The Genera Lithothamnium, Leptophytum (nov. gen.) and Phymatolithon in the Gulf of Maine

by

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INTRODUCTION

This is the fourth in a series of papers on the biosystematics and ecology of the crustose corallines of the Gulf of Maine. The earlier papers treated the genera *Phymatolithon* (ADEY, 1964), *Clathromorphum* (ADEY, 1965) and *Pseudolithopyllum* (ADEY, 1966). This paper deals primarily with the two remaining genera of the non-epiphytic crustose coralline flora of the region, though an additional species of *Phymatolithon* is also treated.

The writer is presently planning to begin a study of the types of the North Atlantic crustose coralline flora during a visit to Europe in 1966. Until all of the crustose coralline types, especially the generic types, have been re-studied from a modern point of view, there will remain nomenclatural uncertainties. There are certain assumptions regarding the types which are made in this paper. Most are probably valid, but a more certain stabilization of the nomenclature will only follow type re-study.

Only two species of branching *Lithothamnium* are distinguished here. These two types are generally easily separable on the basis of anatomy and surface morphology. However, it is apparent that both of these species develop a wide variety of branch forms, depending upon the ecological conditions under which they grow, and it seems

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likely that the larger number of species described for the northwest North Atlantic in older works are a reflection of this (see the compilation of TAYLOR, 1957). Many species of branching *Lithothamnium* were distinguished by the older workers in the northeast North Atlantic, and it remains to be seen whether or not these are valid. Until all of the type specimens involved can be restudied, definite determinations of branching *Lithothamnium* in this region would invite additional nomenclatural confusion. Temporarily the two species involved in this work will be given only the designations *Lithothamnium* "a" and *Lithothamnium* "b".

Although these two species differ in branch form, color and conceptacle and pit body size, they are alike in bearing a large-celled intercalary meristem, similar to that found in *Clathromorphum.* However, the meristem is overlain only by a thin, non-photosynthetic epithallium, the cells of which have a morphology peculiar to branching *Lithothamnium.* In both of these respects they differ markedly from the thin crustose types originally placed in *Lithothamnium* and now treated as *Phymatolithon* and *Leptophytum.* It is primarily on the basis of this uniformity in anatomy in parallel with the branching habit that the genus *Lithothamnium* is here restricted to species having these characteristics.

Only *Lithothamnium laeve* and *L. foecundum* are now being placed in the new genus *Leptophytum.* In many respects, these plants are similar anatomically to the members of *Phymatolithon.* However, they differ in having a much shallower conceptacle primordium, distinctive "pore cells" in the asexual conceptacle roof, and a lateral development of gonimoblasts. *Lithothamnium lenormandi* is intermediate between *Phymatolithon* and *Leptophytum* with regard to conceptacle primordial position. However, in all other respects it is similar to *Phymatolithon* and is here placed in that genus.

Lithothamnium "a" and *Leptophytum laeve* occur throughout the Gulf of Maine and are the dominant coralline species in deep water. *Lithothamnium* "b" also occurs throughout the Gulf, but it is a plant primarily of the shallow sublittoral. *Phymatolithon lenormandi* is restricted to the western and eastern Gulf and is almost exclusively intertidal in occurrence. *Leptophytum foecundum* is primarily an arctic plant. It is the rarest of the Gulf of Maine crustose corallines and very sporadic in its occurrence in this region.

TAXONOMIC SYNOPSIS

Lithothamnium Phillipi, emend.

Plants initially crustose, eventually developing protuberances and becoming branched to various degrees; hypothallium sub-parallel to the substrate, filaments primarily turning up to form the perithallium, short dead-ended filaments also bending downward; epithallium non-photosynthetic and generally a single layer (sometimes 3 or 4) of thick-walled cells of somewhat rectangular cross-section; meristem intercalary, consisting of large cells; perithallial cells nearly maximum length before being cut-off from the meristem; conceptacle primordia formed directly from meristem; asexual sporangia with thick cap walls (i.e. conceptacles with many pores) that stain darkly with phosphotungstic hematoxylin; male and female conceptacles formed by overgrowing of lateral perithallial tissue; spermatangia borne in dendroid clusters completely clothing the conceptacle walls.

Lithothamnium "a"

Plants initially thin crusts, with a tendency to develop very small, white growth ridges, shortly producing low mounds which develop into branches characteristically 2—3 mm in diam.; branch form and relative development of basal crust highly variable depending on environmental conditions, plants becoming as much as 10 cm thick, large or small fragments breaking from the substrate and continuing to develop free in forms ranging from individual, contorted branches to subspherical masses; yellowish-pink; hypothallium 4—17 cells, 28—98μ thick, cells 13.5—36.5μ long and 5—11.5μ diam.; perithallial cells 3.5—14μ long and 3—10μ diam. (cell lumen), meristem the uppermost layer of cells, conspicuous; epithallium generally present, thin, 1—3 cytologically distinct cells; sporangial conceptacle primordia developed directly from perithallial meristem; mature conceptacle roofs 80—310μ diam. with 13—56 pores, bisporic, rarely tetrasporic, cavity 148—309μ diam., 90—158μ high; single male plant, no female plants found in the Gulf of Maine.

Lithothamnium "b"

Plants initially thin, smooth crusts, eventually producing low mounds which develop into branches characteristically 0.5—2 mm diam.; branch form and relative importance of the development of the basal crust highly variable depending on environmental conditions, tendency for basal crust to be well-developed, plants becoming as much as 7 cm thick, large fragments occasionally breaking free from the substrate and continuing to develop free as subspherical masses; pink-violet to brown; hypothallium 10—38 cells, 42—220μ thick, cells 11.5—34.5μ long, 3.5—8.5μ diam.; perithallial cells 3.5—12.5μ long, 2—7.5μ diam. (cell lumen), meristem the uppermost layer of cells, conspicuous; epithallium generally present, thin, 1—3 cytologically distinct cells; sporangial conceptacle primordia developed directly from perithallial meristem, mature conceptacle roofs 120—280μ diam. with 11—83 pores, bisporic, cavity 178—315μ diam., 135—180μ high; no sexual plants found in the Gulf of Maine.

Leptophytum ADEY, gen nov.

Plantae tenuiter crustacea; hypothallium multilaminatum substrato subparallelum; epithallium ex cellulis rotundatis non photosyntheticis parietibus tenuibus constitutum; meristemma prope superficiem, cellulis perithallialibus gradatim elongatis cum profunditatem; conceptaculi primordium ex perithallio superiore ex adventicio sub strato 1—3 cellulis latum formatum; conceptacula asexualia multiporosa, cellulae porae praesentes; gonimoblasti ex cellulo irregulari ex fusuris constito lateraliter producti; spermatangia parietes conceptaculi masculini ubique investientia.

Species typica: *Leptophytum laeve* (STRÖMFELT) ADEY, comb. nov. (*Lithophyllum laeve* STRÖMFELT in Om Algvegetationen vid Islands Kuster, H. E. G STRÖMFELT, 1886, Academisk afhandling, Göteborg.)

Plants thin crusts; hypothallium subparallel to the substrate, turning up to form the perithallium, short dead-ended filaments also turning downward; epithallium absent or of a few, thin-walled, rounded, non-photosynthetic cells; small-celled meristem near surface, perithallial cells gradually lengthening with burial; conceptacle primordia formed adventitiously from the upper perithallial cells, the overlying sheet of one to three cells raised up and sloughed off; asexual sporangia with thick cap walls (i.e., conceptacles with many pores), distinct "pore cells" present; male and female conceptacle roofs formed by overgrowing of lateral perithallial tissue; gonimoblasts developed laterally from an irregular fusion cell; spermatangia completely clothing the conceptacle walls.

Leptophytum laeve (STRÖMFELT) ADEY, comb. nov.

Lithothamnium laeve (STRÖMFELT) FOSLIE.

FOSLIE, 1898, p. 7; ROSENVINGE, 1899, p. 14; FOSLIE, 1901, p. 15; JONSSON, 1901, p. 153; BØRGESON, 1902, p. 401; JONSSON, 1904, p. 6; DE TONI, 1905, p. 1757; FOSLIE, 1905, pp. 16, 131, 1906, p. 3, 1908, p. 6; ROSENVINGE, 1910, p. 100; LEMOINE, 1911, p. 74; ROSENVINGE, 1917, p. 215, 1926, p. 36; HOWE, 1927, p. 26; FOSLIE, 1929, pp. 43, 51; ROSENVINGE, 1935, p. 10; TAYLOR, 1957, p. 246; LUND, 1959, p. 198.

Lithophyllum laeve STRÖMFELT.

STRÖMFELT, 1886, p. 21; FOSLIE, 1891a, p. 10;

Lithophyllum lenormandi f. *laeve* (STRÖMFELT) FOSLIE

FOSLIE, 1891b, p. 45.

Lithothamnium stromfeltii FOSLIE, f. *tenuissima* FOSLIE

FOSLIE, 1895, p. 173, in part.

Plants crustose, 50μ to 320μ thick; the vegetative surface often quite smooth, though sometimes bearing faint marginal growth ridges and central growth patches; pink to pink-violet; hypothallium 2—8 cells, 14—110μ thick with cells 8.5—36.5μ long, 3.5—14.5μ diam.; perithallial cells 1.5—16μ long, 3.5—14μ diam. (cell lumen), not markedly zonate or layered, meristem surficial or nearly so; epithallium single layer of cells or not present; conceptacle primordia developed adventitiously a few cells below the top of the perithallium; cover of one to two cells sloughed off; all conceptacles elevated at maturity; sporangial conceptacles producing tetraspores or bispores, often covering the surface of the plant, pore plate 270—480μ in diam. with 33—150 sporangia, conceptacle cavity 320—580μ diam., 130—300μ high; spermatangial conceptacles 90—190μ high, cavity 150—385μ in diameter, spermatangia dendritic-borne on all walls of the cavity; carpogonial conceptacles 130—320μ high, cavity 155—320μ in diameter; procarp consisting of a supporting auxiliary cell with one or two sterile cells and a single, two-celled carpogonial filament, fragmentary fusion cell developed primarily by fusion of the auxiliary cells, gonimoblasts and large carpospores produced laterally.

Lepthophytum foecundum (KJELLMAN) ADEY, comb. nov.

Lithothamnium foecundum KJELLMAN.

KJELLMAN, 1883, p. 99; FOSLIE, 1895, p. 137; ROSENVINGE, 1899, p. 12; FOSLIE, 1898, p. 12; JONSSON, 1901, p. 153; DE TONI, 1905, p. 1739; FOSLIE, 1905, p. 21; ROSENVINGE, 1910, p. 100, 1926, p. 37; FOSLIE, 1929, p. 40; ZINOVA, 1955, p. 85; TAYLOR, 1957, p. 246; LUND, 1959, p. 198.

Plants crustose, 74—500μ thick; the vegetative surface generally quite smooth, though sometimes bearing faint marginal growth ridges and central growth patches; pink to pink-violet, very glossy; hypothallium 4—8 cells, 18—70μ thick with cells 10.5—24.5μ long, 4—14μ diameter; perithallial cells 2—14μ long and 3—10μ diameter (cell lumen), not layered but sometimes zonate, meristem surficial or nearly so; epithallium single layer of cells or not present; sporangial conceptacle primordia developed adventitiously a few cells below the top of the perithallium, cover of one to two cells sloughed off, conceptacles lightly raised at maturity and with a marked, raised margin, usually densely covering much of the surface of the plant; sporangia bisporic or tetrasporic, pore plate 137—210μ in diameter with 26—62 sporangia, conceptacle cavity 245—360μ in diameter, 125—170μ high, asexual conceptacles often continuing to grow apically after internal degeneration becoming short, narrow "pseudobranches"; spermatangial, carpogonial and carposporic conceptacles unknown in this study.

Phymatolithon FOSLIE emend. ADEY
(see ADEY 1964)

Phymatolithon lenormandi (ARESCHOUG) ADEY, comb. nov.

Lithothamnium lenormandi (ARESCHOUG) FOSLIE.

FOSLIE, 1895, p. 179; HEYDRICH, 1900, p. 78; JONSSON, 1901, p. 154; BØRGESON, 1902, p. 401; FOSLIE, 1905, p. 12; DE TONI, 1905, p. 1756; LEMOINE, 1911, p. 81; ROSENVINGE, 1917, p. 216; MAZZA, 1922, p. 1103; LEMOINE, 1923, p. 465; ROSENVINGE, 1926, pp. 43, 51; LEMOINE, 1931a, p. 4, 1931b, p. 61; KNIGHT & PARKE, 1931, p. 103; ROSENVINGE, 1935, p. 10; SUNESON, 1943, p. 4; HAMEL & LEMOINE, 1953, p. 88; ZINOVA, 1955, p. 83; TAYLOR, 1957, p. 245; DAWSON, 1960, p. 20; MASAKI & TOKIDA, 1961, p. 163.

Lithophyllum lenormandi (ARESCHOUG) ROSANOFF

ROSANOFF, 1866, p. 85; SOLMS-LAUBACH, 1881, p. 15; HAUK, 1885, p. 267; FOSLIE, 1891a, p. 9.

Melobesia lenormandi ARESCHOUG

ARESCHOUG, 1852, p. 514; FARLOW, 1881, p. 181.

Squamolithon lenormandi (ARESCHOUG) HEYDRICH

HEYDRICH, 1911, p. 32.

Lithothamnium squamulosum FOSLIE

FOSLIE, 1895, p. 183.

Plants crustose, 40—210μ thick; the vegetative surface smooth to lightly-irregular when young, sometimes becoming squamulose; pink-violet to violet, very glossy when vegetative; hypothallium 4 -10 cells 14 -75μ thick with cells 8—35μ long and 3—11μ diameter; perithallial cells 1.5—12μ long, 3.5—10μ diam. (cell lumen), meristem surficial or nearly so; epithallium when present a single layer of cells, frequently sloughed off and absent; all conceptacles developed adventitously from a sunken primordium centrally 5—7 cells below the surface, at maturity raised above the surrounding surface; sporangial conceptacles mostly producing bisporangia, some tetrasporangia, conceptacles heavily crowded centrally giving the plants a rough appearance, pore plate with 6—34 pores, 80—210μ diam., conceptacle cavity 122—267μ diam., 80—138μ high; spermatangial conceptacle cavity 136—210μ diam., 73—122μ high; carpogonial conceptacles always hermaphroditic (Gulf of Maine) with at least a limited development of spermatangial clusters included, conceptacle cavities 97—145μ diam., 57—115μ high; carpogonial filaments developed over entire conceptacle bottom, at maturity filaments typically consisting of an auxiliary cell supporting a single sterile cell and a two-celled carpogonial filament-supporting cells and carpogonium; evidence of fertilization or development of oöblasts, or general fusions lacking, carpospores apparently developed directly from auxiliary cells over much of the bottom excepting the centermost area; at maturity cystocarpic conceptacle cavities 145—275μ diam. and 95—160μ high.

VEGETATIVE ANATOMY

Both *Lithothamnium* "a" and *Lithothamnium* "b" develop initially as crusts on a hard substrate. Such plants, when young and less than about one-half centimeter in diameter, often lack evidence of branches and can be very difficult to identify with certainty without sections. Larger plants would generally show protuberances, and seldom offer any problems of generic differentiation, even with superficial examination.

The diameter and density of the initial protuberances, and eventually the branches, are quite variable in both species and depend markedly upon the ecological conditions. Typically *Lithothamnium* "a" has densely-spaced branches having a diameter of 2—3 mm (Figs.

10—A, B; 12), while in *Lithothamnium* "b" they are more scattered and smaller, 0.5—2 mm in diameter (Fig. 14). However, *Lithothamnium* "a" can develop very small branches (Figs. 9—B, 11—D, E) as well as a lower branch density (Figs. 10—C, 11—A) than generally found. Also, *Lithothamnium* "b" can be very densely-branched (Fig. 18), and the branches can develop to quite a large diameter (Fig. 16). Usually, when both species are growing together under the same conditions, they are easily distinguished on the basis of branch diameter and density (Fig. 14). However, the matter can be further complicated by one species growing over the other.

The relative development of basal crust (interbranch area) and branch length in both species is apparently also a function of ecological conditions. Although it is more often true of *Lithothamnium* "b", in either species the basal crust, after the initial appearance of the protuberance, can develop nearly as rapidly as the branch tips. The result is a relatively thick crust and short branches (Fig. 17). On the other hand, in both cases the basal crust development can be suppressed, the branches then becoming relatively long and branched to higher orders. Figures 12 and 13 show the strong effect on branching that position can have. The plants on the top-side of the boulder are densely-branched and the basal crust strongly-developed. The same plants, where they extend into the lateral surface, exhibit a relatively sparse branching with a strongly-suppressed basal crust. This specimen was taken from the northwest coast of Newfoundland, but is shown here since it demonstrates quite well characters used in the past for species differentiation in the same plant.

The branching pattern is further complicated by the presence of boring organisms (especially clams and worms), which can be responsible for a large amount of dissection (Fig. 18). It is primarily the *Lithothamnium* and *Clathromorphum* species, which produce, when bored, the porous, biostromal character of the coralline bottom in many areas. Such boring along with wave action and the activities of larger organisms also eventually result in the breaking up of the plants. Plant fragments of both species (though most abundantly *Lithothamnium* "a") when falling on a pebble or finer bottom under the influence of an intermediate amount of wave action continue to develop on all sides, producing the specimens called "free" plants (Fig. 11). The branch size and density in the free plants is also highly variable, apparently depending primarily on the weight of the initial specimen and the coarseness of the bottom. Although from southern Labrador, the specimen in figure 11—E is included, since it also shows so well in the same plant (there is no question of this) characters of branching which past workers would have deemed quite sufficient for specific differentiation.

In summary, branch form in these species apparently has a genetic basis, but is strongly modified by ecological conditions, especially grain size of substrate, weight and size of specimen and light and wave action. Although branch form certainly can be used for specific determination, it necessarily must be used with great care.

Lithothamnium "a" and *Lithothamnium* "b" generally differ from each other strongly with regard to color and texture. The latter species is somewhat darker than *Lithothamnium* "a" and generally is brownish-red rather than pink or light red. Also the surface is usually glossier than it is in *Lithothamnium* "a". However, these are also characters that must be used with care, especially since the intensity of the color depends to a very large extent on the amount of exposure the plant has had to light while growing. Once familiar with the plants in the field, differentiation between the species on the basis of branching, color, and texture is usually not too difficult, though in some cases sections are necessary.

Leptophytum laeve and *L. foecundum* are thin crustose species (Figs. 21—24). Neither shows any major surface irregularities, except those created by overgrowing of an irregular substrate, though both tend to have vague marginal "growth ridges." Overgrowth of one plant by another seems to be quite rare in both species, and continued development of the perithallium is restricted. The maximum thickness that has been encountered in *L. laeve* is about 450 μ (mean 227 μ), in *L. foecundum* a maximum of 500 μ (mean 175 μ). Although buried asexual conceptacles were never encountered in *L. laeve*, they are frequent in *L. foecundum*.

As will be discussed below, the asexual conceptacles of the two species are makedly different in surface appearance. Since conceptacles are very common and those in *Leptophytum foecundum* are smaller and bear a distinct raised rim, identification is not too much of a problem (Figs. 22, 24). Also *L. foecundum* under similar circumstances is darker in color, somewhat more purplish and glossier than *L. laeve*.

Phymatolithon lenormandi is also a thin, crustose species. In this case local overgrowth is frequent and the plants are often somewhat imbricate (Fig. 26). However, this increases the thickness little, the maximum encountered being 210 μ. The conceptacles, which are generally present centrally in the plants are small and very densely-spaced, creating a very fine, rough appearance which is quite characteristic (Figs. 25, 26).

In all of the species treated in this paper, the hypothallium consists of filaments of elongate cells lying subparallel to the substrate and oriented lengthwise in the direction of lateral growth (Figs. 27, 31, 35, 47). In each case, the thickness at the growing margins is primarily that of the hypothallium, additional plant thickness being formed by perithallium. As in all of the species previously covered by the writer, the hypothallium consists largely of upward arching filaments, though downward arching dead-ended filaments also occur.

Numerical data for the hypothallia of the plants studied are given in Table I. The data were not separated according to depth. An attempt was made to differentiate between shallow and deep water plants in *Leptophytum laeve*, but no significant difference in cell dimensions could be demonstrated.

Lithothamnium "b" as a population possesses a hypothallium which is markedly thicker than *Lithothamnium* "a". However, the cells of *Lithothamnium* "b" are consistently smaller than those of *Lithothamnium* "a", paralleling the condition in the perithallium (see below).

The hypothallial cells of *Leptophytum laeve* are somewhat larger than those of *L. foecundum.* This difference is especially marked in cell diameter. Although *L. laeve* showed significantly fewer cell layers in the hypothallium, the larger cells present produce a tissue thickness which is close to that in *L. foecundum.*

Phymatolithon lenormandi has hypothallial cells which are essentially the same size as those found in *Ph. laevigatum.* However, there are significantly more layers of cells present in *Ph. lenormandi* and the tissue is markedly thicker. *Ph. rugulosum* with its very narrow cells is intermediate between the other species with regard to hypothallial thickness.

Anatomical drawings of the uppermost perithallium and epithallium of each of the saxicolous Lithothamnieae found in the Gulf of Maine are given in Plate X. These are based only on light microscopy. Although the cell dimension and density in each case are drawn from particular examples, details such as cell thickness are composite being derived from many slides stained in phosphotungstic hematoxylin as well as Delafields.

Both *Lithothamnium* "a" and *Lithothamnium* "b" possess epithallial cells of distinctive morphology (Figs. 51, 52). The inner walls of these cells are relatively thick and somewhat rectangular in vertical section, while the upper parts tend to "flare-out." This is also true of all of the North Atlantic branching Lithothamnieae that the author has had the opportunity to examine in section, including a collection of 14 species identified by FOSLIE. In both *Lithothamnium* "a" and *Lithothamnium* "b" the meristem cell tends to be somewhat large and distinct, a situation similar to that found in *Clathromorphum*, but markedly different from the pattern in *Phymatolithon* and *Leptophytum.* Also, in the cytoplasm of the uppermost parts of the meristem cells, the branching species have a distinctive hyaline cap,

Table I
Hypothallia Data

Species			Lithothamnium "a"	Lithothamnium "b"	Leptophytum laeve	Leptophytum foecundum	Phymatolithon lenormandi	P. rugulosum (see Adey, 1964)	P. laevigatum (see Adey, 1964)
		Data from	30 cells 20 plants 14 stations	30 cells 19 plants 15 stations	111 cells 29 plants 20 stat.	48 cells 8 plants 8 stations	45 cells 12 plants 9 stations		
Cell Length (µ)		max.	36.5	34.5	36.5	24.5	35	31	31
		mean	20	18.5	20.5	18	16.5	17	17
		min.	13.5	11.5	8.5	10.5	8	8	8.5
Cell Diameter(µ)		max.	11.5	8.5	14.5	14	11	7	8.5
		mean	7	6	9	6.5	6	4.5	6
		min.	5	3.5	3.5	4	3	3	3
Hypothallial Thickness	No. of cells	max.	17	38	8	8	10	8	5
		mean	9	17	4	6	6	5	4
		min.	4	10	2	4	4	3	2
	(µ)	max.	98	220	110	70	75	50	36
		mean	57	112	42	40	36	30	23
		min.	28	42	14	18	14	17	13

which has not been found elsewhere among the crustose corallines.

The "pit bodies" found in both of these plants are similar to those found in both *Leptophytum* and *Phymatolithon*. However, those in *Lithothamnium* "b" are generally larger than those in *Lithothamnium* "a" (Figs. 51, 52 & Table II). This is a very useful distinction and can be applied to relatively small fragments of tissue, though, in general, the conceptacle roof tissue if available, provides the strongest differentiation.

The arrangement of perithallial cells into horizontal layers has been generally considered to be a characteristic of the Lithophylleae and *Mesophyllum* (JOHNSON, 1961). However, it is also developed to some extent in branching *Lithothamnium* (Figs. 29, 33). Of the two species considered here, it is most strongly developed in *Lithothamnium* "b" (Table II). Zonation, or the development of a horizontal cell layering pattern of second order, also appears in these plants, though here again it is most strongly developed in *Lithothamnium* "b" (Table II).

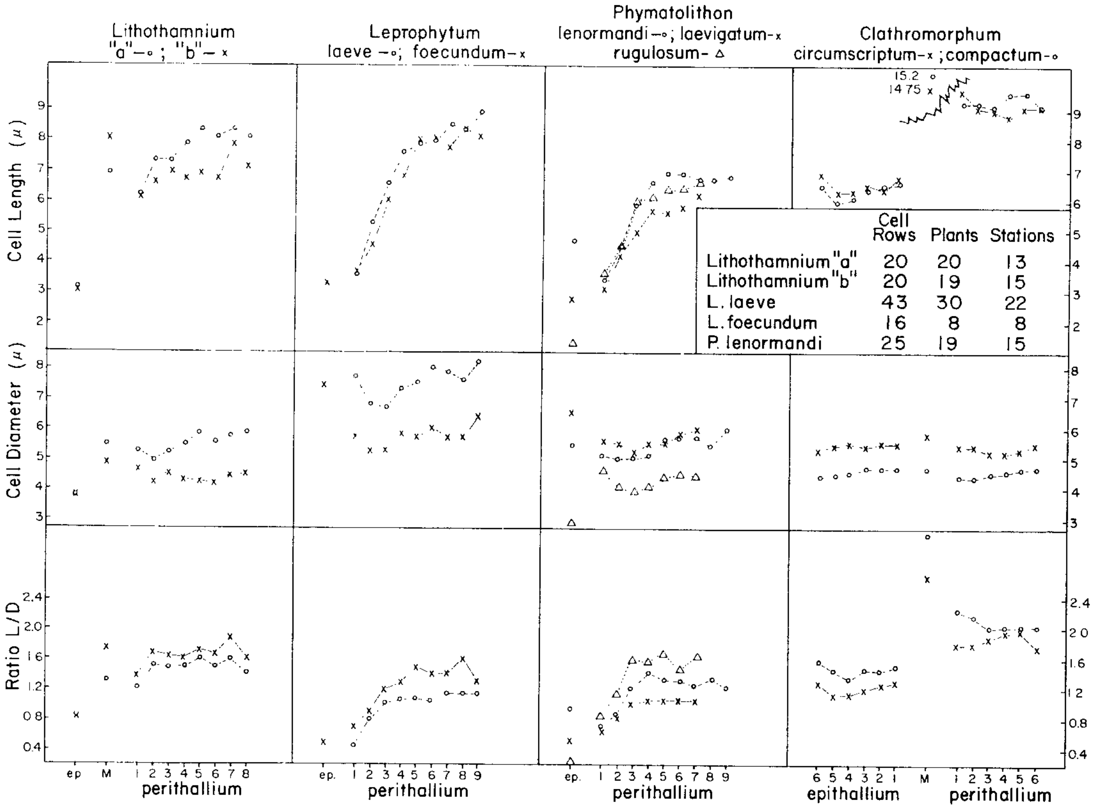
Phymatolithon and *Leptophytum* are quite similar with regard to epithallial and perithallial anatomy. It is on the basis of reproductive structures that these closely-related genera are separated. As discussed previously (ADEY, 1965a), in the *Clathromorphum* species, the epithallium is thick and has become specialized for photosynthesis (Figs. 58, 59 – Note: due to space limitations, for these illustrations examples were chosen with relatively thin epithallia). Thus, with regard to epithallial and perithallial anatomy, the Lithothamnieae of the region fall into three distinct groups; *Lithothamnium*, *Phymatolithon-Leptophytum* and *Clathromorphum*. With only a very small fragment of vegetative tissue from the upper parts of a crust it is possible to place a plant in one of these groups. *Pseudolithophyllum orbiculatum* is the only primary rock-encrustor found in the region which does not fall into the grouping. However, because of its secondary pits and relatively thick but non-photosynthetic epithallium, it is very easily distinguished in section.

The mean length (pit to pit), diameter (lumen) and length/diameter ratio of the epithallial, meristem and perithallial cells of the species being treated are plotted in Figure 1. Except for *Leptophytum foecundum*, for which only summer plants were available, the data are means of seasonal means and are derived more or less evenly throughout the depth range of each species. The data from the earlier *Phymatolithon* and *Clathromorphum* papers, reduced to the same basis, are also included for comparison. The epithallial and perithallial tissues are separated in all cases. In *Lithothamnium* and *Clathromorphum*, the meristem is also separated since in these genera it is morphologically distinct. In the other genera the meristem is not shown

Table II Characteristics of Pit Bodies, Layering and Zonation in *Lithothamnium*

		Pit Bodies					Zonation			Layering		
		State of Development										
	Tissue	Large	Medium	Small	Very Sm.	Apparently rings or plates	Strong	Present	Weak or Absent	Strong	Present	Weak or Absent
Lithothamnium "a"	Uppermost Perithal=lium	0/20	0/20	7/20	10.5/20	2.5/20						
	Lower Perithal-lium	1/20	0/20	1/20	2/20	16/20	0/20	6/20	14/20	2/20	3/20	15/20
	Asexual Concep-tacle Roof	0/12	0/12	4/12	8/12	8/12						
	Hypothal-lium	0/9	0/9	0/9	2/9	7/9						
Lithothamnium "b"	Uppermost Perithal-lium	15/20	2/20	3/20	0/20	0/20						
	Lower Perithal-lium	2/20	1/20	9/20	8/20	0/20	5/20	8/20	7/20	8/20	6/20	6/20
	Asexual Concep-tacle Roof	7/7	0/7	0/7	0/7	0/7						
	Hypothal-lium	5/11	0/11	4/11	1/11	1/11						

Fig. I



	Cell Rows	Plants	Stations
Lithothamnium "a"	20	20	13
Lithothamnium "b"	20	19	15
L. laeve	43	30	22
L. foecundum	16	8	8
P. lenormandi	25	19	15

separated, though normally it would be the uppermost cell below the epithallium.

Disregarding the great difference in the development of the epithallium, the growth patterns in the two species of *Lithothamnium* are somewhat similar to those of *Clathromorphum.* However, the meristem cells are not as elongate relative to the underlying and overlying tissues. Also, apparently there is some elongation of the perithallial cells after they are cut off in the meristem, though it is not nearly as marked as in *Leptophytum* or *Phymatolithon.* Both of the species of *Lithothamnium* show basically the same pattern. In parallel with the situation in the hypothallium, the cells of *Lithothamnium* "a" are generally larger than those of *Lithothamnium* "b".

In *Phymatolithon* and *Leptophytum* the basic patterns of development of the perithallium and epithallium are the same in both genera, though the species of the former genus treated here tend to have larger cells than *Phymatolithon.* Because of the much larger cell size in well-developed perithallium and hypothallium, in section it would be difficult to confuse *Leptophytum laeve* with any of the other species, even lacking reproductive structures and surface data. Also, in this region, because of the "staining bodies" of *Phymatolithon laevigatum*, the general overlapping habit of *P. lenormandi* and the narrow cell of *P. rugulosum* it would generally be possible to distinguish these from *Leptophytum foecundum* and from each other in section even without reproductive structures. Also, asexual conceptacles are generally present in the latter species, and these are quite distinctive.

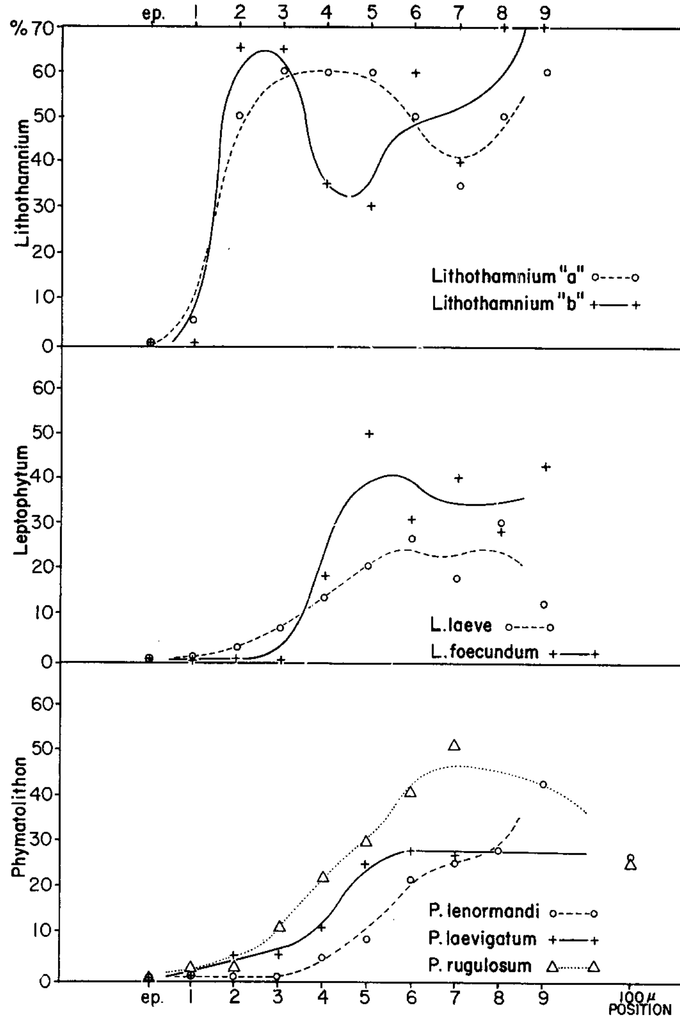
In *Leptophytum laeve* attempts were made to distinguish between the perithallial cell size of the following groups: (a) summer plants vs. winter plants, (b) plants from less than 9 meters vs. those from deeper water, (c) plants less than 70 μ thick vs. thicker plants. In no case could a significant difference be obtained.

The percentage of cell fusions between adjacent cells as seen in vertical sections are given in figure 2. The curves drawn are bi-cell moving averages. In magnitude and form, the *Leptophytum* species and *Phymatolithon lenormandi* have a fusion pattern which is quite similar to that found for *P. laevigatum* and *P. rugulosum* (also included in figure 2 for reference). In contrast, the *Lithothamnium* species show high and irregular percentages of fusions, quite high values being reached immediately below the meristem.

ASEXUAL REPRODUCTION

The general pattern of development of the asexual conceptacles in the Lithothamnieae was discussed in an earlier paper on *Phymatoli-*

Fig. 2



thon (Adey, 1964). It was pointed out that members of *Phymatolithon* develop their conceptacle primordia adventitiously, deep in the perithallium. The same pattern is found in *P. lenormandi*, though the depth of the primordium is not nearly as great (only five to seven cells centrally, Figs. 43, 99), and the resulting disc is not as conspicuous.

In *Leptophytum laeve* and *L. foecundum*, the conceptacle primordia are also adventitious below the meristem (Figs. 60, 96), but typically it is derived from the third cell layer. In these cases, the "disc" is only a thin, white "skin" which sloughs off in fragments. Thus, with regard to the position of the conceptacle primordia, as well as the pattern of division and growth in the upper perithallium, *Phymatolithon laevigatum*, *P. rugulosum*, *P. lenormandi*, *Leptophytum laeve* and *L. foecundum* are quite similar. There is a range in primordial depth from the deeply sunken condition in the first two species, to the very shallow condition in the last two species, with *Phymatolithon lenormandi* being intermediate. Probably the genera are closely related. However, the *Leptophytum* species possess differentiated pore cells (heavily-stained cytoplasm with phosphotungstic hematoxylin) in the asexual conceptacle roof (Figs. 62, 98) and these are lacking in the *Phymatolithon* species, including *P. lenormandi*. Also, as will be discussed below, cystocarpic development in all the *Phymatolithon* species is peculiar while in *Leptophytum laeve*, development apparently follows the classical pattern. Unfortunately, in this regard, the situation in *L. foecundum* is not known. It may be, in time, that the *Leptophytum* species can be placed in *Phymatolithon*. However, since they must be removed from *Lithothamnium* it seems best to keep them separate until more information is available.

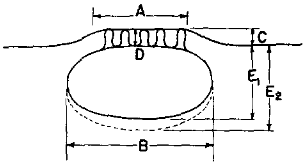
The *Lithothamnium* species on the other hand have conceptacle primordia which develop directly from the large-celled meristem (Figs. 28, 32) as in *Clathromorphum* (ADEY, 1965). However, in this case, only the usually single-layered, non-photosynthetic epithallium overlies the meristem. In all of the Lithothamnieae species of the region, the sporangial plugs stain heavily with Delafield's Hematoxylin. However, the *Lithothamnium* species are sharply marked from all of the other species involved by showing a similar heavy staining in phosphotungstic hematoxylin (Figs. 30, 34). In all other cases, the plugs are translucent and without color in this stain.

Developmental series for the asexual conceptacles of the species in question are given in the following figures: *Lithothamnium* "a" Figs. 28—30; *Lithothamnium* "b", Figs. 32—34; *Leptophytum laeve*, Figs. 60—62; *L. foecundum*, Figs. 96—98; and *Phymatolithon lenormandi*, Figs. 99—101. Data for the mature asexual conceptacles of the plants appears in Tables III, IV and V. Surface views of the conceptacles are given in figures 19, 20, 22, 24 & 26; and a plot of pore plate diameter as a function of the number of sporangia for each species is given in figure 3.

In mean dimensions, the asexual conceptacles of *Lithothamnium* "b" are larger in all respects than those of *Lithothamnium* "a". However, with regard to the relationship between roof size and the number of sporangia, there is a stronger overlap between the two than is found among members of any other genus in the region. In general, it would not be possible to use conceptacle dimensions in this case to

Table III

Dimensions of asexual conceptacles (μ)



		A			B			C			D			E_1			E_2		
		min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max
Lithothamnium "a"	24 concs. 13 plants 12 stations	98	146	242	148	226	309	-32	24	49	19	24	29	73	111	146	90	130	158
Lithothamnium "b"	15 concs. 9 plants 7 stations	113	163	210	178	262	315	0	38	81	20	26	32	122	138	162	135	162	180

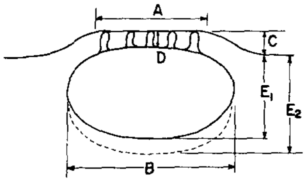
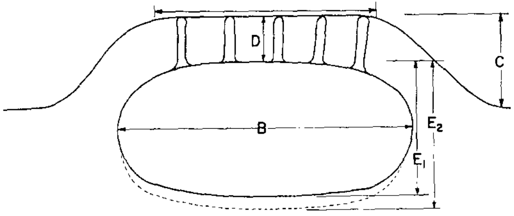


Table IV

Dimensions of asexual conceptacles (μ)



		A			B			C			D			E_1			E_2		
		min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max
Leptophytum laeve	23 concs. 13 plants 12 stations	270	350	480	320	455	580	90	140	255	48	70	95	130	200	300	140	225	310
Leptophytum foecundum	13 concs. 5 plants 5stations	218	270	340	245	293	360	21	52	88	27	37	54	125	152	170			

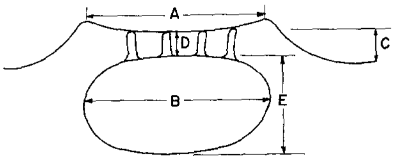
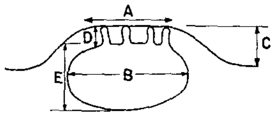


Table V

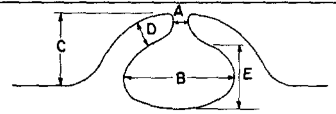
Dimensions of conceptacles of Phymatolithon lenormandi (μ)

asexual



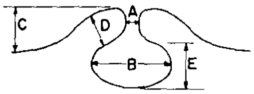
18 concs.	A			B			C			D			E		
9 plants	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max
7stations	113	135	195	122	183	267	10	63	135	18	28	49	80	104	138

male



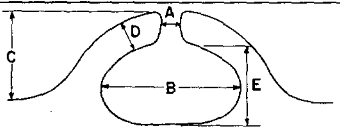
5 concs.	A			B			C			D			E		
2 plants	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max
2stations	16	26	32	136	174	210	65	105	160	24	42	65	73	101	122

female



5 concs.	A			B			C			D			E		
3 plants	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max
3stations	10	21	24	97	120	145	16	68	105	40	47	57	57	75	115

cystocarpic

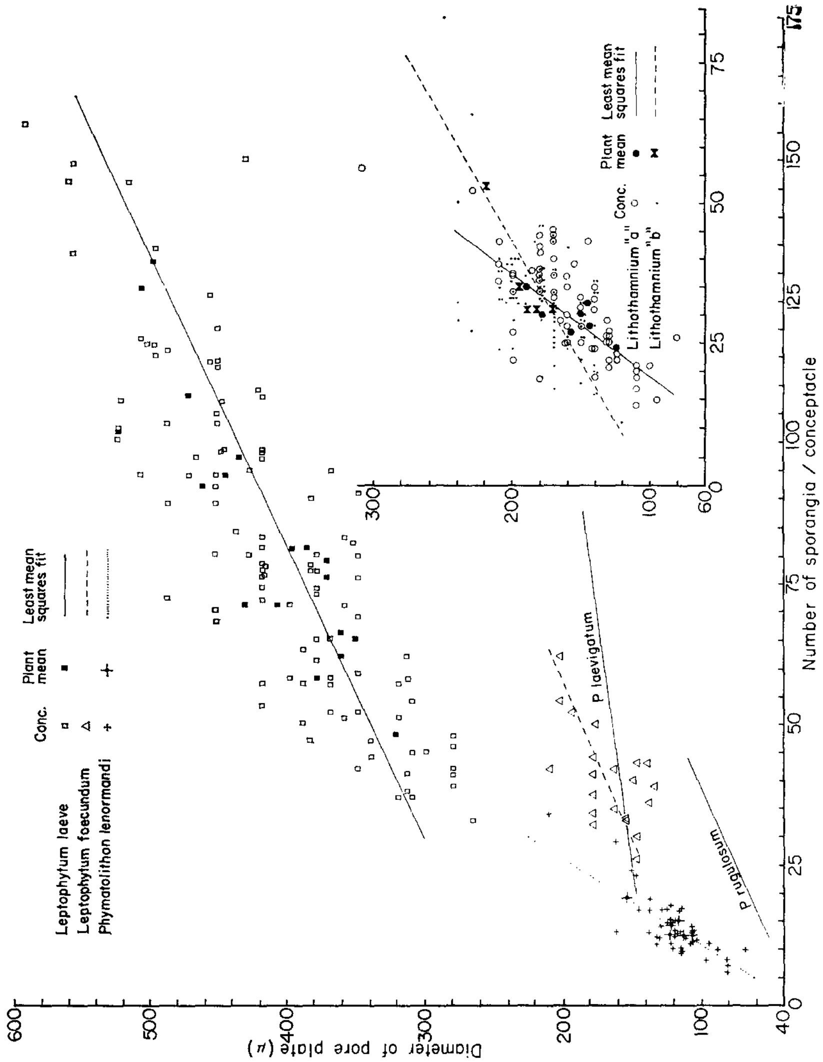


5 concs.	A			B			C			D			E		
2 plants	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max
2 stations	16	29	40	145	217	275	113	138	160	32	48	64	95	136	160

distinguish the species. In the case of *Leptohytum*, the asexual conceptacles of *L. laeve* are so much larger in all respects than those of *L. foecundum*, or any other species in the region, that differentiation would rarely be a problem.

In *Phymatolithon lenormandi*, the mean asexual conceptacle dimensions are intermediate between *P. laevigatum* and *P. rugulosum*. However, there is a marked difference in the relative number of sporangia per conceptacle and in the position of the mature conceptacle roof relative to the plant surface. In general, it would not be a problem to distinguish members of *Phymatolithon* in this region if they are bearing conceptacles. On the other hand, *P. laevigatum* and *Leptophytum foecundum* are quite similar in most asexual conceptacle dimensions, and they both possess similar rings around the conceptacles. However, in *Leptophytum foecundum* the conceptacles are

Fig. 3

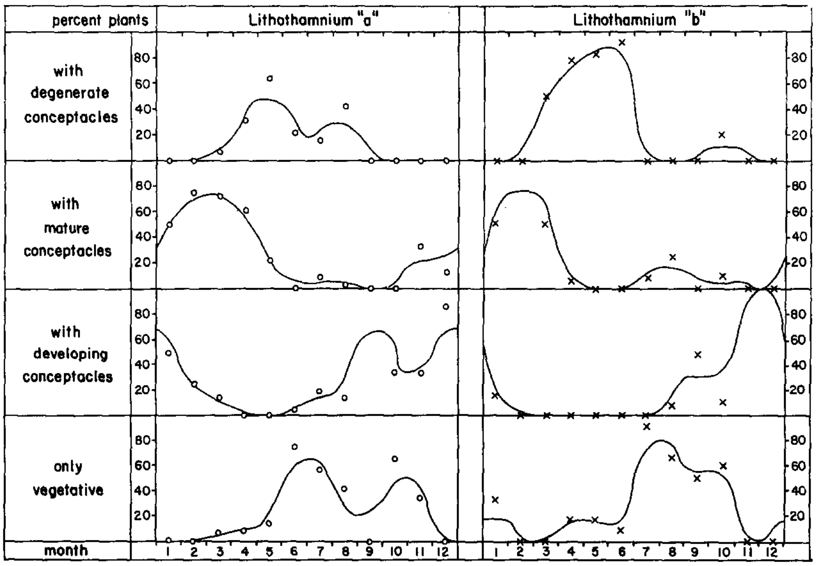

Leptophytum laeve
Leptophytum foecundum
Phymatolithon lenormandi
Conc.
Plant mean
Least mean squares fit
Diameter of pore plate (μ)
600
500
400
300
200
100
40
0
25
50
75
100
125
150
175
Number of sporangia / conceptacle
P laevigatum
P rugulosum
Lithothamnium "a"
Lithothamnium "b"
300
200
100
60
0
25
50
75

generally-raised whereas in *Phymatolithon laevigatum* they are not. If, from the surface, conceptacles are not sufficient to distinguish the plants, sectioning for "staining bodies" and "pore cells" should do so.

For *Phymatolithon* and *Clathromorphum* it was possible to work out asexual reproductive cycles by determining the areal percentages of collected material in different reproductive stages for each month of the year. In the *Lithothamnium* species, this would be very difficult to do on the basis of surface examination. The cap over the conceptacle primordia is the same layer of epithallium that covers the remainder of the thallus and only in the later stages is it easily distinguished. Also, typically the degenerate conceptacles are gradually buried with a new growth of tissue rather than breaking out, and it is often very difficult to differentiate between a mature conceptacle and a quite degenerate conceptacle. However, for both of these plants enough sectioned material was available from all months of the year to allow the working-out of similar reproductive cycles.

Each section of the *Lithothamnium* species was examined with regard to its reproductive state. This information was tabulated on the basis of the value 1 for plants with conceptacles all in the same state and ½—½ for plants with conceptacles in two states. More than two states of surface conceptacles were not found in the same plant. The results were averaged for each species on a monthly basis and are presented in figure 4. Here, the curves drawn are bi-monthly moving averages of the monthly means.

Fig. 4



As would be expected with the more limited data available, the curves are not so regular as those found for *Phymatolithon* and *Clathromorphum*. However, the same basic pattern is also found for these species. The conceptacles begin their development during the summer. In the measured population, the greatest abundance of developing conceptacles occurred in the fall, while the mature conceptacles reached a peak of abundance in mid-winter. Degenerating conceptacles were most abundant during the spring.

For the *Leptophytum* species enough data was not obtained to be certain of any asexual reproductive cycles. In the Gulf of Maine, *L. foecundum* is a relatively rare plant and not enough information is available for any season. *L. laeve* occurs primarily in deep water in this region and sufficient winter material from deep water was not obtained. A fair amount of material was available year-round for *Phymatolithon lenormandi*. However, it was not possible to show any definite pattern for the species, and young to mature asexual conceptacles were found in every season.

In general, bispores are the primary asexual spores in the Lithothamnieae of the Gulf of Maine. In this region, tetraspores were not found in *Lithothamnium* "b" and in *Clathromorphum compactum*. In most of the other species tetraspores occur but are somewhat rare. However, in *Leptophytum laeve* about 70% of the asexual conceptacles used in the dimension tabulation showed tetraspores. In both *L. laeve* and *Phymatolithon lenormandi* conceptacles have been found bearing both tetraspores and bispores.

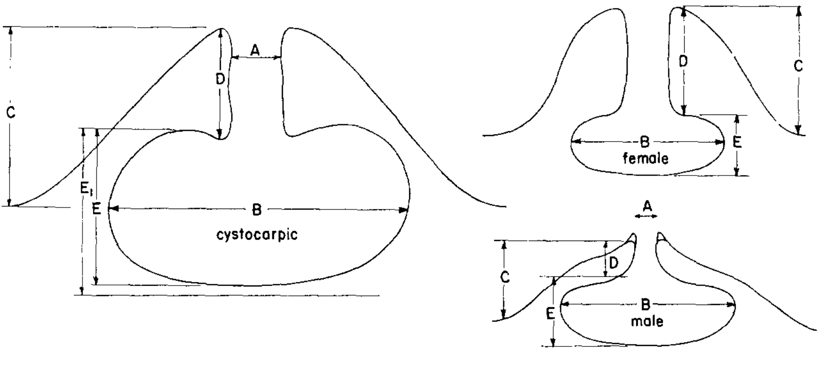
SEXUAL REPRODUCTION

The abundance of plants bearing sexual conceptacles seems to essentially parallel the occurrence of tetrasporic plants in this region. Tetraspores in the *Lithothamnium* species were rare in the Gulf of Maine and only a single sexual plant, a male of *Lithothamnium* "a", was recorded. During the field season of 1964, which the writer spent on the western Atlantic coast from Nova Scotia to northern Labrador, many male and female plants of *Lithothamnium* "a" were taken. A discussion of sexual structures in *Lithothamnium* is thus postponed until this material can be analyzed in some detail. Unfortunately, sexual plants of either *Lithothamnium* "b" or *Leptophytum foecundum* have not yet been found.

As might be expected from the abundance of tetrasporangia, sexual plants are quite common in *Leptophytum laeve*. Plants of *L. laeve* generally bear conceptacles (76.5% of those sectioned) and a tabulation of 64 sectioned plants of the species shows a nearly equal division of reproductive plants into asexual, male, and female-cystocarpic. The female-cystocarpic plants were about two-thirds cystocarps and about one-third female. Sexual conceptacle dimensions for *L. laeve* are given in Table VI.

Table VI

Dimensions of sexual conceptacles of Leptophytum laeve (μ)



		A			B			C			D			E			E$_1$		
		min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max	min	mean	max
male	15 concs. 8 plants 8stations	22	40	58	150	270	385	90	125	190	32	55	80	64	110	160			
female	8 concs. 5 plants 4stations	38	70	95	155	235	320	130	200	320	115	160	220	50	100	130			
cystocarpic	12concs. 5 plants 8 stations	51	80	130	340	470	580	165	270	370	109	165	225	130	225	350	145	240	370

The development of the male conceptacles and filaments of *L. laeve* is given in Figs. 81—90. The position of the conceptacle primordium here is the same as in the asexual conceptacles, and the "growing over" of the roof and lack of decalcification and crushing is characteristic for Lithothamnieae. However, in the early stages the male filaments are characterized by the presence of single or paired elongate cells, which have not yet been seen in other species.

The development of the female conceptacles and carpogonial filaments of *L. laeve* is given in figures 63—75. Up to this point, development is typical for Lithothamnieae. Although the "auxiliary cell" generally bears only a single sterile cell in addition to the carpogonial filament, pairs of sterile cells have been seen (Fig. 71). Also, a single case of a pair of carpogonial filaments with a single sterile filament has been encountered. At maturity, the carpogonial filament is composed of a hypogynous cell and a carpogonium, both of which develop an intense staining state near the time of fertilization.

Although cystocarp development in *L. laeve* is superficially what is considered characteristic for the Lithothamnieae, there are a number of important peculiarities (Figs. 76—80). Fusions of carpogonia with hypogynous cells apparently following fertilization have been seen (Fig. 78). Fusion at or near the level of the auxiliary cell is also quite general, and both the supporting cells and the hypogynous or sterile cells can be involved (Fig. 80). Thus, although no separate ooblast filament has been encountered, nuclear transport would certainly be possible due to the fusions. However, it remains to be determined for certain whether or not actual fertilization and transfer of a diploid nucleus occurs.

Centrally in the cystocarpic conceptacle a small, irregular fusion cell is usually present (Fig. 77). Between the central fusion cell and the base of the gonimoblast filaments, a number of separate smaller fusion cells also occur. However, the maze of fusion cells is always connected radially by pitted cell walls and in no case has a single open passage from central region to gonimoblast base been seen. If there is a diploid nucleus transfer from the central region it must occur before the walls with their pits are developed. Although large numbers of mature female and cystocarpic conceptacles have been examined no stages in such a peculiar secondary wall development have been seen. It is possible that these walls with their large pits represent original connections within female filaments, one cell of an adjacent pair having fused in one direction, the other in another. If this is the case, then the question remains as to how nuclear transport occurs.

SUNESEN (1943), ROSENVINGE (1917) and MASAKI & TOKIDA (1961) have treated the sexual reproduction of *Phymatolithon lenormandi*. However, none of them had either complete or properly-prepared living material. Both male and female conceptacle primordia are produced at a depth of up to five to six cells as in the asexual conceptacles. The characteristic structural development for the female is given in figures 102, 103, and the male pattern is quite similar. A detail showing the development of the male filament is given in figures 91—95.

In this region, the female conceptacles of *P. lenormandi* are peculiar in that they are invariably actually hermaphroditic (Figs. 48, 49, 104—106). To varying degrees all of the mature conceptacles examined had developed apparent spermatangia in addition to the carpogonia. This feature had also been previously described for a Roscoff collection of the species (HEYDRICH, 1911). The mature procarp consists of an auxiliary cell supporting a single sterile cell and a two-celled carpogonial filament. The mature female conceptacle is shown in figure 104, and intermediate and mature cystocarpic conceptacles in figures 105, 106. No evidence of ooblasts or fusions of any cells of the fertile complex have been seen. The carpospores appear to be formed directly by the enlarging of certain auxiliary cells. The origin of the specialized cell immediately below the carpospore is not certain. It seems likely that it too develops directly by enlarging of the carpogonial filament supporting cell, but it could be derived by division of the auxiliary cell.

As peculiar as these observations may seem, they are based on well-prepared material and essentially correspond with similar but generally unaccepted observations in *Phymatolithon polymorphum* (HEYDRICH, 1900). It is especially desirable at this point to restudy *P. polymorphum* and to complete the study of *P. rugulosum* (ADEY, 1964). A special effort needs to be placed on finding and describing the female-cystocarpic structures of *P. laevigatum*, since a similar pattern probably occurs here as well.

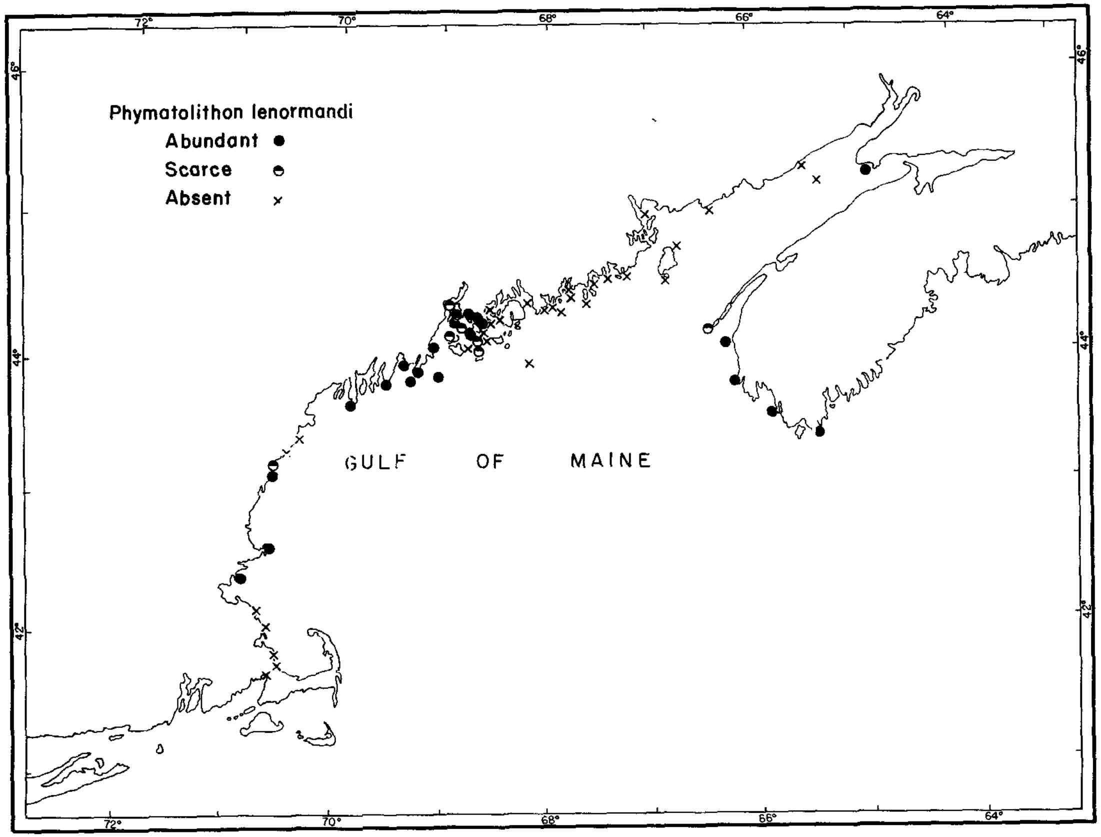
ECOLOGY

General discussions on crustose coralline ecology have appeared in the earlier papers of this series on the Gulf of Maine corallines. Data specifically applicable to the five species now being treated will be presented here. Stations from which the data are derived are indicated in the first paper on *Phymatolithon*.

Phymatolithon lenormandi is primarily an intertidal plant in the Gulf of Maine. It has been found in the sublittoral, but only in shallow water and in very small amounts. The total sublittoral relative abundance was 0.3%, less than any other species. As has been discussed in the earlier papers covering *Phymatolithon laevigatum* and *Clathromorphum circumscriptum* it tends to be restricted to emerging ledge, especially beneath the cover of fuci. In areas where it occurs, it is generally most abundant beneath a heavy cover of *Ascophyllum*.

The intertidal distribution of *Phymatolithon lenormandi* at localities specifically searched for the plant is given in figure 5. It has been found in the western and central Gulf from Boston to Penobscot Bay and along the Nova Scotia coast. From Casco Bay to western Penobscot Bay and in south-western Nova Scotia, it is very abundant. There is no obvious explanation for the peculiar distribution in terms of oceanographic conditions. However, there does seem to be a regional correlation between a high abundance of the plant and the occurrence of schistose rock substrate. Since it occurs on emerged rock, this could be related to the drying characteristics on the substrate.

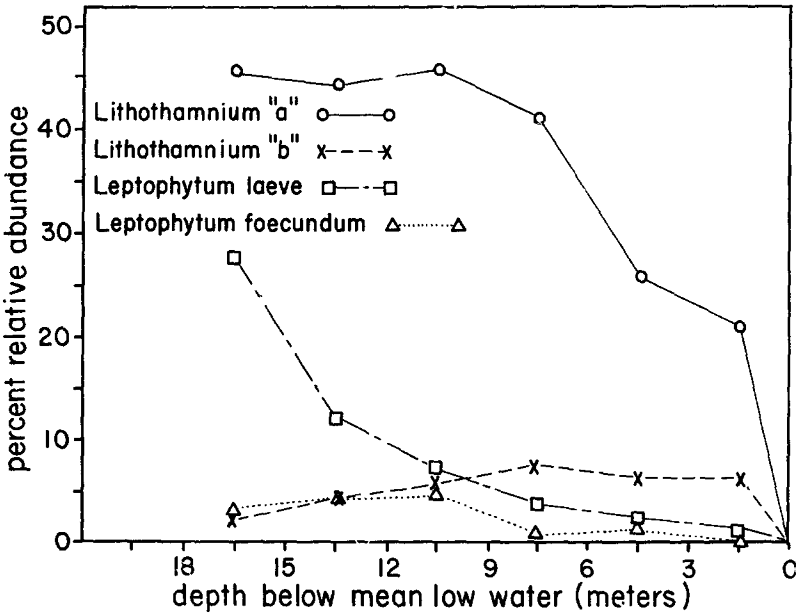
Fig. 5


Phymatolithon lenormandi
Abundant ●
Scarce ◐
Absent ×
GULF OF MAINE
72°
70°
68°
66°
64°
46°
44°
42°

Phymatolithon lenormandi was not found in the intertidal south of Cape Cod. However, in this region a very similar plant formed about 12% of the coralline collected in the sublittoral. These differed from the *P. lenormandi* population in the Gulf in a number of ways, and until further information is available they are being treated as a separate species. DAWSON (1960) has discussed the apparent widespread occurrence of *P. lenormandi* and also suggested that many similar forms actually belong to this species. The problem will only be solved after a thorough analysis of each of the populations involved.

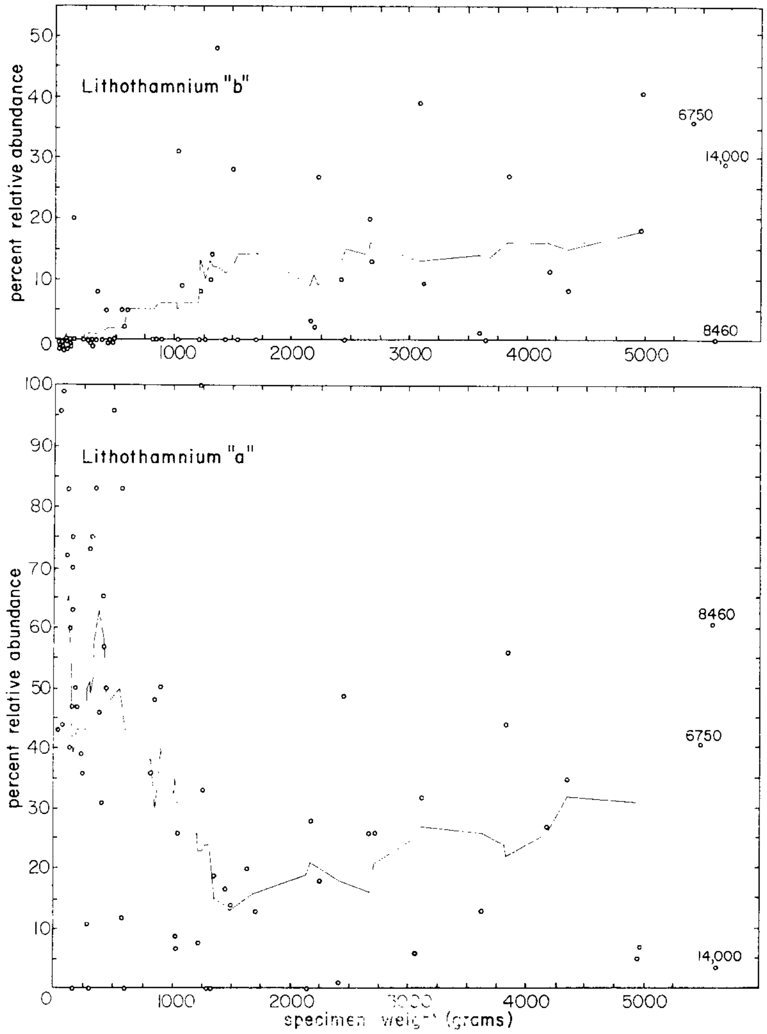
In the Gulf of Maine proper, *Lithothamnium* "a" was the most abundant species collected, forming 38.4% of the total collection. *Lithothamnium* "b" and *Leptopytum laeve* formed 11.4% and 6.3% respectively of the total collection, while *L. foecundum* was quite rare forming only 0.5% of the total collected material. *L. foecundum* was found in much greater abundance during the past seasons' work in northern Newfoundland and Labrador and has been reported in quantity in East Greenland (LUND, 1959). It seems likely that it is a high arctic element. Its tendency to be restricted to deep water in the Gulf of Maine (Fig. 6) may be a reflection of this.

Fig. 6



In this study the *Lithothamnium* and *Leptophytum* species were not found south of Cape Cod. However, none of them exhibited a clear relationship between regional relative abundance and maximum summer temperature within the Gulf itself. At least for *Lithothamnium* "a" and the *Leptophytum* species, this would be expected since these are primarily deep-water plants (Fig. 6). In the earlier papers the near-surface temperature distribution and its correlation with the relative abundance of the shallow water corallines was discussed. It should be noted, however, that this temperature gradient which results primarily from tidal current mixing is actually reversed in the 12—18 meter band.

Fig. 7 and 8



The relationship between substrate size distribution and coralline relative abundance was discussed in the earlier papers on *Phymatolithon* and *Clathromorphum.* Data for relative abundance as a function of substrate-specimen weight at a single station off Merchant Island in Penobscot Bay was presented for *Phymatolithon rugulosum* and *Clathromorphum circumscriptum.* Similar data for *Lithothamnium* "a" and *Lithothamnium* "b" from the same station are presented in figures 7 and 8. *Lithothamnium* "b" is similar to *Phymatolithon rugulosum* in that it tends not to develop on the smaller pebbles. However, the relative abundance of *P. rugulosum* shows a rapid rise to about the 1000 gram size and is relatively constant thereafter, whereas in *Lithothamnium* "b" relative abundance shows a more gradual but consistent rise up to 5000 grams. Visual observation also indicates that *Lithothamnium* "b" is considerably more abundant on large boulders and ledge than on the smaller fraction, and this species is probably not so well represented in the collections as it should be due to the difficulties of collecting on such substrate. However, this probably does not apply to *Phymatolithon rugulosum* since the range of 1000—5000 grams is easily collected.

Lithothamnium "a" is similar to *Clathromorphum circumscriptum* in that it is well-represented on the smaller fraction. These two plants develop almost to the exclusion of other species on the pebble bottoms, which are fairly abundant in protected waters in this region.

SUMMARY

This paper is the fourth of a series covering the crustose corallines of the Gulf of Maine. Information on anatomy, cytology and the development of the reproductive structures is presented to show that *Lithothamnium* and *Leptophytum* (new genus) are distinct from *Clathromorphum* and *Phymatolithon.* An additional species, *P. lenormandi,* is placed in *Phymatolithon.* The reproductive patterns and geographic and bathymetric distributions of the five species involved are presented and discussed.

LITERATURE

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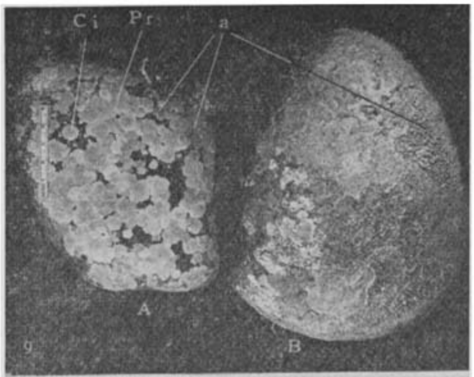
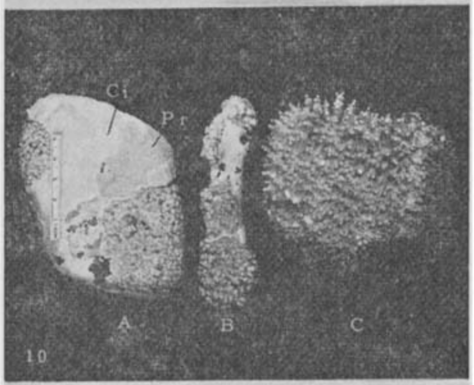
PLATES

SYMBOLS USED

a	*Lithothamnium „a"*
b	*Lithothamnium „b"*
Ll	*Leptophytum laeve*
Lf	*Leptophytum foecundum*
Pr	*Phymatolithon rugulosum*
Ps	*Pseudolithophyllum orbiculatum*
Co	*Clathromorphum compactum*
Ci	*Clathromorphum circumscriptum*
Hp	Hypothallium
Per	Perithallium
Ep	Epithallium
Pri	Conceptacle primordium
Splg	Sporangial plug
Ysp	Young sporangium
Cp	Carpospore

Plate I.





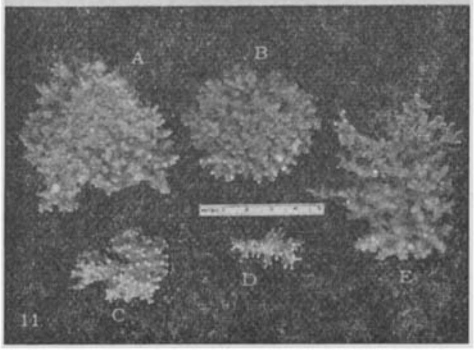
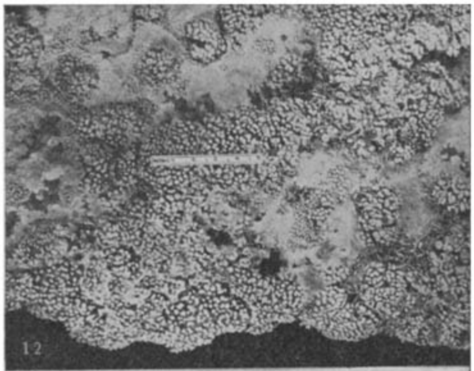


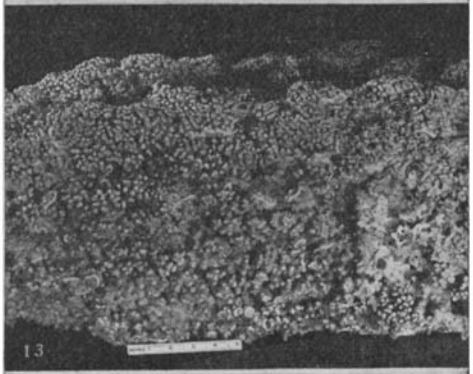
Fig. 9. Characteristic branching patterns in *Lithothamnium* "a" from a deep water, exposed locality, (A) young plants. (B) Well-developed plants. Both collected at 40 meters, Cape Roseway, Nova Scotia.

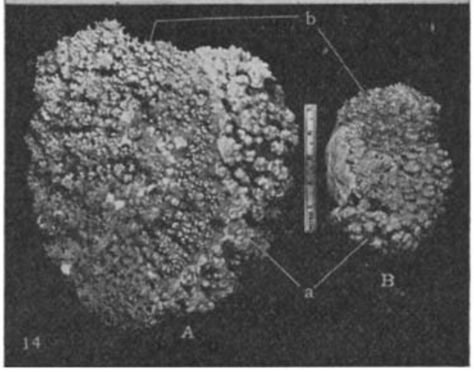
Fig. 10. *Lithothamnium* "a" on pebbles from exposed localities. (A) Collected at 3—4.5 meters, Merchant Is., Penobscot Bay. (B) 0—4.5 m, Long Porcupine Is., Frenchman Bay. (C) 4.5—9 m, Bradbury Is., Penobscot Bay.

Fig. 11. *Lithothamnium* "a" on small pebble (A) and growing "free" (B—E). (E) shows an older coarse branching (bottom) and a younger very fine branching, probably as a result of a change of position due to wave action (coarse to fine bottom). (A—D) 3—4.5 m, North Haven, Penobscot Bay. (E) 9—15 m, White Bear Arm, Labrador.

Plate II.



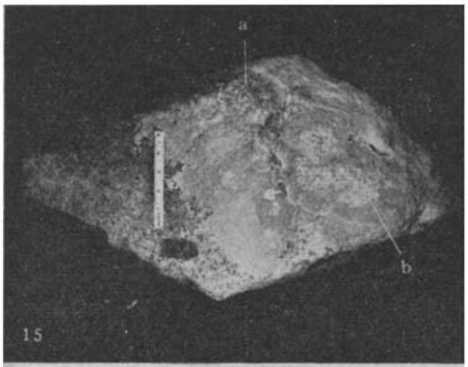


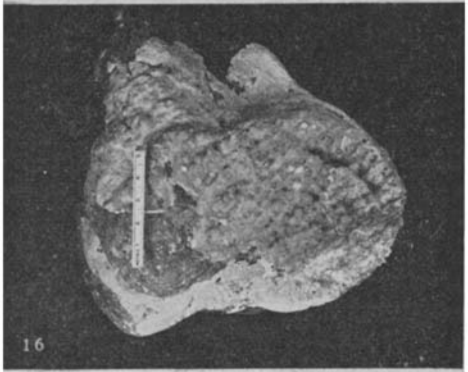


Figs. 12 & 13. *Lithothamnium* "a" on a portion of a boulder. Fig. 12 - upper face, Fig. 13, lateral face. The branching is dense on the upper plants and open on the lateral plants. Individual plants at the edge show both types. 9—15 m, James Is., St. John Bay, W. coast of Newfoundland.

Fig. 14. *Lithothamnium* "a" and *Lithothamnium* "b" growing together on pebbles. (A) 1—3 m., Eagle Is., Penobscot Bay. (B) 0—4.5 m, Long Porcupine Is., Frenchman Bay.

Plate III.





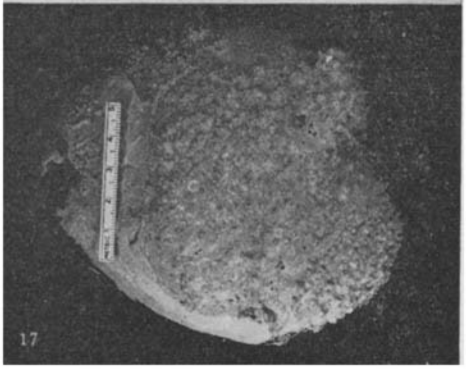
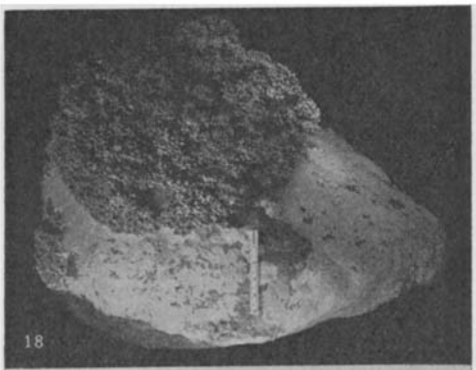


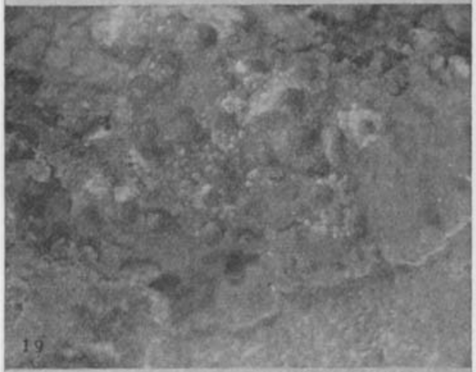
Fig. 15. Weakly-branched *Lithothamnium* ‘b” on small cobble. (see also Fig. 20). 18 m, Isle au Haut, Maine.

Fig. 16. *Lithothamnium* “b” with scattered branches developing to a relatively large diameter. 0—10.5 m, Cape Porpoise, Maine.

Fig. 17. *Lithothamnium* “b” with a well-developed crust. The plant ranges up to 1 cm thick but has a maximum branch length of only about 2 mm. 0—6 m, North Haven Is., Penobscot Bay.

Plate IV.





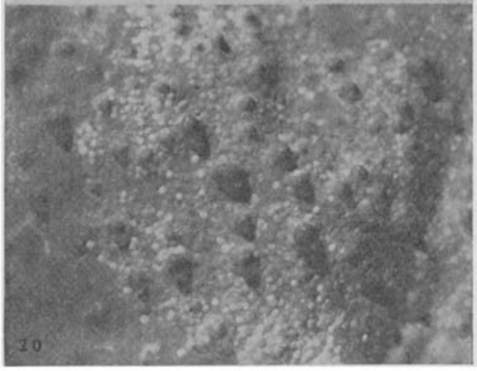
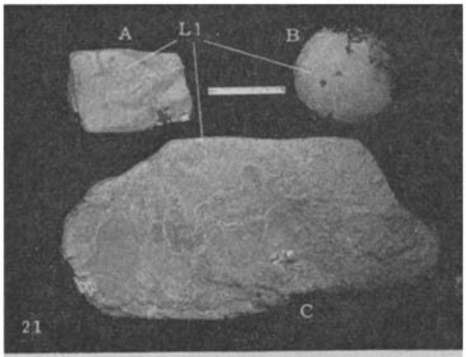


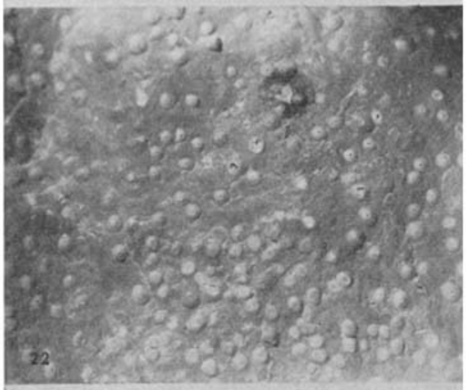
Fig. 18. Highly-developed *Lithothamnium* "b" on large cobble. Plant ranges up to 6 cm thick. 1—3 m, Eagle Is., Penobscot Bay.

Fig. 19. Close-up of *Lithothamnium* "a" shown in Fig. 15. X 4.5. The asexual conceptacles range from young (white caps)to mature.

Fig. 20. Close-up of *Lithothamnium* "b" shown in Fig. 15. X 4.5. The asexual conceptacles here also range from young (white caps) to mature.

Plate V.





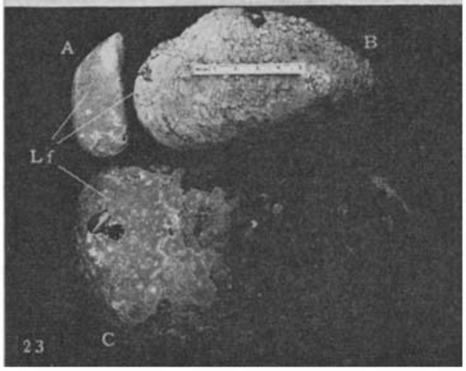
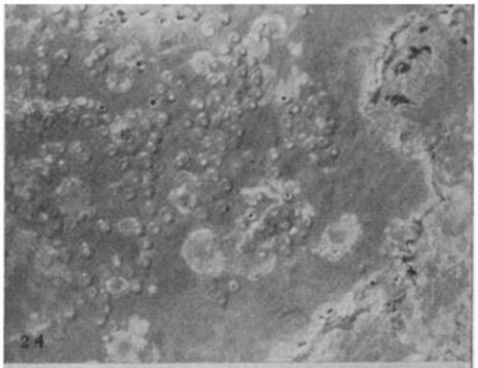
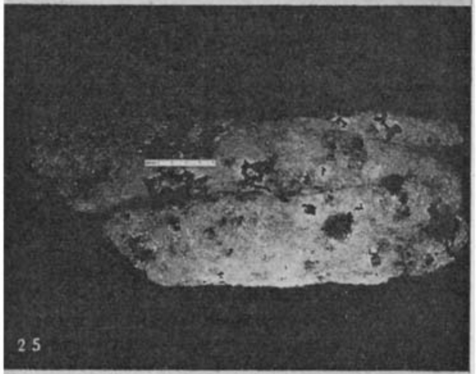


Fig. 21. *Leptophytum laeve*. The white speckling on the plants is derived from the white caps of developing and degenerating conceptacles.

Fig. 22. Close-up of *Leptophytum laeve* as indicated in Fig. 21. X 4.5. The plant in the lower center is mature asexual; the remainder are mature female to cystocarpic.

Fig. 23. *Leptophytum foecundum* on *Mytilis*, *Modiolus* and a small cobble. (A) 1—4.5 m, Quaco Bay, Bay of Fundy. (B) 9—13.5 m, Smuttynose Is., Isles of Shoals. (C) 6—9 m, Eagle Is., Penobscot Bay.





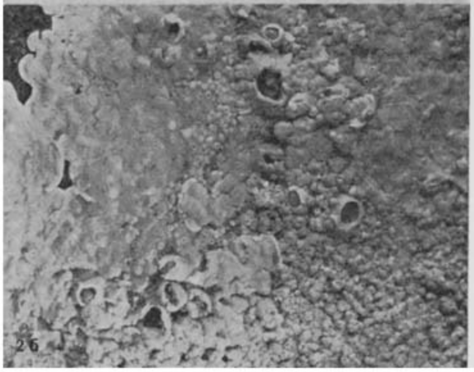


Plate VI.

Fig. 24. Close up of *Leptophytum foecundum* as indicated in Fig. 23—C. X 4.5. The conceptacles are mature asexual.

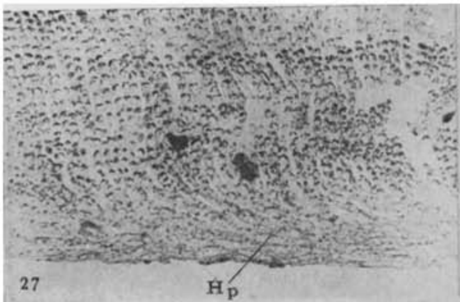
Fig. 25. Heavy growth of *Phymatolithon lenormandi* on a fragment of biotite schist ledge. Intertidal, Pemaquid Point, Maine.

Fig. 26. Close-up of a portion of the *Phymatolithon lenormandi* shown in Fig. 25. X 4.5. Note the scattered overlapping growths and the heavy concentration of asexual conceptacles in the lower right.

Plate VII

Figs. 27—30. *Lithothamnium* "a", all X 120.
Fig. 27. Hypothallium and lower perithallium.
Fig. 28. Asexual conceptacle primordium.
Fig. 29. Mid stage of development of an asexual conceptacle.
Fig. 30. Mature bisporic asexual conceptacle. Note the staining of the sporangial plugs — compare with Figs. 36, 42 & 44. All are stained with phosphotungstic hematoxylin.
Figs. 31—34. *Lithothamnium* "b," all X 120.
Fig. 31. Hypothallium and lower perithallium.
Fig. 32. Asexual conceptcale primordium.
Fig. 33. Mid stage of development of an asexual conceptacle. Note the developing sporangial plugs.
Fig. 34. Mature bisporic asexual conceptacle.

Plate VII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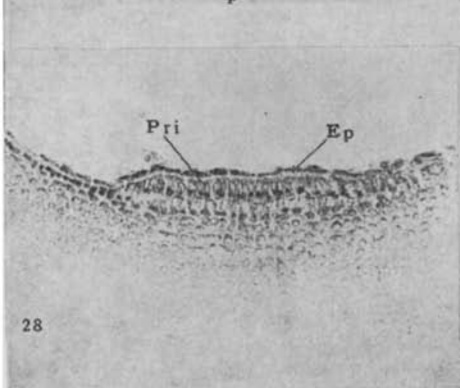
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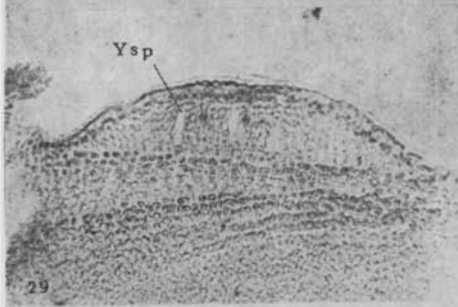
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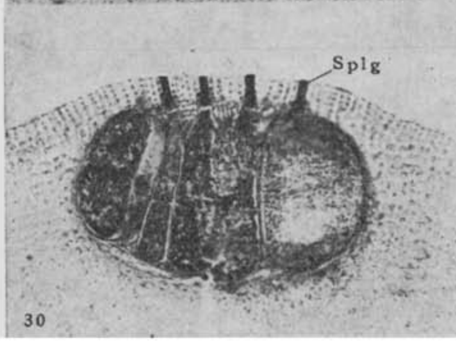
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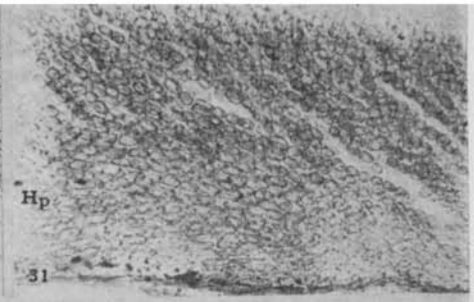
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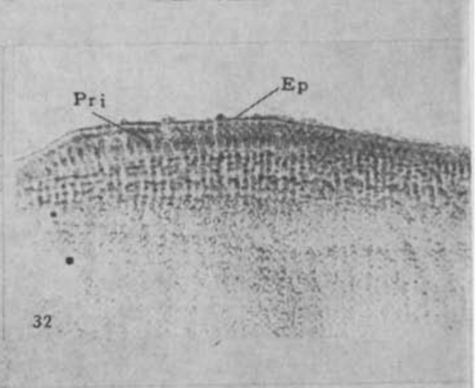
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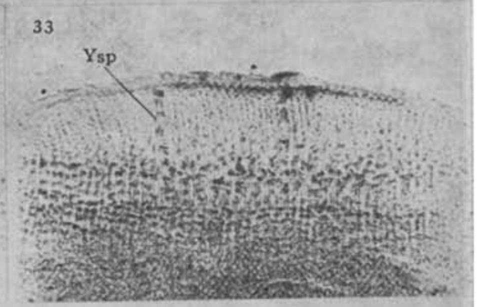
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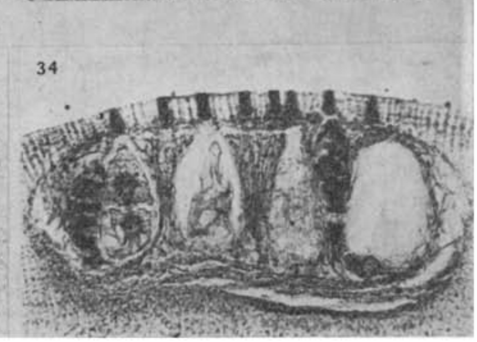
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Plate VIII

Fig. 35. Young thallus of *Leptophytum laeve* showing hypothallium and perithallium. X 100.

Fig. 36. Nearly mature tetrasporic asexual conceptacle of *Leptophytum laeve.* X 75.

Fig. 37. Primordial male conceptacle of *Leptophytum laeve.* X 100.

Fig. 38. Primordial asexual conceptacle of *Leptophytum foecundum.* The primordial tissue has not stained here and appears as a lighter layer overlain by the thin, darker conceptacle cap. X 50.

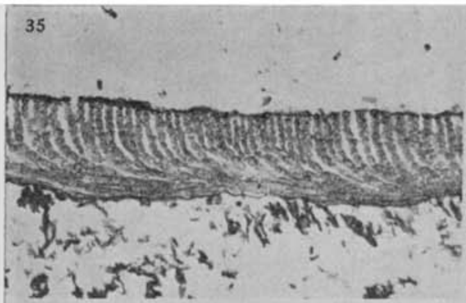
Fig. 39. Mature female conceptacle of *Leptophytum laeve.* X 75.

Fig. 40. Mature cystocarpic conceptacle of *Leptophytum laeve.* X 75.

Fig. 41. Mature male conceptacle of *Leptophytum laeve.* X 100.

Fig. 42. Mature bisporic asexual conceptacle of *Leptophytumfoecundum.* X 120.

Plate VIII.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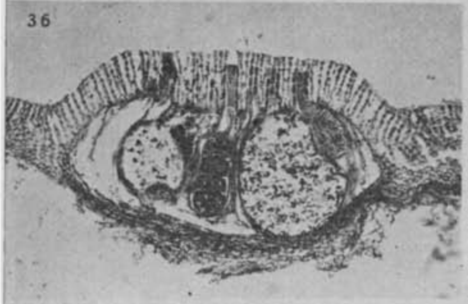
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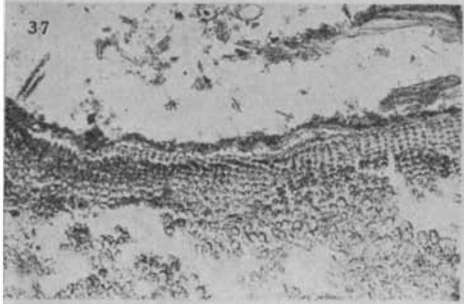
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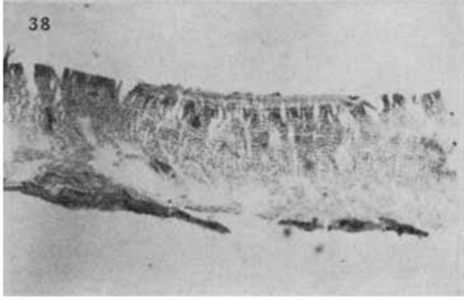
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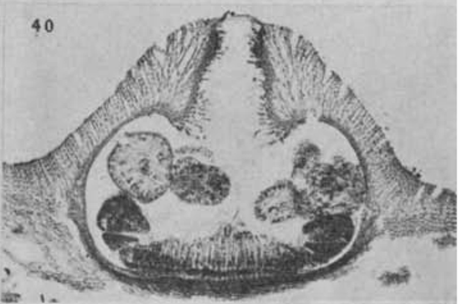
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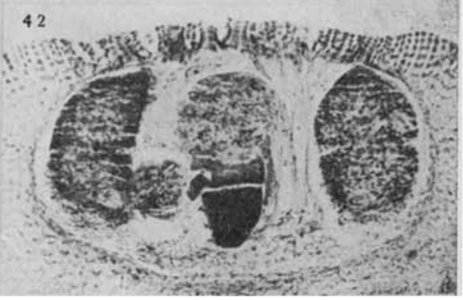
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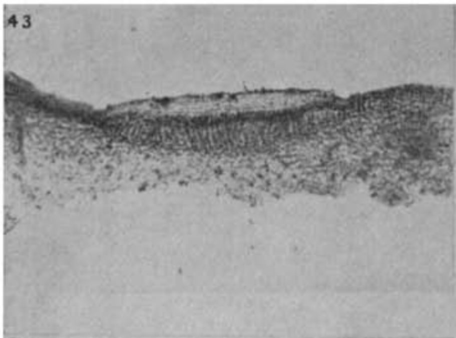
Plate IX

Figs. 43—50. *Phymatolithon lenormandi.*
Fig. 43. Asexual conceptacle primordium. X 100.
Fig. 44. Mature bisporic asexual conceptacle. X 100.
Fig. 45. Developing male conceptacle. X 100.
Fig. 46. Mature male conceptacle. X 100.
Fig. 47. Hypothallium and perithallium. X 200.
Fig. 48. Primordial female conceptacle. X 100.
Fig. 49. Hermaphroditic conceptacle. X 150. Note the developing carpospore, lower left.
Fig. 50. Mature cystocarpic conceptacle. X 100.

Plate IX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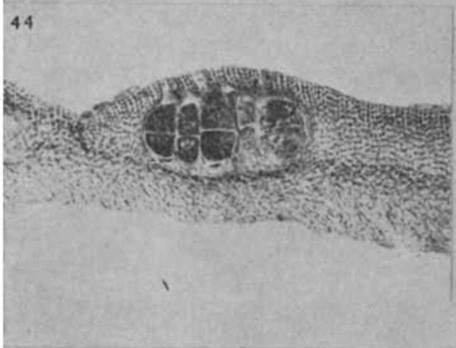
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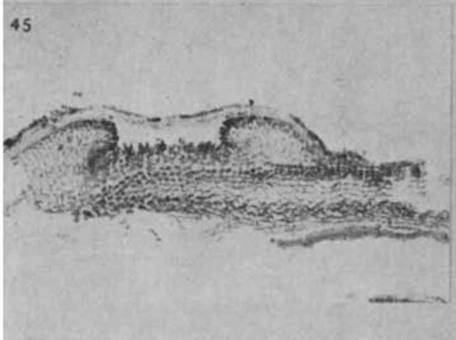
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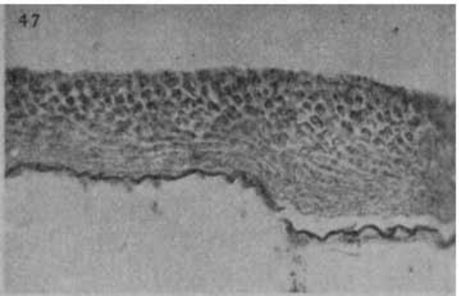
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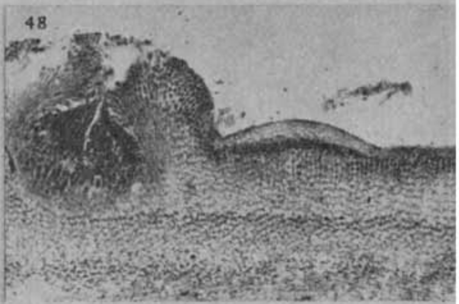
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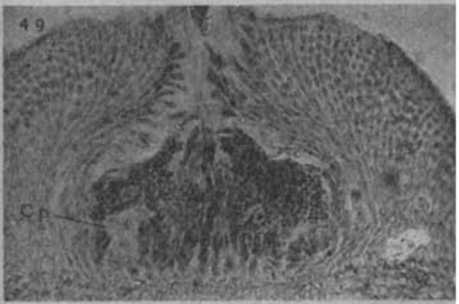
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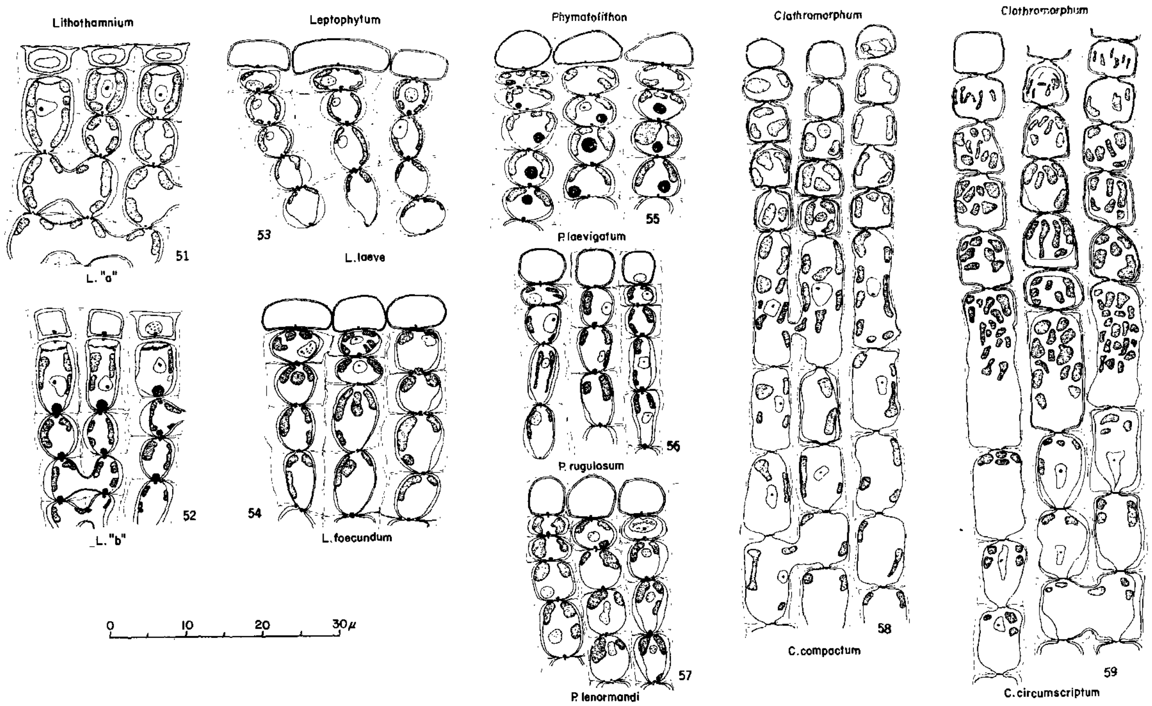
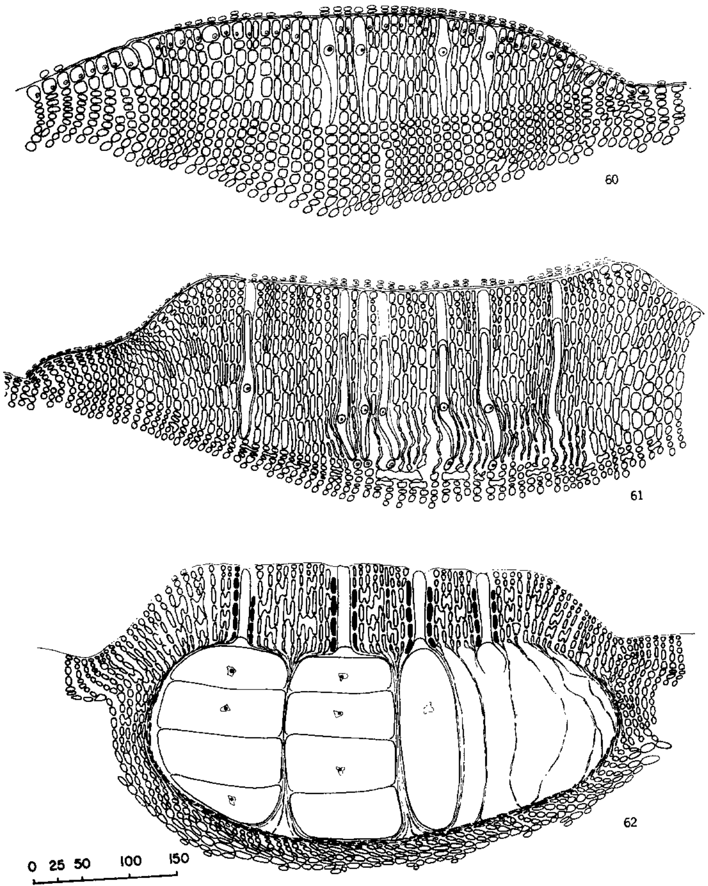
Plate X.



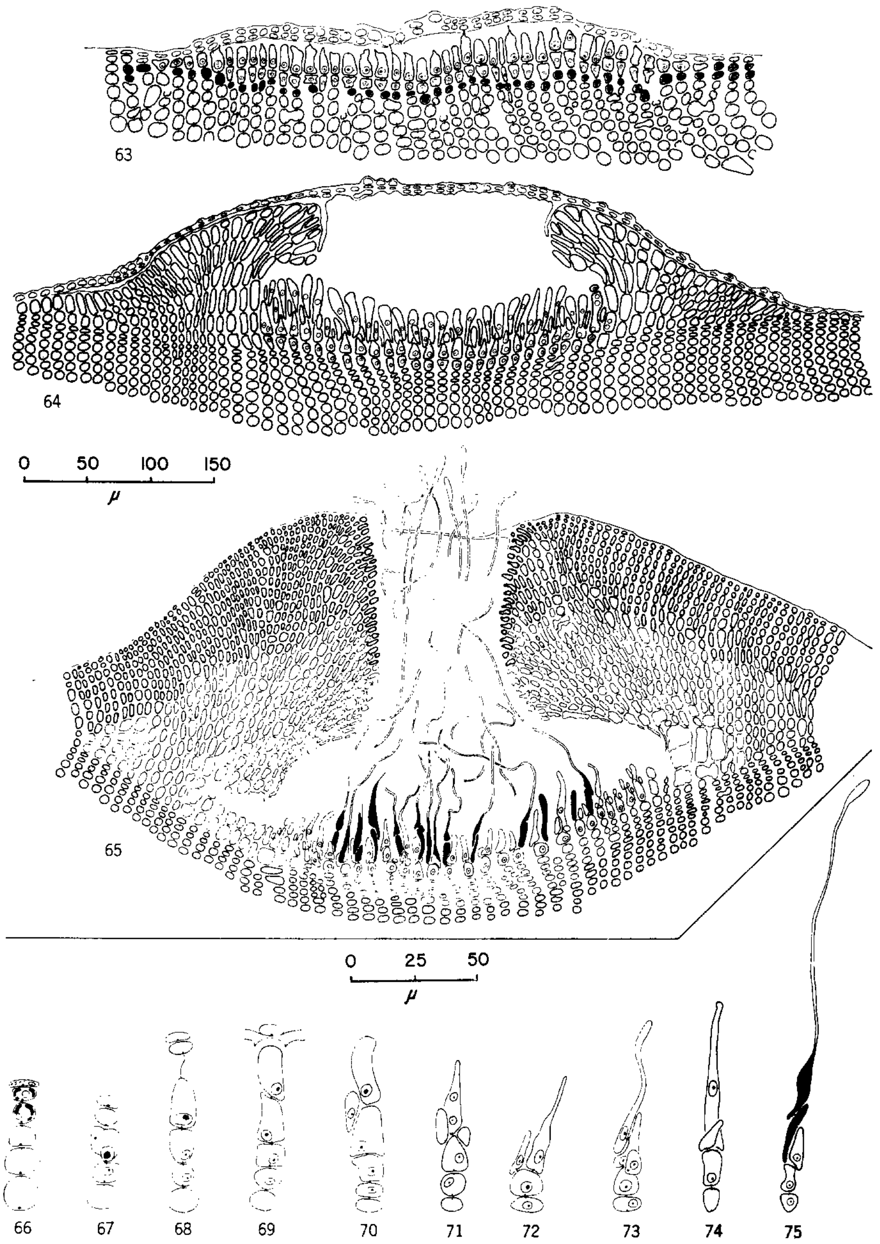
Figs. 51—59. Anatomy of the uppermost perithallium, meristem, and epithallium of the species of Lithothamnieae occurring in the Gulf of Maine.

Plate XI.



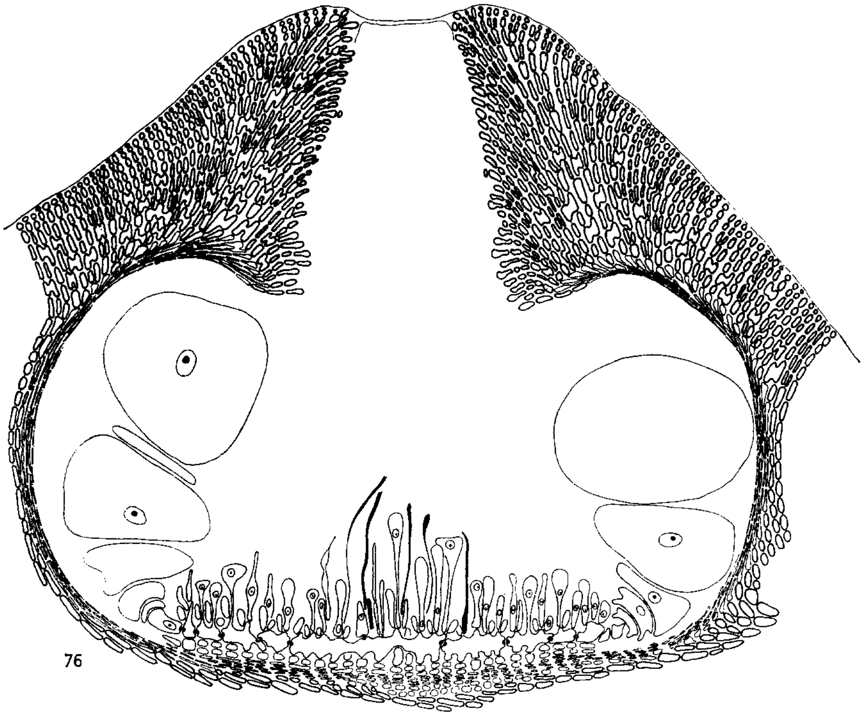
Figs. 60—62. Asexual conceptacle development in *Leptophytum laeve*.

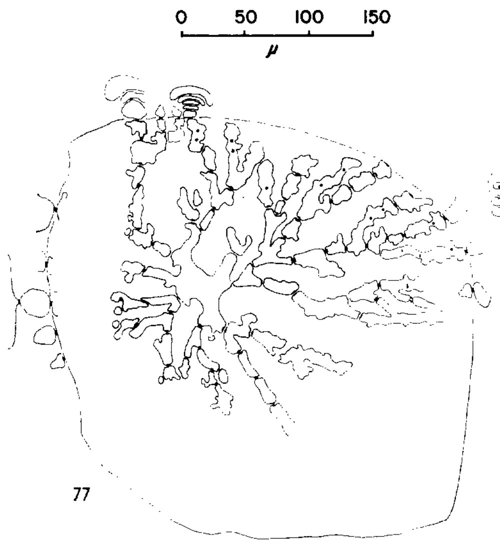
Plate XII

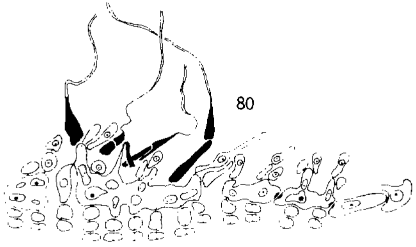


Figs. 63—65. Development of the female conceptacle of *Leptopytum laeve.*
Figs. 66—75. Development of the carpogonial filament of *Leptophytum laeve.*

Plate XIII.







Figs. 76—80. *Leptophytum laeve.*

Fig. 76. Mature cystocarpic conceptacle. Note the large pit connections within the "fusion cell."

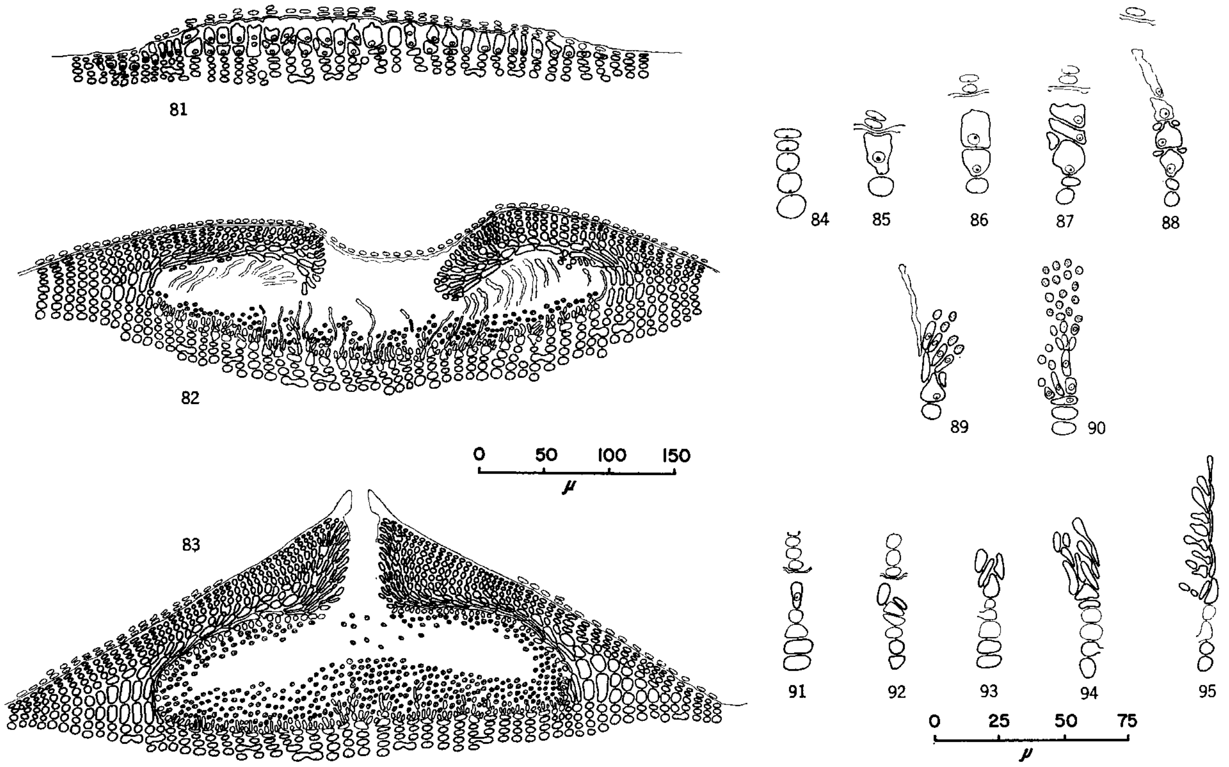
Fig. 77. Horizontal section of the fusion cell. Only the fusion cell elements and the gonimoblasts present in the section drawn are shown. A few scattered fertile filaments were not included in the fusion cell and occur between the arms — these are not shown.

Fig. 78. Fusion of carpogonium with hypogynous cell.

Fig. 79. Pair of carpogonial filaments and a sterile cell on a single auxiliary cell. One of the carpogonial filaments has developed the wall stain, the other has not.

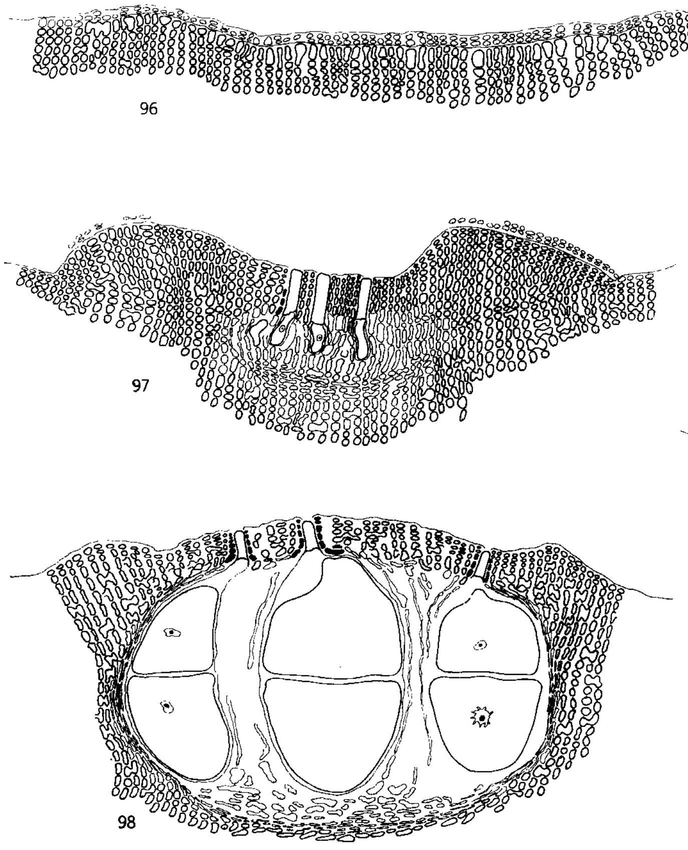
Fig. 80. Early stage in the development of a gonimoblast filament.

Plate XIV.



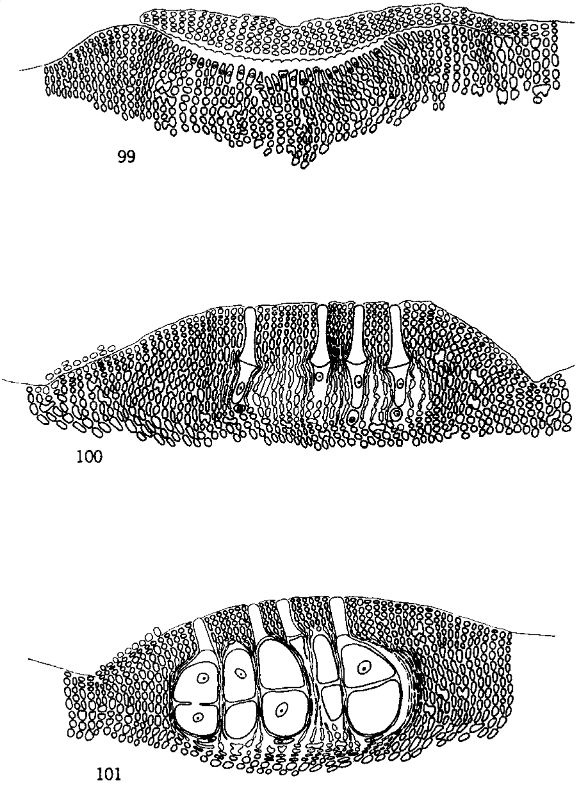
Figs. 81—90. *Leptophytum laeve.*
Figs. 81—83. Development of male conceptacle.
Figs. 84—90. Development of male filaments and spermatangia.
Figs. 91—95. *Phymatolithon lenormandi,* development of male filaments and spermatangia.

Plate XV.


96

97

98

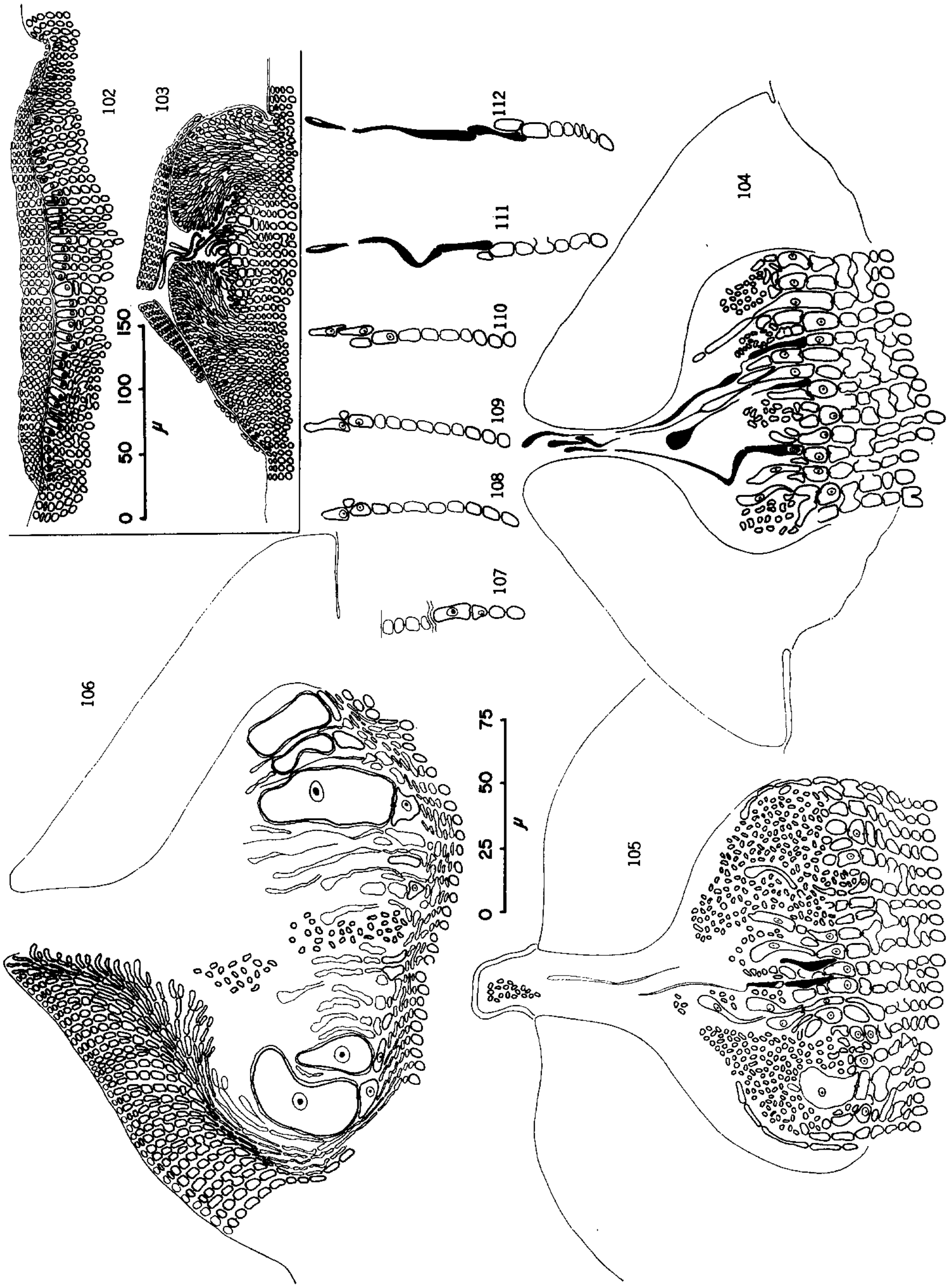

99

100

101

Figs. 96—98. Development of the asexual conceptacles of *Leptophytum foecundum*.
Figs. 99—101. Development of the asexual conceptacles of *Phymatolithon lenormandi*.

Plate XVI.



Figs. 102—112. *Phymatolithon lenormandi.*
Figs. 102—104. Development of the female conceptacle. The conceptacle is actually hermaphroditic, as were all the female conceptacles encountered in this species. Separate male conceptacles with only spermatangia are common.
Figs. 105— 106. Development of cystocarpix conceptacle.
Figs. 107—112. Development of carpogonial filament.