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THE CRUSTOSE CORALLINACEAE

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INTRODUCTION

Although two excellent surveys of the Rhodophyta have recently appeared in this journal (Dixon, 1963, 1970), these included only general information on the crustose Corallinaceae. There has been no comprehensive treatment concerning our knowledge of these algae published elsewhere at any time. Because coralline algae are the only members of the red algae for which there is any semblance of a fossil record, they hold considerable interest for both phycologists and palaeobiologists. Possible correlations exist between the petroleum deposits of the world and the coralline deposits of antiquity. The crustose Corallinaceae are of considerable importance in all of the world's seas, both in the littoral and sublittoral down to considerable depths.

Albeit several hundred papers have appeared on living crustose corallines, most of these are merely floristic treatments. Ecological information is scarce due to a lack of measurement techniques for obtaining quantitative data concerning crustose coralline algal biology and productivity. The only extensive account of the crustose Corallinaceae appeared in the second volume of Fritsch's (1945) *Structure and Reproduction of the Algae*. This treatment was not comprehensive yet, even so, only Kylin's (1956) treatise on the Rhodophyceae has treated the whole group since Fritsch. Kylin's work presented only the morphology and taxonomy of genera and higher taxa. Recently, the genera of crustose Corallinaceae contained in the Foslie Herbarium have been re-studied (Adey, 1970a) and, in many cases, re-defined in the light of modern systematics.

The primary intent of this paper is to indicate in a comprehensive manner those works which have advanced the fundamental knowledge of the group and, to a lesser extent, also to serve as a broad and detailed index to the literature on crustose coralline algae.

NATURE OF CRUSTOSE CORALLINACEAE

CLASSIFICATION

Two of the earliest published references to any organisms in the Corallinaceae, as this group is recognized today, were by Sloane (1707) and by Rae

(1724) to *Corallium* now considered to be *Lithothamnium*. On the other hand, the coralline algae were grouped by Ellis (1755) with what are considered today as corals. Ellis recognized that the articulated forms have a cell structure which differs from the corals and he arranged the former in a special group including two genera that are now designated as *Halimeda* and *Corallina*: he also described two genera now considered as the melobesioids, *Lithothamnium* and *Lithophyllum*. Coralline algal forms were described subsequently by Pallas (1766) under the name *Millepora*, and his treatment was followed by Linnaeus (1767). The attitude of the eighteenth-century workers concerning coralline algae is reflected in the observation of Linnaeus (1767, p. 1,304) that all calcareous substances are surely of animal production; and because corallines partly consist of those substances, Linnaeus thought that they indubitably belonged to the animal kingdom. Similarly, the group of coralline "animals" lacking pores was recognized by Gunnerus (1768) as being distinct from other "polypers" and he established the genus *Apora* to include those without pores.

Melobesia, described by Lamouroux (1812), is a coralline alga which he thought was an animal. This is the only 'animal' genus that is retained in the crustose Corallinaceae. Lamouroux's classical contributions of 1812 and 1816 are extremely important. He divided what he thought were corals into four groups and some Chlorophyta and Rhodophyta were included in a group which he called limestone corals. Lamouroux was followed by Lamarck (1816) who likewise placed all the known calcareous algae into coral groups, including eight species of crustose corallines that were grouped in the genus *Millepora*. Lamarck divided the genus *Millepora* of Pallas (1766) into two genera; one called *Millepora* and the other called *Nullipora* which he considered to be hydrozoa. All of the crustose corallines were removed to the genus *Nullipora* in a later publication (Lamarck, 1836).

A short time after Lamouroux's publications, Schweigger (1819) reemphasized the "plant nature" of calcareous algae. Yet, contrary to the opinions Sloane, Ray, and Schweigger, several leading scientists continued to consider calcareous algae as animals. For this reason the calcareous algae were not included in C. A. Agardh's (1824) *Systema Algarum*, and Harvey's (1841) *Manual of British Algae* contained no calcareous Rhodophyta.

The establishment of the botanical nature of the crustose red algae should be credited to Philippi (1837) whose two generic names for them are still used today. Philippi's distinctions were based solely on external features with *Lithothamnium* being used for the erect and branched forms and *Lithophyllum* for the crustose and flat forms. Although the generic concepts have changed considerably, some *Lithophyllum* species described by Philippi are still recognized.

Tenarea undulosa was described as a crustose calcareous alga by Bory de Saint-Vincent (1832) although it had been described previously by Esper (1791) as the coral *Millepora*. Bory de Saint-Vincent's treatment was not recognized until much later (Lemoine, 1911) and this resulted in the general belief that Philippi's (1837) generic names *Lithothamnium* and *Lithophyllum* were the first algal designations of the group. *Tenarea* is recognized (Lemoine, 1911; Huvé, 1957; Johansen, 1969; Adey, 1970a) as valid and this makes *T. undulosa* the oldest species name originally applied to the crustose Corallinaceae in a botanical context.

The algal nature of *Halimeda, Udotea, Acetabularia* and *Corallina* (previously confused with corals) was indicated by Link (1834) yet he believed that melobesioids were only non-living calcareous deposits. Link's opinion was based on the fact that very little remained of his crustose coralline specimens after acid treatment. This suggests that the material he studied was either poorly preserved or that his techniques were faulty. The incorporation of organic matter as well as calcareous compounds in crustose corallines was recognized by Blainville (1834) who also interpreted them to be non-living. Blainville, contrary to Link, placed such algae as *Corallina, Galaxaura, Amphiroa* and *Udotea* in the animal kingdom.

An interesting opinion presented by Johnston (1842) is understandable in light of the state of knowledge at that time. According to him, the crustose corallines are all various states of *Corallina officinalis* Linnaeus, a species which is capable of great variation under different environmental conditions. A major contribution of Johnston was his assessment of previous information, which led him to the correct conclusion concerning the plant nature of corallines.

Decaisne's (1842) contribution of useful anatomical information, based on microscopical studies of freshly collected melobesoids, represented a significant taxonomic advance. The algal nature of crustose corallines was further demonstrated and the reproductive apparatus was utilized as a basis for distinguishing the genera *Corallina, Jania, Amphiroa* and *Melobesia.* His concept of the genus *Melobesia*, however, also included forms now considered to be *Lithothamnium* or *Lithophyllum.* This classification was adopted by Harvey (1849) in the *Manual of British Marine Algae*, and Harvey concluded that the following were distinctive because of their characteristic reproductive structures:

Corallineae (subfamily)	Nulliporeae (subfamily)
Jania (genus)	*Melobesia* (genus)
Corallina	*Hildenbrandia*

Several new genera were proposed in the *Phycologia Generalis* of Kützing (1843). At this time *Lithothamnium* and *Lithophyllum* were reduced to subgenera of the newly created (Kützing, 1841) and now invalid genus *Spongites. Spongites* was used as the type genus for the family Spongitae (Kützing, 1849) in the following classification:

Spongitae (family)

Hapalidium (genus)	*Mastophora* (genus)
Pneophyllum	*Spongites*
Melobesia	*Lithothamnium* (subgenus)
	Lithophyllum

Some *Mastophora, Melobesia* and *Spongites* species are illustrated in Kützing's (1869) *Tabulae Phycologicae.*

The family Corallinaceae was proposed by Areschoug in J. Agardh's (1852) *Species, Genera et Ordines Algarum.* The beliefs of Philippi (1837) were also revived when Areschoug re-defined the Melobesioideae as two groups, one with only crustose flat thalli (*Melobesia* and *Hapalidium*) and another having erect thalli (*Lithothamnium* and *Mastophora*). The genus *Melobesia* contained

two subgenera: (1) *Melobesia*, which also included species recognized today as *Lithophyllum* and *Lithothamnium*; and (2) *Lithophyllum*, which included forms still placed in this genus. Areschoug could determine no internal difference between *Lithothamnium* and *Lithophyllum*.

Rosanoff's (1866) recognition of two tissue layers in some melobesioids and his use of internal structure as a basis for classification was a major advance. Subsequently, anatomical studies were based upon Rosanoff's work and his illustrations have been widely reproduced: the first cell fusions between the adjacent filaments of certain melobesioids were also described by Rosanoff.

Solms-Laubach (1881) published a monograph on the Corallinacea and, after his studies of *Amphiroa*, *Melobesia* and *Corallina*, he suggested that the reproductive organs might be used more widely to distinguish genera. Four years later Hauck (1885) divided the Corallinaceae into articulated and non-articulated groups, and this formed the foundation for the modern systematics of coralline algae. Although Hauck's species and genera do not agree with modern ones, his classification is worthy of presentation:

Corallinaceae (family)

Melobesieae (subfamily)	Corallineae (subfamily)
Melobesia (genus)	*Amphiroa* (genus)
Lithothamnium	*Corallina*
Lithophyllum	

The genera *Lithophyllum* and *Lithothamnium* were first delimited in a tenable manner by Rothpletz (1891) who used reproductive structures for distinguishing fossil forms: reproductive criteria apply equally well to living forms and are now used to characterize genera and tribes. A new genus, *Archaeolithothamnium*, was suggested (Rothpletz, 1891) to include a large number of fossil species with sporangia not in conceptacles; however, Rothpletz failed to apply the genus name in a binomial. Subsequently, living species of *Archaeolithothamnium* have been described. A revision by Rothpletz (1891) of the genus *Lithophyllum* to *Lithothamniscum* was not accepted by later workers. Rothpletz's major contribution was to formulate a foundation upon which generic relationships could be examined phylogenetically.

Schmitz and Hauptfleisch (1897) proposed that *Melobesia*, *Mastophora Lithothamnium*, and *Lithophyllum* be distinguished solely by their externa, appearance: according to them, *Lithothamnium* forms excrescences, *Lithophyllum* consists of flat crusts, *Mastophora* is not densely calcified and forms sheets, and *Melobesia* consists of at most a few layers of cells. This system proved relatively useless because of numerous exceptions.

Upon the extensive foundation laid by the early workers, Foslie [1881–1909] and Heydrich [1894–1911] began to build our modern classification systems: however, these workers seldom agreed with each other and frequently modified their systems, thereby illustrating the extreme difficulties encountered in the systematics of this group.

A classification based on vegetative characters was formulated by Heydrich (1897a) and, later (1897b) he suggested another system based on tetrasporangial arrangement. Subsequently he (1900c) used cystocarp development and the characteristics of the rhizoids to define a third system. Heydrich's (1897a) classification is as follows:

Melobesieae (tribe)

Chloronema (genus)
Melobesia
Mastophora
Lithophyllum
Eulithophyllum (subgenus)
Pterolithon
Lithothamnium (genus)
Leptolithon (subgenus)
Heteroptychon
Lithomorphum
Heterolithon
Eulithothamnium

The descriptions given by Heydrich were largely inadequate and many of his views are not accepted by modern workers.

Foslie (1895a) showed that *Apora* and *Nullipora* were both *Lithothamnium* which, he further suggested, be retained since it had been accepted and applied for almost sixty years. Foslie's major contributions were his numerous taxonomic works on the crustose Corallinaceae (many in Norwegian) and his competence has been widely recognized. Foslie's taxonomic concepts were based mainly on the morphology of the reproductive structures. He was occasionally inconsistent and by necessity, his opinion changed frequently. Excluding all of the developmental modifications and later changes made by Foslie, the following is his basic classification (Foslie, 1904c), with modifications made in the following year (Foslie, 1905c) indicated by an asterisk:

Lithothamnioneae (tribe)
Lithothamnium (genus)
**Eulithothamnium* (subgenus)
Crustacea (group)
Subramosa
Ramosa
**Epilithon*
Archaeolithothamnium
**Phymatolithon*
**Euphymatolithon*
**Clathromorphum*
Mastophoreae
Mastophora
Eumastophora
Lithoporella

Melobesieae (tribe)
Goniolithon (genus)
Crustacea (*Herpolithon*) (group)
Ramosa (*Cladolithon*)
Melobesia
Eumelobesia (subgenus)
Heteroderma
Lithophyllum
Eulithophyllum
Crustacea
Ramosa
Lepidomorphum
Crustacea
Subramosa
Ramosa
**Dermatolithon*

Many crustose coralline species were described by Foslie, and it is his work which forms the basis for current melobesioid systematics. Foslie was working on a monograph of the coralline algae at the time of his death in 1909: his incomplete material was edited by H. Printz and published twenty years later (Foslie, 1929).

Foslie's classification was modified by De Toni (1903) and *Chloronema* and *Chaetolithon* were treated as uncalcified genera. Other genera and subgenera in this system are as follows:

Archaeolithothamnium (genus)
Phymatolithon
Clathromorphum
Lithothamnium
Eulithothamnium (subgenus)
Epilithon
Melobesia (genus)
Mastophora
Lithophyllum
Eulithophyllum (subgenus)
Carpolithon
Lepidomorphum
Goniolithon

An attempt was made by Lemoine (1909) to distinguish between *Lithophyllum* and *Lithothamnium* solely by internal vegetative morphology and this method was extended later (Lemoine, 1911) to other melobesioid genera. Three basic forms were distinguished (Lemoine, 1911): a *Lithothamnium*-type; a *Lithophyllum*-type; and a *Melobesia*-type. This system is inconsistent with systems now used by those who study living crustose Corallinaceae (from the viewpoint of developmental morphology); however, it has been accepted and applied by palaeobotanists. Lemoine (1911) rejected the genera *Phymatolithon*, *Clathromorphum*, *Goniolithon*, *Perispermum*, *Sphaeranthera*, *Paraspora*, *Stichospora*, *Hyperantherella* and *Stereophyllum* which had been established either by Heydrich or by Foslie. The genus *Tenarea* was revived and the following genera were considered (Lemoine, 1911) to be in the crustose Corallinaceae: *Archaeolithothamnium*, *Lithothamnium*, *Lithophyllum*, *Porolithon*, *Tenarea*, *Mastophora*, *Melobesia*, *Epilithon* and *Mesophyllum*. To this list should be added the genus *Fosliella* established by Howe (1920a), with *Fosliella farinosa* (Lamouroux) Howe as the type: exception was, however, taken to this later by Kylin (1956).

A new subfamily, Mastophoreae, was proposed by Setchell (1943) with *Mastophora* as the type genus. Setchell's suprageneric classification is:

Corallinaceae (family)

Corallineae (subfamily)	Sporolitheae (subfamily)
Mastophoreae	Lithothamnieae
	Lithophylleae

According to Setchell, the Mastophoreae have at most only feeble differentiation of tissues and include the genera *Metamastophora*, *Mastophora*, *Goniolithon*, *Lithoporella* and *Litholepis*. In another paper during the same year (Setchell and Mason, 1943a), the genus *Neogoniolithon* was proposed and the older genus *Goniolithon* was re-defined.

In the excellent floristic work by Hamel and Lemoine (1952), the Corallinaceae were divided in the following manner:

Corallinées (subfamily)
- *Corallina* (genus)
- *Jania*
- *Amphiroa*

Melobesiées
- Lithophyllées (tribe)
  - *Porolithon*
  - *Neogoniolithon*
  - *Lithophyllum*
  - *Dermatolithon*
  - *Tenarea*
  - *Pseudolithophyllum*
- Archaeolithothamniées
  - *Archaeolithothamnium*
- Lithothamniées (tribe)
  - *Mesophyllum* (genus)
  - *Lithothamnium*
- Mastophorées
  - *Melobesia*
  - *Litholepis*
  - *Metamastophora*
  - *Mastophora*
  - *Lithoporella*
  - *Chloronema*
- Epilithonées
  - *Epilithon*
  - *Chaetolithon*
- Schmitziellées
  - *Schmitziella*

In the important taxonomic treatment of Pacific North American crustose Corallinaceae by Mason (1953), Hauck's (1885) subdivision of the Corallinaceae into articulated and non-articulated groups was also endorsed. A new hemiparasitic genus *Polyporolithon* (Mason, 1953) was included in the melo-

besioid tribe Lithothamnieae; the other tribe is the Lithophylleae. Later workers (e.g. Dawson, 1960b; Masaki, 1968; Adey, 1970a) have followed classification schemes which are essentially similar to Mason's.

Descriptions of present crustose coralline genera have been provided by Kylin (1956) as he interpreted them. A compilation of general information on the group has been included as well; Kylin's classification is as follows:

Sporolithon (group)
Sporolithon (genus)

Lithothamnium (group)
Phymatolithon (genus)
Lithothamnium
Mesophyllum
Epilithon
Chaetolithon

Lithophyllum (group)
Metamastophora (genus)
Lithophyllum
Tenarea
Porolithon
Crodelia
Dermatolithon
Hydrolithon
Melobesia
Chloronema
Schmitziella

Kylin saw fit to use the name *Sporolithon* for living forms and *Archaeolithothamnium* for fossil forms of the same taxon and Dawson (1960a) followed his example.

Recently, a revision of the classification of the coralline algae has been proposed by Johansen (1969) in a paper dealing mainly with articulated forms, in particular *Calliarthron*. The crustose corallines are classified by Johansen as follows:

Melobesioideae (subfamily)
Melobesieae (tribe)
Melobesia (genus)
Chaetolithon
Clathromorphum
Leptophytum
Lithothamnium
Mesophyllum
Phymatolithon
Polyporolithon
Sporolitheae
Sporolithon

Schmitzielloideae (subfamily)
Schmitzielleae (tribe)
Schmitziella (genus)
Lithophylloideae
Lithophylleae
Lithophyllum
Dermatolithon
Pseudolithophyllum
Tenarea

Mastophoroideae (subfamily)
Mastophoreae (tribe)
Mastophora (genus)
Chloronema
Fosliella
Goniolithon
Heteroderma
Hydrolithon
Lithoporella
Litholepis
Metamastophora
Neogoniolithon
Porolithon

Two tribes were considered (Johansen, 1969) as subfamilies and two new subfamilies were recognized. As Johansen pointed out, *Archaeolithothamnium* was used only provisionally by Rothpletz (1891) and, therefore, Heydrich's (1897a) generic epithet, *Sporolithon*, should be applied.

FLORISTIC INFORMATION

In addition to the taxonomic works already cited there are many floristic works which do not always include ecological data. While these papers contribute new records and distributional data, only the relatively more informative (Table I) are included within the scope of this review.

Lemoine's works [1909–1971] have contributed a great deal to our knowledge of the distribution and systematics of crustose coralline algae and the illustrated coralline algal flora (Hamel and Lemoine, 1952) of France and French North Africa is particularly useful. The papers by Mason (1953) and

TABLE I

Geographical listing of papers contributing floristic information on living melobesioids.

Atlantic Arctic
Adey, 1968
Jónsson, 1902
Kjellman, 1883
Rosenvinge, 1926
Strömfelt, 1886

Northwestern Pacific
Masaki, 1968
Masaki and Tokida, 1960a,b, 1961,a,b, 1963
Segawa, 1954
Tokida and Masaki, 1959, 1960

Northeastern Pacific
Dawson, 1965
Doty, 1947
Hollenberg and Abbott, 1966
Mason, 1953
Nichols, 1909
Saunders, 1901
Setchell and Mason, 1943b
Smith, 1944

Northwestern Atlantic
Adey, 1964, 1965, 1966a,b,c
Taylor, 1937

Northeastern Atlantic
Feldmann, 1939
Foslie, 1895a
Gayral, 1966
Lancelot, 1961
Lemoine, 1913b, 1928a, 1931
Parke and Dixon, 1968
Rosenvinge, 1917, 1935
Suneson, 1943, 1958

Pacific Islands
Chapman, 1971
Dawson, 1957
Johnson, 1954, 1964b
Lee, 1967
Lemoine, 1923, 1929a
Levring, 1943a,b
Taylor, 1945, 1950
Womersley and Bailey, 1969, 1970

Atlantic Islands
Foslie and Howe, 1906a
Lemoine, 1929b
Hoek, 1969

Florida and Caribbean
Dawson, 1962b
Foslie and Howe, 1906a,b
Lemoine, 1917a,b
Taylor, 1960

Mediterranean and Red Sea
Hamel and Lemoine, 1952
Huvé, 1956, 1962
Lemoine, 1915a, 1931, 1939b, 1966
Lewalle, 1960
Papenfuss, 1968

Pacific, South America and Central America
Dawson, 1960a,b, 1962a
Dawson, Acleto and Foldvik, 1964
Lemoine, 1920, 1929a
Levring, 1960

North Africa
Gayral, 1958
Hamel and Lemoine, 1952
Lemoine, 1924a, 1926
Pilger, 1919

Indian Ocean and Southeast Asia
Desikachary and Ganesan, 1967
Foslie, 1902, 1907f
Ganesan, 1962, 1963
Pilger, 1908
Weber-Van Bosse and Foslie, 1904

Antarctic and Subantarctic
Foslie, 1907c
Lemoine, 1917c
Papenfuss, 1964

Dawson (1960b) are systematic accounts covering the Pacific coasts of North America and Mexico respectively. Detailed bio-systematic papers on the melobesioid algae were published by Adey (1964, 1965, 1966a,b, 1970b) covering the northwestern North Atlantic coast and extending through the intertidal into the subtidal areas. A similar melobesioid analysis (Adey, 1968) was made along Icelandic coasts. An excellent treatment of the crustose corallines (especially temperate species) of Japan by Masaki (1968) includes superb illustrations and photographs of the species he found.

DEVELOPMENTAL MORPHOLOGY

Work on the developmental morphology of crustose coralline algae is scanty and, consequently, the available information is difficult to evaluate. Among those who have noted depth effects is Lemoine (1940). She reported a general reduction in the size of cells, particularly of the hypothallus, in *Lithothamnium polymorphum* (L.) Aresch. and *L. lenormandii* (Aresch.) Foslie as depth increased. A decrease in the number of conceptacles as depth increased was also recorded. Similar trends have been noted (Johnson, 1954) in the Mediterranean, the Cape Verde Islands and a few places in the tropics.

The morphological differences between *Melobesia*, *Lithophyllum*, *Lithothamnium*, *Epilithon* and *Mesophyllum* (Suneson, 1943) have been contrasted. Data concerning the development of conceptacles, procarps, gonimoblasts, spermatangia, and tetra- and bispores also were compiled and reviewed by Suneson (1937) for the relatively few species studied. Additional information of this sort comprises a major contribution of Adey [1964–1966], consisting of detailed accounts of vegetative development and spore formation in *Phymatolithon laevigatum* (Foslie) Foslie, *P. rugulosum* Adey, *P. lenormandii* (Areschoug) Adey, *Clathromorphum circumscriptum* (Strömfelt) Foslie, *C. compactum* (Kjellman) Foslie, *Pseudolithophyllum orbiculatum* (Foslie) Lemoine, *Lithothamnium glaciale* Kjellman, *Lithothamnium lemoineae* Adey, *Lithothamnium trophiforme* Unger, *Leptophytum foecundum* (Kjellman) Adey, and *Leptophytum laeve* (Strömfelt) Adey from the Gulf of Maine. Recent trends in crustose coralline systematics [Adey, 1964–1970a] show an increasing use of developmental criteria as taxonomic characters.

The morphology of crustose corallines from the coasts of Brittany have been compared by Cabioch (1966a) who found two species to be present with two varieties and eleven forms. In another paper (Cabioch, 1966b), the spore development in *Lithothamnium*, *Lithophyllum* and *Mesophyllum* were reported to be identical. The unusual manner of trichocyte formation in *Neogoniolithon notarisii* (Dufour) Setchell and Mason was described (Cabioch, 1968) in a third paper. The developmental morphology of the epiphytic *Melobesia mediocris* has been discussed in detail by Lee (1970) who analysed both the vegetative and reproductive ontogeny. The paper by Adey and Sperapani (1971), describing the vegetative and reproductive development of *Kvaleya epilaeve*, should stand as an example to be followed by those describing new taxa of algae.

LIFE HISTORIES

Research on melobesioid life histories is as scarce as developmental information. Based on frequency of collection (Suneson, 1943), the occurrence

of tetra- and bispores in some Swedish Corallinaceae has been reported. The significance of bispores in the Corallinaceae was later revealed by Suneson (1950), who noted that uninucleate bispores are formed following mitotic division only, while tetrasporangia are produced following meiosis. Uninucleate bispores give rise to tetrasporophytes, while binucleate bispores and tetraspores, produce gametophytes. Dixon (1970) has commented on the frequently cited report (Bauch, 1937) of the occurrence of monosporangia in *Lithophyllum incrustans* Philippi. He points out that the structures illustrated as monosporangia by Bauch are in reality aberrant bisporangia. According to Foslie (1905b), bisporic Melobesioideae are more abundant in colder waters and are absent in the tropics. *Fosliella farinosa* (Lamx.) Howe, as *Melobesia callithamnioides* Falkenberg, appears unique (Solms-Laubach, 1881) among corallines in reproducing vegetatively by means of triangular, plate-like gemmae.

The reproductive stages were discussed and illustrated by Adey (1964, 1965, 1966a,b) for *Clathromorphum compactum*, *C. circumscriptum*, *Pseudolithophyllum orbiculatum*, *Leptophytum laeve*, *Leptophytum foecundum*, *Lithothamnium glaciale*, *Lithothamnium lemoineae* and *Phymatolithon lenormandii* in the Gulf of Maine.

PHYLOGENETIC RELATIONSHIPS

Knowledge concerning the phylogenetic affinities of the crustose Corallinaceae has been supplied almost entirely by workers with a geological approach. As stated above, the early work of Rothpletz (1891) provided a basis for determining generic and hence phylogenetic affinities of crustose corallines. Reviews of crustose coralline algal phylogenetic relationships were presented by Ishijima (1954) and by Johnson (1956b, 1963a), and both of these workers agree that *Sporolithon* is the most primitive of the crustose corallines, followed by *Lithophyllum* and *Lithothamnium*, respectively.

DISTRIBUTION OF CRUSTOSE CORALLINACEAE

PHYTOGEOGRAPHICAL STUDIES

While it may be said that crustose corallines are found from the littoral zones to great depths in all modern seas, no comprehensive study had been made of the geographical distribution of the melobesioid algae prior to Adey's (1970a) preliminary treatment. According to Johnson (1962b), *Lithothamnium* has the widest geographical distribution of any genus in the Corallinaceae. The greatest development of this genus occurs in the colder water of temperate and arctic seas; however, *Lithothamnium* extends from pole to pole wherever conditions are favourable.

Lemoine (1940) and Johnson (1954) stated that *Porolithon*, *Lithoporella* and *Goniolithon* are essentially tropical and notably absent from the Mediterranean Sea and that *Mesophyllum* is also restricted to warm seas. All of the existing species of *Sporolithon* have been found in tropical and subtropical waters and the available evidence indicates (Johnson, 1963b) that fossil species occurred in a similar environment. Most of the recent species of *Sporolithon*

have been collected from the tropical Pacific, some extend into the Indian Ocean, Red Sea and Mediterranean Sea, one species is known from Mexico's west coast, and another from the Bahamas area of the Atlantic. The Recent species of this genus and their geographical distributions are given in Figure 10 of Johnson's (1963b) paper. It has been recorded (Johnson and Adey, 1965) that members of the Lithophylleae, while extending into cold areas, are generally found in temperate and tropical regions, with their greatest development in tropical seas.

Adey (1970a) provided world-wide distributional maps showing the percentage of total melobesioids contributed by the genera *Tenarea*, *Lithophyllum*, *Neogoniolithon*, *Porolithon*, *Hydrolithon*, *Pseudolithophyllum*, *Lithoporella*, *Lithothamnium*, *Sporolithon* (as *Archaeolithothamnium*), *Mesophyllum*, *Clathromorphum*, *Phymatolithon* and *Leptophytum* for the various geographical regions of Ekman (1967). These maps were compiled from the Foslie Herbarium collection data and from seventy other species for which Adey considers the data sufficiently reliable.

GEOLOGICAL WORK

Geologists have studied the crustose coralline algae because these organisms abound in limestone deposits from the late Cretaceous to the present day. Therefore, much of the basic information concerning the Melobesioideae has been contributed by workers with a geological background.

Thoroughly annotated bibliographies, recently compiled by Johnson (1957a, 1967), list most of the pertinent literature concerning fossil melobesioids; the more noteworthy of these will be mentioned here. Most of these studies emphasize that the part played by calcareous algae in the formation of both ancient and living reef deposits is conspicuous or even dominant. For example, an early and excellent quantitative study by Pollock (1928) on Hawaiian fossil reefs, showed them to be composed primarily of crustose coralline algae.

The usefulness of the "*Lithothamnium*-zone" has been proposed (David and Sweet, 1904) as a valuable geological indicator of oscillatory vertical shoreline movements. That lime-secreting algae serve as prehistoric climatic indicators (Glock, 1923), usually of warmer climates, has also been indicated.

Bergmann and Lester (1940) were the first to propose that 'coral' reefs should be considered as possible sources of petroleum because much lipid material is present in corals and reefs may act as gigantic accumulators of waxes, by trapping and removing them from circulation. It was later pointed out (Ladd, 1950) that only ancient reefs are known to produce oil and these ancient structures differ from existing reefs; caution is therefore required when interpreting the old in terms of the new. The additional point has been made (Cloud, 1952) that an increased awareness of the importance of ancient reefs in the localization of oil has led to increased research into reef structure, their lithic nature and palaeontological peculiarities. As a result, there has been a great number of drillings into modern reefs, studies of their surface features and ecology, deep dredgings and geophysical investigations of atolls, seamounts and their environments.

In reiterating the importance of algae in forming biotic reefs, Cumings (1932) indicated that the term 'reef' no longer had a precise meaning.

Consequently, he proposed the terms "bioherm" for structures with a reef-like, lens-like, or bank-like form built chiefly by sedentary organisms, and "biostrome" for those with a strictly bedded or layered aspect. Reef types and associated structures have been defined, described and illustrated (Cloud, 1952) and such workers as MacNeil (1954) and Tracey, Cloud and Emery (1955) have expounded upon and clarified these definitions further.

Archaeolithothamnium episporum Howe (described as a Recent and Pleistocene species) and three other fossil melobesioids, two being new to science, were recorded (Howe, 1918b) from the Panama Canal zone. Howe pointed out that prior to 1918, fossil melobesioid taxonomy was an untouched field in America. Extensive taxonomic treatments, enumerating and describing melobesioids from many deposits of various ages, have been published by Lemoine [1909–1971] and Johnson [1937–1968], who are perhaps the two greatest investigators of the fossil melobesioid algae. A noteworthy and comprehensive treatment of the Cenozoic coralline algae from the Western Pacific has been given in which numerous fossil species were described (Ishijima, 1954).

QUALITATIVE APPRAISALS OF STANDING CROP

The occurrence in Indo-Pacific reefs of crustose corallines as well as corals was reported (Darwin, 1842) well over a century ago: however, the importance of these seaweeds as reef builders was first emphasized by Agassiz (1888), particularly as regards their contribution to total mass.

Numerous workers throughout the world have observed that one of the most important roles that melobesioid algae play is in determining the physical and chemical structure of the ocean floor from the littoral zone to depths of hundreds of metres. According to Kjellman (1883), along the northern coast of Norway *Lithothamnium soriferum* Kjellman covers the bottom in great masses and *L. glaciale* extends over miles of deep-water bottoms. Kjellman was first to express the opinion as to the great importance of these organisms in the formation of future strata of the earth's crust. The particular abundance of *Lithothamnium* in arctic seas (Seward, 1931) also has been emphasized.

Non-articulated species of coralline algae have long been known to form very large banks or fringing ridges of calcium carbonate deposits. Many of the world's reefs have this sort of ridge which commonly may be composed entirely of from one to several of various crustose corallines; in some cases other algae, as well as corals, echinoids and molluscs may become locally abundant. Early emphasis (Foslie, 1895a) placed on this type of so-called *Lithothamnium*-bank was based on investigations along the coast of Norway, although *Lithothamnium*- and *Lithophyllum*-banks had been mentioned earlier (Walther, 1885) in the Bay of Naples. According to Kjellman (1883), the banks at Novaya Zemlya and Spitzbergen are composed predominantly of *Lithothamnium glaciale*, while those in Iceland and along Norway's northern coast are formed by *L. ungeri* Kjellman. *Lithothamnium*-banks have also been described (Masaki and Tokida, 1963) at Yashima in the Ariake Sea, Kumamoto Prefecture, Miumaya Bay, Higashe Tsarugun and Aomori Prefecture in Japan.

A tropical crustose coralline bank from the mouth of a bay at Bonaire,

Netherlands Antilles, was described somewhat superficially by Zaneveld (1958). Zaneveld stated that tropical banks are very different from reefs but did not clearly distinguish either. He recorded *Lithothamnium erubescens* Foslie as the major bank-forming species but, as pointed out by Hoek (1969), his identification was not critical because he did not investigate the histology; according to a note added to Zaneveld's paper, W. R. Taylor considered Zaneveld's material to belong to *Goniolithon spectabile* Foslie.

Transects estimating the relative abundance at Bikini Atoll (Tracey, Ladd and Hoffmeister, 1948) revealed that the marginal ridge zone of a windward reef was made up of 90–95% melobesioids and 5–10% corals. These extensive melobesioid-dominated ridges at Bikini (Taylor, 1950) are reported to be composed of several *Porolithon* species. Another example of algal-ridge structure is the typical reef rim under conditions of moderate wave action in the Solomon Islands. This habitat is characterized (Womersley and Bailey, 1969) by *Lithophyllum moluccense* Foslie, *Neogoniolithon myriocarpum* (Foslie) Setchell and Mason and *Porolithon onkodes* (Heydrich) Foslie; under heavy surf action *P. onkodes* is the dominant organism and *Neogoniolithon myriocarpum* also is present. The above authors also emphasized the importance of *Porolithon onkodes* and *P. gardineri* as reef-building species in the Marshall Islands. They state that, on Indian Ocean atolls (Maldives, Chagos, etc.), *P. craspedium* (Foslie) Foslie and *P. onkodes* are dominant on the reef rim under strong surf and *P. gardineri* is of less importance. The importance of *Neogoniolithon frustescens* (Foslie) Setchell and Mason in the reef-moat area of Pacific atolls, in Indonesia and in the Indian Ocean was also indicated. Similarly, according to Guilcher, Denizot and Berthois (1966), the outer ridges at Mopelia Atoll of the Society Islands and nearby atolls and barriers in French Polynesia consist mostly of *Porolithon onkodes* and *P. craspedium* growing on old ledges. At present, coral growth plays an insignificant role on these ridges, which resemble comparable ridges of the Marshall Islands. The Funafuti expeditions (1896–1898) provided major contributions toward elucidating the role of reef-building melobesioid algae. Descriptive transects were made (Finckh, 1904) across Funafuti Atoll and the order of importance of reef-forming organisms in contributing to bulk was as follows: crustose coralline algae (lichenous form, thinly branched form, knobbed form), *Halimeda*, foraminifera and corals. Finckh's study marks the first recorded assessment of the standing stock of crustose coralline algae, emphasizing the erosion-resisting melobesioid belt which forms the outermost and exposed broad zone and pointing out the critical cementing function of these algae in the consolidation of reef components. During the same year, David, Halligan and Finckh (1904) gave some results of dredging in the deeper waters of Funafuti Atoll. Living melobesioids were found down to 200 fathoms where they grew as thin crusts; the four chief reef-forming organisms on the oceanward slope of the atoll were: foraminifera, Melobesioideae, *Halimeda* and corals. An unbranched form of crustose coralline is ubiquitous around Funafuti Atoll (David, Halligan and Finckh, 1904) and is the great cementing agent of the sand and rubble on the ocean slope of the reef and in the lagoon below low water along the shores. Although the authors indicated that this alga grows slowly, they emphasized that it would be difficult to overestimate its importance as a former of reef rock. The role of melobesioids in deposition and cementation in building reefs and lime-

stones has been emphasized by Glock (1923), particularly where waters are relatively warm, i.e. in tropical and subtropical regions.

It was Foslie (1907f) who first showed that although crustose corallines are the dominant components of tropical reefs, the number of species is small and each occurs in great abundance: he firmly established that over wide areas of the Indian and Pacific Oceans three or four species, namely, *Neogoniolithon frutescens*, *Porolithon onkodes*, *P. craspedium* and *P. gardineri* are the important reef builders in the littoral and shallow sublittoral zones, while *Lithothamnium indicum* Foslie and *L. australe* Foslie are the great builders of deeper (60 fathoms) strata. Gardiner (1903) agreed with Foslie in emphasizing that the number of species of Melobesioideae in any one coral reef is seldom more than a dozen. He also stated that no known coral reef in the Indo-Pacific could have reached the surface and maintained a wave-resistant front without their presence: Gardiner (1903), however, noted that many Indo-Pacific reefs often have a higher percentage of corals in their composition.

Early in the history of biotic reef studies, Howe (1912) pointed out that previous studies of reef-building processes had greatly underestimated the importance of lime-secreting algae, and that crustose corallines are effective reef formers at greater depths than are the corals. These points were carried several steps further by Setchell (1926a) as a result of his qualitative appraisals of standing stocks during his studies in the Samoan Islands and Tahiti. Setchell's (1926a) contribution toward elucidation of the role of crustose coralline algae may be summarized in the following six points: (1) there can be no reef formation without crustose corallines; (2) the biological depth limit in reef formation based on coral peculiarities may be abandoned; (3) reef interconvertibility from fringing reef to barrier reef to atoll is an unnecessary assumption: (4) "coral" reef formation where sea level changes have occurred needs to be evaluated; probably those changes took place before, rather than during, the growth of these reefs and are incidental rather than causal; (5) encrusting animals rank second to crustose corallines in importance; and (6) barrier and atoll reefs originate at depths below those at which reef-forming coral can grow, and this deep growth is of crustose corallines.

According to Setchell (1924), the reef margin of Rose Atoll in the Samoan Islands is dominated by *Porolithon gardineri* f. *abbreviata* (Foslie) Lee, as *P. craspedium* f. *mayorii* (Foslie) Howe, which has been almost the sole agent in forming the compact reef. In contrast, *P. onkodes* is (Setchell, 1926b) the most conspicuous organism of both Tutuila's and Tahiti's fringing and barrier reefs, especially in wave exposed areas. Tahiti's barrier reefs, in Setchell's (1926b) opinion, have arisen in water up to 30 fathoms deep almost exclusively from crustose corallines, one of which, *Lithothamnium dickiei* Foslie, is said to have probably formed an entire bank near Papeete, which was then covered by corals almost to the surface, where *Porolithon onkodes* overgrew them. In Tahiti, corals are reported (Crossland, 1938) to be absent where crustose corallines grow best. It is curious that although Crossland indicated melobesioids to be the most conspicuous of all surface constituents, he asserted, apparently with no confirming data, that they are making no permanent addition to Tahitian reefs.

In addition to the above reports, Gardiner (1903) observed that in the Atlantic off certain bays in the Cape Verde Islands, there are

fringing reefs which also consist almost entirely of melobesioid algae. Moreover, along the Brazilian coast (Gardiner, 1903) melobesioids are the chief agents which consolidate the sand and build reefs from 18° latitude to the almost fresh waters of the Amazon River mouth.

The efficiency of the melobesioid spur and groove area in absorbing wave energy has been discussed by Tracey, Ladd and Hoffmeister (1948), and the ecological influence of the crustose-coralline outer edge in controlling zonation of the various atoll reef-types has also been emphasized. The spur and groove area of the reef at Raroia Atoll (Doty and Morrison, 1954) is composed of massive amounts of *Porolithon onkodes* with only traces of other corallines. The surface of the reef is uniformly coated with *P. onkodes* which throughout the ridge area is dominant. Doty (1954) found that with variations in reef exposure and local topography, other species of *Porolithon* become locally abundant at Raroia, but they rarely dominate. In rare instances, a species of *Neogoniolithon* appeared in numbers, but only well shoreward on the reef flat. As Doty (1954) asserted, the term "*Lithothamnium*-ridge" is certainly not appropriate for the seaward edge of outer reefs because *Lithothamnium* (uncommon in the Tuamotus) is not likely to be common on any reef edge where *Porolithon* is found. That "*Lithothamnium*-ridge" and "Nullipore-ridge" are misnomers was again emphasized by Johnson (1954) and the term, algal ridge, was suggested.

The coralline development at Raroia Atoll (Newell, 1954) has been described further. The unequal width of the ridge and spur area was postulated to have resulted from the growth of the algal buttresses into the surf at unequal rates. Coverage on the flat tops of the spurs was estimated (Newell, 1954) to be 50% *Porolithon onkodes* and 25% *Pocillopora elegans* (the coral). Wherever the biota of the Raroia algal ridge is healthy, the ridge is covered by pink, blister-like crusts of *P. onkodes*, with scattered small hemispheres of *P. gardineri*: *P. onkodes* is truly a rock former, effectively binding corals and foraminiferal deposits together into a rigid framework.

Based on their observations at Raroia Atoll, Doty and Morrison (1954) suggested that since *Porolithon onkodes* is apparently of extreme importance in reef development, the sudden appearance and spread of such a species would partly explain the noticeable uniformity of atoll reefs. From observations at Johnston Island, Raroia and elsewhere, Doty (1954) suggested that an atoll could form without an emergent sea mount. Because *Porolithon*, the dominant builder, actively begins at a definite depth, Doty reasoned that if a submerged sea mount remains stable, the lagoon might become filled in and the reefs broader such as is seen in Canton in the Phoenix group and Christmas Island in the Line Islands. If the sea mount sinks steadily, the reefs might become narrow and develop a deep lagoon: examples of this type are shown by Raroia and most of the Tuamotu Archipelago. The rising of a seamount faster than its erosion could result in a raised reef such as the northernmost corner of Anaa, or a raised atoll such as Henderson or Makatea in the Tuamotus. On the other hand the sea mount might sink rapidly enough to escape from the surface, and this could result in a structure similar to the southeastern portion of Johnston Island. Doty (1954) also proposed that the solution and production of sediment in situ from the solid algal (and coral) material does not take place as abundantly as the local formation of fragments, which to a large extent become deposited in the lagoon or on the reef

flat. The important feature in this (Doty, 1954) is the removal of fragments which provides new sites favourable for coralline growth.

Work at Rongelap Atoll (Lee, 1967) verified that *Porolithon onkodes*, *Neogoniolithon frutescens*, *Porolithon craspedium* and *P. gardineri* are well adapted to the atoll-type of reef habitat where they produce a dominant, homogeneous melobesioid community to the partial exclusion of other organisms. The notable lack of systematic and ecological data concerning the melobesioid algae was also stressed by Lee (1967) who also stated that these algae are the dominating organisms and the major components of nearly all atoll reefs.

QUANTITATIVE APPRAISALS OF STANDING CROP

The first measurement of crustose coralline coverage was carried out by Pollock (1928) upon fringing and fossil reefs of Oahu Island, Hawaii. A metal grid was devised and used as a movable quadrat along transects to estimate proportions of calcareous animals and seaweeds. Pollock's transects on living reefs went only as deep as wading permitted and the large stands of crustose corallines near the algal rim were not studied. Coralline algae were recognized as either crustaceous, nodular or branching "*Lithothamnium*" and were not identified further; however, Pollock's results showed that corals were subordinate to crustose coralline algae in all of the living (2·9% coral and 4·6% melobesioids) and fossil (24% corals and 44% melobesioids) reefs examined. Pollock's study and its techniques have remained unnoticed and for unexplained reasons have been rarely cited by later workers.

Ecological zones at Eniwetok Atoll were investigated by Stearns (1945) using two low-resolution transects; one transect was located on the outer reef of Eniwetok Island and the other on the inter-island reef north of Eniwetok Island. He reported four zones which in order shoreward are: (1) "*Lithothamnium*"-ridge, (2) pool and pothole zone, (3) bevelled limestone platform, and (4) beach conglomerate. Living corals are scanty and, inland of the ridge, the reef is wave-eroded limestone. The reef was denoted as being in a decadent state, supposedly due (Stearns, 1945) to a recent local change of a few feet in the sea level. Later, Odum and Odum (1955), on another inter-island reef at Eniwetok Atoll, used a transect series of quadrats to measure coral and crustose algal standing crops. This work elucidated some interrelationships and trophodynamics of melobesioids in relation to other organisms.

Hoek (1969) recently described algal "vegetation-types" along the open coasts of Curaçao, Netherlands Antilles. He employed the European system whereby an arbitrary phytosociological scale is used to describe vegetation. *Porolithon pachydermum* (Foslie) is a very important encrusting organism in the surf platform on the seaward edge of the northeast coast and *Lithophyllum daedaleum* Foslie and Howe and an unidentified species of *Lithophyllum* are also present in this zone. On the calmer southwest coast, *Porolithon pachydermum* plays an important role in cementing together corals down to a depth of about 7 m.

A technique for estimating the relative abundances of crustose corallines on collected substrata was developed by Adey (1964, 1965, 1966a,b,c, 1968) in biosystematic studies of the northwestern North Atlantic and Icelandic coasts. *Clathromorphum circumscriptum* is the most important intertidal

melobesioid (13·8% of the total coverage) in the Gulf of Maine, while *Lithothamnium glaciale* is the most abundant species in the whole collection. *Lithothamnium lemoineae* and *Leptophytum laeve* cover 11·4 and 6·3% of the collected substrata respectively, and *Leptophytum foecundum* is more abundant relatively deeper and more northward. In Nova Scotia and Labrador, relative abundances as a function of depth were found (Adey, 1966c) to be comparable to those recorded in the Gulf of Maine, except that the whole spectrum is shifted deeper owing to cleaner water. *Phymatolithon lenormandii* and *Lithothamnium trophiforme* have total mean sublittoral coverages (Adey, 1966c) of 0·1 and 0·4%, respectively. A similar treatment (Adey, 1968) of the distribution of crustose corallines on the coast of Iceland has revealed occurrences and abundances similar to those in the northwestern North Atlantic.

STUDIES ON STRATIFICATION PHENOMENA

Although there are no direct studies of stratification of melobesioids, the literature does contain some descriptive information. For example, *Halicystis*, a marine green algal epiphyte (Kuckuck, 1907), typically grows on *Lithothamnium*. Furthermore, it has been noted that in the spur area at Raroia Atoll (Doty and Morrison, 1954), a prostrate *Gelidium* and a *Ceramium* grow in small concavities of the *Porolithon onkodes* along with *Herposiphonia tenella* (C. A. Agardh) Naegeli. Few if any macroscopic algae grow upon the *Porolithon onkodes* of the groove areas.

Another Tuamotuan atoll, Mururoa, was examined in detail by Chevalier, Denizot, Mougin, Plessis and Salvat (1968). They reported a little-known alga, *Chevaliericrusta polynesiae* Denizot, to be an abundant encrusting form in the algal ridge above 10 m in depth which often overgrows *Porolithon onkodes*. Other species of algae which commonly grow on the above two species in the outer-ridge area are *P. craspedium*, *Lithophyllum kaiserii* Heydrich, *Caulerpa pickeringii* Harvey and Bailey, *C. urvilliana* Montagne, *Pocockiella variegata* (Lamouroux) Papenfuss, *Dictyosphaeria* sp., *Liagora* sp., and *Microdictyon* sp. A species of *Jania* is abundant on the *Porolithon onkodes* in isolated areas.

The melobesioids on shallow rocky bottoms in the Gulf of Maine (Adey, 1966c) are usually covered with heavy growths of filamentous, leafy and fleshy algae. In addition, these microbiostromes contain an abundant epifauna of molluscs and echinoderms as well as an extensively developed infauna of boring pelecypods and ophiurans. *Phymatolithon lenormandii* in the Gulf of Maine (Adey, 1966c) tends to be restricted to emerging ledges beneath the cover of Fucales, being generally most abundant beneath a heavy cover of *Ascophyllum*. In southern Nova Scotia, Newfoundland, southern Labrador, and the northern Gulf of St Lawrence, the overlaying algae occur in relatively less abundance (Adey, 1966c).

STUDIES ON ZONATION

Many authors have reported zonation phenomena in relation to the distribution of crustose corallines. Lemoine (1940) has given an account of a vertical melobesioid zonation in the Bay of Fundy and the English Channel where crusts grow as much as 3 m above low-tide level in caves and areas bathed in

spray. Littoral melobesioids are usually non-branching encrusted forms (Johnson, 1954), but the reef flat at Haingsisi Island (Indonesia) is reportedly covered (Weber-Van Bosse and Foslie, 1904) by rounded heads of the branching *Lithothamnium erubescens* Foslie exposed at extreme low tide.

Maximum depths from which crustose coralline algae have been collected have been tabulated by Lemoine (1940) using all available data. So far, only *Lithothamnium* spp. have been found at depths exceeding 100 m.

Such accounts also include descriptive observations of vertical zonation at Funafuti Atoll (Finckh, 1904; David, Halligan and Finckh, 1904) and at the Juan Fernandez Islands (Skottsberg, 1943). The branched and knobbed forms of crustose corallines, as well as the reef-building corals, were found to be limited at Funafuti mainly to a depth of 20 m (David et al., 1904). In the Juan Fernandez Islands (Skottsberg, 1943), the major crustose corallines are *Lithothamnium validum* Foslie and *Pseudolithophyllum discoideum* (Foslie) Lemoine which form a deep-water association on stones, pebbles and old shells, all of which become thickly encrusted. Another association possibly consists of *Lithophyllum decipiens* Foslie and *L. fernandezianum* Lemoine and these develop as a thin cover on rock in littoral pools and in the surf zone. Foslie (1907f) has given species lists and depth distributional data for the Chagos and Seychelles Archipelagos. A similarly brief report of Strauss (1962) gives a qualitative description of melobesioid zonation with depth in the Mediterranean. According to Strauss, *Lithothamnium lenormandii* is found in the supralittoral, *Lithophyllum tortuosum* (Esper) Foslie forms a littoral pavement and *Neogoniolithon mamillosum* (Hauck) Setchell and Mason and *Pseudolithophyllum expansum* (Philippi) Lemoine build coralline bottoms in the lower infralittoral.

Setchell (1926b, 1928) has given another qualitative account of horizontal reef zonation for the fringing and barrier reefs of Tahiti. Although the zones differ in detail among reef-types, an outer *Porolithon onkodes* belt is, in general, present, followed by a *Sargassum*-zone and then a *Turbinaria*-zone immediately shoreward, with the last-named finally becoming either a coral or a rubble area. The horizontal zonation of melobesioids has been reported at Funafuti by Finckh (1904) and at the Marshall Islands atolls by Tracey, Ladd and Hoffmeister (1948).

Both horizontal and vertical distributional patterns have been given for Raroia Atoll's melobesioid algae by Doty and Morrison (1954). More detailed biosystematic studies, including quantitative determinations of relative abundance (Adey, 1964, 1965, 1966a,b), have shown that the latitudinal, horizontal, and vertical zonation patterns of crustose corallines were correlated most strongly with depth and temperature in the Gulf of Maine.

PRODUCTION BY CRUSTOSE CORALLINACEAE

SIZE INCREASE

The first growth measurements on crustose coralline algae were made by Finckh (1904) using fragments of a non-branched form (*Porolithon*) grown in boxes at Funafuti Atoll: no growth could be detected over a 5-month period. Thin, crust-like, pink patches on the reef were found to increase in

diameter at an average rate of 1·0 in./10·0 months; in one instance, 1·0 in./6·6 months was observed. Finckh concluded that the growth of crustose coralline algae is extremely slow.

The *Porolithon onkodes* association of the barrier reef near Papeete, Tahiti was reported by Setchell (1926b) to increase 0·3–0·5 mm/year in thickness; however, just how this was determined is not clear.

Lithophyllum incrustans and *Phymatolithon lenormandii* were found by Lemoine (1913a, 1940) to extend their margins at rates of 2–7 mm/year at Roscoff, France. According to Huvé (1954), young thalli of *Lithophyllum tortuosum* in the western Mediterranean attain a diameter of 1–2 cm in 7–8 months. Mature *Clathromorphum circumscriptum* grows (Adey, 1965) 3·0 mm/year laterally, while *C. compactum* increases about 0·2–0·3 mm/year in thickness in the eastern Gulf of Maine. Adey (1970c) was the first to use increases in area of Norwegian melobesioids grown in experimental conditions in an attempt to relate light and temperature effects to distributional patterns. Areal increases comparable to those of Norwegian crustose corallines were reported by Adey and McKibbon (1970) for *Phymatolithon calcareum* (Pallas) Adey and McKibbon and *Lithothamnium coralloides* Crouan from the Rio de Vigo. Most of the growth took place during the summer months with little or no growth during winter.

WEIGHT INCREASE

Weight increases have been measured (Smith, 1970) for *Lithothamnium* sp. and *Lithophyllum* sp. from California: four fragments of *Lithothamnium*, showed an increase in weight of 210% of total weight/year for the first 28 days and 105%/year during the next 74 days. The average rates for these two genera were about 3%/week.

ORGANIC PRODUCTION

Some work has been done on overall reef productivity and in some cases the role of coralline algae is indicated. For example, 'flow respirometry' was used by Sargent and Austin (1949, 1954) to determine the productivity of atoll reefs in the Marshall Islands. The density of crustose corallines on the seaward face of the reef at Rongelap Atoll, inside and outside the surf zone, led them to presume that the area has high productivity. They also measured net oxygen production of various reef organisms in jars set in the flowing inter-island waters. Three measurements of a single *Porolithon* thallus yielded oxygen production rates (based on sample wet weight) comparable to those of corals.

Flow respirometry has been used subsequently to measure productivity on an inter-island reef at Eniwetok Atoll (Odum and Odum, 1955), on a fringing reef on Kauai Island, Hawaii (Kohn and Helfrich, 1957) and on Coconut Island reef in Kaneohe Bay, Oahu Island, Hawaii (Gordon and Kelly, 1962). All of these studies indicate that crustose corallines are important organisms in the economy of living reefs.

The first published measurements (Goreau, 1963) of carbon fixation and calcium carbonate deposition rates for various reef-building algae were obtained by using radioisotope techniques (^{14}C and ^{45}Ca simultaneously), but problems arising from the chemical and taxonomic methods employed

leave many of these data open to question. For example, Goreau reported the uptake rates in terms of μM carbon or calcium fixed per mg nitrogen per hour, which is impossible to relate to either standing stock or to sediment studies. Recently, Marsh (1970) has measured the productivity of unidentified melobesioids from an island reef at Eniwetok Atoll and from Kaneohe Bay, Oahu Island, Hawaii. He used a specially constructed, dissolved-oxygen electrode and found that crustose Corallinaceae, while within the same order of magnitude, had the lowest productivity of all photosynthetic reef organisms examined.

INORGANIC PRODUCTION

While there has been no work specifically concerned with inorganic productivity, several studies have dealt with the production of inorganic substances and related phenomena and, will therefore be treated here. Indirectly related to inorganic production are the mineralized membranes characteristic of the articulated species; those of *Corallina officinalis* and *Amphiroa dorbigniana* Decaisne were found by Bass-Becking and Galliher (1931) to be optically similar to those of the melobesioid genera *Melobesia*, *Lithothamnium* and *Lithophyllum*. The walls were found to be non-cellulosic, probably pectin or pectin-like, birefringent in longitudinal section and isotropic in cross section. The wall fibres are probably tangential elongate lamellae interspersed with concentrically arranged interstices in which calcite is deposited initially and magnesium carbonate secondarily.

Relatively early in the history of knowledge concerning carbonate deposition by crustose corallines, Lemoine (1911) pointed out that tropical species contain relatively more magnesium carbonate than temperate or subarctic species. The calcite of melobesioid coralline algae contains a higher percentage of magnesium carbonate than the aragonite of other algae (Clarke and Wheeler, 1917; Chave, 1954). Different species were found by Chave (1954) to incorporate different percentages of magnesium carbonate, but all incorporated more magnesium with increasing temperature. Moberly (1968), however, employing electron microprobe analysis, found that the magnesian content of coralline algae is not primarily dependent on water temperature but is a function of all the variables that determine growth rate. Calcite algal skeletons containing higher percentages of magnesium carbonate were found to be relatively more soluble by Chave, et al. (1962) in sea water.

SEDIMENT PRODUCTION

Quantitative data concerning coralline algal sediment production remain scanty although many have felt that the contribution of crustose corallines must be considerable. Newell, Rigby, Whiteman and Bradley (1951), have recorded extensive sediment producing communities of stony corals and melobesioids which build long reefs along the seaward face of the northwest coast of the Andros Island barrier reef. The prominence of crustose coralline algae along the lee margin indicated to them that the lagoon may receive a disproportionate quantity of algal detritus as compared with that of stony corals. Further investigation revealed that *Neogoniolithon strictum* (Foslie) Setchell and Mason is effective in lagoon sand production. Coralline algae contribute 32·6% to total lagoon sand and in this respect are more important

than coelenterate corals. Another quantitative examination of beach sediments by Moberly and Chamberlain (1964) indicated that calcareous Hawaiian Rhodophyta were subordinate in importance only to foraminiferans and molluscs in sand formation.

According to Chave and Wheeler (1965), *Clathromorphum compactum* growing in the Gulf of Maine deposits approximately 0·5 mm of carbonate sediments annually. Seasonal increments, identified by localization of gametangia (or tetrasporangia?) produced in the autumn, showed that thicker layers are produced in the summer than in the winter. A more sophisticated technique, utilizing an infrared analyser, has been applied by Smith (1970) to determine the percentage of calcium carbonate changes in articulated coralline algae: from the data it was estimated that the annual calcium carbonate production for some Californian articulated species is about 150% of the standing crop and that crustose species might be expected to show similar rates.

CRUSTOSE CORALLINACEAE IN RELATION TO THEIR ENVIRONMENT

PHYSICAL FACTORS OF THE ENVIRONMENT

Substratum

Although most information about the substrata on which melobesioids grow consists merely of records, several studies have taken a more ecologically oriented approach and these will be mentioned here. Ladd (1950) observed that crustose coralline algae, as well as other reef organisms, generally require a solid bottom for fixation. On the other hand, while most species of *Archaeolithothamnium* appear to grow attached to a firm bottom or coral heads as well as to other coralline algae (Johnson, 1963b), highly branched species such as *A. timorense* Foslie have been dredged from sandy bottoms where they are apparently lying free. In addition, Johnson (1963b) has suggested that broken fragments from many of the saxicolous species often continue to grow unattached. Examples of this phenomenon are forms of *Lithothamnium calcareum* (Pallas) Areschoug and *L. fruticulosum* (Kützing) Foslie, which grow abundantly (Lemoine, 1940) in sandy regions of the Mediterranean Sea and along the coasts of Ireland and France. Other melobesioid species show no substratum preference, growing equally well on rock, pebbles, mollusc shells, glass, barnacles, anchor chains, cables, coral, porcelain and other algae (Johnson, 1954).

The most thorough studies of melobesioid occurrence in relation to the type of substratum (Adey, 1964, 1965, 1966a,b, 1970d) were made in the North Atlantic. The percentages of area occupied on each collected rock specimen by each Gulf of Maine melobesioid as a function of the rock size (Adey, 1965) was utilized as a useful indicator of substratum preference. Crustose corallines, growing below mean low water, were found to form the dominant incrustation on bottoms with a predominant grain-size larger than 1–2 cm (Adey, 1964). The same technique was applied by Adey (1970d) to quantify the substrata relationships of Icelandic Melobesioideae as a function of

depth: *Clathromorphum circumscriptum* is the only species that showed no relationship to substratum size in its depth distribution. *Leptophytum laeve* increases on the smaller-sized substrata as a function of increasing depth. It appears able to grow on finer particles than other crustose corallines, possibly because of its more rapid growth (Adey, 1970d). The larger rocks are more extensively covered by *Pseudolithophyllum orbiculatum* relative to *Leptophytum laeve*. *Lithothamnium* increases in overall abundance as a function of increased depth, but its abundance on the smaller rocks decreases.

Temperature

Detailed studies of temperature as a factor in crustose coralline biology are few. A discussion of reef distribution (Ladd, 1950) on a world-wide basis has emphasized that the most influential factor controlling reef growth is temperature which, in a large part, gives rise to the extensive reef developments in the relatively warmer, western tropical parts of oceans.

The genus *Sporolithon* (as *Archaeolithothamnium*) throughout its history (Johnson, 1954) seems to have been restricted to warm waters. *Lithothamnium* is widespread but it predominates in cool temperate and polar waters. *Lithophyllum*, *Goniolithon* (including *Neogoniolithon*) and *Porolithon* are all very important in warm seas today (Johnson, 1954), *Lithophyllum* being most important in species numbers and *Goniolithon* and *Porolithon* represented by relatively fewer, widely distributed species. Lemoine (1940) has reported that in the Galapagos Islands some crustose corallines are able to endure temperature changes of up to 10° C during a single day.

Temperature has been shown to be one of the most important controlling factors (Adey, 1964, 1965, 1966a,b,c, 1969, 1971) in the regional and local distributions of North Atlantic crustose species. *Kvaleya epilaeve*, a parasite on *Leptophytum laeve*, reaches maximum abundance below 3° C and does not occur above 9°–10° C in the North Atlantic (Adey and Sperapani, 1971). *Leptophytum laeve* extends into warmer waters but is limited by a requirement for winter temperatures below 6° C (Adey and Sperapani, 1971). Another temperature effect is exemplified by *Clathromorphum compactum* in the Gulf of Maine. This alga shows a 40% change in carbonate composition during the year (Chave and Wheeler, 1965), and more rapid calcification occurs during warmer periods.

In calcite-secreting marine organisms (Clarke and Wheeler, 1917) the percentage of magnesium was observed to increase almost linearly with increases in water temperature from 0 to 30° C. Tropical crustose corallines have also been shown (Lemoine, 1911; Chave, 1954) to have a higher magnesium carbonate content than their colder-water counterparts.

Illumination

That reef organisms need strong light and that shallow tropical regions provide optimum conditions has been emphasized by Ladd (1950). That some crustose corallines are, however, adapted to habitats of low light energies is implicit in the report of David, Halligan and Finckh (1904) of a thin melobesioid crust living at depths of at least 400 m; the ability of red algae to grow under conditions of reduced light has been postulated as possibly due to the presence of phycoerythrin, which enables them to use blue light in photosynthesis

(Strain, 1951). Unfortunately, this has never been investigated in the Melobesioideae.

Johnson (1954) noted that during low tides, the algal-ridge melobesioids are exposed to full sunlight for considerable lengths of time without losing their colour: however, he remarked that these areas are nearly always kept moist by the action of breakers and this suggests that these algae will tolerate bright light but not heating or desiccation. It has been suggested (Doty and Morrison, 1954) that perhaps the ridge-forming *Porolithon onkodes* at Raroia Atoll, differs physiologically from other melobesioids. It appears able to develop rapidly, withstand intense illumination and a certain degree of emergence. In general it seems that tropical melobesioids can tolerate greater light intensities than their deeper growing counterparts in temperate regions. The interesting hypothesis has been proposed by Johnson (1954) that tropical species, by their higher content of magnesium carbonate, are somehow enabled to influence the quantity of light which they tolerate and absorb.

According to Adey (1964), *Phymatolithon rugulosum* reaches a greater abundance at shallower depths than in the offshore waters of the Gulf of Maine bays. This appears to be attributed to clearer water and greater light further offshore. Light was also considered (Adey, 1965) probably to be the dominant cause of the peak of abundance of *Clathromorphum circumscriptum* which occurs between mean low water to 1 m in depth. In the eastern areas of the northwestern North Atlantic, where the substratum is favourable, crustose corallines extend deeper than in the coastal Gulf of Maine (Adey, 1966c) owing to cleaner water and deeper light penetration. *Lithothamnium coralloides* and *Phymatolithon calcareum* in the Ria de Vigo grew best (Adey and McKibbon, 1970) in tanks under light and temperature regimes that closest approximated those conditions characteristic of spring. A critical experiment has been reported (Smith, 1970) in which *Lithothamnium* sp. and *Lithophyllum* sp. increased in mass from low to intermediate light energies.

Prevailing Currents

The one account in the literature of current effects involved the (steady?) current across an inter-island reef at Eniwetok Atoll (Odum and Odum, 1955). This current yields a very distinctive distribution of surface encrusting algae. The quantitative coverage by surface encrusting algae (and corals), correlated with mean current velocities, was found (Odum and Odum, 1955) to decrease, while the abundance of subsurface algae (Cyanophyta) increases shoreward across the reef. This distribution suggests a transition from a water filtering source of nutrients near the reef rim to a subsurface decomposition source nearer the lagoon.

Turbulence

Research involving turbulence effects upon crustose coralline algae is restricted to several qualitative observations. Ladd (1950) implied that reef organisms seem to require some agitation or water circulation because of their sessile nature, which necessitates that food be brought to them. In agreement with this statement are numerous observations that melobesioid abundance often appears to coincide with the degree of water agitation. In Hawaii,

localization of different crustose coralline forms appears (Pollock, 1928) to be related to nearness of surf. The reef edge is characterized by encrusting forms and compact branching masses growing exposed to tremendous wave forces. Other forms which develop as free nodules are found (Pollock, 1928) in depressions behind the outer reef front where they are rolled about occasionally. It appeared to Johnson (1954) that branching species represent adaptations to agitated water of variable intensity and that they assume different growth forms in response to changes in current. Furthermore, these forms do not occur in habitats where circulation is restricted.

Odum and Odum (1955) and Marsh (1970) speculated that the foam and combers on algal–coral ridges have their effect by diminishing the light penetration significantly and this possibly causes the dominance of crustose corallines.

Another effect of waves has been mentioned (Adey, 1966c) in reference to semi-exposed bays and fjords in the northwestern North Atlantic. Species of thick *Lithothamnium* are broken free from the shallow ledge-boulder bottom and continue to grow as they are carried deeper or accumulate in crevices. In some areas this process results in the formation of a thick, narrow marl zone developing below the ledge-boulder cobble bottom.

Exposure to Desiccation

The upper limit of crustose coralline growth at Funafuti has been said (Finckh, 1904) to be governed entirely by the distance to which waves extend their wash landward at low-water spring tides and the evidence for this is as follows. On several occasions the water was extremely calm at low-water spring tide so that the wave wash did not reach its usual mark. Considerable areas of crustose coralline, especially on the mounds surrounding the channel heads of the seaward reef face, remained dry and exposed to sunlight for nearly an hour and this caused the algae to die and turn white. After several days of re-immersion, pink growths reappeared, always starting from some small depression, spreading outward concentrically and meeting with other similar growths. Complete restoration of the pink living cover took less than 2 weeks and this process is probably responsible for the mounds at the ends of the channels.

Newell (1954) believed that erosion surpasses new accumulation at Raroia Atoll. This erosion is correlated with depopulation of the coralline algae and corals, but the factors responsible remain obscure. Possibly a slight drop (several centimetres) in the ocean level might account for this.

Some observations have been recorded of melobesioids interacting with other organisms in response to desiccation: e.g. it has been suspected (Johnson, 1954) that barnacles may assist in keeping some intertidal forms of crustose corallines moist during periods of exposure to air. All of the littoral melobesioids considered by Adey (1964, 1966b) seem to require some means for keeping wet during low tide: e.g. *Phymatolithon laevigatum* is found only in small pools and along fractures kept moist by rivulets, when littoral. *Clathromorphum circumscriptum* occupies (Adey, 1965) the larger pools intertidally, while *Phymatolithon lenormandii* is found (Adey, 1964, 1966b) intertidally on emergent rocks, but only when under a dense cover of non-crustose algae.

CHEMICAL FACTORS OF THE ENVIRONMENT

Salinity

The literature is almost completely lacking in any quantitative discussion of salinity as related to the melobesioid algae. The observation has been made (Lemoine, 1940) that crustose corallines are generally found in waters of 'normal' salinity; but, studies along the coast of France have shown that some species can grow near estuaries where the salinity is appreciably reduced. Adey and McKibbon (1970) have given some preliminary data concerning the effects of three different salinities on *Phymatolithon calcareum* and *Lithothamnium coralloides*. They found that low salinity was probably of little importance in increasing the mortality of these species in non-estuarine habitats. *L. coralloides* was more sensitive to lowered salinity than was *Phymatolithon calcareum*.

Carbon dioxide

One of the earliest workers who considered chemical factors in relation to melobesioid occurrence was J. Stanley Gardiner who, according to Foslie (1907f), presumed the poor development of calcareous algae in lagoons or enclosed waters (e.g. the Seychelles Bank) to be caused by churning-up of the water and the removal from it of carbon dioxide by seaweeds before it reached the islands. This statement was probably inaccurate, yet no one has investigated either carbon dioxide or dissolved oxygen changes in relation to crustose coralline algae.

Phosphate and Nitrate

The superficial similarity between the heterocysts (megacells) of crustose corallines and those of blue–green algae was pointed out by Womersley and Bailey (1969), who suggest that since those Cyanophyta having heterocysts are able to fix nitrogen, it would be of interest to examine *Porolithon* for this capability.

Phosphorus was reported to be more abundant (Odum and Odum, 1955) in relation to needs than nitrogen on the Eniwetok Atoll reef: they further postulated that reef surfaces, living coral, living calcareous algae, and dead skeletons may act as a soil in conserving phosphorus and nitrogen nutrients which might then be available to boring blue–green algae. The large proportion of boring blue–green algae in the corals and melobesioids further suggested, to Odum and Odum a low nitrogen environment, and extensive recycling of nitrogen by Cyanophyta.

Organic factors

The low nutrient content of the water at Eniwetok Atoll and the (definite?) correlation of surface encrusting algae with high current velocities were noted by Odum and Odum (1955), who were led to suspect that melobesioids may have a relatively high requirement for organic (and inorganic) nutrients, since the habitat that these algae occupy is more favourable (owing to reduced concentration gradients against diffusion) for uptake of nutrients. This appears

to be the only mention of organic factors in relation to crustose coralline biology.

BIOTIC FACTORS OF THE ENVIRONMENT

Competition

The crustose corallines at Funafuti Atoll (Finckh, 1904) have been implicated as the major destroyers of coral. These algae are said to kill the coral by overgrowing it and Finckh claimed this process to be necessary for an increase in size of the reef. In addition, Hoek (1969) reported that *Porolithon* at Curaçao often encroaches upon corals and kills them by "smothering". Further evidence for direct spatial competition between encrusting corals and encrusting corallines (Ladd, 1950) has been shown by sections which often reveal alternate overlapping of one organism by the other. From observations of the seaward margin of the surf platform at Curaçao, Hoek (1969) proposed that the *Porolithon* development is an indirect result of increased light owing to the removal of frondose algae by heavy surf.

An early report (Nadson, 1900) showed that boring Cyanophyta are a principal cause of the disintegration of melobesioids and other limestone-producing organisms. Later, he (Nadson, 1927) stated that these blue–green algae may contribute to the breaking down of the older, central parts of atolls. Another example of this phenomenon has been reported by Purdy and Kornicker (1958) along Bahamian coasts where the algal-stained rocks characteristically flake off in irregular patches, one of the causes being shown to be boring blue–green algae, which weaken the outer portion of the algal layer. This last report emphasizes that boring blue–green algae are among the most important destroyers of coastal limestone.

Predation

That burrowing organisms interfere with coralline algal growth was emphasized first by Finckh (1904) from his observations at Funafuti Atoll. The major borers on the eastern rim of the atoll are two sipunculids. One of these was observed to feed off the crustose coralline which surrounds its burrow and the entire melobesioid zone is riddled by these creatures. The extremely pitted nature of the oceanward slope of reef platforms (Finckh, 1904), caused by innumerable echinoid excavations, indicates that these and other boring or eroding organisms must contribute substantially to reef destruction. Finckh hastened to point out that if it were not for the growth of crustose corallines, the ocean platform would undergo decided diminution. At Raroia Atoll, a similar destruction of the coralline algal ridge by boring echinoderms, worms and other organisms has been observed (Doty, 1954; Doty and Morrison, 1954; Newell, 1954). Another probable effect of sea urchins has been reported for the Gulf of Maine (Adey, 1965), where extensive and deep scraping in mid-winter contributes to the morphological irregularity of *Clathromorphum circumscriptum*.

On the southwestern coast of Curaçao (Hoek, 1969) corals are abundant but *Porolithon* is clearly dominant. Frondose algae although showing a broad species diversity are continuously removed by grazing fish and by large numbers of *Diadema antillarum*. The *Porolithon* itself is also grazed (Hoek,

1969), as shown by the scars on its surface, but apparently its growth exceeds grazing losses. Kempf (1962) experimentally demonstrated that the activities of sea urchins near Marseille favour the development of *Lithophyllum incrustans* although the urchins also graze on this melobesioid.

Hoek (1969) proposed that the *Porolithon pachydermum*-coral formation of the southwestern coast is a stable ecosystem maintained by grazing and not a stage in a degradation series. He further supposed that undergrazing could lead to a gradual degradation of the *Porolithon*-coral formation. Consequently, he believed this region to have great potential as an indicator of fishing pressure and other factors that might diminish the herbivorous fish population. Parrot fish (Scaridae), by eating *Porolithon onkodes*, may play an important role at Raroia and other atolls (Doty, 1954) in establishing a phytoplankton population. These fish, by defaecating 'fertilizer' salts (as well as calcareous sand), tend to enrich the otherwise nutrient impoverished waters. The importance of this process in explaining the population increases of plankton, plankton feeders and fishes in the proximity of atolls could be quite large (Doty, 1954). On a Bermuda reef the most important raspers, Acanthuridae and Scaridae, were estimated (Bardach, 1961) to consume 600 kg and 700 kg of calcareous material/hectare/year, respectively. At Heron Island, Queensland, Australia, fish browsing was estimated by Stephenson (1961) to remove a thickness of about 0·5 mm of rock/year. Newell, Rigby, Whiteman and Bradley (1951) observed *Cerithium* sp. feeding on the surface slime of *Neogoniolithon strictum* at Andros Island in the Bahamas.

Parasitism and mutualism

The colourless *Kvaleya epilaeve* parasitizes *Leptophytum laeve* by means of haustoria (Adey and Sperapani, 1971) which penetrate the host's cells. Parasitism of both *Neogoniolithon notarisii* and *Porolithon onkodes* by the juvenile stages of *Amphiroa rigida*, and *Pseudolithophyllum expansum* parasitized by *Amphiroa verruculosa* has been reported by Cabioch (1969). *Lithoporella melobesioides* has been reported (Lemoine, 1970) as being both its own host and parasite; a phenomenon referred to by Lemoine as autospecific endophytism. The green layer of boring blue–green algae found just under the red surfaces of crustose coralline algae, as well as under coral surfaces at Eniwetok Atoll (Odum and Odum, 1955), may indicate a possible parasitic or mutualistic role, as does the occurrence (Batters, 1892) of the melobesioid *Schmitziella endophloea* Bornet and Batters endophytic in *Cladophora pellucida*, *Chloronema thuretii* (Bornet) Schmitz on articulated corallines such as *Jania rubens*, and *Chaetolithon deformans* (Solms-Laubach) Foslie which deforms the apices of *Corallina natalensis*: however, in these last three cases the interactions are unstudied and unknown.

In summarizing the ecological relationships, the above findings justify a tentative picture of an algal group able to grow at greater depths and in light perhaps more feeble than other algae can. *Porolithon onkodes* is exceptional in being able to stand a certain amount of desiccation and exposure to direct sunlight. Some crustose corallines seem tolerant of, or even favoured by, extremes of temperature such as are characteristic of tropical tide pools on the one hand and Arctic and Antarctic deeps on the other. Many forms flourish in agitated water, possibly because of mechanical factors, oxygenation, light

screening, or reduced competition, and the group is generally rather less vulnerable to herbivore grazing than would be true of the softer algae.

Previous workers (e.g. Setchell, 1926a, 1928; Crossland, 1938) have debated at length the relative importances of calcareous organisms in the reef environment. Biologists, in their arguments, have stressed the importance of standing stock (usually in subjective terms) and geologists have emphasized sediment measurements. These approaches have not resolved the question of the biological roles played by reef-building organisms, because there has been little correlation between standing stock and the skeletal components that remain after such events as grazing, export, and resolution have occurred. As Goreau (1963) pointed out, the missing quantity is a productivity parameter. To date only two studies (Goreau, 1963; Marsh, 1970) have attempted to measure coralline algal productivity.

The attempt has been made above to review, and evaluate where possible, the literature pertinent to crustose coralline algae and, thereby, lead the reader to an understanding of the current evidence in the field. It should be apparent that many investigations (e.g. some of the early taxonomic works and many of the descriptive field observations) have suffered from repetitious and unimaginative reporting of what was generally already known, while other aspects have been neglected. For instance, the point is here made that investigations of dissolved organic uptake and production, parasitism, mutualism, inhibition, dispersal, periodicity phenomena, succession, species-numbers relationships, ecotones, community energetics, light quality and quantity effects, salinity and pH responses and inorganic-substratum uptake remain virtually untouched in respect to our knowledge of crustose coralline algae.

The taxonomy of this group is also presently in a very confusing state. Hopefully much of this confusion will end in the near future as a result of recent re-investigations (Adey, 1970a; Masaki, unpubl.) of the Foslie type specimens in Trondheim, Norway.

While several quantitative and numerous qualitative observations of crustose coralline standing stock have been made, these lack sufficient critical detail for the evaluation of the interrelationships between melobesioids and possible causal environmental factors. As pointed out in the paper by Littler (1971) this lack has been largely due to a need for high-resolution measurement techniques which can be applied to crustose corallines.

Also, once detailed measurements of standing stock in conjunction with environmental factors have been determined in the field, hypotheses derived from the relationships observed must be carefully evaluated in controlled experiments (e.g. Adey, 1970c; Adey and McKibbon, 1970). At present it seems that the acquisition of these kinds of data has the greatest potential for significantly advancing our knowledge concerning the biological role of reef-building crustose Corallinaceae.

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