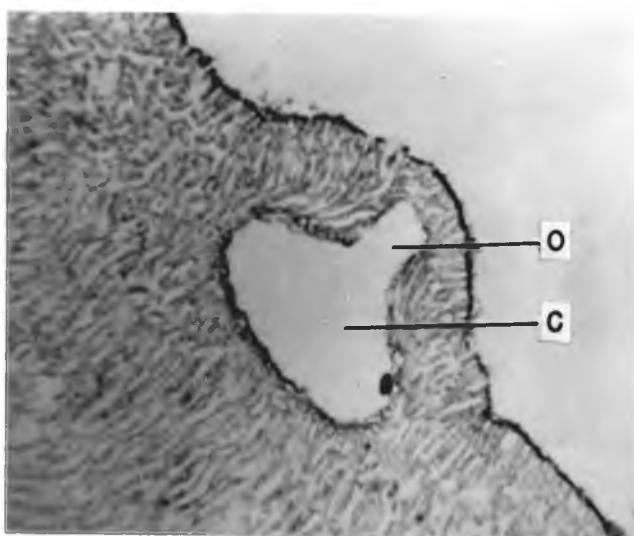


FIG. 7. *N. frutescens*. Longisection of a tetrasporangial conceptacle:
O, ostiole; C, cavity.
1 cm = 80 u.

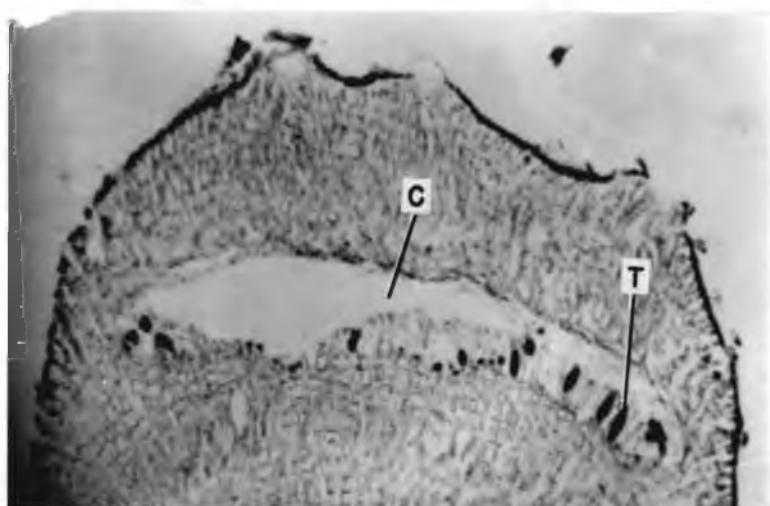


FIG. 8. *M. frutescens*. Cross section of a branch tip with an abnormal tetrasporangial conceptacle: T, tetraspore; C, cavity. 1 cm = 100 u.

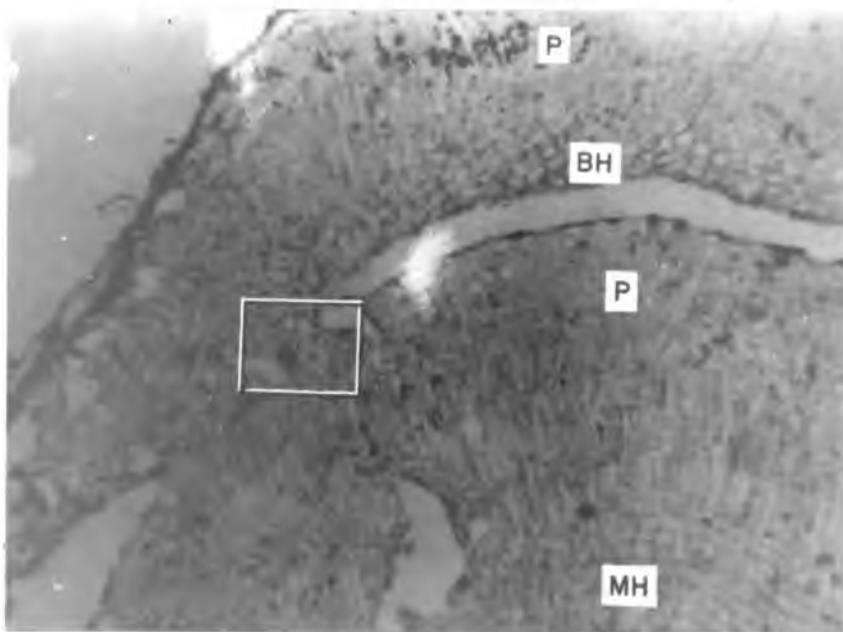


FIG. 9. *M. frutescens*. Branch (MH portion) cross section and surrounding crust (BH portion) sectioned perpendicular to its surface: P, perithallium; MH, medullary hypothallium; BH, basal hypothallium. 1 cm = 130 u.

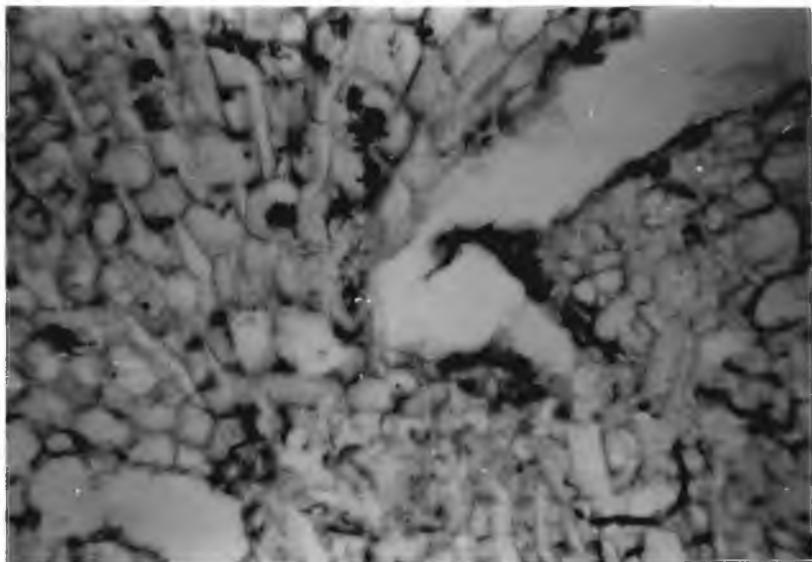


FIG. 10. *M. frutescens*. Enlargement of boxed section in Fig. 9. 1 cm = 32 u.

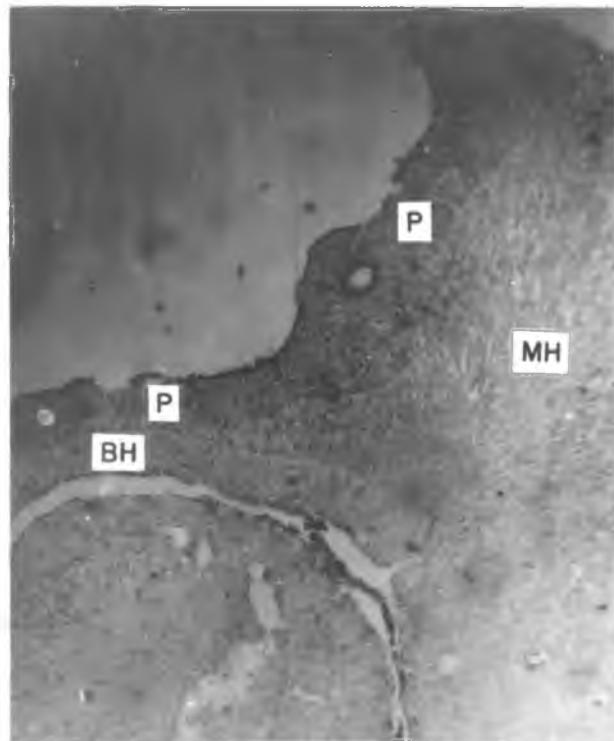


FIG. 11. *M. frutescens*. Cross section of a branch from which has developed a crust (MH portion) and which, in turn, has given rise to a branch (MH portion): P, perithallium; BH, basal hypothallium; MH, medullary hypothallium.

1 cm = 323 u.

Porolithon (Foslie) Foslie, Kgl. Norske Vidensk. Selsk. Skr. 1909, No. 2,
p. 57, 1909.

Lithophyllum subgenus Porolithon Foslie, Kgl. Norske Vidensk. Selsk.
Skr. 1906, No. 2, p. 24, 1906.

Thallus crustose or fruticulose, surface texture chalky and dull; filaments differentiated into hypothallium and perithallium; when crustose, basal hypothallium thin, 1-14 cell layers thick, perithallial tissue broad; when fruticulose, coaxial medullary hypothallium thicker than perithallium; lateral fusion between adjacent cells present in both tissues; megacells in cross sections grouped in horizontal plates of 18-24; tetrasporangial conceptacles perforated by one pore; sexual conceptacles unknown.

Lectotype: Porolithon onkodes (Heydrich) Foslie, 1909.

Geographical range: northern and southern temperate to tropical waters.

The three species recognized at Rongelap may be separated by use of the following key:

Since Foslie did not designate a type for Porolithon, I have arbitrarily chosen the above lectotype species. It was included in the original circumscription of the taxon, first in the subgenus Porolithon (Foslie,

1906: 25) and later in the genus Porolithon (Foslie, 1909: 57). Also, it is the earliest described of the species (Lithothamnium okodes Heydrich, 1897a: 6) now referred to this genus.

The distinguishing feature that sets apart members of Porolithon from all other melobesicoids is the presence of horizontal plates of megacells (Figs. 13 & 14), which are dispersed throughout the perithallar tissue. Except for the presence of these megacells, this genus is similar to Lithophyllum because of the hypothallar and perithallar tissues each being of several layers of cells and there being a single pore opening in each tetrasporangial conceptacle. Without microsection studies, it is not known whether Porolithon specimens can be separated from other lithophylloids--as is possible with Meogoniolithon specimens.

However, the problem of naming the genera without microscopic examination is minimized in an area such as Rongelap because the reef-building melobesicoid population comprises, essentially, of only two genera, Meogoniolithon and Porolithon. It is not unreasonable to suppose that other genera, for example Lithophyllum, Lithothamnium or even Archaeolithothamnium, may be present, but they were not found at Rongelap. Thus, if a specimen collected from Rongelap has no striations on the branches, and has a dull chalky textured surface, one can be fairly sure that it is a member of the genus Porolithon.

It seems that while certain anatomical characteristics are useful in separating the genera, none is sufficiently distinct in the Porolithon specimens studied to serve as a qualitative criterion. Subsequently, after considering the anatomical and morphological characteristics, the circumscriptions of P. craspedium and P. gardineri have been modified.

As treated here, three species of this genus are presumed to be present on Rongelap. These are P. craspedium, P. gardineri and P. onkodes. Taylor (1950: 128 & 132) ascribed two other fruticulose Porolithon species to Rongelap, P. marshallense (as a new entity) and P. sequinoctiale (as "prox."). P. marshallense, which is considered here to be the name for a superfluous species, is reduced to synonymy under a proposed new combination, P. gardineri f. abbreviata (Foslie) comb. nov. A specimen (#644) I have not been able to satisfactorily identify closely resembles a photograph of a specimen labeled P. sequinoctiale by Taylor (1950: 132, Pl. 68), which he had named with "some diffidence." I would prefer, if anything, to consider my specimen to be an aberrant form of P. gardineri.

Porolithon onkodes (Heydrich) Foslie, Kgl. Norske Vidensk. Selsk. Skr.

1909, No. 2, p. 57, 1909.

Lithophyllum (subgenus Porolithon) onkodes (Heydrich) Heydrich, in
Foslie, Kgl. Norske Vidensk. Selsk. Skr. 1906, No. 2, p. 25, 1906.

Lithophyllum oncodes (Heydrich) Heydrich, Ber. Deut. Botan. Ges.
15: 410, 1897.

Lithothamnion onkodes Heydrich, Bibliotheca Botan. 7(41): 6, 1897.

Thallus crustose, 0.1-5.0 mm thick, usually superimposed forming thick coherent masses; hypothallar tissue 3-14 cell layers thick, perithallar tissue many more cell layers thick, composing most of crust; megacell plates numerous, in longisection of a plate up to 22 cells show; cavity of tetrasporangial conceptacles reniform or oval in longisection, 154-217 μ wide, 70-140 μ high, imbedded.

Type locality: Dutch New Guinea.

Geographical range: tropical waters of the Pacific and Indian Oceans.

One growth form (Fig. 12) recognized at Rongelap: forma onkodes.

Specimens examined: 563, four meters in from ridge at seaward reef margin between Rongelap and Bokujarito; 594, ridge at seaward reef margin opposite Eniaetok; 620, in channel, at the 2-3 meter depth, between Kabelle and Aniriu; 645, middle of seaward reef flat opposite Maen; 663, ridge at seaward reef margin opposite Maen; 688, 690 & 691, three meters in from ridge at seaward reef opposite Cogan; 719, marginal region of seaward reef flat opposite Burok.

In accordance with Article 26 of the 1956 International Code of Botanical Nomenclature, the combination Lithophyllum onkodes f. typica Poslie (1909: 38) is changed to L. onkodes f. onkodes--now P. onkodes f. onkodes--because it apparently includes the nomenclatural type of the species.

As far as I have been able to determine, all of the Pacific crustose forms of Porolithon are referred to as P. onkodes. It was the only crustose malobesiod collected at Rongelap.

The shape of the crust depends on the substrate upon which it is growing. The crustose habit of the alga, as in specimens 645 & 690 (Fig. 12B illustrating specimen 690) is not always evident from the gross appearances. Both of the specimens were thought, at first, to belong to a fruticulose Porolithon species, but examination of a broken piece of "branch" shows them to be a crustose form overlying dead coralline material. Microscopic study of sections obtained from this material confirmed this.

On the other hand, a longisection taken from the basal portion of specimen 690 shows the development of a knob measuring 4 mm high and 3 mm wide without differentiation of a medullary hypothallium. This accelerated growth in a restricted area may represent the beginning of the development of a branch. If this is the case, then specimen 690 may be the basal crust of some fruticulose Porolithon species. The crust may have developed from the underlying fruticulose coralline just as the development of basal material from a branch was noted above for M. frutescens.

In comparison, a crust-like melobesicoid specimen collected from Saipan, Marianna Islands, has, according to Johnson (1957: 232, Pl. 59, Figs. 1 & 2), slight knobs that have some differentiation of medullary hypothallar tissue. Johnson remarked, without elaboration, that it anatomically resembled the type material of *P. craspedium*, and that it had a resemblance in growth form to Foslie's *forma subtilis* of that species.

However, since the knobs of the Rongelap specimens have no differentiation of medullary hypothallium (i.e., a "true branch" is absent), they are assigned to *P. onkodes*.

Depending on the specimen, the Rongelap *P. onkodes* has hypothallar cells that may be square ($12 \mu \times 12 \mu$), rectangular ($11.2 \mu \times 12.6 \mu$) or elongate ($6.3-8.4 \mu \times 13.5-15.4 \mu$). As in the fruticulose Porolithon species (Figs. 20 & 21), the individual hypothallar cells are distinctive in shape and size, but the perithallar cells are greatly distorted and vary in size and shape within a given specimen.

In thicker crusts the perithallium appears to have two horizontal zones. The uppermost zone has loosely packed filaments with cells that are irregular in shape. The lower zone is of closely packed filaments. These filaments consist of distinctly shaped (square or elongate) cells that are layered in irregularly arranged horizontal rows as well as cells that are irregular in shape. The cells in the upper zone, including the megacells present (Fig. 14), are filled with protoplasmic contents as evidenced in fixed microsections. The cells in the lower zone, like those of the hypothallar tissue, lack cytoplasmic material. It seems likely that these cells in the lower or inner portions of a living thallus

are filled with inorganic carbonate compounds. A crust measuring 0.74 mm thick had 0.32 mm composed of the "upper" type of perithallial tissue, 0.41 mm of the "lower" perithallial tissue, and less than 0.01 mm of hypothallial tissue. Another crust measuring 2.2 mm thick had 0.4 mm composed of "upper" perithallial tissue, 1.6 mm of "lower" perithallial tissue, and 0.2 mm of hypothallial tissue. Apparently the living cells of a crust comprise a greater portion of the thallus than one might be led to suspect. Certainly, contrary to what some observers have assumed, more than just the superficial cell layer of a thallus is "living."

Plates of megacells are numerous (Fig. 13) and a plate usually has 5-14 megacells in longisection. Occasionally, as in specimen 690, 22 megacells may be present in a plate longisection. The number of megacells present in the longisection of a plate depends on the area through which the section passes. The plates are, roughly, circular in tangential section and, thus, a vertical section may include only a few of the cells from near the periphery of a given plate. The megacells measured 16.8-28.0 μ long and 8.5-15.0 μ wide.

Conceptacles are numerous, and all of those observed were tetrasporic. They are always imbedded in the thallus, i.e., the conceptacle roof does not protrude from the thallus surface. In at least two specimens, the sections show conceptacles that are deeply imbedded (as in Fig. 13) with tetraspores still in them. Evidently vigorous vegetative growth has overcome the more slowly developing reproductive elements or they remain intact a long time.

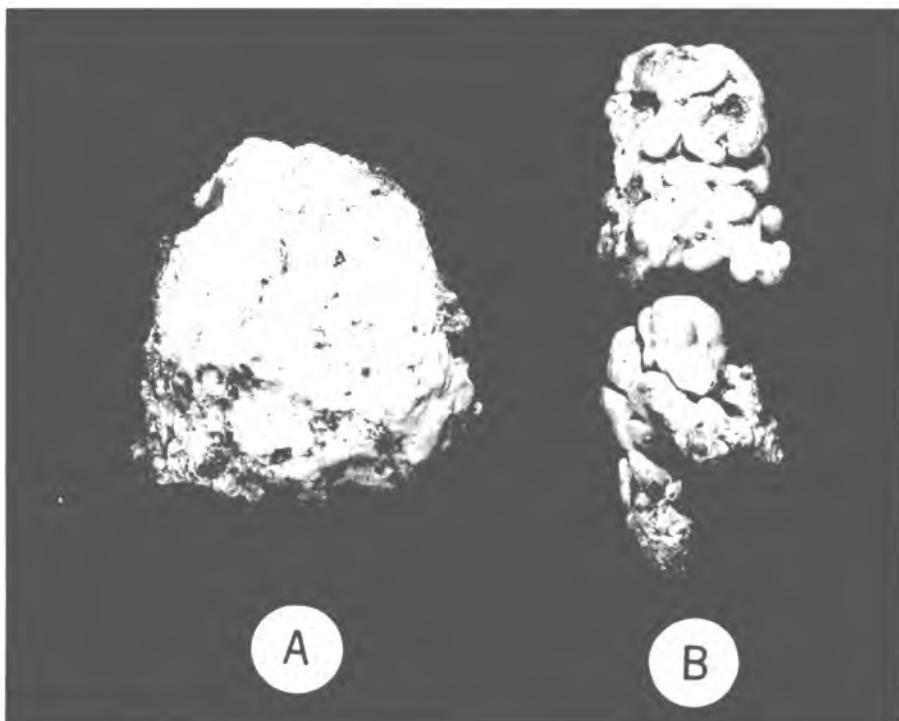


FIG. 12. *P. onkodes*. Growth forms of forma *onkodes*: A, crustose nature obvious; B, crustose nature not obvious.

1 mm = 1.55 mm.

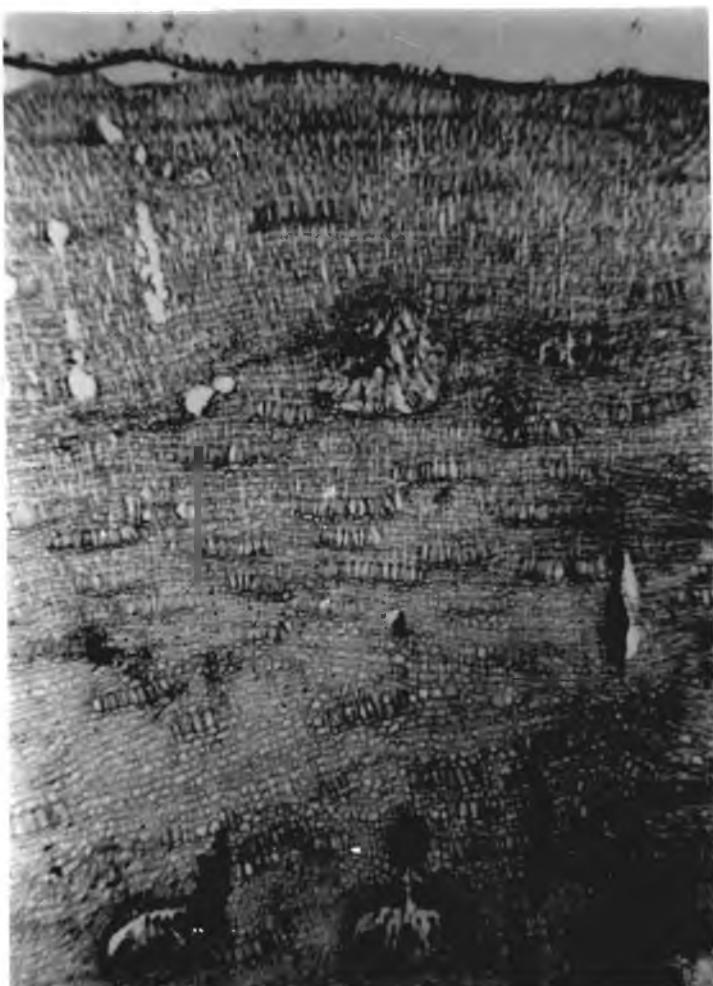


FIG. 13. *P. onkodes*. Portion of perithallium sectioned perpendicular to the crust surface with deeply imbedded conceptacles and numerous megacell plates. 1 cm = 109 u.

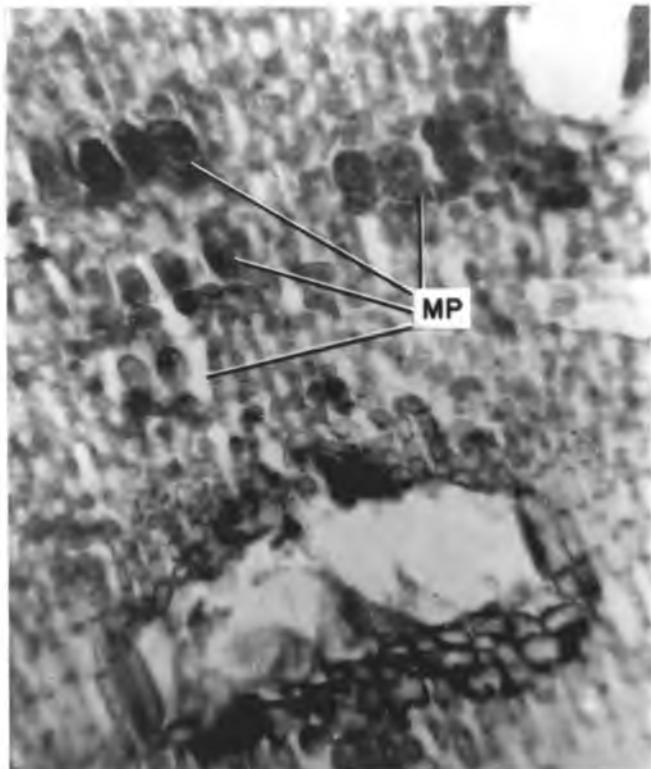


FIG. 14. *P. onkodes*. Portion of peri-thallium sectioned perpendicular to the crust's surface with a concep-tacle and megacell plates (MP); the megacells are filled with protoplasmic material.
1 cm = 22 u.

Porolithon craspedium (Foslie) Foslie, Kgl. Norske Vidensk. Selsk. Skr.

1909, No. 2, p. 57, 1909.

Lithophyllum (subgenus Porolithon) craspedium Foslie, Kgl. Norske Vidensk. Selsk. Skr. 1906, No. 2, p. 25, 1906.

Lithophyllum craspedium Foslie, Kgl. Norske Vidensk. Selsk. Skr.

1899, No. 5, p. 26, 1900.

Thallus fruticulose, often up to 12 cm wide and 17 cm high; branching sparse; individual branches short and columnar, fused below, terete to complanate, tips 5-12 mm wide; fused branches forming complanate structures up to 10 cm wide; megacell plates numerous, in longisection of a plate 2-6 cells show, in cross section 20-24 cells show; cavity of tetrasporangial conceptacles reniform or oval in longisection, 123-275 μ wide, 52-105 μ high, imbedded.

Type locality: Onotoa Atoll, Gilbert Islands.

Geographical range: tropical waters of the Pacific and Indian Oceans.

One growth form (Fig. 15) recognized at Rongelap: forma craspedium.

Specimens examined: 661A, ridge at seaward reef margin opposite Maen; 718 & 720, margins of seaward reef opposite Burok.

When P. craspedium was first described by Foslie (1900a: 26) as Lithophyllum craspedium, it was based on a specimen (British Museum No. A27) which he later (1900b: 8) referred to as forma compressa. Since the proposed combination P. craspedium f. compressa would include the nomenclatural type, the combination is referred to here as P. craspedium f.

craspedium in accordance with Article 26 of the 1956 International Code of Botanical Nomenclature.

The combination Lithophyllum craspedium f. abbreviata Foslie (1900b: 7) was later changed by Foslie (1909: 43) to L. craspedium f. typica; apparently to designate this form to be the typical morphological form of the species. In so doing, Foslie innocently ignored the type method of botanical nomenclature for at that time this feature of nomenclature was not applied by Europeans. The later epithet forma typica is rejected and forma abbreviata is reinstated since it is the first legitimate epithet available. As treated here, this form is removed to P. gardineri. L. craspedium f. abbreviata thus falls into synonymy.

Because of similarities in their morphological and anatomical characteristics, the taxonomic features of P. craspedium and P. gardineri are discussed together in the section below.

Porolithon gardineri (Foslie) Foslie, Kgl. Norske Vidensk. Selsk. Skr.

1909, No. 2, p. 57, 1909.

Lithophyllum (subgenus Porolithon) gardineri Foslie, Kgl. Norske Vidensk. Selsk. Skr. 1906, No. 8, p. 30, 1907.

Thallus fruticulose, various in shape, up to 20 cm or more wide; branching dense, irregular, dichotomous to monopodial, localized fusions between adjacent branches common; individual branches terete to complanate, with acute or truncate tips that are 0.7-3.0 mm wide to the club-shaped tips that are 1.5-7.0 mm wide; fused branch tips forming flabellate structures with tips up to 15 mm wide; megacell plates numerous, in longisection of a plate 2-9 cells show, in cross section 18-20 cells show; cavity of tetrasporangial conceptacles reniform or oval in longisection, 92-210 μ wide, 56-91 μ high, imbedded.

Type locality: Salomon & Egmont Atolls, Chagos Archipelago, and Coevity Island.

Geographical range: tropical waters of the Pacific and Indian Oceans.

The three growth forms recognized at Rongelap may be separated by use of the following key:

1. Thallus 10-14 cm high and 14-20 cm or more wide (Fig. 19)
 - forma subhemisphaerica (Foslie) Taylor, 1950
1. Thallus less than 10 cm high or 14 cm wide 2
 2. Branch tips acute or truncate, 0.7-3.0 mm wide (Fig. 18) . .
 - forma gardineri
 2. Branch tips round and expanded, 1.5-7.0 mm wide (Figs. 16 &

17) forma abbreviata (Foslie) comb. nov.

Specimens examined: f. subhemisphaerica--560 & 562, ridge at seaward margin between Rongelap and Bokujarito; 597-598 & 599-600, ridge at seaward reef margin opposite Eniaatok.

f. gardineri--561, ridge at seaward reef margin between Rongelap and Bokujarito; 658, 660 & 661, ridge at seaward reef margin opposite Naen; 685, 686 & 687, ridge at seaward reef margin opposite Gogan.

f. abbreviata--662, ridge at seaward reef margin opposite Naen; 714, 715, 716 & 717, edge of seaward reef opposite Burok.

Lithophyllum gardineri f. typica Foslie (1907: 30) is accepted here as including the nomenclatural type of the species, and the combination is therefore changed to Porolithon gardineri f. gardineri in accordance with Article 26 of the 1956 International Code of Botanical Nomenclature.

Forma abbreviata of Lithophyllum craspedium is the first legitimate epithet available for a form of Porolithon gardineri, which, as proposed here, includes as synonyms those combinations as listed below.

Porolithon gardineri f. abbreviata (Foslie) comb. nov.

Lithophyllum craspedium f. abbreviata Foslie, 1900b: 7 (basionym).

L. craspedium f. typica Foslie, 1909: 43.

L. gardineri f. obpyramidata Foslie, 1907: 30.

Porolithon craspedium f. mayorii Howe, in Setchell, 1924: 252.

P. marshallense Taylor, 1950: 128.

Howe (in Setchell, 1924: 252) in establishing forma mayorii noted the presence in the filaments of one, two or three long cells alternating with one short cell in the longisections of branches. He further described

these as appearing in regularly alternating layers of long and short cells. This alternation of layers agrees with Foslie's interpretation of P. craspedium.

Foslie (1907-09) mentioned that P. craspedium closely resembled P. gardineri in habit, but that P. craspedium was in general a coarser, more vigorously developed alga. In some cases, as between L. craspedium f. abbreviata and L. gardineri f. obpyramidata, he said it was difficult to distinguish one from the other. However, he further stated that the two species may be separated on the basis of the number of elongate cells in the layers alternating with the row of short cells in the medullary hypothallium. His statements (1907-09: 191) that the ". . . medullary hypothallic cells of Lithoph. craspedium form a row of short cells, rather regularly alternating with one or two or up to three rows of long ones, whereas" as he mentioned earlier (1907-09: 189), in P. gardineri there is ". . . one row of short cells and two or four or sometimes up to seven rows of long ones," are, at best, indefinite. Aside from reconciling the matter of layers of 1-3 and 2-4 cells in the rows, the Rongelap specimens show no regular alternation of such layers of cells.

L. craspedium f. abbreviata at times does show some alternation of layers consisting of two long cells (13.6-18.7 μ long) and one short cell (5.1-7.8 μ long) in the cell rows, but this is found only in localized areas of a microsection. On the other hand, Taylor (1950: 130) mentioned this same irregularly occurring sequence of two long cells and one short cell layers in P. gardineri f. subhemisphaerica. Taylor made no comment on the alternation of these cell types for other forms of P. gardineri or for P. craspedium. Johnson (1957: 232) made no comment either on

their presence or absence in P. craspedium, which was the only fruticulose Porolithon he found at Saipan Island.

Thus, while one can visualize and perhaps nebulously observe Foslie's distinction between these two species, his criteria actually seem to have had no taxonomic utility.

The irregularity or lack of zonation in cell sizes could be explained by the fact that the tissue is filamentous. A study of the variation and consistency in character of the filaments themselves may prove to be of greater value, taxonomically, and possibly have more validity, biologically, in identifying the species. I have made some studies of individual filaments, using EDTA solution as a decalcifying agent and aniline blue to stain the cell walls of the separated filaments. Though feeling this to be a prospectively profitable source of taxonomic criteria, such criteria were not sufficiently established to justify any statement at this time concerning their taxonomic application.

A tabular evaluation of other anatomical characteristics, essentially the dimensions of various anatomical parts, showed no significant difference between the two species. As shown in Table I, which gives certain anatomical measurements of the Rongelap specimens and of those provided by Foslie and by Taylor in their diagnostic discussions of the two species, the dimensions from the different sources overlap even where the same species is concerned.

On the basis of gross morphological characteristics then, L. craspedium f. abbreviata, L. gardineri f. obpyramidata, P. craspedium f. mayori and P. marshallense are grouped under P. gardineri f. abbreviata.

TABLE I. MICRON DIMENSIONS OF VARIOUS ANATOMICAL
STRUCTURES PUBLISHED BY M. FOSLIE AND BY W. R.
TAYLOR, AND THOSE OBTAINED DIRECTLY FROM
RONGELAP SPECIMENS.

Species	Source	Perithallic Cells-L X W	Hypothallic Cells-L X W	Megacells L X W	Concep. Cavity L X W
<i>P. crasspedium</i>	Foslie 1909: 43	9-14(18) X 7-9(11)	9-22(29) X 9(7)-11	22(18)-36(47) X 9-14(18)	95-115 X 200-230
	Taylor 1950: 127	7.5-11.5 X 8.5-10.0	9.5-13.0(19) X 6.5-11.0	15.0-21.0 X 9.5-17.0	85-190 X 170-250
	Rongelap Specimens	3.8-12.0 X 4.5-7.5	5.0-18.7 X 5.2-8.0	18.7-28.9 X 7.5-12.2	52-105 X 123-275
<i>P. gardineri</i>	Foslie 1909: 44	4-11(14) X 7-11	7-25(29) X 7-11	18-36 X 11-22	80-95 X 200-300
	Taylor 1950: 130	7.5-19.0 X 9.5-11.0	9-30 X 9-13	28.0-35.0 X 9.5-18.0	68-110 X 110-152
	Rongelap Specimens	5.0-15.3 X 4.9-13.6	10.1-20.4 X 5.1-11.9	20.4-30.6 X 7.5-17.0	56-91 X 92-210

P. marshallense was erected by Taylor (1950: 129) on the assumption that P. craspedium f. mayorii and H. gardineri f. obpyramidata, both of which he asserted had no relationship to the species to which they had been assigned, should fall into synonymy. Evidently Taylor considered the gross form in delimiting P. marshallense from P. craspedium and P. gardineri, for he stated (1950: 129) that his P. marshallense specimens ". . . are certainly the same in growth habit and anatomical characters as Howe's P. craspedium f. mayorii" However, P. craspedium f. mayorii with its dense, short, 3-9 mm thick, bluntly round-tipped branches (Howe, in Satchell, 1924: 251, Pl. 36, Figs. 1 & 2) is also identical to the description given by Foslie (1900b: 7) for forms abbreviata of the same species.

P. marshallense is considered to be superfluous because the growth habit of P. gardineri f. abbreviata (Foslie) comb. nov. seems to be a developmental stage of P. gardineri f. gardineri. Figure 17 illustrates a possible intermediate stage between forms gardineri type branches and forms abbreviata type branches. It seems that after the branches of a thallus have reached a certain growth stage (e.g., as in forms gardineri, Figs. 18 & 19) the uppermost regions of the branches revert to the development of crustose outgrowths; hence, the club-shaped branch tips. Micro-sectioned material indicates that the crustose outgrowths have developed from the perithallar cells. The formation of crustose material by the perithallar cells of a branch was also noted above for H. frutescens.

As in P. onkodes, the hypothallar filaments of P. craspedium and P. gardineri are closely packed, while the perithallar filaments are loosely packed. This is shown in Figures 20 & 21, which also illustrates the

marked irregularity of the size and shape of the perithallar cells. The perithallar cells, which constitute but a small portion of a branch, contain cytoplasmic material. The hypothallar cells apparently contain no living intracellular material.

In both species, megacell plates are numerous, each of which usually consists of 18-24 megacells in cross section (Fig. 23). The megacells (Fig. 22), which seem to be restricted to the perithallar tissue, have cytoplasm in them.

In four of the specimens of P. gardinari studied (597, 589, 561 & 716), abnormally formed conceptacles (Figs. 24 & 25) are present. The width of the "cavity" of these conceptacles is the same as the height (49 u X 49 u), while the width of the normal type conceptacle cavity (Fig. 23 & 24) is much greater than the height. The tetraspores contained in the abnormal conceptacles are about half the size of those found in normal conceptacles. These abnormally formed tetraspores apparently escape through the spaces between the loosely arranged filaments since no ostiole is apparent.



FIG. 15. *P. craspedium* f. *craspedium*.
Growth form. 1 mm = 1.5 mm.

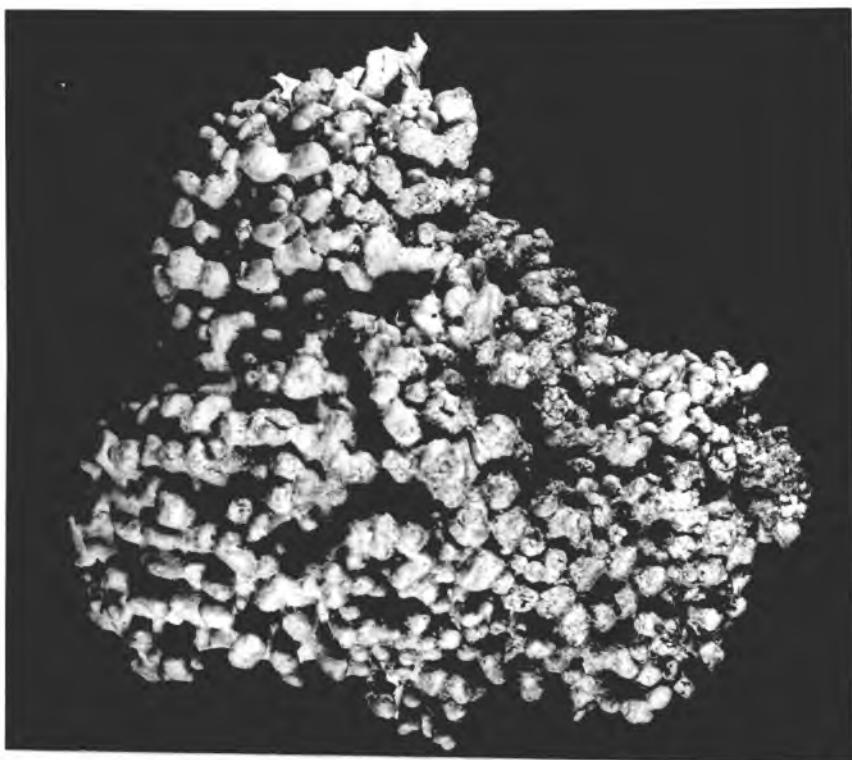


FIG. 16. P. gardineri f. abbreviata.
Growth form. 1 mm = 1.5 mm.

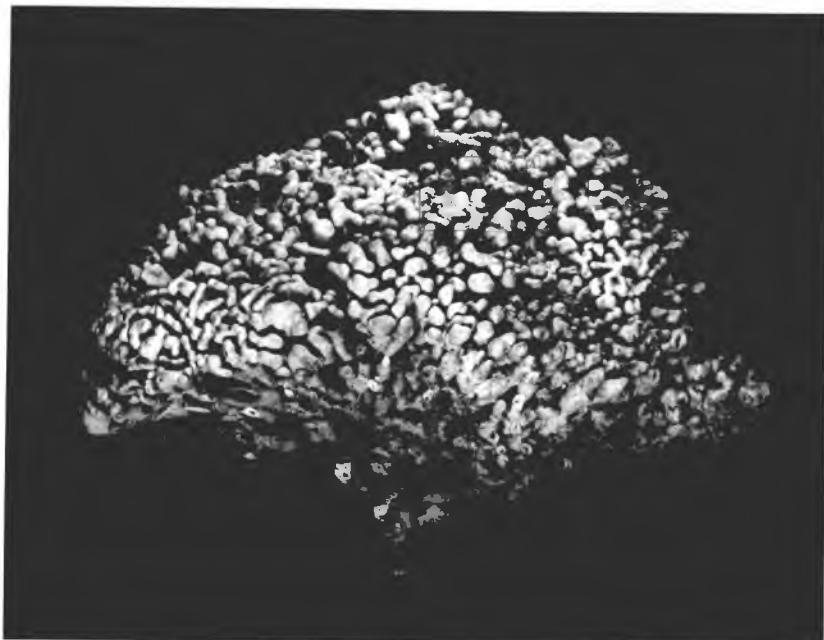


FIG. 17. P. gardineri f. abbreviata.
Growth form. 1 mm = 1.5 mm.



FIG. 18. *P. gardineri* f. *gardineri*.
Growth form. 1 mm = 1.5 mm.



FIG. 19. *P. gardineri* f. subhemispherica.
Growth form. 1 mm = 1.5 mm.

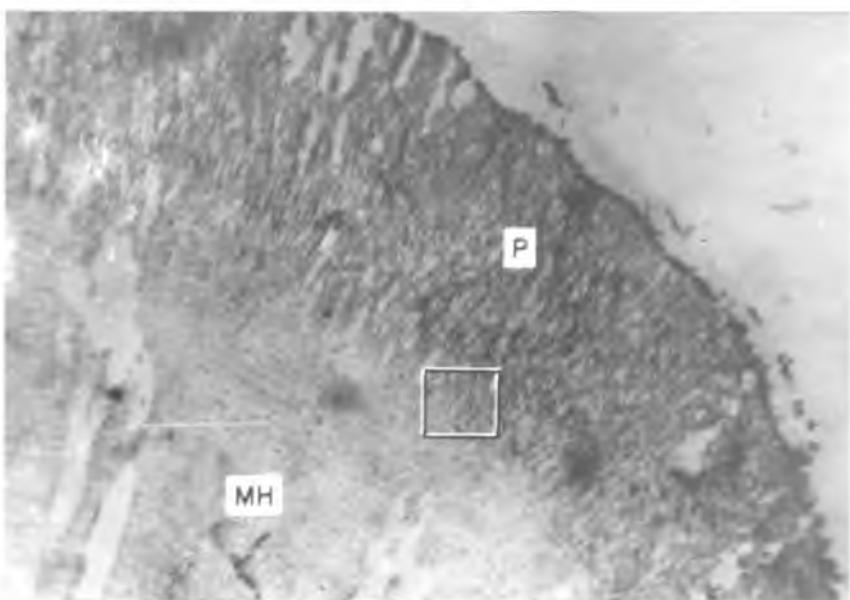


FIG. 20. *L. gardineri*. Portion of a branch cross section: P, parithallium; MH, medullary hypothallium.
1 cm = 109 u.

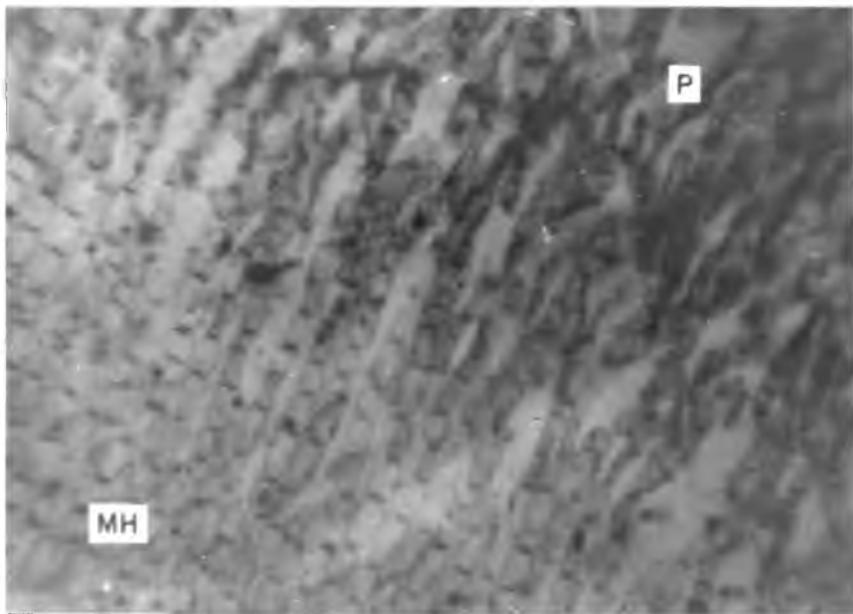


FIG. 21. *L. gardineri*. Enlargement of boxed section in Fig. 20: P, parithallium; MH, medullary hypothallium.
1 cm = 40 u.

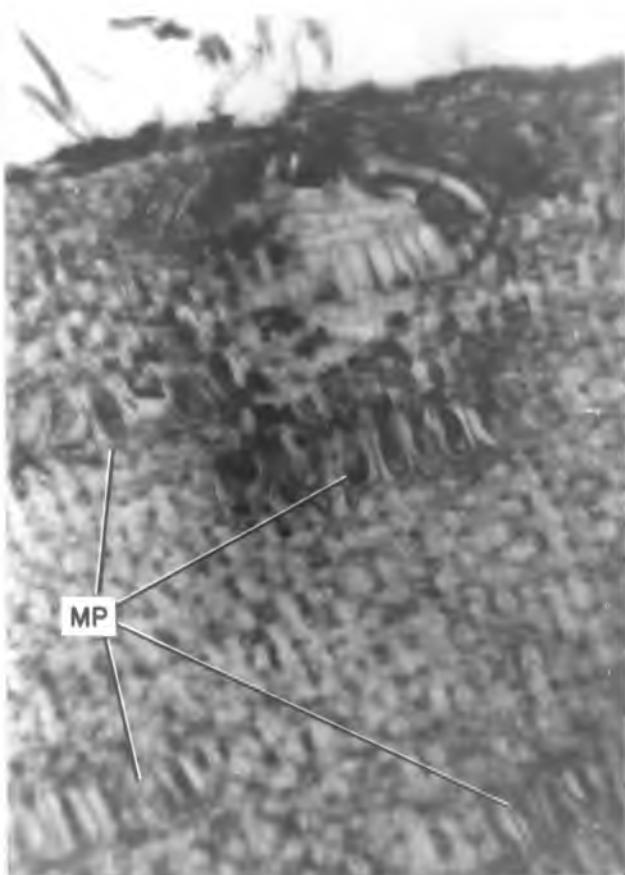


FIG. 22. *P. gardineri*. Longisec-
tion of perithallium portion of
a branch with darkly stained
megacells (MP). 1 cm = 32 u.

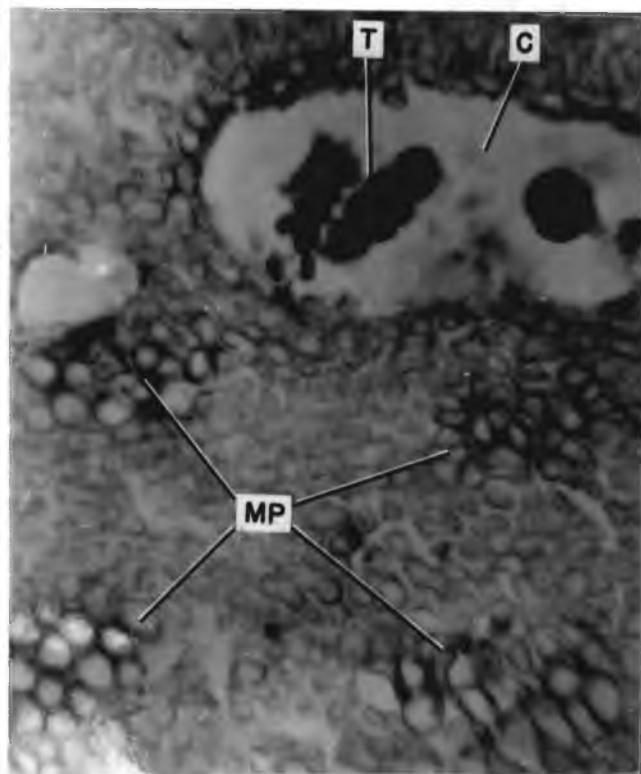


FIG. 23. *L. sardinari*. Slightly oblique cross sections of megasporangial conceptacles (C) and tetrasporangia (T) with tetraspores (MP).
1 cm = 26 u.

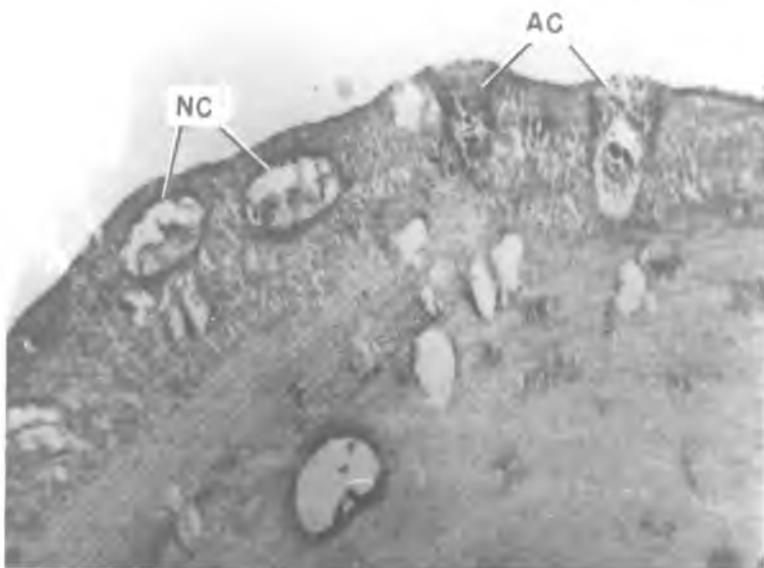


FIG. 24. *P. gardineri*. Portion of branch cross section with normal conceptacles (NC) and abnormal conceptacles (AC).
1 cm = 109 u.



FIG. 25. *P. gardineri*. Portion of branch cross section with an abnormal conceptacle: T, tetraspore; C, cavity.
1 cm = 25 u.

GEOGRAPHICAL AND LOCAL DISTRIBUTION
OF THE RONGELAP SPECIES

A thorough investigation of the geographical distribution of the four species found at Rongelap, M. frutescens, P. onkodes, P. craspedium and P. gardineri, is hampered, since only a few areas have been explored with respect to the melobesioid corallines. However, the available literature dealing with these organisms seems to indicate that the species found at Rongelap are restricted to the Pacific and Indian Oceans.

Much of our knowledge concerning the Indian Ocean melobesioids is based on specimens collected by J. Stanley Gardiner, who on two expeditions (Foslie, 1903 & 1907-09) collected them from various island groups and banks in the area. The specimens were sent to Foslie for determination, who made distributional inferences based on the relative number of specimen-types he received and on the collector's own observations.

At Coevity Island, and at Salomon and Egmont Atolls of the Chagos Archipelago, Foslie (1907-09: 178) considered P. craspedium, P. onkodes, P. gardineri and M. frutescens to be the most commonly occurring coralline algae. P. gardineri was not present according to him (1903: 462 & 469, 1907-09: 181) in the Maldives and Laccadive Islands, but the other Rongelap species mentioned above for the Chagos Archipelago and Coevity Island were collected from these areas. None of the Rongelap species appeared in collections made from the Seychelles Group, Admirante Islands, Car-gados Carajos Bank or the Saya de Malha Bank. These areas together with the Chagos, Maldives and Laccadives had other melobesioid members present (Foslie, 1903 & 1907-09), most of which apparently were obtained as dredged material and only a few vera collected from the reef flat proper.

The collection made from Coevity Island had (Foslie, 1907-09: 179) only the four Rongelap species.

From the Mascarene Islands, which were not visited by the Gardiner expeditions, Bérugesen (1943: 16) listed only P. onkodes of the four species concerned as being present at Mauritius Island.

The first extensive collection of melobesioids collected in the Pacific area, was made (Foslie, 1904) during the Siboga Expedition in the Indonesian Archipelago, and it too was sent to Foslie for determination. It included specimens of M. frutescens and P. onkodes (Foslie, 1904: 53 & 59), but specimens of P. craspedium and P. gardineri were absent. Judging from the number of specimens he received from a given locality, Foslie (1904: 54 & 59) was led to believe that although the two Rongelap species present were widely distributed in the area, apparently they did not occur in abundance. Foslie (1904: 54) mentioned that M. frutescens probably occurred less frequently in Indonesia than in the Maldives or at Funafuti Atoll.

Melobesiod specimens from Funafuti Atoll, Ellice Islands, and Onotoa Atoll, Gilbert Islands, were collected apparently by Alfred E. Finckh (Foslie, 1900a: 26 & 1900b: 8) and sent to Foslie for determination. The Funafuti collection had (Foslie, 1900b) P. craspedium f. craspedium (as Lithophyllum craspedium f. compressa), P. gardineri f. abbreviata (as Lithophyllum craspedium f. abbreviata), P. onkodes, M. frutescens (as a new entity), and Lithothamnium philippi in it. The last species, as was noted by Foslie (1900b: 3), was collected in depths of 38-86 fathoms "from deep water around the atoll" At Onotoa Foslie (1900a: 27 & 1900: 8) recognized only P. craspedium f. craspedium (as Lithophyllum

craspedium f. compressa) and it was considered to be the most important reef-builder on the atoll.

According to Setchell (1924: 253), who assembled the Samoan algal materials and data collected by Alfred G. Mayor, the reef margins of Rose Atoll were dominated by P. gardineri f. abbreviata (as P. craspedium f. mayorii). By contrast, at the island of Tahiti Setchell (1926: 318) found only P. onkodes. He said this species was the most conspicuous organism present on the fringing and barrier reefs of the island. No other melobesioids were identified from Tahiti or Rose.

Setchell (1924: 154) collected several melobesiod genera from Tutuila of the Samoan Islands, but of the species found at Rongelap only M. frutescens and P. onkodes were present. Johnson (1957: 231 & 232) found on Saipan of the Mariannas Islands a varied melobesiod population, including the three Rongelap species, P. craspedium, P. onkodes and M. frutescens.

Taylor (1950: 123-132) collected M. frutescens, P. onkodes, P. craspedium, P. gardineri, P. marshallense, P. aquinoctiale and an unidentified Lithothamnium species from the northern Marshall atolls. With the exception of M. frutescens and the Lithothamnium species, which were not found at Rongelap, they appeared in collections made at Eniwetok, Bikini, Rongerik and Rongelap. The improbable assignment of P. marshallense and P. aquinoctiale to these atolls was discussed in the Porolithon section above. The Lithothamnium species was obtained from material dredged from the lagoon of Bikini Atoll and cannot be construed as being a significant reef-builder in the area.

The collection made by Dr. F. R. Fosberg in the Marshall Island atolls, Ujue, Bikar, Taka and Likiep, as far as I could determine, had two specimens of Lithophyllum, but the remainder of the some 30 odd specimens consisted of the four Rongelap species, P. gardineri, P. crassum, P. okodes and M. frutescens.

From the preceding geographical discussion it seems that P. okodes and M. frutescens have the widest geographical distribution among the four Rongelap species, since they apparently are not as restricted to atoll-type reefs as P. crassum and P. gardineri seem to be. Among the four species, P. okodes seems to have the widest range and P. gardineri the narrowest.

All four species seem to be most adapted to the atoll-type reef environment, where their dominating presence produces a simple, homogeneous melobesicoid vegetation. It is only on reefs associated with basalt islands that one might expect the melobesicoid vegetation to be more heterogeneous.

At Rongelap, the three Porolithon species were the dominating organisms from the margins of the seaward reef inward about ten meters toward the inner reef flat. M. frutescens, which was reported (Foslie, 1903: 462) to be "abundant" in the Maldives Islands and at Funafuti, was rather scarce at Rongelap. As Gardiner had observed (as quoted in Foslie, 1903: 463), this species as found in the Maldives was always in situations ". . . where they are never uncovered and the water circulates freely." This was the situation found in the inner regions of some reef flats at Rongelap, and these were the only areas in which M. frutescens was found.

Also, at Raroia, an atoll in the Tuamotu Archipelago, Doty (1954: 9) observed that Goniolithon occurred only on the inner reef flat proper.

At Gagan Islet, located on the eastern rim of Rongelap (Fig. 1), M. frutescens was found growing about seven meters in from the seaward reef edge adjacent to an area which had no elevated ridge at the reef edge so that at low tide the surging waves were not hampered as they normally would have been.

The ridges, which are discussed in more detail below, are growths of Porolithon, species of which form areas elevated up to half a meter or more along the seaward margins of the reef. During low tides, they impede the movement of water onto the reef flat proper as they break the force of the incoming waves. A noticeable result of this effect on the water circulation was that the waters of the reef flat became warmer in-shore of the ridge.

Apparently M. frutescens is adapted to areas of the inner reef flat that provide free circulation of water. However, it does not seem adapted to very turbulent waters for it is not found growing in positions where it might be subjected to strong currents such as are found at the reef margins. This species has slender, rather fragile branches, and is probably not able to persist in a vigorously turbulent environment. The Porolithon species, if found growing in the "M. frutescens habitat," were P. onkodes or the small P. gardineri f. gardineri. However, these two corallines were much more common in an area five meters in from the algal ridge and outward to the very edges of the seaward reef.

The Porolithon species apparently are adapted to strong surf and inter-tidal conditions. Along the windward rim of the northern and

eastern faces of the atoll, the reef was often conspicuously ridged marginally at its seaward edge by extensive growths of P. onkodes and two forms of P. gardineri, forms subhemisphaerica and gardineri. The area in which they were maximally developed extended outward toward the rim of the reef much to the exclusion of other organisms. There they formed overhanging ledges which could be readily observed as conspicuous features of the surge channels. Form subhemisphaerica of P. gardineri was the most conspicuous element of the ridges and also of the seaward reef face to the very edges of the reef. On the fringing-type reefs surrounding Tahiti, on the other hand, according to Satchell (1926: 309) ". . . the outer margin of the exposed fringing reef overhangs and is a pure P. onkodes association . . . forming a pavement-like outer bank." Also the reef margins at Rose Atoll, as mentioned earlier, were, according to Satchell (1924: 253), dominated by P. gardineri f. abbreviata (as P. craspedium f. abbreviata).

During low tides, the algal ridges at Rongelap become elevated above sea level and are exposed to the atmosphere except for intermittent submersion by the surging waves. The height of the algal ridge appeared to be limited only by the height of the wave action at low tide. The ridges present along the northern rim were not as conspicuous as those found on the eastern rim. In at least the eastern reef area opposite Gogau Islet, the Porolithon growth at the reef edge was broken by two intervals of about twenty meters each that had no obvious living algae on them; certainly no melobesiacoids were present. The role these organisms may have elsewhere in checking reef erosion caused by wave action was evidenced by the marked indentation of the reef at these barren areas.

A striking feature of the northern rim was its broad reef flat, more than a thousand meters wide in some instances. An interesting aspect of coralline growth was found on one of these broad areas. In a reef area of about three hundred meters beginning at Maea Islet, the reef of which extended for another four hundred meters or so to the seaward edge, specimens of three malobesioid species, M. frutescens (#646), P. onkodes (#645) and an unidentified fruticulose Porolithon species (#644) were found only loosely attached to, usually, the sides of slightly elevated limerock material. The crustose P. onkodes specimen collected encrusted a piece of calcareous material, which in turn was attached by what appeared to be a calcareous sponge. The fruticulose specimens were also attached to the substrate by this same calcareous sponge.

At low tide, this broad reef flat was covered by less than one-half meter of rather quiet water; a type of environment which does not seem natural for these species. Also, the fruticulose specimens had branches which were not as well developed as those found growing in freely circulating water. It is possible, however, that the abnormal branch development may have been caused by activities of the sponge. Unfortunately the exact nature of the relationship between the sponge and the algae can not be determined without making further field observations.

The essentially surfless leeward reef margins along the southern rim of the atoll were markedly in contrast to windward rim areas in regard to coralline growth. Growth of corallines was relatively scarce and coelenterate coral growth, although still sparse, was more evident here than to the windward. The algal ridge so conspicuous in windward areas was absent.

P. gardineri f. gardineri and P. onkodes were the most common algae growing on the seaward reef margin opposite Burok Islet. The most conspicuous alga here was the coarse columnar P. craspedium f. craspedium and it towered over all other organisms growing on the reef. Forma abbreviata of P. gardineri was also collected from here. Both P. craspedium f. craspedium and P. gardineri f. abbreviata were found growing on the seaward reef margin opposite Naen Islet along the northeastern rim as well.

It seems that P. gardineri f. gardineri and P. onkodes have the widest distribution on the reef flat at Rongelap. Of these two, P. onkodes is apparently the more versatile species in being able to grow in turbulent to non-turbulent water conditions. P. gardineri f. gardineri, while more or less confined to a ten meter zone extending inward from the seaward reef edge toward the inner reef flat, has a wide local range in that it grows on both the leeward and windward rims of the atoll. M. frutescens, P. gardineri f. subhemisphaerica, P. gardineri f. abbreviata, and P. craspedium f. craspedium seem to be restricted to definite ecological habitats. M. frutescens is an inner reef flat species, growing apparently only in areas that provide moderate water movement. P. gardineri f. subhemisphaerica seems to be restricted to the windward reef margins where it is the dominating organism and provides the bulk of the ridge material. If this form truly represents a later growth stage of the smaller forma abbreviata and forma gardineri, then one can only conclude that optimum growth of the species is attained in an intertidal environment accompanied by vigorous wave action. P. craspedium f. craspedium and P. gardineri f. abbreviata, relatively uncommon at Rongelap, seem to

be restricted to the marginal areas and were found growing only on the northern and southern rims of the atoll.

BIBLIOGRAPHY

- Areschoug, J. E. 1852. Ordo XII. Corallinaeae, pp. 506-576. In
J. G. Agradh, Species genera et ordines algarum. Vol. 2, Pt. 2.
- Batters, E. A. L. 1892. On Schmitziella; a new genus of endophytic
algae, belonging to the order Corallinaceae. Ann. Botany, Vol. 6.
(Not seen.)
- Børgesen, F. 1943. Some marine algae from the Mauritius, III.
Rhodophyceae, Part 2, Gelidiales, Cryptonemiales, Gigartinales.
Kgl. Danske Vidensk. Selsk., Biol. Medd. 19(1): 1-85.
- Bory de Saint-Vincent, J. B. G. M. 1832. Notice sur les polypiers de la
Grèce. Expéd. Sci. Morée, Zoologie, Vol. 3. (Not seen.)
- Decaisne, J. 1842. Essais sur une classification des algues et des
polypieres calcifères de Lamouroux. Ann. Sci. Nat., Ser. 2, 17:
297-380; Pls. 14-17.
- Doty, M. S. 1954. Floristic and ecological notes on Rarotonga. Part I.
Atoll Res. Bull. 33, 41 pp.
- Ellis, J. and D. Solander. 1786. Natural history of many curious and
uncommon zoophytes. London. 208 pp., Pls. 1-69.
- Foslie, M. H. 1895. The Norwegian forms of Lithothamnion. Kgl. Norske
Vidensk. Selsk. Skr. 1894. 180 pp., Pls. 1-23.
- _____. 1898a. Systematical survey of the Lithothamnia. Kgl.
Norske Vidensk. Selsk. Skr. 1898, No. 2. 7 pp.
- _____. 1898b. List of species of the Lithothamnia. Kgl. Norske
Vidensk. Selsk. Skr. 1898, No. 3. 11 pp.

Foslie, M. H. 1898c. Remarks on the nomenclature of the Lithothamnia.

Kgl. Norske Vidensk. Selsk. Skr. 1898, No. 9. 7 pp.

_____. 1900a. New or critical calcareous algae. Kgl. Norske Vidensk. Selsk. Skr. 1899, No. 5. 34 pp.

_____. 1900b. Calcareous algae from Funafuti. Kgl. Norske Vidensk. Selsk. Skr. 1900, No. 1. 12 pp.

_____. 1900c. Revised systematical survey of the Malobesiace.

Kgl. Norske Vidensk. Selsk. Skr. 1900, No. 5. 22 pp.

_____. 1901. New Malobesiace. Kgl. Norske Vidensk. Selsk. Skr. 1900, No. 6. 24 pp.

_____. 1903. The lithothamnia of the Maldives and Laccadives, pp. 460-471, Pls. 24 & 25. In J. S. Gardiner (ed.), The Fauna and geography of the Maldivian and Laccadive archipelagoes. Cambridge, Vol. 1.

_____. 1904. Lithothamnionaceae, Malobesiace, Mastophorace, pp. 10-77, Pls. 1-13. In A. Weber-van Bosse and M. Foslie, The Corallinaceae of the Siboga Expedition. Siboga Expeditie 61.

_____. 1905. New Lithothamnia and systematical remarks. Kgl. Norske Vidensk. Selsk. Skr. 1905, No. 5. 9 pp.

_____. 1906. Algologiske notiser, II. Kgl. Norske Vidensk. Selsk. Skr. 1906, No. 2. 28 pp.

_____. 1907. Algologiske notiser, III. Kgl. Norske Vidensk. Selsk. Skr. 1906. No. 8. 34 pp.

_____. 1907-1909. The Lithothamnia, pp. 177-192, Pls. 19 & 20.

In Reports of the Percy Sladen Trust Expedition to the Indian Ocean

- in 1905, under the leadership of Mr. J. Stanley Gardiner, Vol. 1.
 Trans. Linnean Soc. London, Ser. 2 (Zoology), Vol. 12.
- Foslie, M. H. 1909. Algologiske notiser, VI. Kgl. Norske Vidensk.
 Selsk. Skr. 1909, No. 2. 63 pp.
- Gunnerus, J. E. 1768. Om nogle Norske Coraller. Kgl. Norske Vidensk.
 Selsk. Skr. (Not seen.)
- Hauke, F. 1885. Die Meeresalgen Deutschlands und Oesterreichs. Dr. L.
 Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der
 Schweiz, 2nd ed. 2: 1-375; Pls. 1-5.
- Meydrich, F. 1897a. Neue Kalkalgen von Deutsch-New-Guinea (Kaiser
 Wilhelms-Land). Bibliotheca Botan. 7(41): 1-11; Pl. 1.
- _____. 1897b. Corallinaceae, insbesondere Malobesiae. Ber.
 Deut. Botan. Ges. 15: 34-70; Pl. 3.
- _____. 1897c. Malobesiae. Ber. Deut. Botan. Ges. 15: 403-420;
 Pl. 18.
- _____. 1900. Weiterer Ausbau des Corallinesystems. Ber. Deut.
 Botan. Ges. 18: 310-317.
- _____. 1911. Lithophyllum incrassans. Phil., mit einem Nachtrag
 "über Paraspore fruticulosa (Kts.) Meydr. Bibliotheca Botan., Vol.
 18. (Not seen.)
- Howe, M. A. 1920. Class 2. Algae, pp. 553-618. In N. L. Britton and
 C. P. Millspaugh, The Bahama flora. Published by the authors.
- Ishijima, W. 1954. Cenozoic coralline algae from the western Pacific.
 Published by the author. 87 pp. Pls. 1-49.

- Johnson, J. H. 1954. An introduction to the study of rock building algae and algal limestones. *Quart. Colorado School Mines* 49(2): 1-117.
- _____. 1957. Calcareous algae, pp. 209-246, Pls. 37-60. In *Geology of Saipan, Mariana Islands*. U. S. Geol. Survey Professional Paper 280, Z-J.
- Kylin, H. 1956. Die Gattungen der Rhodophyceen. CWK Gleerups Förlag, Lund. 673 pp.
- Lamarck, J. B. 1801. *Système des animaux sans vertèbres*. Paris. 432 pp.
- Lamouroux, J. V. F. 1812. Extrait d'un mémoire sur la classification des polypiers coralligènes non entièrement pierreux. *Nouv. Bull. Sci. Soc. Philom. Paris* 3: 181-188.
- Lemoine, Mme P. 1911. Structura anatomique des Malobésées, application à la classification. *Ann. l'Institut Océanogr.* 2(2): 1-213; Pls. 1-5.
- _____. 1928. Un nouveau genre de Malobésées: Mesophyllum. *Bull. Soc. Bot. France* 75: 251-254. (Not seen.)
- Linnæus, C. 1767. *Systema naturae*. Ed. 12. 1(2): 533-1327.
- Mason, L. R. 1953. The crustaceous coralline algae of the Pacific Coast of the United States, Canada and Alaska. Univ. California Publ. Botany 26(4): 313-389; Pls. 27-46.
- Pallas, P. S. 1766. *Elenchus scophytorum*. *Hague Comitum*. (Not seen.)
- Philippi, R. A. 1837. Beweis, dass die Nulliporen Pflanzen sind, pp. 387-393, Pl. 9. In A. F. A. Wiegmann (ed.), *Archiv für Naturgeschichte*, 3rd Set, Vol. 1.

- Printz, H. (ed.). 1929. M. Foslie. Contributions to a monograph of the Lithothamnia. Kgl. Norske Vidensk. Selsk. Museet. 60 pp., Pls. 1-75.
- Rosanoff, S. 1866. Recherches anatomiques sur les Malobésiaes. Mem. Soc. Imp. Sci. Nat. Cherbourg, Vol. 12. (Not seen.)
- Rothpletz, A. 1891. Fossile Kalkalgen aus den Familien der Codiaceen und der Corallineen. Z. Deut. Geol. Ges. 40(2): 295-322; Pls. 15-17.
- Schmitz, F. 1889. Systematische Übersicht der bisher bekannten Gattungen der Florideen. Flora 72: 435-456. (Not seen.)
- Setchell, W. A. 1924. American Samoa: Part I. Vegetation of Tutuila Island, Part II. Ethnobotany of the Samoans, Part III. Vegetation of Rose Atoll. Carnegie Inst. Washington, Dept. Marine Biol., Publ. No. 341, 20: 1-275; Pls. 1-37.
- _____. 1926. Phytogeographical notes on Tahiti, II. Marine vegetation. Univ. California Publ. Botany 12(8): 291-324.
- _____. 1943. Mastophora and the Mastophoreae: genus and subfamily of Corallinaceae. Proc. Nat. Acad. Sci. 29(5): 127-135.
- _____. and L. R. Mason. 1943. Goniolithon and Neogoniolithon: two genera of crustaceous coralline algae. Proc. Nat. Acad. Sci. 29: 87-92.
- Solms-Laubach, H. 1881. Die Corallinenalgen des Golfes von Neapel. Fauna und Flora des Golfes von Neapel, Leipzig 4: 1-64; Pls. 1-3.
- Suneson, S. 1937. Studien über die Entwicklungsgeschichte der Corallinaceen. Lunds Univ. Årsskrift, New Series 33(2): 1-102; Pls. 1-4.
- _____. 1943. The structure, life-history and taxonomy of the Swedish Corallinaceae. Lunds Univ. Årsskrift, New Series 39(9): 1-66; Pls. 1-9.

Taylor, W. R. 1950. Plants of Bikini and other Northern Marshall Islands. Univ. Michigan Studies, Scientific Series 18: 1-227; Pls. 1-79.