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MAERL-FORMING CORALLINE ALGAE AND ASSOCIATED PHYTOBENTHOS FROM THE MALTESE ISLANDS

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ABSTRACT

Maerl grounds consist mainly of unattached non-geniculate coralline algae, known as rhodoliths, and their algal debris. The recent discovery of such grounds around the Maltese Islands led to the present study of rhodolith-forming species. Gross morphology of the rhodoliths was highly variable so identifications were based on microscopic examination of fertile material. Investigations using optical and scanning electron microscopy confirmed that five main species of rhodolith-forming coralline algae were present: *Lithophyllum racemus, Lithothamnion corallioides, Lithothamnion minervae, Mesophyllum alternans* and *Phymatolithon calcareum.* Two other heavily calcified species, tentatively identified as *Peyssonnelia rosa-marina* and *Neogoniolithon brassica-florida* on the basis of gross morphology, were also important contributors to Maltese maerl deposits. Seasonal monitoring of the phytobenthos associated with maerl revealed that *Flabellia petiolata* and *Womersleyella setacea* were consistently the dominant species present.

INTRODUCTION

The term maerl is used to describe biogenic sediments composed of live and dead unattached calcareous algae, mainly in the Order Corallinales. As with many seaweeds, these coralline algae can reproduce both by fragmentation and through the production of spores that settle and grow on hard substrata. Maerl is formed in both of these ways. Thus fragments that break off attached thalli may be transported by currents and form maerl through continued growth and fragmentation at the redeposition site (Freiwald, 1995). Alternatively, free-living algal nodules can form by the settlement and growth of spores on suitable sediment particles. Eventually the spores grow to form a thallus that completely encloses the original sediment grain (Bosence, 1976). Resulting unattached coralline algae typically have an inorganic core although the cores can also be of biogenic origin, such as mollusc shells (Adey, 1986).

While some authors refer to uncored algal thalli as 'maerl', and to cored algal nodules as 'rhodoliths' (e.g. Irvine & Chamberlain, 1994), here we use 'rhodoliths' to describe both types of free-living coralline algae, following the terminology of Bosence (1983b), Basso & Tomaselli (1994) and Steller & Foster (1995). Such rhodoliths show an enormous range of morphologies (Woelkerling, 1988).

Rhodoliths can have a highly irregular shape or be more or less spherical; they can also take the form of branched thalli or unbranched crustose layers enveloping a sediment particle. Branched rhodoliths show variations in branching density ranging from open to compact branching. These different morphologies have little taxonomic value since the same species can exhibit a wide spectrum of rhodolith shapes and branching densities, while different species can display a similar gross morphology.

Variations in rhodolith morphology are thought to result primarily in response to different intensities of physical disturbance, and therefore can be used as indicators of environmental conditions at the site of growth (Steneck, 1986). Bosence (1976; 1983a) related rhodolith shape and branching density with environmental parameters and concluded that sphaeroidal densely branched rhodoliths are formed in areas where water movement is significant, while open branched rhodoliths are formed in quieter waters. Because of their potential as bioindicators of environmental conditions and because rhodoliths fossilise readily, they are regarded as useful palaeoecological indicators (Basso, 1995a; Basso & Tomaselli, 1994). However, some authors dispute this view, at least in the case of rhodoliths formed by fragmentation of attached forms, suggesting that the different rhodolith shapes simply reflect different stages in their formation, being more compact or spherical when mature (Freiwald, 1995; Wehrmann *et al.*, 1995; Freiwald & Henrich, 1994).

Due to this plasticity in the gross morphology of rhodoliths within the same population, the identification of rhodolith-forming coralline algae must be based on detailed examination of microscopic characteristics such as their reproductive conceptacles (Adey & McKibbin, 1970). This generally involves optical microscopy of decalcified sections and the use of scanning electron microscopy (Woelkerling, 1988). Thus the identification of rhodolith-forming algae is time consuming, especially since diagnostic reproductive structures may occur infrequently (Adey & McKibbin, 1970). However, despite wide

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variability in external form, some species often show recognisable characteristics in gross morphology on which tentative identifications can be made (Lanfranco, 1998).

Maerl grounds in the Mediterranean are characterised by several species of coralline algae that are able to live under conditions of low light. In the Western Mediterranean maerl occurs to ca.100m while in the clearer waters of the Eastern Mediterranean it is found to ca.180m (Basso, 1996). Maerl grounds require periods of moderate water movement to overturn the algae – this allows concentric growth of the rhodoliths and prevents burial by fine particles (Bosence, 1983b; Basso & Tomaselli, 1994; Hall-Spencer, 1998). They also require a degree of shelter from wave action to avoid dispersal into non-suitable environments (Hall-Spencer, 1998).

Live rhodoliths have been collected from various sites around the Maltese Islands at depths ranging from 5m to 103m. Not all these rhodoliths come from maerl grounds; some form very sparse accumulations on soft sediments, amongst seagrass beds, and even on rock. The most extensive maerl ground known to date lies off the Northeastern coast of the islands, and covers about 20km^2 of the seabed. This maerl ground was recently discovered during a UNESCO sponsored oceanographic survey (Borg *et al.*, 1998).

The first record for a maerl-forming alga from the Maltese Islands appears to be that of Sommier & Caruana Gatto (1915) who list "*Lithothamnion polymorphum* (L.) Aresch." This taxon as represented in the Mediterranean is generally held to be synonymous with *Phymatolithon calcareum* (Woelkerling & Irvine, 1986; Cormaci *et al.*, 1997). However the authors state that it is "..*comune sulle conchilie*", which is hardly descriptive of the habitat and status of this species, which only occurs as unattached rhodoliths!

MATERIALS AND METHODS

Over a two year period (1996-1998), seasonal samples of rhodoliths were obtained from a maerl ground located at depths of between 45m and 55m off Is-Sikka l-Bajda (Borg *et al.*, 1998). On each sampling occasion 3-6 replicate 0.1m^2 van Veen grab samples and one biological dredge sample were obtained.

The phytobenthos was first removed and preserved in 10% seawater formaldehyde for subsequent identification. Maerl was then sieved over a 1mm mesh, washed to remove salt and debris, and air-dried. Preliminary sorting of the dried maerl was then carried out on the basis of gross morphology using published keys (Preda, 1908; Hamel & Lemoine, 1952; Giaccone, 1972/3). A x 40 stereo-microscope was then used to select fertile thalli for detailed examination using x 1000 optical and x 4000 scanning electron microscopes following methods given by Irvine & Chamberlain (1994).

Identifications based on these detailed observations were made by comparison with the most recent descriptions of European coralline algae (e.g. Irvine & Chamberlain, 1994; Basso, 1995b; Basso *et al.*, 1996; Cabioch & Mendoza, 1998).

RESULTS

Detailed study of the microscopic structure of Maltese rhodolith-forming algae revealed that five main species occurred at Is-Sikka l-Bajda: *Lithophyllum racemus, Lithothamnion minervae, Lithothamnion corallioides, Phymatolithon calcareum* and *Mesophyllum alternans.* A brief description of their gross morphology is given below:

Lithophyllum racemus (Lamarck) Foslie
(Plate 1: Figure A)

This was the only rhodolith-forming species found that was attributable to the coralline subfamily Lithophylloideae. Diagnostic features included the presence of sporangia in uniporate conceptacles, a lack of cell fusions and abundant secondary pit connections. The specimens generally had short, thick, densely spaced branches broadened at the apex and conformed in every detail to descriptions of the species provided by Basso *et al.* (1996). The shape of these rhodoliths is thought to be an adaptation to high water movement: abrasion by water movement causes broadening of the branch tips but the sides of the branches remain unaffected (Basso *et al.* 1996). This species was thinly dispersed on the Maltese grounds studied, but its rhodoliths had a distinctive shape and could be quite easily recognised on the basis of gross morphology. Due to the structure of the branches, this species formed spherical rhodoliths in which the broadened apices of the thalli nearly make contact with each other and leave very few open spaces on the outer surface.

The four other rhodolith-forming species that were common at Is-Sikka l-Bajda were all attributable to the coralline subfamily Melobesioideae on the basis that sporangia were borne in multiporate conceptacles, secondary pit connections were absent, and cell fusions were abundant (see Woelkerling, 1988).

Lithothamnion corallioides Crouan P.L. & Crouan H.M.
(Plate I : Figure B)

This species was also sparsely distributed on the Maltese ground studied. Several features, including flared epithallial cells, generally thin branches and multiporate conceptacles were concordant with descriptions of this species provided by Cabioch (1966, 1970, 1972), Adey & McKibbin (1970), Cabioch & Giraud (1978), Irvine & Chamberlain (1994) and Basso (1995b). Throughout southern Europe this species is most commonly found as unattached branches, or rarely as nodules enveloping pebbles or biogenic remains (Irvine & Chamberlain, 1994; Basso, 1995b). Rhodolith shape and branching density is extremely variable although the branches tend to be thin (ca.1mm diameter) and are not known to exceed 1.8mm in diameter (Basso, 1995b). On Maltese maerl grounds *L. corallioides* was present only as fragile open branched rhodoliths and was not found enveloping sediment particles. Cabioch (1966, 1970) found it useful to describe two varieties of *L. corallioides* on the French Atlantic coast; var. *minima* had narrow branches (< 1mm in diameter) and thrived on fine sandy and muddy bottoms while var. *corallioides* had thicker branches (up to 1.8mm in diameter) and thrived on coarse detritic bottoms. Both varieties of *L. corallioides* were present on the Maltese maerl ground studied, and they were

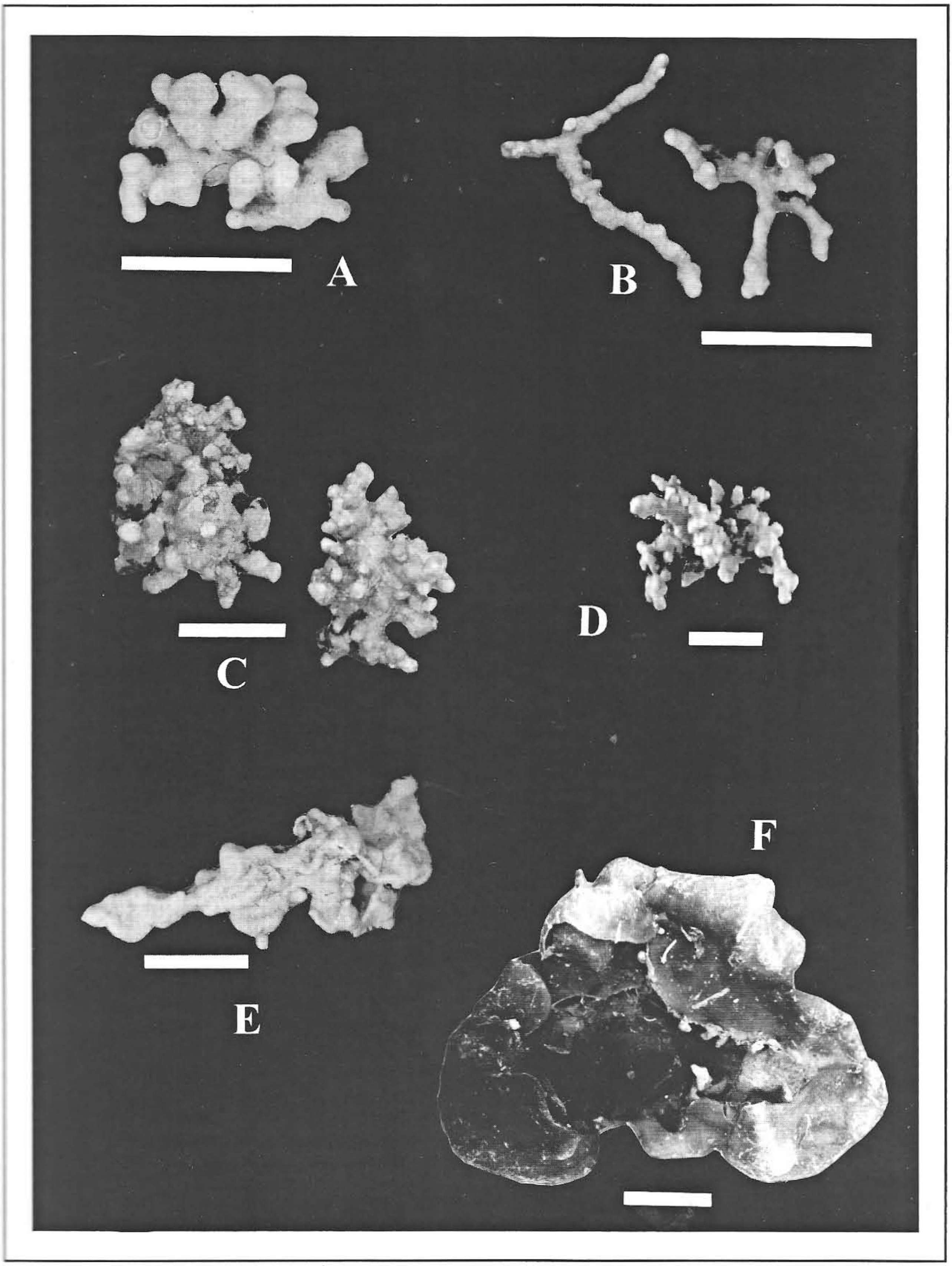

Plate I Representative examples of the main rhodolith-forming species of algae from the maerl ground off Is-Sikka l-Bajda. A: ***Lithophyllum racemus*** (Lamarck) Foslie B: ***Lithothamnion corallioides*** Crouan P.L. & Crouan H.M. C: ***Lithothamnion minervae*** Basso D: ***Phymatolithon calcareum*** (Pallas) Adey & McKibbin E: ***Mesophyllum alternans*** (Foslie) Cabioch & Mendoza F: ***Peyssonnelia rosa-marina*** Boudouresque & Denizot. (All scale bars represent 10 mm).

particularly abundant at a station that was characterised by a relatively high mud content.

Lithothamnion minervae **Basso** (Plate I : Figure C)

This was the most abundant rhodolith-forming species present at Is-Sikka l-Bajda with specimens conforming well to descriptions given by Basso (1995b). As with *L. corallioides,* flared epithallial cells were present. A notable difference between these species was that reproductive conceptacles were abundant year-round in *L. minervae* but were infrequently seen on the other rhodolith-forming species present. These algae may occur as unattached branches or may encrust sediment or biogenic particles. The rhodoliths formed by this species are more or less densely branched, the branches having a diameter ranging from 1-3mm. On Maltese maerl grounds *L. minervae* formed very compact and more or less spherical densely branched rhodoliths, with relatively short branches. These attained quite large sizes with rhodoliths of up to 80 mm diameter.

***Phymatolithon calcareum* (Pallas) Adey & McKibbin** (Plate I: Figure D)

Specimens were attributed to this species by comparison with descriptions of the neotype specimen (Woelkerling & Irvine, 1986). Anatomical and reproductive studies led Adey & McKibbin (1970) to place this species in the genus *Phymatolithon.* Descriptions of the habit and branching pattern are given by Cabioch (1966), Irvine & Chamberlain (1994) and Basso (1996). As with all rhodolith-forming species, *P. calcareum* can be found either as unattached branches or enveloping sediment or biogenic particles. While the shape and branching density of these rhodoliths is extremely variable; the diameter of the branches tends to be thick and is typically in the range of 1.5 - 3 mm.

On Maltese maerl grounds the rhodoliths formed by this species were sparsely distributed as highly variable, irregularly branched, unattached thalli. In contrast to many Mediterranean and Atlantic maerl grounds (Jacquotte, 1962; Grall & Glemarec, 1997; Hall-Spencer, 1998), it was not one of the dominant species present. It could usually be distinguished by the naked eye on the basis of a more robust structure and a thicker branching pattern than in *Lithothamnion corallioides*, while it has a more open branching pattern than *Lithothamnion minervae.* Specimens of *P. calcareum* were easily separated from species of *Lithothamnion* on the basis of epithallial cell shape, being domed in *Phymatolithon* and flared in *Lithothamnion* (see Woelkerling, 1988).

***Mesophyllum alternans* (Foslie) Cabioch & Mendoza** (Plate I : Figure E)

This species was quite frequent on the Maltese maerl grounds studied, where it forms small irregularly shaped rhodoliths with a very characteristic lamellate structure. These lamellae overlap each other and enclose sediment particles.

Other Species

Two other species, *Peyssonnelia rosa-marina* and *Neogoniolithon brassica-florida* were tentatively identified on the basis of gross morphology. The identification of the former is almost certainly correct, but for the latter species it needs to be confirmed by microscopic examination of fertile material, which is not yet available.

***Peyssonnelia rosa-marina* Boudouresque & Denizot** (Plate 1 : Figure F)

Unlike all the other maerl-forming species, which are corallines (Order Corallinales; Family Corallinaceae), this alga is a member of the family Peyssonneliaceae (Order Gigartinales). It was quite frequent in the Maltese maerl beds studied where it formed fragile monospecific nodules made up of a series of smooth overlapping lamellae.

***Neogoniolithon brassica-florida* (Harvey) Setchell & Mason**

This species is generally found attached to hard substrata but it also encrusts pebbles or biogenic particles to form highly irregular rhodoliths.

DISCUSSION

In the Maltese maerl grounds so far examined, the dominant rhodolith-forming algae are *Lithothamnion minervae* and *Lithothamnion corallioides.* The former is a recently described species, having been formerly confused with the normally attached *Spongites fruticulosa* (Basso, 1995). Accompanying rhodolith-forming species include *Phymatolithon calcareum*, *Lithophyllum racemus* and *Mesophyllum alternans.* Other rhodolith-forming species include *Neogoniolithon brassica-florida*, which also occurs commonly in the attached state, and *Peyssonnelia rosa-marina* (Family Peyssonneliaceae; Order Gigartinales). Several rhodoliths are 'stained' with blood-red patches which have been provisionally identified as the red alga *Cruoria cruoriaeformis* (P.L. & H.M. Crouan) Denizot. Also abundant on the rhodoliths, as well as on other algae growing on the maerl, is the tiny encrusting coralline *Hydrolithon farinosum* (Lamouroux) Penrose.

The complex architecture of the rhodoliths gives rise to a very heterogeneous environment and in fact maerl beds provide a very important habitat with a high biodiversity. Apart from the species already mentioned, the maerl grounds studied support a variety of upright and creeping macroalgae. The most abundant is *Flabellia petiolata* (Turra) Nizamuddin, a species with an erect leaf-like thallus subtended by a creeping system of stolons anchored into the sediment by abundant rhizoids which permeate the whole fabric of the maerl surface. Less conspicuous but nevertheless very abundant is the creeping red alga *Womersleyella setacea* (Hollenberg) R.E. Norris, a species of recent introduction in the Mediterranean (Verlaque, 1989) and which is rapidly spreading. This employs numerous disc-shaped attachments to anchor itself to sediments, including rhodoliths and other seaweeds. The dark-green ball-shaped *Codium bursa* (L.) C. Agardh, which is attached by means of a dense system of rhizoids, *Osmundaria volubilis* (L.) R.E. Norris with dark spirally-twisted thalli, and the brown *Cystoseira corniculata* (Wulfen) Zanardini with creeping axes, are also common. Among the more notable of the other species are the red *Cryptonemia tunaeformis* (Bertolini) Zanardini, a species which seems to occur almost exclusively on maerl, and the green net-like *Microdictyon tenuius* (C. Agardh) Decaisne. Numerous red algae of the family Rhodomelaceae, especially from the genera *Polysiphonia* and *Laurencia* (s.l.) also occur.

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