CORALLINE ALGAE FROM
THE MIOCENE OF MALTA

by DANIEL W. J. BOSENCE

ABSTRACT. The morphology and systematics of ten coralline algae are described from the Miocene of Malta. The corallines occur in great abundance and are the principal constructors of rhodoliths and frameworks of the Coralline Algal Biostrome. The corallines are well preserved and many show previously undescribed reproductive structures. The eleven species comprise two species of *Archaeolithothamnium*, two of *Lithothamnium*, two of *Mesophyllum*, four of *Lithophyllum*, and one species of *Lithoporella*. Two new species of *Lithophyllum* (*L. bahrijense* and *L. mgarrense*) are described.

    The morphology of the framework-building *Mesophyllum commune* is described in detail. The success of this species as a limestone constructor is attributed to its foliaceous growth habit combined with various methods of crust division, fusion, and branch growth.

    This coralline flora is most similar to that of the Miocene of North Africa.

THE algae described in this paper are the dominant rock builders of the Miocene Coralline Algal Biostrome of the Maltese Islands (Pedley 1978, Bosence and Pedley 1982). The biostrome (20 × 5 km × 16 m thick) outcrops along the western coast and plateaus of Malta and the eastern coast of Gozo (text-fig. 1). It is cut by a number of NNE/WSW growth faults. Bosence and Pedley (1982) have described the sedimentology and palaeoecology of the biostrome and we have divided it into six facies. Three of the facies contain limestones constructed by more or less *in situ* coralline algae, the remaining three being derived and transported equivalents of these facies. Each facies is characterized by particular types of rhodolith.

In situ coralline algal sediments	Transported coralline algal sediments
Crustose Algal Marl facies	Algal Debris Wackestone facies
Rhodolith Pavement facies	Algal Branch Packstone facies
Crustose Pavement facies	Algal Crust Packstone facies

    Beneath and to the west of the biostrome *Heterostegina*, rich biomicrites of the Ghajn Znuber and Zebbug Beds occur. To the east are micritic sediments of the Mtarfa member (text-fig. 1).

    The biostrome develops on a series of relic sand ridges of the Ghajn Znuber Beds (text-fig. 1). Sheltered areas between ridges accumulate 1–2 m thick sequences of Crustose Algal Marl and Algal Debris Wackestone facies. The Crustose Algal Marl facies contains a high algal, bryozoan, brachiopod, and crustacean biota preserved largely *in situ*. Leafy rhodoliths of *Mesophyllum commune* (Lemoine) grow from turned crusts originally growing over the marl surface. Open branched rhodoliths of *M. commune*, *Lithophyllum albanense* (Lemoine) and *L. mgarrense* (n.sp.) also occur. The Algal Debris Wackestone facies occurs interbedded and laterally adjacent to the Crustose Algal Marls. Fossils are fragmented and aligned along bedding planes. Rhodoliths are mainly discoidal (being derived from planar crusts); they are larger and more densely branched than those from the preceding facies. These wackestones are considered to be transported from pre-existing sediment of the Crustose Algal Marl facies. The Rhodolith Pavement facies is the most abundant facies and dominates the centre of the biostrome with units up to 14 m thick and 10 km wide. The sediments are plane or trough cross-bedded and are composed of alternating
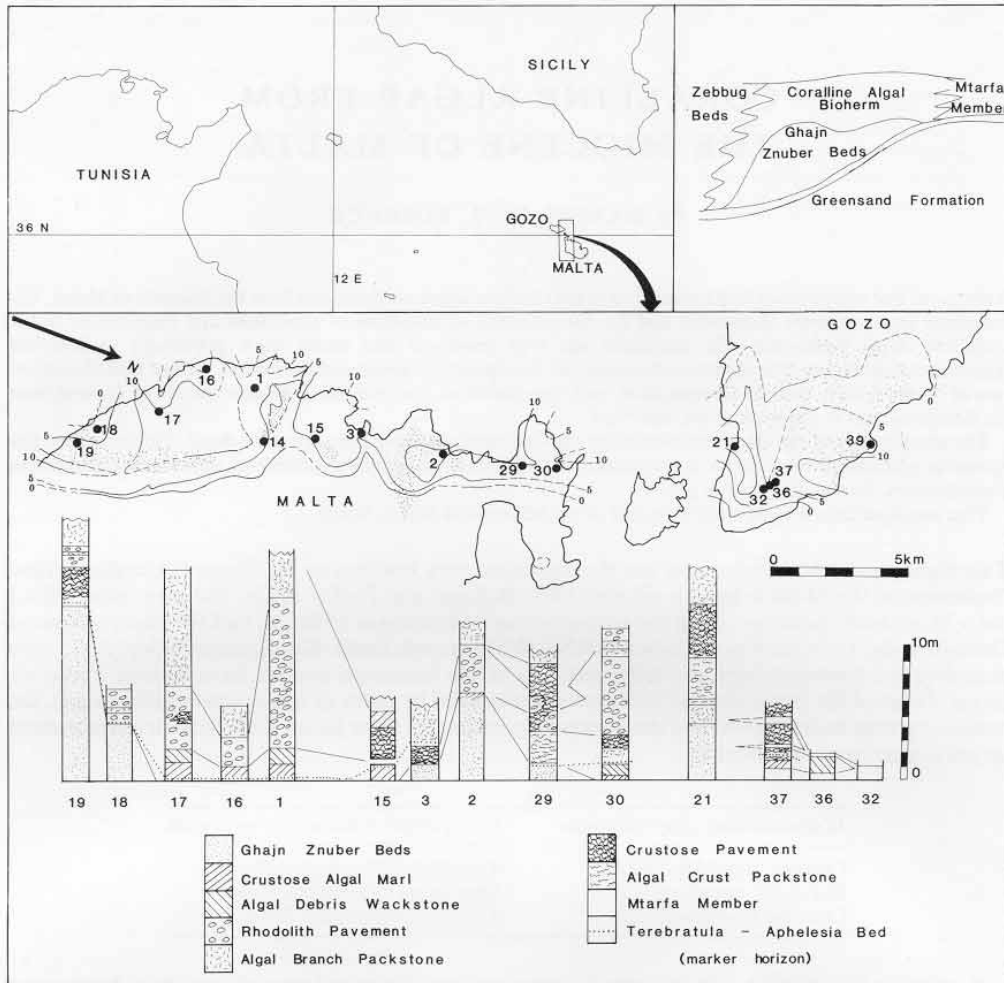
TEXT-FIG. 1. Location, stratigraphic setting, isopachytes (at 5 m intervals), and sections through Coralline Algal Biostrome, Malta and Gozo.

rhodoliths and biomicrites. Within fault-bound biostrome units rhodoliths have similar long axis orientations which are normal to palaeocurrents obtained from cross-beds and channels. The mainly ellipsoidal rhodoliths originate from laminar cores of *M. commune* and *Lithoporella melobesioides* (Foslie), to columns of *M. commune*, *Lithophyllum albanense*, *L. mgarrense*, *L. bahrijense* (n.sp.) and *Archaeolithothamnium affine* (Howe). Growth sequences occur from branched, through branches with flattened apices and lateral branches, to laminar concentric growths: they record periods of turbulence during rhodolith growth. The biomicrites are thought to have been deposited in quieter periods. Closely associated with this facies is the Algal Branch Packstone facies which is rich in coralline debris and smaller, spheroidal abraded rhodoliths of the same taxa as those of the preceding facies. This facies frequently terminates the biostrome and represents higher energy conditions of deposition.

The Crustose Pavement facies represents the only *in situ* framework within the bioherm. This framework is constructed of leafy growths of *M. commune* with *Lithoporella melobesioides*. The construction of this framework is described in detail in this paper. The framework had little original relief and provided a suitable hard substrate for bryozoans, serpulids, foraminifers, and brachiopods. Discoidal rhodoliths, derived from eroded crusts, are preserved along erosion surfaces in the Crustose Pavement facies. The rhodoliths from this facies contain many species of corallines. Laminar concentric cores of *M. commune*, *L. melobesioides*, *Lithophyllum bahrijense*, and *Lithothamnium praefructiculosum* (Maslov) are succeeded by outer branches and columns of *M. commune*, *Lithophyllum albanense*, *L. bahrijense*, *Lithothamnium magnum*, and *L. praefructiculosum*. Interbedded with the Crustose Pavement facies occurs the Algal Crust Packstone facies. This facies is composed of eroded and transported coralline crusts with discoidal rhodoliths of *M. commune*, *Lithophyllum albanense*, and *Lithothamnium magnum* and represents a transported Crustose Pavement facies.

The biostrome had little original relief and the facies would have occurred as a mosaic on the sea bed at any one time (text-fig. 1). The closest modern analogue known is the 'Coralligène de Plateau' of the Mediterranean (Laborel 1961; Pérès 1967). This occurs in depths of 50–150 m and contains leafy *in situ* coralline frameworks, rhodoliths, and coralline and shell gravels. These water depths are also indicated in the Miocene material by the present-day depth ranges of the coralline genera.

In this paper I describe the morphology and taxonomy of these limestone building coralline algae, and is the first description of Maltese coralline algae apart from the early, inadequately described, and unillustrated work of Samsonoff (1917a, b). A more thorough statistical approach to the description of fossil corallines is presented and two new species of *Lithophyllum* are described. The constructional abilities of the polymorphic *M. commune* are described. Details of the reproductive structures of many of these corallines are described and illustrated for the first time.

METHODS AND PROBLEMS IN CLASSIFICATION

About forty well-exposed localities (text-fig. 1) were visited in August/September 1978. The sections were logged and the majority of the corallines were collected as rhodoliths. Others were from coralline frameworks and some occurred as fragmented grains in sediment samples. Samples were impregnated in green stained Araldite 800 prior to sectioning and staining. For the study of the corallines, sections were taken only when carefully oriented normal to the crusts. All measurements of tissue and cell sizes were carried out with calibrated micrographs.

There are many problems concerning the taxonomy of fossil corallines at both the generic and specific levels. At the generic level there are recent taxa where diagnostic morphological features have not been recognized in fossil material. For example, the differentiation of *Lithothamnium*, *Leptophytum*, and *Phymatolithon* is to a large extent based on epithallial and staining characteristics (Adey 1970). The coralline epithallus has not to my knowledge been recognized in fossil material and therefore these genera are still grouped under *Lithothamnium* until fossilizable characteristics can be differentiated. Recent keys for generic identification of corallines (Adey and MacIntyre 1973) contain epithallial characteristics and pit connections, which again have not been found in fossil corallines. However, these do not alter the traditional generic groupings. Poignant (1979) gives a key for identification of fossil coralline genera.

At the specific level the major problems concern the small number of taxonomic criteria, their variability, and the lack of detail in previous descriptions. The main taxonomic criteria at species level are cell and conceptacle sizes. These vary with the orientation of the section, with zoned thalli and with interruptions to growth. Some species are more variable than others. Unfortunately previous workers have only given size ranges with no indication of the number of measurements made, thus making comparisons sometimes impossible. In this paper I record means, standard deviations, and ranges (e.g. mean (standard deviation), range is recorded as 10 μm (1·6), 5–16 μm). It is hoped in the future to use numerical taxonomy to differentiate fossil species.

The following data are taken from 10 to 40 measurements of up to eight parameters on sixty-six oriented specimens. Cells are measured from their middle cell walls and conceptacles at their widest and highest measurements in vertical section. Unipored conceptacles are measured from the lowest point of the floor to the base of the pore.

SYSTEMATIC PALAEONTOLOGY

Holotypes or representative material of each species are housed at the British Museum (Natural History), BM(NH), under numbers V.60922–V.60931.

Class RHODOPHYTA Wettstein, 1901
Order CRYPTONEMIALES Schmidtz, in Eugler 1892
Family CORALLINACEAE (Lamouroux) Harvey 1849
Subfamily MELOBESIODEAE Lemoine 1939
Genus ARCHAEOLITHOTHAMNIUM Rothpletz 1891
Archaeolithothamnium affine Howe 1919

Plate 15, figs. 1–2; text-fig. 2

1919   *Archaeolithothamnium affine* Howe, pp. 11–12, pl. 4, fig. 1; pl. 5.
1939   *Archaeolithothamnium affine* Howe; Lemoine, p. 60, pl. 11, fig. 8; text-fig. 25.

Description. Laminar crusts giving rise to columnar perithallial tissue. Columns 1·8–3·7 mm in diameter and up to 3 mm high. A poorly developed hypothallium is seen in one specimen only. The hypothallium is 90–150 μm thick with cells measuring 25 μm (s.d. 6·7), 18–35 μm long × 12 μm (s.d. 2·2), 10–15 μm wide. Perithallium multistromatic with cells either arranged in rows or in filaments. Cells are square and measure 10 μm (s.d. 1·6), 5–16 × 9 μm (s.d. 1·1), 7–13 μm (Pl. 15, figs. 1–2). Sporangia are ellipsoidal and measure 75 μm (s.d. 1·5), 55–85 μm high and 43 μm (s.d. 3·3), 28–55 μm wide.

Remarks. These specimens are close to Howe's (1919) material except for the perithallial cell length which he records as 8–28 μm. Howe's (1919) figure may be on the high side as his illustrated sections appear slightly oblique. Howe does not record a mean value.

Occurrence. A. affine occurs occasionally in rhodoliths from the Rhodolith Pavement and Crustose Pavement facies. It either forms monospecific rhodoliths or is intergrown with *M. commune* and *Lithothamnium praefructiculosum*, Maslov.

Archaeolithothamnium intermedium Raineri 1924

Plate 15, figs. 3–5; text-fig. 2

1924   *Archaeolithothamnium intermedium* Raineri, p. 29, fig. 1.

Description. Columnar growths 2·5 mm in diameter and up to 2 mm high. The hypothallus 50 μm thick, non-coaxial but too poorly preserved to measure cell dimensions. Perithallium multistromatic with rectangular cells arranged in filaments (Pl. 15, figs. 4–5) and measure 17 μm (s.d. 3·9), 11–26 μm long × 12 μm (s.d. 1·9), 10–17 μm wide. Sporangia occur in rows usually arched over the apical region of columns. They are elliptical and measure 61 μm (s.d. 7·2), 50–75 μm wide and 101 μm (s.d. 14·4), 75–120 μm high.

Occurrence. A multispecific rhodolith composed dominantly of *A. intermedium* with outer laminae of *M. commune* was found in the Algal Bank Packstone facies. A broken fragment was also found in the Algal Debris Wackestone facies.

EXPLANATION OF PLATE 15

Figs. 1, 2. *Archaeolithothamnium affine*. 1, basal non-coaxial hypothallium and perithallium with filament walls dominating. Loc. 20, × 80. 2, zoned columnar perithallium with ellipsoidal sporangia borne in rows. Loc. 15, × 80. BM(NH) V.60921.

Figs. 3, 4. *Archaeolithothamnium intermedium*. 3, overgrowing fertile branch of *Mesophyllum commune* and overgrown by large oblique celled *Lithoporella melobesioides* and foraminifera. Loc. 21, × 30. BM(NH) V.60922. 4, detail of perithallium with thick filament walls and sporangia. Loc. 21, × 80. BM(NH) V.60922.
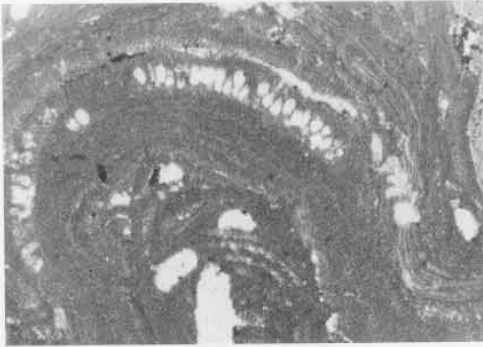
Figs. 5–7. *Lithothamnium magnum*. 5, zoned medullary tissue from branch. Loc. 30, × 120. BM(NH) V.60924. 6, perithallium in crust with filament walls dominating structure. Loc. 16, × 80. 7, fertile branch with large hemispherical multipored conceptacles. Loc. 16, × 20. BM(NH) V.60924.
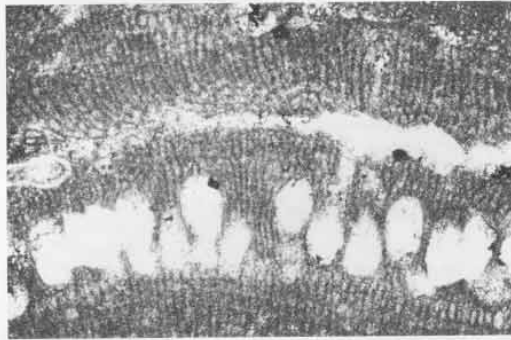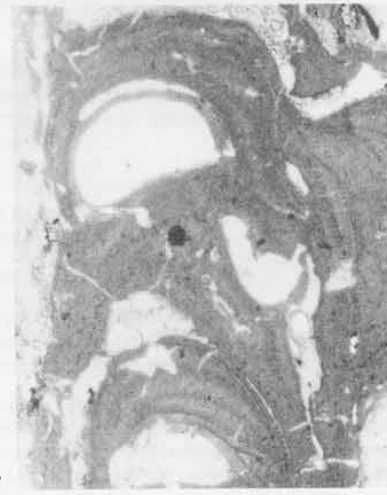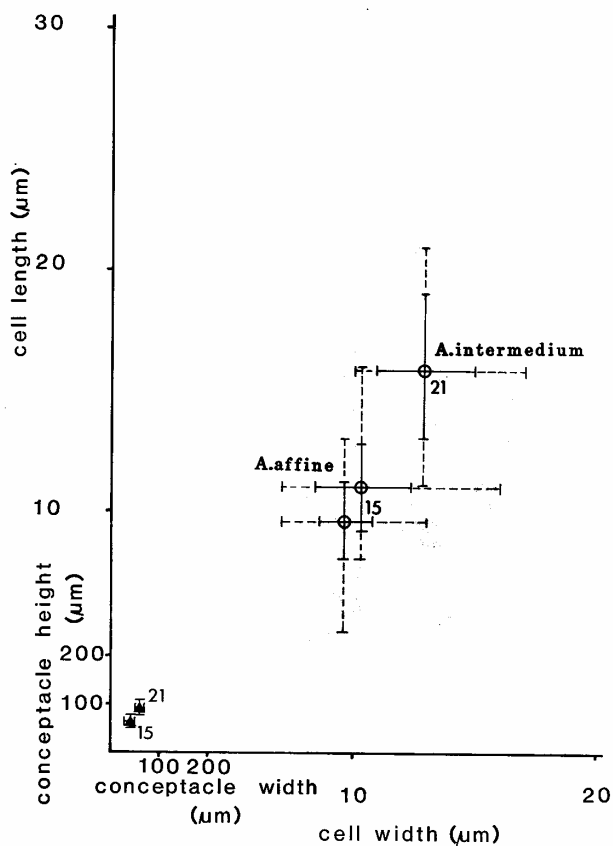
PLATE 15
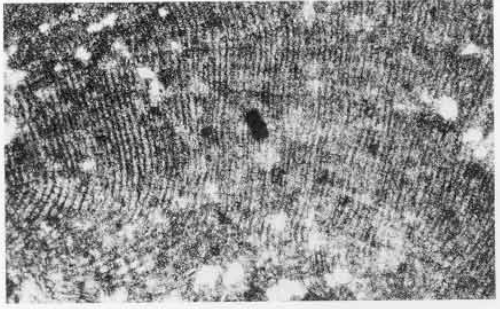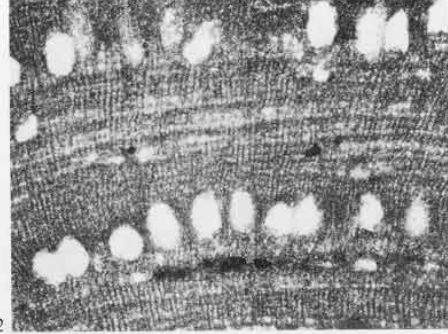
BOSENCE, Miocene coralline algae

TEXT-FIG. 2. *Archaeolithothamnium intermedium* and *A. affine*: Peri-thallial cell length and width (mean O, standard deviation ⊢—⊣ , and range ⊢— —⊣) and conceptacle height and width (mean ▲ and range ⊢— —⊣) from localities 15 and 21 (see text-fig. 1).

Genus LITHOTHAMNIUM Philippi 1835
Lithothamnium magnum Capeder 1900

Plate 15, figs. 6-7; text-fig. 3

1900   *Lithothamnium magnum* Capeder, p. 179, pl. vi, fig. 10.
1926   *Lithothamnium magnum* Capeder; Lemoine, pp. 248-249, text-figs. 7, 8.
1939   *Lithothamnium magnum* Capeder; Lemoine, p. 73, text-figs. 34, 35.

Description. Branching thalli with very large distinctive semicircular superficial conceptacles. Branches measure 2 mm (s.d. 0·5) in diameter and up to 5·6 mm long. Also occurs as 0·4-0·6 mm thick crusts with multistromatic perithallus. No hypothallium has been seen. Branches are constructed of distinctively and regularly zoned (107 μm (s.d. 3·5) thick) perithallium with a central medullary tissue (Pl. 15, figs. 6-7) arranged in filaments with rectangular cells measuring 13·3 μm (s.d. 3·6), 9-20 μm long and 10 μm (s.d. 1·9), 7-13 μm wide. Conceptacles are
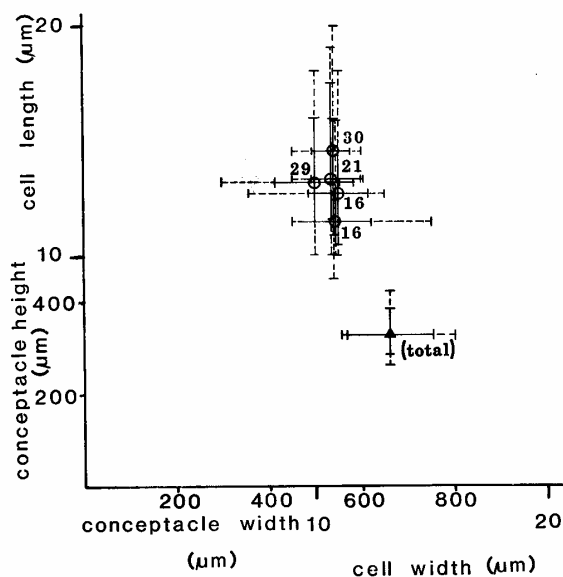
TEXT-FIG. 3. *Lithothamnium magnum*: Perithallial and conceptacle measurements. (Symbols as for text-fig. 2.)

superficial and commonly apical in position on branches. The multipored conceptacles are covered by a roof 5–10 cell thick. Conceptacles have a flat base and a distinctive semicircular vertical cross-section (Pl. 15, fig. 7). Conceptacle dimensions are 652 μm (s.d. 92), 557–800 μm at their widest point and 342 μm (s.d. 60), 287–430 μm at their highest.

Remarks. Perithallial cells are larger (but overlap) with those of Lemoine (4–9 μm long: 1926, 1939). Although her drawings (fig. 34) suggest common cell-lengths of around 10 μm. The distinctive conceptacles suggest that this is the same species showing some variability in cell size.

Occurrence. L. magnum is found occasionally in the Crustose Pavement facies. Here it occurs on the outer layers of multispecific rhodoliths coating *M. commune*. Similar examples are also found in rhodoliths of the transported sediments of the Algal Crust Packstone facies. One branching rhodolith was found in the Rhodolith Pavement facies.

Lithothamnium praefructiculosum Maslov 1956

Plate 16, figs. 1–2; text-fig. 4

1956 *Lithothamnium praefructiculosum* Maslov, p. 149, pl. lii, figs. 1–3.

Description. Occasional fertile crusts 0·5–0·7 m thick in rhodoliths. Hypothallium weakly developed, non-coaxial (60 μm thick) with rectangular cells measuring 20 μm (s.d. 2·3), 17–22 μm long and 9·7 μm (s.d. 1·7), 8–10 μm wide. Perithallial tissue is multistromatic, weakly zoned with cells arranged in sinuously curved filaments. Cells measure 9 μm (s.d. 1·6), 5–12 μm long and 10 μm (s.d. 1·4), 7–13 μm wide. The multipored conceptacles have vertical walls and flat tops giving distinctive rectangular vertical sections (Pl. 16, fig. 1). Conceptacles measure 437 μm, 407–467 μm wide, and 129 μm (s.d. 17·9), 112–145 μm high.
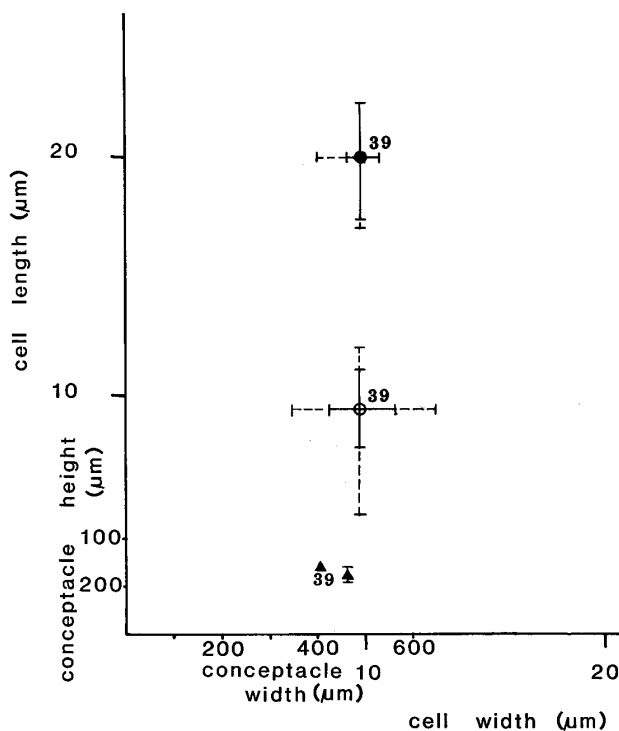
TEXT-FIG. 4. *Lithothamnium praefructiculosum*: Perithallial, hypo-
thallial (mean ●, standard deviation ⊢——⊣, and range ⊢— —⊣) cell and
conceptacle measurements. (Symbols as for text-fig. 2.)

EXPLANATION OF PLATE 16

Figs. 1, 2. *Lithothamnium praefructiculosum*. 1, fertile crust with multipored sporangial conceptacles. Loc. 39,
×20. BM(NH) V.60925. 2, detail of fig. 1 illustrating poorly preserved hypothallium and weakly zoned
perithallus with conceptacle. Loc. 39, ×80. BM(NH) V.60925.

Figs. 3–7. *Mesophyllum commune*. 3, typical crust with variable (coaxial to non-coaxial) hypothallium and
perithallium. Loc. 39, ×80. 4, zoned, columnar perithallial tissue. Loc. 39, ×30. 5, fertile column with
multipored asexual conceptacles. Loc. 39, ×20. BM(NH) V.60926. 6, asexual conceptacle with preserved
spores. Loc. 3, ×40. 7, unipored sexual conceptacle. Loc. 1, ×40.

Figs. 8–10. *Mesophyllum koritzae*. 8, fragment of crust with hypothallium, perithallium, and ripe conceptacles.
Loc. 36, ×20. BM(NH) V.60927. 9, detail of fig. 8 showing coaxial hypothallium and grid-like perithallium.
Loc. 36, ×80. BM(NH) V.60927. 10, detail of fig. 8 showing multipored asexual conceptacle with preserved
spores. Loc. 36, ×80. BM(NH) V.60927.

PLATE 16
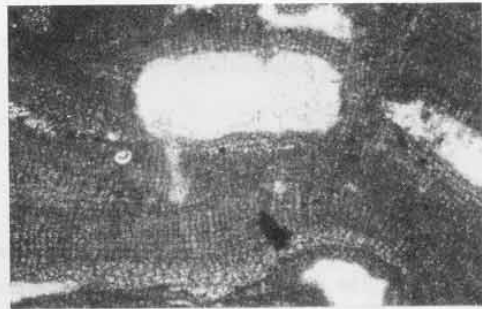
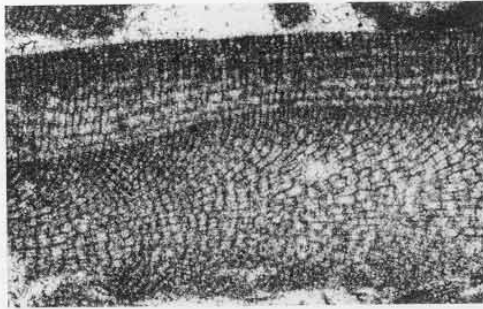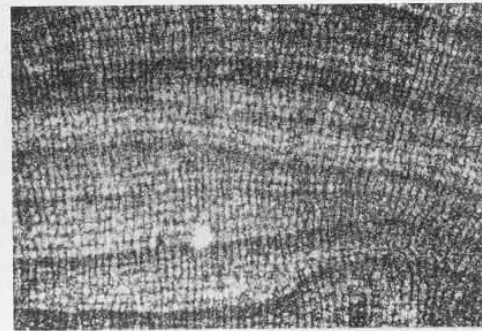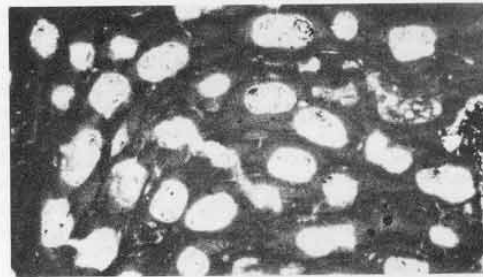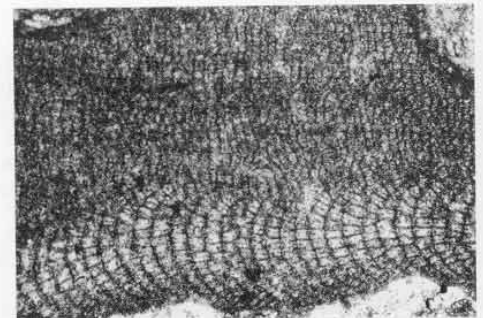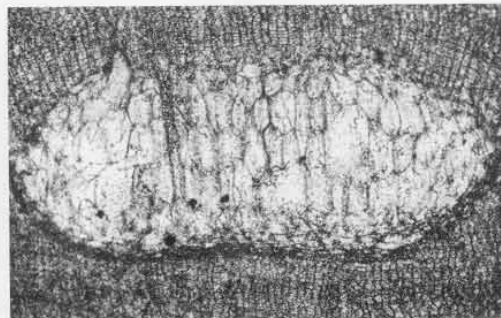BOSENCE, Miocene coralline algae

Remarks. This species has not to my knowledge been found by any workers since Maslov's original description. The hypothallium is first described here.

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Genus MESOPHYLLUM Lemoine 1923
Mesophyllum commune Lemoine 1939

Plate 16, figs. 3-7; Plates 17, 18, figs. 3-6, text-figs. 5, 12

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1939 *Mesophyllum commune* Lemoine, p. 86, text-figs. 54, 56, 57.
1972 *Mesophyllum commune* Lemoine; Orszag-Sperber and Poignant, p. 120.

Description. This polymorphic genus (Orszag-Sperber and Poignant 1972) is the major limestone building alga from the Upper Coralline Limestone Formation of Malta. It occurs as both *in situ* frameworks and rhodoliths as described below (see *Occurrence*, p. 167). Thalli occur as crusts, bifurcating crusts, branches, and columns. Crusts with hypothallium and perithallium are commonly about 350 μm thick but the perithallium may continue growing to produce a thick, multistromatic crust 500-600 μm thick. These thick crusts commonly develop into columns. Columns ('Mammelons' of Lemoine 1939) are distinct from branches by their size and shape 6·6 mm (s.d. 1·7) high and 6·3 mm (s.d. 1·2) wide and a variable internal structure. Columns may be formed by zoned arched layers of perithallial tissue or successive crust layers with both hypothallium and perithallium present. Branches arising from crustose perithallial tissue have diameters of 3·1 mm (s.d. 0·4) and are up to 20 mm high. They have a coaxially zoned central medulla and layered outer cortex. Branches may bifurcate dichotomously or laterally.

The hypothallium is of variable thickness (143 μm (s.d. 45), 70-210 μm) and construction. Filaments may be arranged to form coaxial, partially coaxial, or non-coaxial hypothalli (Pl. 16, fig. 3). Hypothallial cells are rectangular and measure 22 μm (s.d. 3·5), 17-34 μm long and 12 μm (s.d. 1·8), 10-18 μm wide. Perithallial tissue is most commonly arranged in rows or a grid but may also have filament walls dominating. The perithallium is commonly zoned; particularly in columns and branches where the zones measure 80 μm (s.d. 22) thick in the apical region. Perithallial cells in crusts are square and measure 11 μm (s.d. 1·7), 7-16 μm long and 10 μm (s.d. 1·4), 6-13 μm wide. Those in the medullary tissue of columns and branches are longer and measure 13·5 μm (s.d. 3·3), 8-20 μm long and 11 μm (s.d. 1·7), 8-18 μm wide. Asexual conceptacles are multipored, mainly elliptical in vertical section (Pl. 16, figs. 5-6) and measure 397 μm (s.d. 114), 275-630 μm wide and 171 μm (s.d. 41), 120-300 μm high. A possible sexual conceptacle was found measuring 440 μm × 176 μm. The distinctive raised floor of the conceptacle and the single large pore can be seen in Pl. 16, fig. 7.

Remarks. The wide variability in the morphology of this species previously led to its assignment to the genus *Lithothamnium* by Bosence and Pedley (1979). Subsequent study of the variable hypothallium has shown it to be a species of *Mesophyllum* which rarely develops a truly coaxial hypothallium.

For the occurrence and details of framework construction see below: *M. commune*—Occurrence, framework construction, and functional morphology (p. 167).

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EXPLANATION OF PLATE 17

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Figs. 1-4. *Lithophyllum albanense.* 1, crust with coaxial hypothallium and typical irregular grid-like perithallium. Loc. 2, × 80. BM(NH) V.60928. 2, zoned columnar perithallial tissue. Loc. 2, × 80. BM(NH) V.60928. 3, asexual conceptacle illustrating characteristic wide, flared pore with conical infilling by later tissue. Loc. 2, × 80. BM(NH) V.60928. 4, sexual conceptacle with preserved cystocarps? Loc. 14, × 80.

Figs. 5, 6. *Lithophyllum mgarrense.* 5, detail of fig. 6 showing perithallial tissue dominated by filament walls and asexual conceptacle with characteristic elongate roof cells. Loc. 15, × 60. BM(NH) V.60930. 6, fertile crust illustrating perithallial tissue and asexual conceptacles. Loc. 15, × 25. BM(NH) V.60930.

Figs. 7-9. *Lithophyllum bahrijense.* 7, crust illustrating partly coaxial hypothallium and perithallium. Loc. 19, × 60. BM(NH) V.60929. 8, asexual conceptacle. Loc. 19, × 60. BM(NH) V.60929. 9, sexual (cystocarpic) conceptacles. Loc. 1, × 60. BM(NH) V.60929.

Fig. 10. Epilithic crusts of Recent *Lithophyllum* sp. showing growth ridges arising where adjacent crusts meet and attempt to overtop neighbours. Loc. Kimmeridge Bay, Dorset, × 2.

PLATE 17
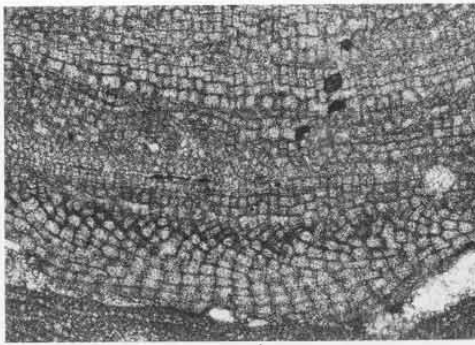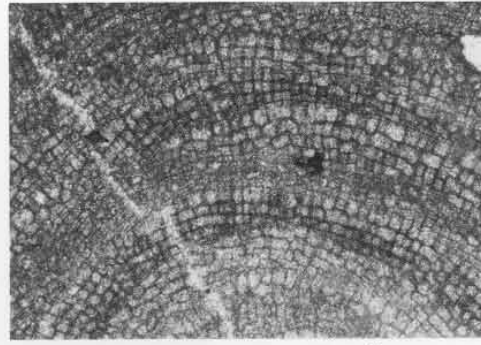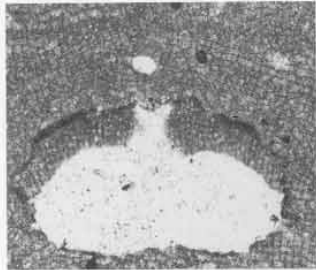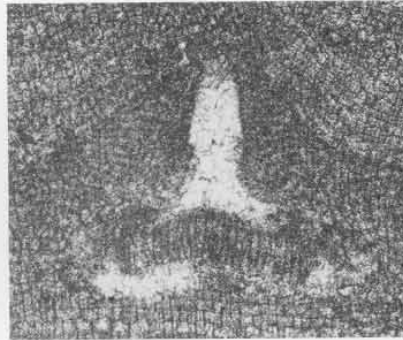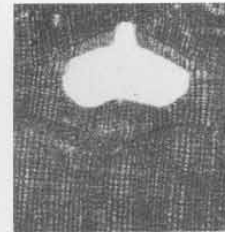

BOSENCE, Miocene coralline algae
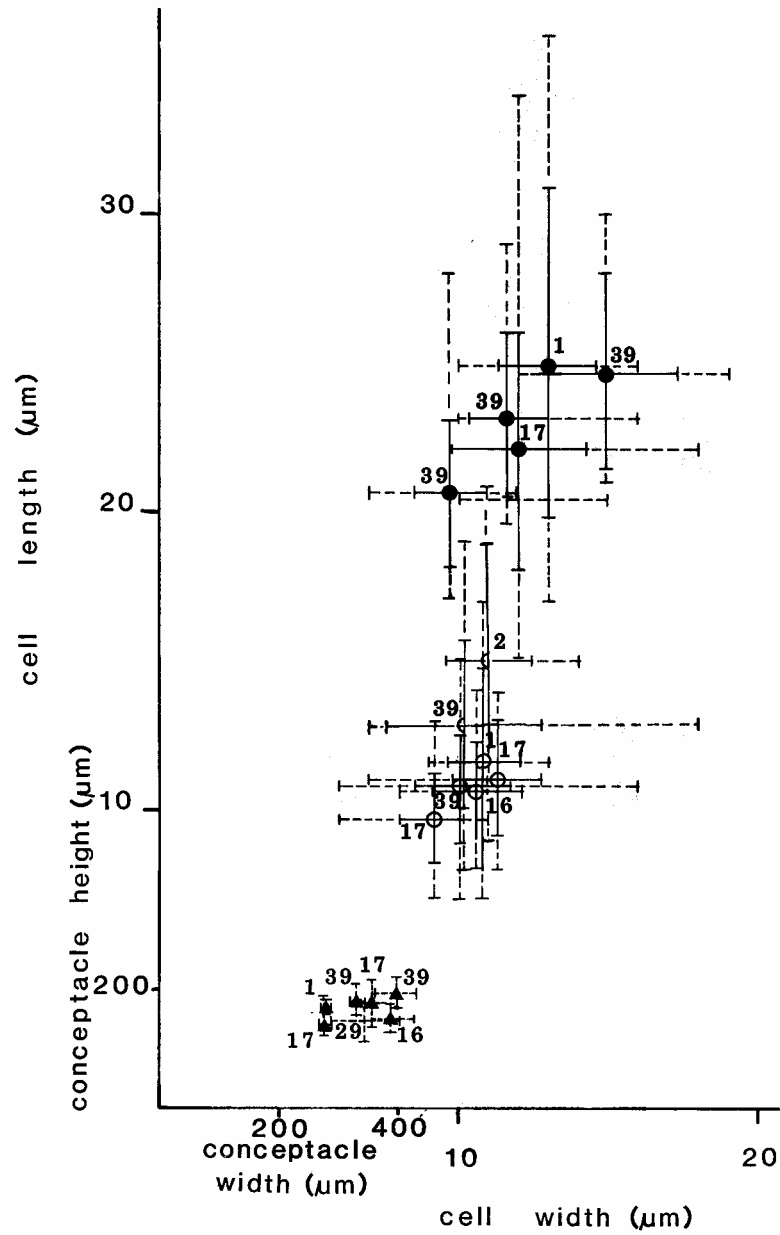
TEXT-FIG. 5. *Mesophyllum commune*: Perithallial (columnar perithallium mean-C), hypothallial and asexual conceptacle measurements. (Symbols as for text-figs. 2-4.)

Mesophyllum koritzae Lemoine 1939

Plate 16, figs. 8-10; text-fig. 6

1939   *Mesophyllum koritzae* Lemoine, p. 84, text-figs. 49, 50, 51.
1972   *Mesophyllum koritzae* Lemoine; Orszag-Sperber and Poignant, p. 120, pls. 2, 5.

TEXT-FIG. 6. *Mesophyllum koritzae*: Hypothallial, perithallial and conceptacle measurements. (Symbols as for text-figs. 2–4.)

Description. M. koritzae occurs rarely as concentric laminar cores to rhodoliths and as fragments of crust. Hypothallium is distinctly coaxial and measures 125 μm (s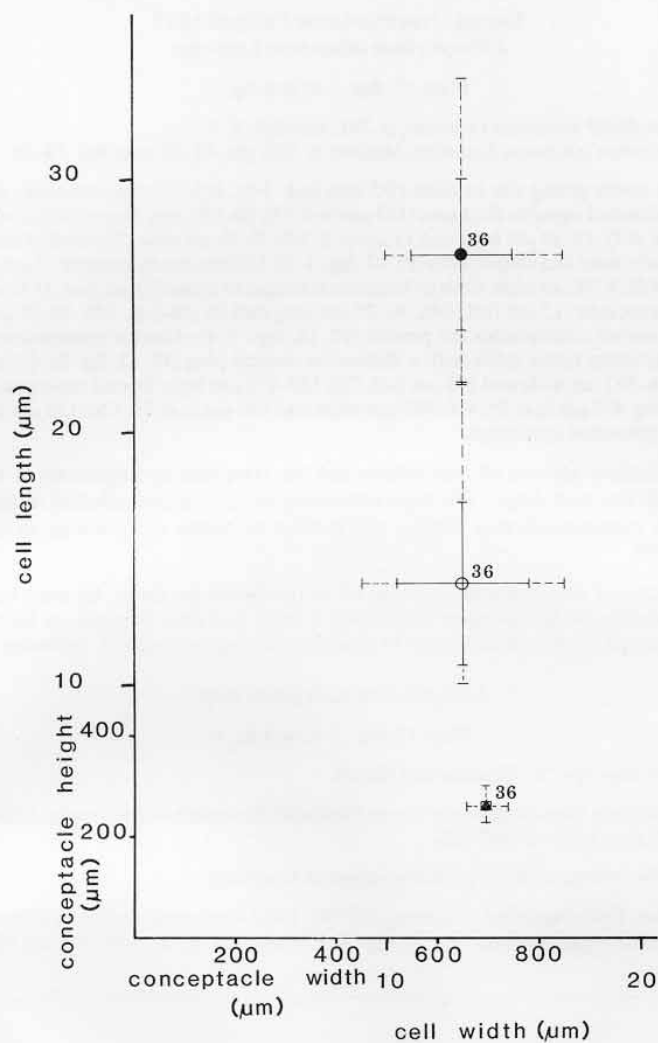.d. 32), 80–175 μm thick. Cells are rectangular measuring 27 μm (s.d. 3), 22–33 μm long and 13 μm (s.d. 2), 10–17 μm wide. Perithallium is unevenly zoned with square cells arranged in rows. Cells measure 12 μm (s.d. 2), 7–22 μm long by 11 μm (s.d. 1·8), 8–17 μm wide. Multipored conceptacles are elliptical and measure 324 μm (s.d. 60), 209–390 μm wide and 149 μm (s.d. 24), 110–180 μm high. Pl. 16, fig. 10 illustrates mature conceptacles with preserved spores.

Occurrence. M. koritzae occurs in discoidal rhodoliths from the Algal Crust Packstone facies and as fragments from the Algal Debris Wackestone facies.

Genus LITHOPHYLLUM Philippi 1837
Lithophyllum albanense Lemoine

Plate 17, figs. 1–4; text-fig. 7

1924 *Lithophyllum?* *albanense* Lemoine, p. 281, text-figs. 8, 9.
1956 *Lithophyllum albanense* Lemoine; Maslov, p. 155, pls. 40–41, text-figs. 78–79.

Description. 1–2 mm crusts giving rise to thick (5·3 mm (s.d. 1·6), 315–7·5 mm) branches up to 25 mm long. Hypothallium coaxial and of variable thickness (183 μm (s.d. 73), 80–380 μm). Hypothallial cells rectangular and measuring 25 μm (s.d. 4·7), 15–39 μm long and 15 μm (s.d. 3·5), 9–23 μm wide. Perithallial cells typically form a zoned grid of irregularly sized and shaped cells (Pl. 17, figs. 1–3). Cells in crusts measure 15 μm (s.d. 4·8), 9–23 μm long and 14 μm (s.d. 4·3), 8–24 μm wide. Cells in branches arranged in zones (73 μm (s.d. 11·6) in apical thickness) and are larger than crust cells (15 μm (s.d. 4·8), 10–25 μm long and 16 μm (s.d. 3·9), 10–25 μm wide).

Both asexual and sexual conceptacles are present (Pl. 16, figs. 3–4). Asexual conceptacles have short/wide pores in which overgrowing tissue infills with a distinctive conical plug (Pl. 17, fig. 3). Conceptacles measure 430 μm (s.d. 108), 316–567 μm wide and 179 μm (s.d. 72), 120–275 μm high. Sexual conceptacles are flatter with longer necks measuring 455 μm (s.d. 9), 450–467 μm wide and 130 μm (s.d. 9), 120–136 μm high. One example (Pl. 17, fig. 4) shows presumed cystocarps.

Remarks. The distinctive aspects of this species are the irregular arrangement of the cells and the variable conceptacle size and shape. The high variability in cell sizes is reflected in the large standard deviations and the conceptacle size ranges are similar to those of Lemoine (350–575 μm wide: Lemoine 1924, 1939).

Occurrence. L. albanense is common and occurs in all of the biostrome facies. Its most frequent habit is to overgrow small rhodoliths of *M. commune* with firstly a crust and then branches to form large branching rhodoliths. Occasionally it forms a laminar core to rhodoliths intergrown with *M. commune.*

Lithophyllum bahrijense n.sp.

Plate 17, figs. 7–9; text-fig. 8

1982 *Lithophyllum* sps. 'b', Bosence and Pedley.

Holotype. BM V.60929 from branching rhodoliths in Rhodolith Pavement facies, locality 1 (Bosence and Pedley 1982). *Times of Malta* map grid. ref. 402 726.

Derivation. Named after village of Bahrija, Malta; adjacent to locality.

Description. Distinctive, finely branched (2·2 mm (s.d. 0·48), 1·4–3·4 mm wide and up to 15 mm long) spheroidal rhodoliths. Partly coaxial hypothallium (Pl. 17, fig. 7) 175 μm (s.d. 43·8), 120–230 μm thick with elongate

EXPLANATION OF PLATE 18

Fig. 1. *Lithoporella melobesioides.* Fertile crust with monostromatic thallus and large ripe conceptacle with preserved spores. Loc. 14, × 80. BM(NH) V.60931.

Fig. 2. Cf. *Lithophyllum prelichenoides.* Fragment of crust illustrating thick, coaxial hypothallium and thinner, poorly preserved perithallium. Loc. 14, × 80.

Figs. 3–6. *Mesophyllum commune.* 3, crustose Pavement facies of coralline Algal Biostrome with leafy, *in situ* framework of *M. commune.* Loc. 14, coin 25 mm. 4, framework with branches arising from subhorizontal leafy crusts. Loc. 14, × ⅓. 5, framework in thin section showing fusion of overgrowing crusts to basal crust. A short vertical branch arises between the two overgrowing crusts. For sketch of filaments and growth zones see text-fig. 12c. Loc. 14, × 20. 6, framework illustrating leafy crusts, crust divisions branches, and encrusting byozoans. Loc. 3, × 1½.

Figs. 7, 8. *Mesophyllum lichenoides* (Recent). 7, side view of framework illustrating crust divisions and fusions, overgrowth of old crusts and articulated corallines. Note epiphytes and debris on older lower crusts. Loc. Kimmeridge Bay, Dorset, × 5. 8, upper surface of leafy framework. Note overgrowth of lower crusts and articulating corallines. Loc. Kimmeridge Bay, Dorset, × 2.

PLATE 18
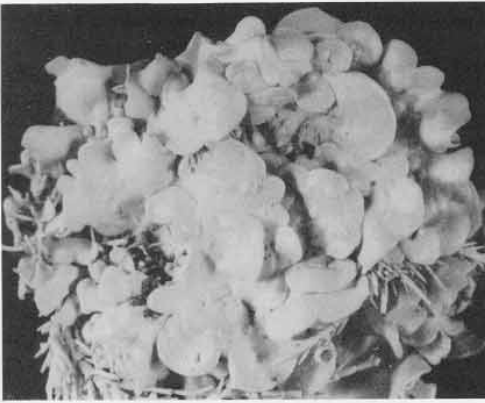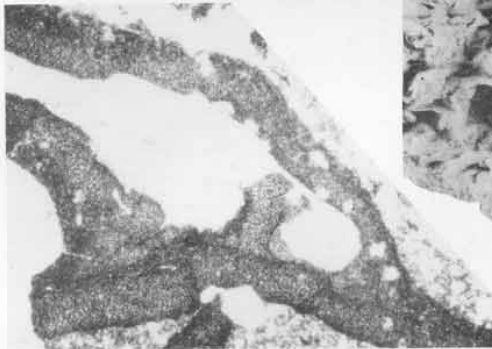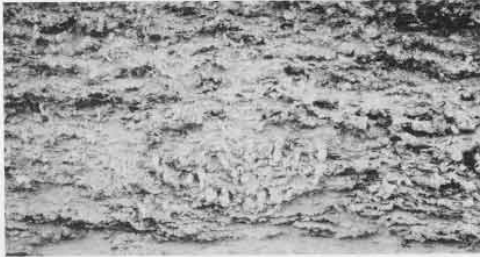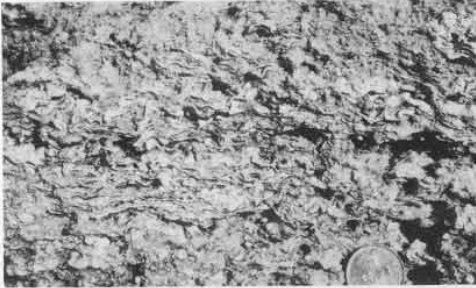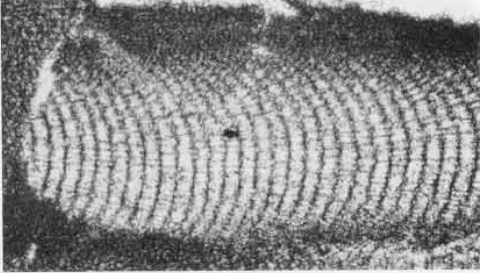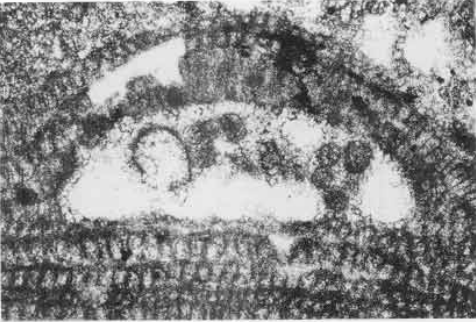
BOSENCE, Miocene coralline algae
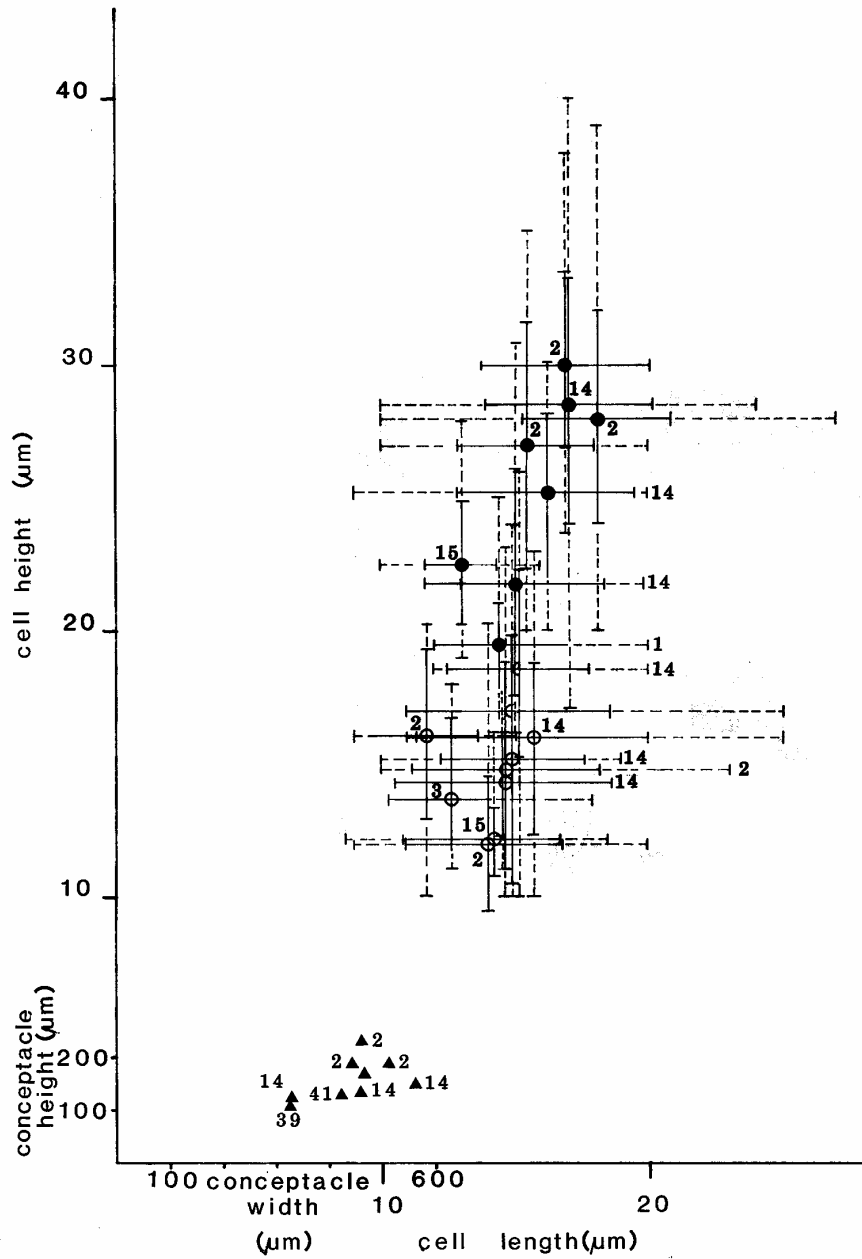
TEXT-FIG. 7. *Lithophyllum albanense*: Hypothallial, perithallial, columnar perithallial (C), asexual (▲), and sexual (■) conceptacle measurements. (Symbols as for text-figs. 2-4.)
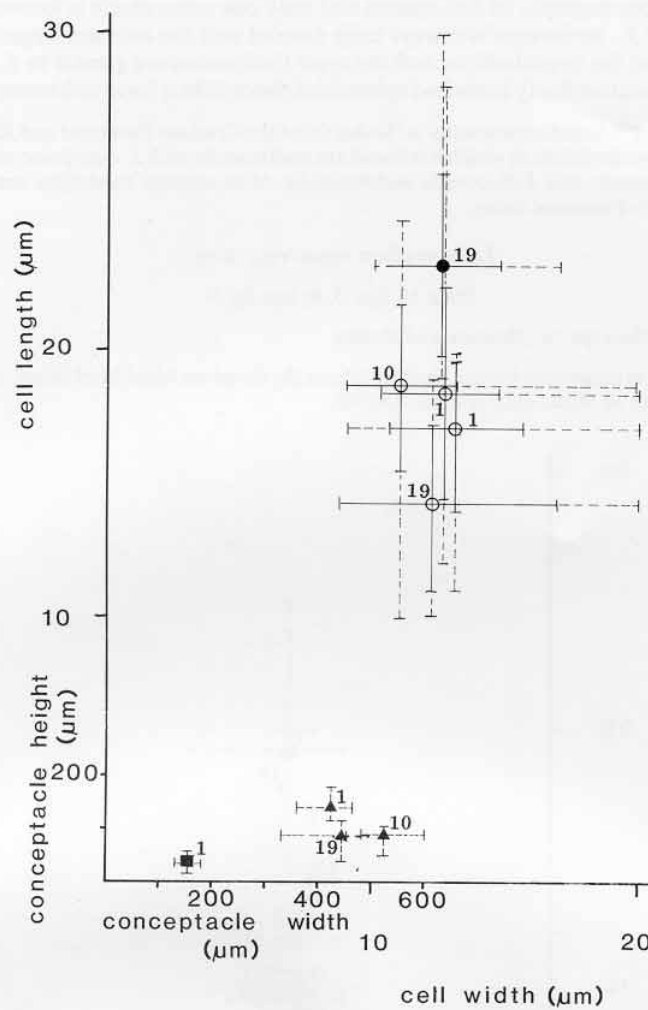
TEXT-FIG. 8. *Lithophyllum bahrijense*: Hypothallial, perithallial, asexual (▲), and sexual (■) conceptacle measurements. (Symbols as for text-figs. 2–4.)

rectangular cells measuring 23 μm (s.d. 3·7), 20–30 μm long and 13 μm (s.d. 2·3), 10–17 μm wide. Perithallium irregularly zoned with cells arranged in rows or a grid. Cells vary in shape from elongate, to square, to depressed, to polygonal (Pl. 17, figs. 7–9). Perithallial cells measure 17 μm (s.d. 2·5), 9–20 μm wide. Asexual conceptacles are characteristically depressed with a short wide conical pore. Conceptacle floors are flat or following undulations of previous cell rows (Pl. 17, fig. 8). Conceptacles measure 459 μm (s.d. 63), 330–600 μm wide and 98 μm (s.d. 36), 40–180 μm high. Smaller crystocarpic conceptacles are also present (Pl. 17, fig. 9) with depressed chambers with a long pore nearly as high as the conceptacles are wide. Conceptacles measure 156 μm (s.d. 26), 140–210 μm wide and 38 μm (s.d. 17), 20–60 μm high.

Remarks. The perithallial tissue of *L. bahrijense* is not significantly different from that of *L. albanense* and without conceptacles these two species cannot be separated. This species is similar in some respects to *Lithophyllum barbarense* Lemoine described from the Oligocene of Algeria (Lemoine

1939). There are no photographs of this species and only one conceptacle is known (450 × 160 μm). The hypothallium of *L. barbarense* is always truly coaxial and the cells are larger than those of *L. bahrijense*. In addition the hypothallium and the crust thicknesses are greater in *L. bahrijense* and it always occurs as distinctive finely branched spheroidal rhodoliths a form unknown in *L. barbarense*.

Occurrence. L. bahrijense is found occasionally in rhodoliths of the Crustose Pavement and Rhodolith Pavement facies. The characteristic rhodoliths in which it is found are multispecific with *L. bahrijense* overgrowing or being grown over by *M. commune* and *Lithoporella melobesioides*. Monospecific rhodoliths are found at the type locality in the Rhodolith Pavement facies.

<center>*Lithophyllum mgarrense* n.sp.</center>

<center>Plate 16, figs. 5, 6; text-fig. 9</center>

1982   *Lithophyllum* sps. 'a', Bosence and Pedley.

Holotype. BM V.60930 in concentric lamina rhodolith from the Crustose Algal Marl facies, locality 15 (Bosence and Pedley, 1982). *Times of Malta* map grid ref. 410 746.
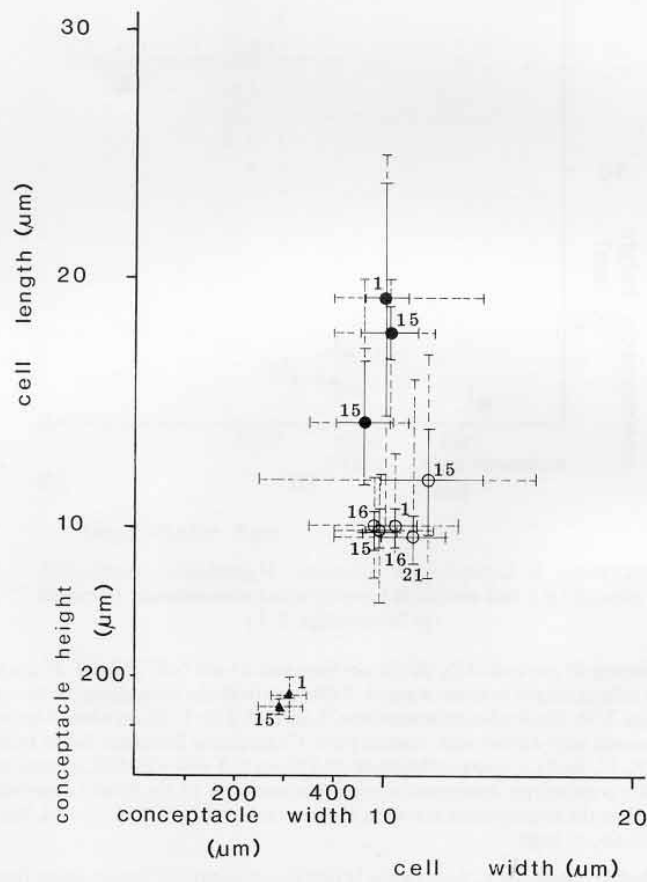
TEXT-FIG. 9. *Lithophyllum mgarrense*: Hypothallial, perithallial, and conceptacle measurements. (Symbols as for text-figs. 2–4.)

Derivation. Named after nearby town of Mgarr, Malta.

Description. L. mgarrense occurs as crusts and columns (6·5 mm (s.d. 2·5), 4–9 mm wide and up to 9 mm high) within rhodoliths. The coaxial hypothallium is thin (60 μm (s.d. 8), 50–70 μm) and often weakly developed and poorly preserved. Cells are rectangular and measure 19 μm (s.d. 5·2), 12–20 μm long and 11 μm (s.d. 1·9), 8–15 μm wide. The perithallium (up to 850 μm thick in crusts) has distinctive thick walled filaments which diverge in fan-shaped zones, particularly around conceptacles (Pl. 17, fig. 5). Perithallial cells in crusts are square and measure 10 μm (s.d. 0·8), 7–12 μm long and 10 μm (s.d. 0·8), 7–13 μm wide. Columnar tissue is zoned (183 μm (s.d. 35), 150–220 μm thick at the apex) and cells are more elongate and variable in length (16 μm (s.d. 4·6), 10–25 μm long and 11 μm (s.d. 1·4), 8–15 μm wide) than crust cells. The unipored conceptacles are oval with either a raised or flat floor. They measure 301 μm (s.d. 40), 260–370 μm wide and 152 μm (s.d. 23), 126–210 μm high and have short wide pores. Conceptacles are commonly roofed with a distinctive row of elongate perithallial cells (Pl. 17, fig. 5).

Remarks. L. mgarrensis has similar ranges of cell sizes as *Lithophyllum uvaria* (Michelin) Lemoine but the latter species has a thicker hypothallium and the perithallium is arranged in rows. Conceptacles are unknown in *L. uvaria.* The distinctive perithallium of *L. mgarrense* is similar to that of *Lithophyllum duplex* Maslov but the latter species has larger cells and characteristic bulbous pored conceptacles.

Occurrence. L. mgarrense is common in branching rhodoliths of the Crustose Algal Marl and Algal Debris Wackestone facies. It also occurs in the Rhodolith Pavement facies and at the top of the Ghajn Znuber Beds. Its commonest habit is to overgrow concentric laminar cores of *M. commune* with crusts and then branches. The occurrence of *L. mgarrense* in the above facies suggests it had a preference for relatively quiet water conditions.

<div style="text-align:center">

cf. *Lithophyllum prelichenoides* Lemoine

Plate 18, fig. 1; text-fig. 10

</div>

1917   *Lithophyllum prelichenoides* Lemoine, p. 262; text-figs. 8–9.

Description. Laminar crusts and dividing leafy crusts of hypothallial and perithallial tissue. Distinctive thick (300 μm (s.d. 79), 800–400 μm) coaxial hypothallium and thin (120 μm (s.d. 47), 80–200 μm) multistromatic perithallus (Pl. 18, fig. 1). Hypothallial cells rectangular, measuring 22 μm (s.d. 3·2), 15–30 μm long and 12 μm (s.d. 2·4), 9–19 μm wide. The perithallial cells which are arranged in filaments are often poorly preserved and measure 19 μm (s.d. 1·7), 16–22 μm long and 16 μm (s.d. 3·9), 10–22 μm wide. No conceptacles are present.

Remarks. Due to the absence of conceptacles no definite generic assignment can be made for this coralline. The size and structure of the hypothallium and perithallium is very similar to those of *L. prelichenoides.* However, the hypothallial cells are smaller (22–38 μm × 10–20 μm) and the perithallial cells larger (7–15 μm × 7–10 μm) than is normal for this species (Lemoine 1939).

Occurrence. As crusts in multispecific rhodoliths. One specimen from the Rhodolith Pavement facies and one from the Crustose Pavement facies.

<div style="text-align:center">

Sub-family MASTOPHOROIDEAE (Svedelius 1911); Setchell 1943
Genus LITHOPORELLA (Foslie 1904); Foslie 1909
Lithoporella melobesioides (Foslie); Foslie

Plate 18, fig. 2; text-fig. 11

</div>

1904   *Mastophora (Lithoporella) melobesioides* Foslie *in* Weber van Bosse and Foslie 1904, pp. 73–77, text-figs. 30–32.
1939   *Melobesia (Lithoporella) melobesioides* (Foslie); Lemoine, pp. 108–110, text-figs. 78–79.
1949   *Lithoporella (Melobesia) melobesioides* (Foslie); Johnson and Ferris, p. 196, pl. 37, figs 4–5; pl. 39, fig. 2.

Description. Monostromatic crusts of hypothallium with successive layers forming crusts up to 500 μm thick.
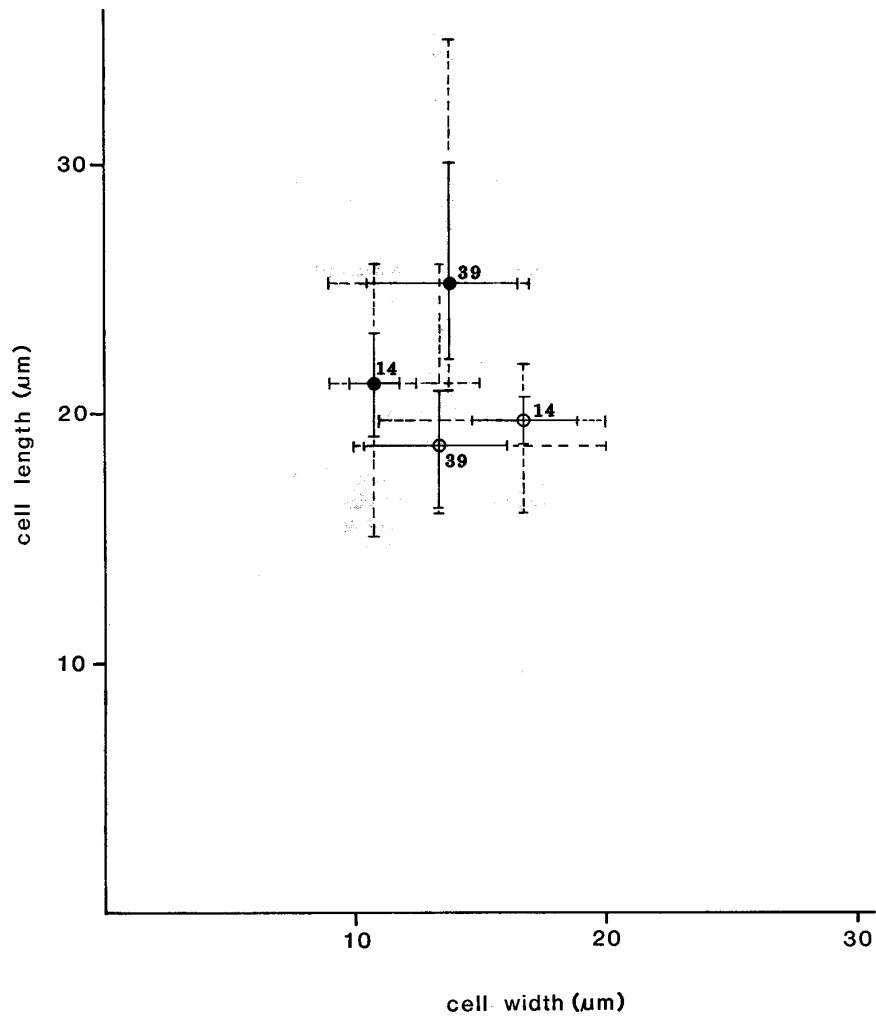
TEXT-FIG. 10. Cf. *Lithophyllum prelichenoides*: Hypothallial and perithallial cell measurements. (Symbols as for text-figs. 2-4.)

Cells often arranged in imbricate patterns with variable cell lengths (text-fig. 11, pl. 18, fig. 2). Cells measure 37 μm (s.d. 23), 15–120 μm long and 18 μm (s.d. 4·5), 8–29 μm wide. One large semicircular conceptacle is present 730 μm wide and 350 μm high. This conceptacle has preserved spherical spores with diameters in section of 45 μm (s.d. 28), 30–105 μm.

Occurrence. L. melobesioides is common as crusts within rhodoliths from all biostrome facies. It is frequently intergrown with crusts of *M. commune. L. melobesioides* is also found as encrusting sheets in the framework of the Crustose Pavement facies. Because of its simple morphology it is never a framework constructor in the manner of *M. commune* as outlined below.

MESOPHYLLUM COMMUNE—OCCURRENCE, FRAMEWORK
CONSTRUCTION, AND FUNCTIONAL MORPHOLOGY

M. commune is abundant in all facies of the Coralline Algal Biostrome. In each facies this alga produces different growth forms in response to different environmental conditions. In the quiet water Crustose Algal Marl facies crusts of *M. commune* grow over the sediment surface; a mode of life unusual for crustose corallines (Adey and MacIntyre 1973). This habit is proven by growth responses
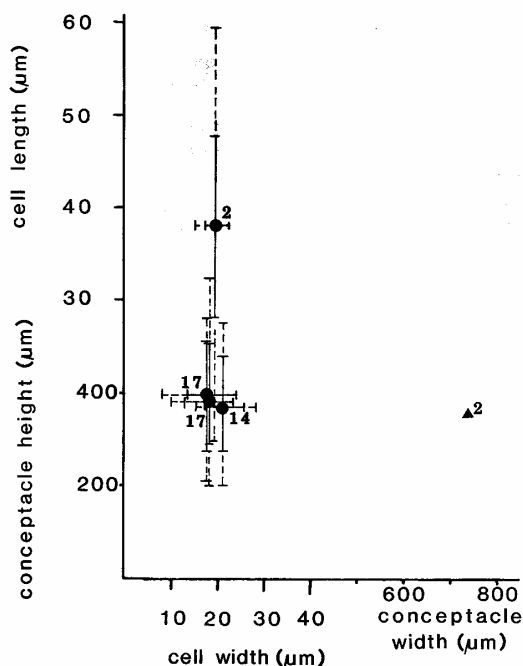
TEXT-FIG. 11. *Lithoporella melobesioides*: Cell lengths and widths and conceptacle measurement. (Symbols as for text-figs. 2–4.)

by the algae to substrate irregularities. Bifurcations and occasional turning of these crusts give rise to leafy rhodoliths (Bosence and Pedley 1982). Large discoidal rhodoliths originating from crusts are found in the Algal Debris Wackestone facies. In addition, open branched rhodoliths of *M. commune* occur in the Crustose Algal Marl facies and denser branched forms in the higher energy Algal Debris Wackestone facies. *M. commune* forms laminar, concentric, and columnar cores to most rhodoliths from the Rhodolith Pavement and Algal Branch Packstone facies. These rhodoliths are overgrown by species of *Lithophyllum*, *Lithothamnium*, and *Lithoporella melobesioides*.

The most striking occurrence of *M. commune* is in the construction of the *in situ* framework in the Crustose Pavement facies (Pl. 18, figs. 3–6). The frameworks are up to 4·5 m thick, covering areas measured in 10,000s of square metres (text-fig. 1). They had an original relief of around 10–20 cm above the sea bed. The sedimentological features and associated fauna of the Crustose Pavement facies is described in Bosence and Pedley (1982). I describe here the morphological details of framework construction and their adaptive significance.

Framework construction

The construction of the framework in the Crustose Pavement facies is basically a combination of foliaceous crust growth, crust divisions, crust fusion (Pl. 18, figs. 3–6), and vertical branch growth (Pl. 18, fig. 4). However, in detail there are a variety of ways in which this is achieved.

(a) *Normal crust division* (text-fig. 12A). Crusts may divide through rejuvenation of previously dormant perithallial meristem to form a surface ridge which grows upwards into an overgrowing crust. The resulting new crust is identical in structure to the original crust and continues growth in the same direction as the underlying crust.

(b) *Reverse crust division* (text-fig. 12B). Divided crusts as in (a) above but the new crust grows in the opposite direction.

(c) *Crust fusion* (Pl. 18, fig. 5; text-fig. 12C). A downward growing crust can fuse on to an underlying crust. Two such examples are shown in Pl. 18, fig. 5 and text-fig. 12C, together with a short vertical branch. Either the upper downward growing, or the lower crust can heal the junction with additional perithallial tissue. The right-hand example has been fused mainly by perithallial tissue from the downward growing crust. The inverted left-hand crust has been fused by perithallial tissue derived from the basal crust.

(d) *Crust bridging* (text-fig. 12D). Bridging between over and underlying crusts can occur with a combination of crust division and crust fusion described above. Text-fig. 12D shows a vertically growing crust of perithallium growing on to the basal hypothallium of an overgrowing crust.

(e) *Enforced crust division* (text-fig. 12E). Divisions and redirected crust growth occur where a crust grows up against an obstruction. The hypothallial meristem ceases division against the obstruction and growth continues through rejuvenation of adjacent perithallal meristem to form an upward growing crust with hypo- and perithallal tissue identical to the original crust.

(f) *Crust overgrowth* (text-fig. 12F). When crusts (presumed to be dead) are overgrown by successive crusts the upper one may grow up and away from its substrate. Similarly juvenile crusts from spore settlement on old crusts may grow away from the substrate with a foliaceous habit.

(g) *Crusts—branch frameworks* (Pl. 18, fig. 4). Distinctive frameworks are also constructed by branches arising from horizontal crusts which are then subsequently overgrown by crusts. Further growth alternates between crusts and branches. Branches usually originate directly above previous branch tips giving the impression of continuous branch growth. Sections indicate that branches originate from raised areas where crusts overgrow previous branches.

Discussion

This variety of crust fusions and division has not, to my knowledge, been described before for one species of fossil or recent coralline. The foliaceous habit of *M. commune* together with its constructional abilities clearly enabled it to become a successful frame-building species in the Miocene.

The morphologies exhibited by Recent frame-building corallines are being investigated by the author (e.g. Bosence 1981), but preliminary examination of material collected from south-west England and W. H. Adey's material at the Smithsonian Institution indicate possible Recent analogues.

The closest analogue for *M. commune* appears to be *Mesophyllum lichenoides* (L) Lemoine. Specimens from intertidal and shallow subtidal rocky shores at Kimmeridge Bay, Dorset, exhibit small-scale frameworks (up to 10 cm across and 1–2 cm thick). In the Mediterranean this species occurs at greater depths as an important constructor in the 'coralligène bioceonose' (Laborel 1961) which is also used as an analogue for the Coralline Algal Biostrome of Malta.

M. lichenoides exhibits the same foliaceous growth as *M. commune* and crust division, crust fusion, enforced crust division, crust bridging, and crust overgrowth can all be recognized (Pl. 18, figs. 7, 8). Similar leafy frameworks are constructed by *Lithophyllum expansion* Phillippi from Naples and

A   Crust   Division

B   Reverse   Crust   Division

0 ___ 500µm

C   Crust   Fusion

D   Crust   Bridging

E   Enforced   Crust   Division

F   Crust   Overgrowth
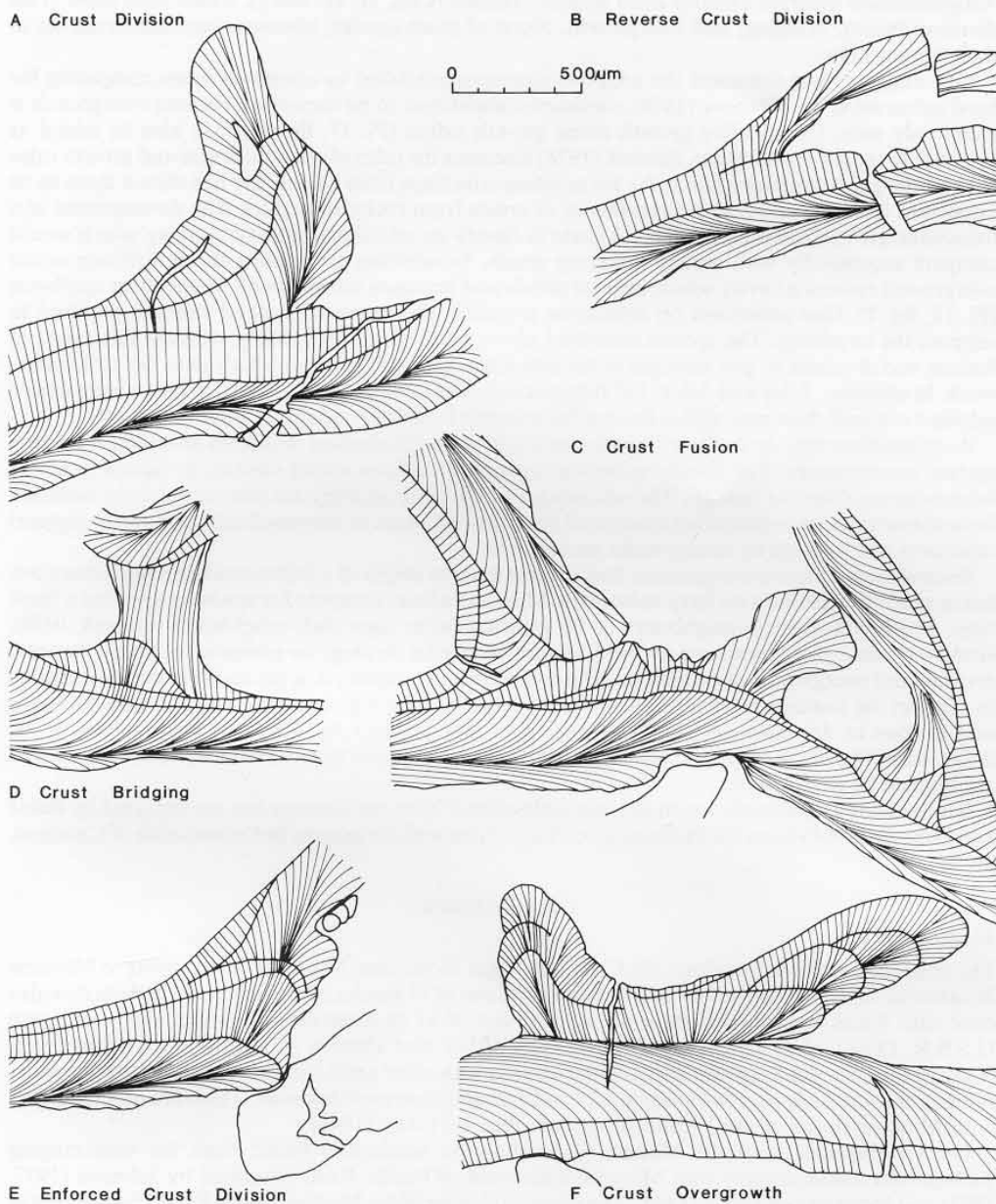
TEXT-FIG. 12A–F. Framework construction by *Mesophyllum commune* (for details see text). Outlines and growth zones in heavy lines. Filaments (lines of cells) indicating direction (divergence) and sequence of growth in fine lines. Note post depositional fracturing of framework (12B, F) and foraminifer in 12E. Sketches from camera lucida drawings of thin sections.

Neogoniolithon notarissi Delfour from Bibane, Tunisia (Coll. W. H. Adey), which both show crust division, fusion, bridging, and overgrowth. None of these species, however, combine branches in their frameworks.

Few authors have discussed the adaptive strategies exhibited by corallines when competing for hard substrate space. Steneck (1978) considers competition to be important because overgrowth is commonly seen. Competitive growth along growth ridges (Pl. 17, fig. 10) may also be added as evidence for space competition. Steneck (1978) discusses the roles of crust thickness and growth rates in producing a competitive hierarchy for crustose corallines from Maine. He has shown these to be important in explaining relative abundance of crusts from rocky substrates. The development of a foliaceous growth habit above the substrate is clearly an additional growth strategy which would compete successfully with closely adhering crusts. In addition to shading the underlying crusts overgrowth creates a cavity which collects debris and becomes infested with filamentous epiphytes (Pl. 18, fig. 7). One constraint on foliaceous growth is the increased skeletal strength required to support the overhang. The species described above have, in all probability, evolved this range of fusions and divisions to give strength to the foliaceous growth form and which gives rise to a frame-work. In addition, Adey and Adey (1973) mention that *M. lichenoides* is unusual in that it increases its calcified cell wall thickness within the thallus possibly to support a foliaceous growth form.

A comparison may be made with Jacksons's (1979) morphological strategies proposed for sessile marine invertebrates. The closely adhering crustose corallines would classify as 'sheets' and the foliaceous corallines as 'plates'. The advantages of the plate strategy are considered to be isolation from the deleterious 'substratum associated processes' at a cost of increased commitment to support structures and damage by strong water movements.

In conclusion, there are arguments that suggest that the origin of a foliaceous coralline framework lies in space competition on hard substrates. Many corallines compete for space by growing a thick crust which will overtop neighbours or by growing faster than their neighbours (Steneck 1978). However, some corallines have evolved a more successful strategy to compete for space by crust division and overgrowth of neighbour. The cost to these corallines is in the construction of a thallus to support the overhangs. *Mesophyllum* has achieved this through a diverse array of crust divisions and fusions in *M. commune* and *M. lichenoides* and possibly by increased calcification in *M. lichenoides*. The result of this growth strategy is the construction of a foliaceous framework so well exemplified by *M. commune*.

Similar leafy frameworks are at present undescribed from the Tertiary but are reported by Babič and Zupanič (1981) from the Palaeocene of Yugoslavia and are present in Eocene reefs of Catalana, Spain.

DISCUSSION

Biogeography

The crustose coralline flora from the Coralline Algal Biostrome, Malta, is most similar to Miocene floras from Algeria described by Lemoine (1939) (8 out of 11 species co-occurrences). Similarities also exist with floras from the Miocene of Egypt (5 out of 11 co-occurrences) (Souya 1963), southern U.S.S.R. (5 out of 11 co-occurrences) (Maslov 1956), and Corsica (4 out of 11 co-occurrences) (Orszag-Sperber and Poignant 1972). Comparisons with other areas can only be made with the wide-ranging species; *Lithoporella melobesioides* and *Lithophyllum prelichenoides*. There are no similarities with Miocene floras of the Vienna Basin described by Conti (1946).

On a world-wide scale the Maltese floras show no similarities (apart from the wide-ranging *Lithoporella melobesioides*) with Miocene limestones of Pacific Reefs described by Johnson (1957, 1961) and Johnson and Ferris (1949). The possible closure of the Mediterranean Pacific connection at around the Oligocene/Miocene boundary is discussed by Adams (1981).

Climate and water depth

The genera from the Miocene of Malta are today found in waters from the tropics to temperate waters (Adey 1970). Tropical to subtropical climates are, however, indicated by the presence of small

patch reefs of *Montastrea* and *Porites*, within the biostrome together with locally abundant *Halimeda* plates. In these climates a flora dominated by *Mesophyllum* is typical of water depths of 60-80 m (Adey and Boykins, in press). Comparison has been made with the 50-130 m 'Coralligène de Plateau' (Pérès 1967) of the present-day Mediterranean (Bosence and Pedley 1982).

TABLE 1. Occurrences of coralline taxa in facies of the Miocene Coralline Algal Biostrome

Facies	Ghajn Znuber Beds	Crustose Algal Marl	Algal Debris Wackestone	Rhodolith Pavement	Algal Branch Packstone	Crustose Pavement	Algal Crust Packstone	Total occurrences of taxa
Taxa per cent								
Archaeolithothamnium affine				2		2		2
A. intermedium					4			1
Lithothamnium magnum				3		2	7	4
L. praefructiculosum					4	9		5
Mesophyllum commune	57	43	36	38	43	45	43	80
M. koritzae			14					3
Lithophyllum albanense	14	19		27	30	14	29	41
L. bahrijense				2		4		3
L. mgarrense	7	19	36	6				14
Cf. *L. prelichenoides*				2		2		3
Lithoporella melobesioides	22	19	14	20	17	21	21	36
Total occurrences in facies	15	21	14	61	23	44	14	192

Distribution of flora in Biostrome

The occurrence of corallines in the biostrome facies is shown in Table 1. The differences in sample sizes precludes a statistical analysis of the diversity and comparisons of floras from each facies. The facies with the greatest numbers of species are the Rhodolith Pavement and Crustose Pavement facies. These two facies contain the greatest volume of *in situ* material and therefore probably represent the richest original floras. The range of taxa in the Rhodolith Pavement facies occurs in multispecific rhodoliths. Species numbers are increased by ecological succession within rhodoliths with inner laminar cores of *M. commune* and *Lithoporella melobesioides* and outer layers with species of *Lithophyllum* and *Lithothamnium*. In the Crustose Pavement facies the corallines of the framework (*M. commune*, *Lithoporella melobesioides*, and *Lithophyllum albanense*) are added to those of rhodoliths occurring along erosion surfaces within the framework.

In general, the floras from each facies are similar and dominated by *M. commune*, *L. melobesioides*, and *L. albanense*. The facies are characterized more by the algal growth forms than by species composition. The one exception is *Lithophyllum mgarrense* which occurs mainly in quieter water sediments.

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