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Non-coralline crustose algae associated with maerl beds in Portugal: a reappraisal of their diversity in the Atlantic Iberian beds

Abstract: In recent years (2007–2009), the distribution and associated flora of maerl beds in southern Portugal (Algarve) were investigated by dredging and SCUBA diving (12–30 m depth). The present work provides the first data on the non-coralline crustose flora associated with maerl beds in Portugal. *Peyssonnelia bornetii* is a new record for Atlantic European coasts, and new records for Portugal are "*Rhododiscus pulcherrimus*" (sporophyte phase of *Atractophora hypnoides*), *Contarinia peyssonneliaeformis*, "*Cruoria rosea*" (sporophyte phase of *Halarachnion ligulatum*), *Peyssonnelia armorica*, and *"Aglaozonia chilosa"* (sporophyte phase of *Cutleria chilosa*). In addition, the records of three other species (*Hildenbrandia crouaniorum*, *Peyssonnelia dubyi*, and *Peyssonnelia harveyana*) completed the distribution gap between the North Iberian Peninsula and the Macaronesian region. The female and carposporangial structures of *C. peyssonneliaeformis* and *P. bornetii* are described for the first time. The diversity and species composition observed are compared with previous studies from maerl beds in the northwestern Iberian Peninsula (Galicia) and neighboring areas in the Atlantic Ocean and Mediterranean Sea. In order to facilitate and promote further studies of the crustose flora of subtidal habitats along European coasts, an identification key is provided for the 26 crustose taxa associated with maerl and gravel beds of the Atlantic coast of the Iberian Peninsula.

Keywords: crustose seaweeds; Iberian Peninsula; maerl; Portugal; Rhodophyta.

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Introduction

Crustose algae are considered an important component in the diversity and structure of marine communities. They also constitute an interesting subject for biogeographic studies due to their wide distribution, slow growth rates, and persistence in the face of mechanical and biological disturbances (Maggs 1990). In addition, studies of crustose algae have contributed to the discovery of new phases in the life histories of species with alternating heteromorphic generations (Sauvageau 1899, Maggs and Guiry 1982, Maggs et al. 1983). European maerl beds are coastal habitats that provide a wide range of ecological niches because of their three-dimensional structure (Barberá et al. 2003). They harbor a high number of algal species, including crustose taxa and phases in heteromorphic life histories, some of them mostly restricted to this habitat (Jacquotte 1962, Maggs and Irvine 1983, Maggs and Guiry 1989, Soto 1990, Ballesteros 1992, Birkett et al. 1998, Mannino et al. 2002, Peña and Bárbara 2010a).

In the Atlantic Iberian Peninsula, a previous study of the diversity of the non-coralline crustose flora associated with the Galician maerl and gravel beds brought the total number of species up to 23 taxa (Peña and Bárbara 2010a). Recently, we were able to record subtidal maerl beds in two areas of southern Portugal (Peña et al. 2009). Up to this date, the flora (and particularly the crustose species) associated with maerl beds of Portugal had not been studied in detail. The present study aims to contribute to a better knowledge of the subtidal benthic flora of the Portuguese coast, which is poorly known in the literature. We provide here the first data on the non-coralline crustose red algae associated with these maerl beds. We also compare the crustose flora of the Atlantic Iberian maerl beds with those reported from adjacent beds of the Atlantic Europe and the Mediterranean Sea. Given the difficulty of identifying crustose species and the scattered information for the species recorded, we provide an identification key, which encompasses all non-coralline crustose species recorded in the maerl and gravel beds of the Atlantic Iberian Peninsula.

Materials and methods

From 2007 to 2009, we carried out 74 subtidal surveys both by SCUBA and dredging (12–30 m depth) in two main areas of southern Portugal (Armaçao de Pêra, 37°01′N, 8°19′W; Bahia de Lagos-Portimao, 37°06′N, 8°38′W). We collected 181 samples from maerl beds with variable maerl cover mixed with gravel, dead shells, and pebbles, sometimes interrupted by rocky outcrops (Figure 1A–D). The samples were preserved in 4% formalin/seawater and kept in total darkness at 4°C. Sections were cut by hand using a razor blade. Observations were made in different planes according to Denizot (1968) and Irvine (1983). The species were identified using specialized literature on crustose red algae (Denizot 1968, Boudouresque and Denizot 1973, 1975, Belsher and Marcot 1975, Maggs and Guiry 1989, Kato et al. 2005, Peña and Bárbara 2010a). Pictures of each species were taken under light microscopy, and the most significant contributions to the European crustose flora were illustrated in the present study.

Representative specimens were deposited in the herbarium SANT (acronyms follow Holmgren et al. 1990). The terms sorus, conceptacle, perithallus, and hypothallus were used according to Peña and Bárbara (2010a). The habitat and occurrence of each species are provided. Present records were also compared with previous phycological studies from the Portuguese coast (Ardré 1970, Araújo et al. 2009, Berecibar et al. 2009, Berecibar 2011). The maerl-associated crustose flora of the Atlantic Iberian Peninsula was compared with those of neighboring Atlantic European and Mediterranean beds according to data compiled by Peña and Bárbara (2008, 2010a). The identification key for non-coralline crustose species associated with Atlantic Iberian maerl and gravel beds was based on Peña and Bárbara (2010a) and the present study.

Results

"*Rhododiscus pulcherrimus*" (sporophyte phase of *Atractophora hypnoides*)

Crust up to 100 μm thickness. Color bright red to carmine red, mucilaginous when fertile. Rhizoids are absent. Monostromatic basal layer composed of branched radial filaments. Each basal cell gives rise to one to two erect filaments, unbranched or rarely branched, separable under pressure. In surface view, cells are round. Tetrasporangia are terminal, cruciately arranged. Paraphyses are absent. The Portuguese material agrees with previous descriptions for this species (Newton 1931, Denizot 1968, Irvine 1983, Peña and Bárbara 2010a). Together with the report of *R. pulcherrimus* in the Canary Islands (Gil-Rodríguez et al. 1985), the present record constitutes the southernmost record for Atlantic Europe.

Habitat and occurrence: tetrasporangia recorded in March. The species was found growing on living maerl, occasionally on dead shells. Depth range: 17–19 m. The present study constitutes the first record for Portugal. The tetrasporophyte phase ("*R. pulcherrimus*") only is cited for the Atlantic maerl beds (Table 1).

Contarinia peyssonneliaeformis

Creeping thallus up to 200 μm in thickness, margin appressed to the substratum (Figure 2A, B). Color bright red to brownish. Rhizoids are multicellular, unbranched or branched. No hypobasal calcification is observed. In vertical section, the thallus has principal axial filaments composed of colorless cells that give rise to one to two dorsal cortical cells pseudodichotomously branched at the second cell. Gland cells are ovoid, immersed among the cortical filaments and also spreading on the surface. Carpogonial branches are produced in sori with multicellular paraphyses. Auxiliary filaments are three to four celled, each 30–37×10 μm, with pit connections between cells (Figure 2C, D). Mature gonimocarps are external globular structures, 75–150×50–75 μm, and contain carpospores, each 10–15×7–13 μm (Figure 2E). The diagnostic vegetative features of the Portuguese specimens match with descriptions provided from the Mediterranean and from the only Atlantic record hitherto known in Galicia (Feldmann 1939, Denizot 1968, Athanasiadis 1987, Peña and Bárbara 2010a). The female structures and gonimocarps are described for the first time in this species. Fertile plants of the Mediterranean species *Contarinia squamariae* were also recently reported from Portugal (Berecibar et al. 2009). The structure of female nemathecia and the development of gonimocarps are similar in both species. Berecibar et al. (2009) also recorded tetrasporangial nemathecia in the Portuguese specimens of *C. squamariae* as dark reddish masses, composed of dense stands of cylindrical tetrasporangia zonately or irregularly zonately divided. By contrast, the tetrasporangia of *C. peyssonneliaeformis* are irregularly cruciate (Denizot 1968).

Habitat and occurrence: female structures recorded only in December. The species was found growing on living maerl, occasionally epilithic on pebbles. Depth range: 15–19 m. This study represents the first record for Portuguese coasts, and it constitutes the second report for

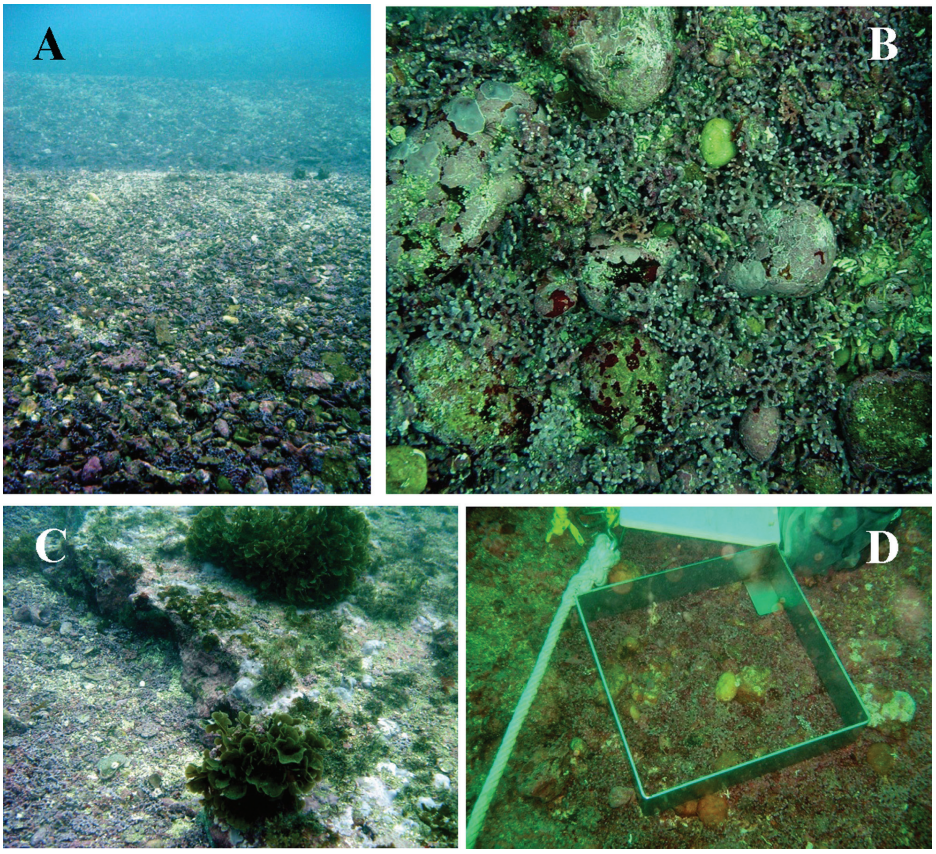

Figure 1 (A) Maerl bed with ripples in Armaçao de Pêra (Algarve). (B) Crustose species overgrowing maerl, gravel, and pebbles. (C) Maerl bed interrupted by rocky outcrop with *Zonaria tournefortii* (Lamouroux) Montagne. (D) Collecting samples in a maerl bed using a metal quadrat, 25×25 cm.

the Atlantic Ocean after Peña and Bárbara (2010a). This species was previously restricted to the Mediterranean, but recent records (Peña and Bárbara 2010a, present study) expand its distribution to Atlantic maerl beds (Table 1).

Cruoria cruoriaeformis

Crust up to 300 µm in thickness, easily squashed. Crusts velvety and bright red in color when alive; they are composed of erect filaments sparsely branched with a basal layer formed by branches that grow horizontally. Rhizoids are absent. Gonimocarps are very apparent among vegetative filaments. Tetrasporangia are zonate, laterally arranged. The Portuguese material agrees with descriptions provided from other Atlantic European regions (Dixon and Irvine 1977, Maggs and Guiry 1989, Peña and Bárbara 2010a) and from the Mediterranean (Feldmann 1939).

Habitat and occurrence: gonimocarps and tetrasporangia recorded in February, March, September, and December. The species was found growing only on living maerl. Depth range: 17–19 m. Although it is commonly cited for Atlantic and Mediterranean maerl beds (Table 1), it was only recently recorded for Portugal (Berecibar 2011) mainly due to the absence of floristic studies of maerl beds from this region.

"*Cruoria rosea*" (sporophyte phase of *Halarachnion ligulatum*)

Crust up to 80 µm in thickness. Color pale rose to red. Thallus composed of erect filaments occasionally branched with a basal layer, which is polyflabellate. Gland cells clavate, 75×10 µm. Rhizoids are absent. Tetrasporangia are zonate, laterally arranged, 45×10 µm. The Portuguese material agrees with previous descriptions for other European Atlantic coasts (Newton 1931, Denizot 1968, Dixon and Irvine 1977, Maggs and Guiry 1989, Peña and Bárbara 2010a).

Habitat and occurrence: tetrasporangia recorded in September and December. The species was found growing

Table 1 Alphabetical list of the non-coralline crustose flora (Rhodophyta and Ochrophyta) associated with maerl beds in Portugal, NW Iberian Peninsula, and on Atlantic European and Mediterranean coasts.

	Continental Portugal (3)	Iberian Peninsula (2)	Atlantic European coast (1–3)	Mediterranean European coast (1)
Rhodophyta				
Contarinia peyssonneliaeformis Zanardini	*	+	+	+
Contarinia squamariae (Meneghini) Denizot				+
"Cruoria arctica" Schmitz (sporophyte phase of *Turnerella pennyi* (Harvey) F. Schmitz			+	
Cruoria cruoriaeformis (P.L. Crouan *et* H.M. Crouan) Denizot	+	+	+	+
Cruoria pellita (Lyngbye) Fries		+	+	
"Cruoria rosea" (P.L. Crouan *et* H.M. Crouan) P.L. Crouan *et* H.M. Crouan (sporophyte phase of *Halarachnion ligulatum* (Woodward) Kützing)	*	+	+	
Cruoriopsis hauckii Batters			+	
"Haematocelis fissurata" P.L. Crouan *et* H.M. Crouan (sporophyte phase of *Sphaerococcus coronopifolius* Stackhouse)		+	+	
"Haematocelis rubens" J. Agardh (sporophyte phase of *Schizymenia dubyi* (Chauvin *ex* Duby) J. Agardh		+	+	+
Hildenbrandia crouaniorum J. Agardh	+	+	+	
Hildenbrandia rubra (Sommerfelt) Meneghini	+	+	+	
"Petrocelis cruenta" J. Agardh (sporophyte phase of *Mastocarpus stellatus* (Stackhouse) Guiry)		+	+	
Peyssonnelia armorica (P.L. Crouan *et* H.M. Crouan) Weber van Bosse *in* Børgesen	*	+	+	+
Peyssonnelia atropurpurea P.L. Crouan *et* H.M. Crouan		+	+	+
Peyssonnelia bornetii Boudouresque *et* Denizot	*	P	P	+
Peyssonnelia coriacea J. Feldmann	+	P	P	
Peyssonnelia crispata Boudouresque *et* Denizot				+
Peyssonnelia dubyi P.L. Crouan *et* H.M. Crouan	+	+	+	+
Peyssonnelia harveyana P.L. Crouan *et* H.M. Crouan *ex* J. Agardh	+	+	+	+
Peyssonnelia immersa Maggs *et* Irvine		+	+	
Peyssonnelia inamoena Pilger				+
Peyssonnelia orientalis (Weber-van Bosse) Cormaci *et* Furnari				+
Peyssonnelia polymorpha (Zanardini) Schmitz *in* Falkenberg				+
Peyssonnelia rosa-marina Boudouresque *et* Denizot				+
Peyssonnelia rubra (Greville) J. Agardh				+
Peyssonnelia squamaria (Gmelin) Decaisne				+
Peyssonnelia stoechas Boudouresque *et* Denizot				+
"Rhododiscus pulcherrimus" P.L. Crouan *et* H.M. Crouan (sporophyte phase of *Atractophora hypnoides* P.L. Crouan *et* H.M. Crouan)	*	+	+	
Rhodophysema elegans (P.L. Crouan *et* H.M. Crouan *ex* J. Agardh) Dixon			+	
Ochrophyta				
"Aglaozonia chilosa" Falkenberg (sporophyte phase of *Cutleria chilosa* (Falkenberg) Silva)	*	P	+	+
"*Aglaozonia melanoidea"* Schousboe *ex* Sauvageau (sporophyte phase of *Cutleria adspersa* (Mertens *ex* Roth) De Notaris)	+	P	P	+
"*Aglaozonia parvula"* (Greville) Zanardini (sporophyte phase of *Cutleria multifida* (Turner) Greville)		+	+	+

(**Table 1** Continued)

	Continental Portugal (3)	Iberian Peninsula (2)	Atlantic European coast (1–3)	Mediterranean European coast (1)
"*Microspongium gelatinosum*" Reinke (sporophyte phase of *Scytosiphon lomentaria* (Lyngbye) Link)		+	+	
Petroderma maculiforme (Wollny) Kuckuck		+	+	
Phycocelis foecunda Strömfelt		+	+	
Pseudolithoderma roscoffense Loiseaux		+	+	
"*Stragularia clavata*" (Harvey) Hamel (sporophyte phase of *Petalonia fascia* (Müller) Kuntze according to Fletcher 1987)		+	+	
Symphyocarpus strangulans Rosenvinge		+	+	

*New records for Portugal; P, records from Portugal that represent new additions to the flora associated with maerl beds of the Atlantic Iberian Peninsula and Atlantic European coasts. Data from 1, Peña and Bárbara (2008); 2, Peña and Bárbara (2010a); 3, present study.

on living maerl and occasionally on dead shells. Depth range: 17–19 m. The present study constitutes the first record for Portugal. The tetrasporophyte phase "*C. rosea*" only is cited for Atlantic maerl beds; however, the gametophyte phase *H. ligulatum* is reported for both Atlantic and Mediterranean beds (Table 1).

Hildenbrandia crouaniorum

Crust up to 110 μm in thickness, closely adherent to the substratum, coriaceous. Color brownish red. Sporangial conceptacles are 100–125 μm in diameter, with zonate tetrasporangia. The Portuguese material agrees with previous descriptions (Denizot 1968, Ardré 1970, Irvine and Chamberlain 1994, Peña and Bárbara 2010a). Zonate tetrasporangia have been also recorded for the species *Hildenbrandia occidentalis* Setchell in the Atlantic Iberian Peninsula (Ardré 1970, Bárbara 1994), but *H. occidentalis* has thicker thalli (350–500 μm) and larger sporangial conceptacles (100–200 μm in diameter).

Habitat and occurrence: tetrasporangial conceptacles recorded in December. It was found growing on pebbles associated with maerl beds. Depth: 17 m. The present study constitutes the first record for Algarve province, although it was previously cited by Ardré (1970) for other Portuguese coasts. This species has been recorded only in Atlantic Iberian maerl beds (Table 1).

Hildenbrandia rubra

Crust coriaceous up to 90 μm in thickness, closely adherent to the substratum. Color dark red. Sporangial conceptacles are 80–110 μm in diameter, tetrasporangia irregularly cruciate. Our material agrees with previous descriptions (Rosenvinge 1909, Denizot 1968, Ardré 1970, Irvine and Chamberlain 1994, Peña and Bárbara 2010a).

Habitat and occurrence: tetrasporangial conceptacles recorded in December. The species was found growing on pebbles associated with maerl beds. Depth: 19 m. This species was recorded in the Atlantic European maerl beds but not in the Mediterranean (Table 1).

Peyssonnelia armorica

Crust closely adherent to the substratum, color bright red to pink. Rhizoids scarce, unicellular. Perithallial filaments, sometimes pseudodichotomously branched, are produced at a very wide angle (>60°) from a basal layer

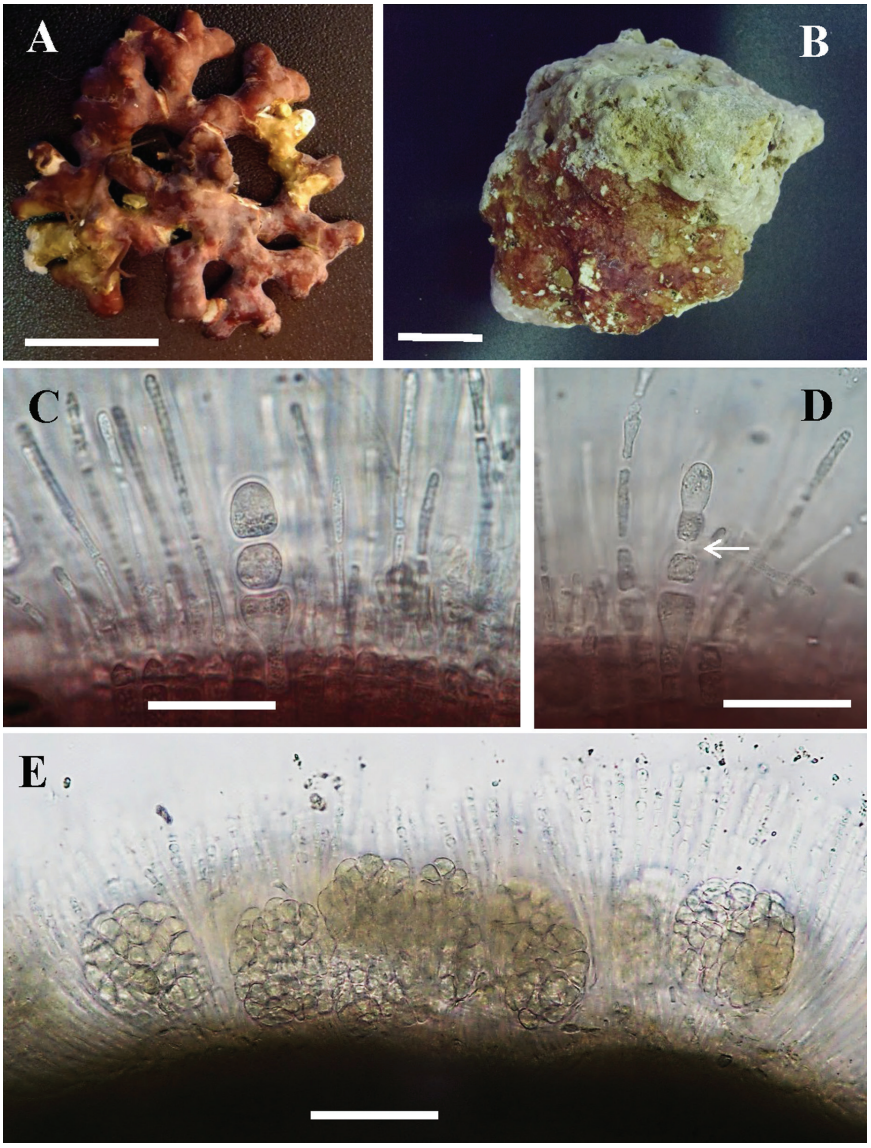

Figure 2 *Contarinia peyssonneliaeformis*. (A, B) Creeping thalli growing on living maerl and pebbles. (C, D) Female sorus with three- to four-celled auxiliary filaments connected by pit connections (arrow) and associated multicellular paraphyses (VS). (E) Groups of globular gonimocarps (VS). VS, vertical section. Scale bars: (A)=1 cm, (B)=2 cm, (C, D)=50 μm, (E)=100 μm.

of hypothallial cells polyflabellate. Carposporangial sori slightly elevated, branched chains of at least nine carposporangia occur laterally on perithallial filaments. Paraphyses branched or unbranched, more slender than other cells. Tetrasporangia are cruciate, in immersed sori, not elevated, terminal on perithallial filaments with a stalk cell or laterally borne, 75×25 μm. The Portuguese material agrees with previous descriptions (Børgesen 1929, Feldmann 1939, Denizot 1968, Guimarães and Fujii 1999, Kato et al. 2005, Peña and Bárbara 2010a).

Habitat and occurrence: carposporangial sori in September and December, tetrasporangial sori in December. The species was found growing on living maerl and dead shells. Depth range: 13–19 m. This constitutes the first record for Portuguese coasts, but the species has also been recorded in other Atlantic and in Mediterranean maerl beds (Table 1).

Peyssonnelia bornetii

Large crusts up to 500 μm in thickness, with loose margins (Figure 3A). Color red brownish. Hypobasal calcification is observed. Rhizoids multicellular, unbranched, generally arising from the anterior end of hypothallial cells, up to 400 μm long, each cell 10–12 μm diameter

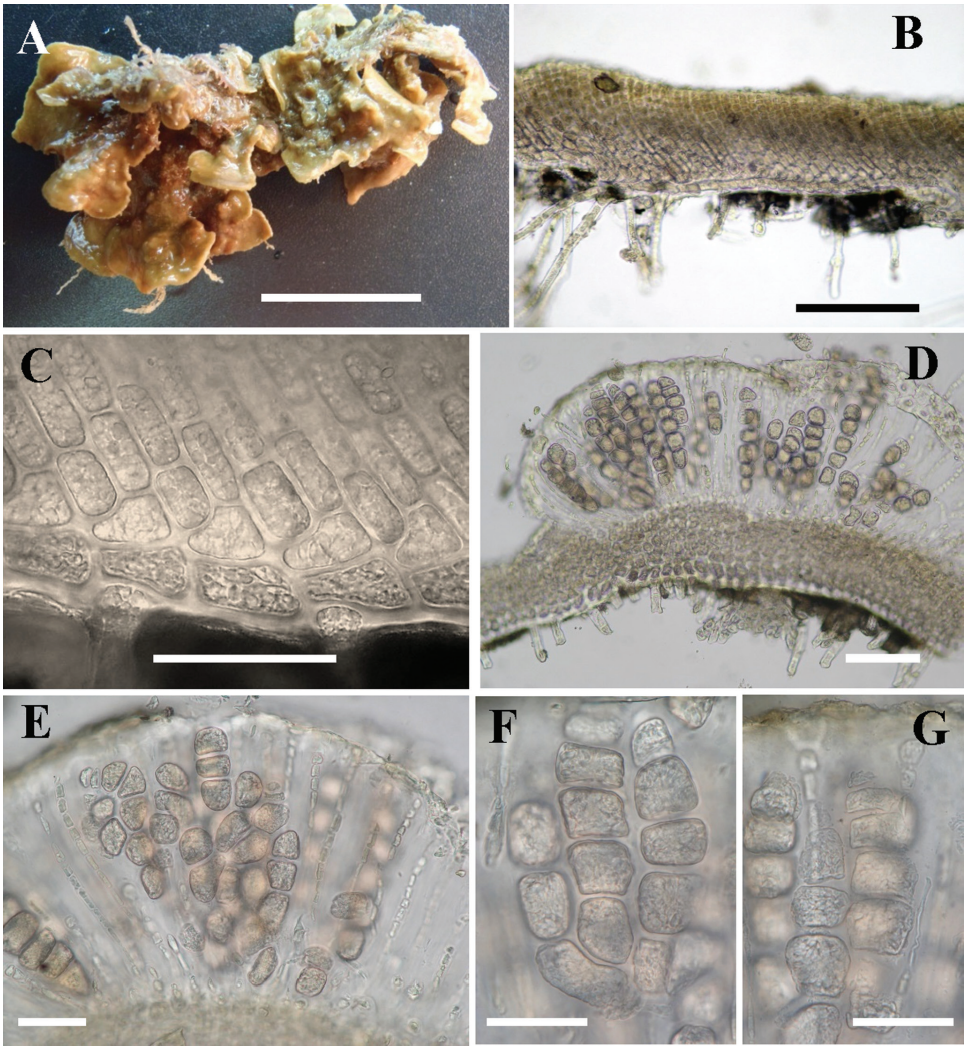

Figure 3 *Peyssonnelia bornetii*. (A) Crust with loose margins. (B) Thallus with hypobasal calcification, unbranched multicellular rhizoids, and ascending perithallial filaments, produced at a narrow angle from hypothallial layer (RVS). (C) Rhizoid produced from anterior end of hypothallial cell (RVS). (D) Raised carposporangial sorus containing chains of carposporangia. (E–G) Branched chains of carposporangia with associated unbranched multicellular paraphyses (RVS). RVS, radial vertical section. Scale bars: (A)=1 cm, (B)=200 µm, (C, E–G)=50 µm, (D)=100 µm.

(Figure 3B, C). Hypothallial filaments are not polyflabellate. Cystoliths are absent. In radial vertical section, two to three ascending perithallial filaments are produced at a narrow angle from hypothallial layer (<60°, Figure 3C). Hypothallial cells are 10–15×20–30 µm, perithallial cells are 12–15×15–20 to 6–8×6–10 µm in the apical part. Carposporangial structures were observed for the first time in this species. Carposporangial sori up to 300 µm high were composed of branched chains of up to eight carposporangia, each 15–20×25–30 µm; the associated paraphyses are unbranched, composed of 10–13 cells, each 3–5×5–10 µm (Figure 3D–G). The diagnostic vegetative features of the Portuguese material agree with descriptions of *P. bornetii* in the Mediterranean (Boudouresque and Denizot 1973, 1975).

Habitat and occurrence: carposporangial sori recorded in February. The species was found growing on living maerl at 17 m depth. This constitutes the first record for Atlantic European coasts. Carposporangial structures were observed for the first time. This species has also been recorded for Mediterranean maerl beds (Table 1).

Peyssonnelia coriacea

Large crusts up to 300 µm thick, with loose margins and concentric grooves on the surface. Color brownish red. Rhizoids arise from hypothallial cells, multicellular, up to 300 µm long, each cell 15–20 µm in diameter. Hypothallial

filaments are not polyflabellate. Cystoliths are absent. In radial vertical section, the thallus is composed of two hypothallial layers, and perithallial filaments are produced at a narrow angle. Hypothallial cells are 12–17×35–50 µm, perithallial cells are 20–25×10–12 µm to 10×10 µm in the apical part. Reproductive structures were not observed. The diagnostic vegetative features of the Portuguese material agree with previous descriptions (Boudouresque and Denizot 1973, 1975). With its type locality in Tangier, Morocco (Athanasiadis 1996), this species is reported along the Atlantic European coast from Biarritz to the Algarve and also in the Mediterranean (Denizot 1957, Ardré 1970, Boudouresque and Denizot 1975, Coppejans and Boudouresque 1983, Gorostiaga et al. 2004, Bárbara et al. 2005).

Habitat and occurrence: The species was found growing on living maerl at 17 m depth. This species was not previously recorded in any European maerl beds, either in the Atlantic or Mediterranean (Table 1).

Peyssonnelia dubyi

Crust closely adherent to the substratum. Color dark red to brownish red, surface wrinkled especially in dried specimens. Rhizoids unicellular, arising from the anterior end of hypothallial cells. Hypothallial filaments are polyflabellate. In radial vertical section, the thallus is composed of pseudodichotomously branched perithallial filaments arising from hypothallial cells at a very wide angle (>60°). Tetrasporangia cruciate, terminal on sterile filaments. Paraphyses are unbranched, more slender than other sorus filaments. The Portuguese material agrees with previous descriptions (Newton 1931, Denizot 1968, Boudouresque and Denizot 1975, Irvine 1983, Maggs and Irvine 1983, Peña and Bárbara 2010a).

Habitat and occurrence: tetrasporangia recorded in March and December. The species was found growing on living maerl, dead shells, and small pebbles associated with maerl beds. Depth range: 17–19 m. This constitutes the first record for the Algarve province. This species had already been recorded in other European maerl beds (Atlantic and Mediterranean, Table 1).

Peyssonnelia harveyana

Thallus up to 400 µm in thickness, closely adherent, with margins free especially in dried specimens. Color bright to dark red, with conspicuous radial markings on the surface, occasionally with concentric, alternating pale and dark bands. Rhizoids unicellular, long, 25–95×10–15 µm, arise from the central part of the hypothallial cells. The hypothallial filaments are arranged in parallel sinuous rows. In radial vertical section, the perithallial filaments are produced at a very wide angle from the hypothallial cells (>60°). Hypothallial cells boot-shaped, 20×30 µm, perithallial cells from 25–28×20 µm to 10×10 µm in the apical part. Spermatangial sori colorless, mucilaginous, elevated up to 80 µm high, containing chains of paired spermatangial filaments without associated paraphyses, each spermatangium measuring 2 µm in diameter. Tetrasporangial sori raised, up to 150 µm in height, tetrasporangia cruciate, terminal on perithallial cells with a stalk cell, 150×50 µm. The Portuguese specimens agree with descriptions from other European Atlantic coasts (Ardré 1970, Irvine 1983, Maggs and Irvine 1983, Peña and Bárbara 2010a), the Mediterranean (Feldmann 1939, Boudouresque and Denizot 1975, Marcot-Coqueugniot and Boudouresque 1976, Marcot-Coqueugniot 1980, Athanasiadis 1987), and from Japan (Kato et al. 2005).

Habitat and occurrence: spermatangial sori recorded in December, tetrasporangial sori in December. The species was found growing on living maerl at 17 m depth. This constitutes the first record for the Algarve province. This species has previously been recorded in Atlantic and Mediterranean maerl beds (Table 1).

Discussion and conclusion

Eleven non-coralline crustose red algal species are associated with maerl beds in Portugal. Two species with heteromorphic life histories (*Atractophora hypnoides* and *Halarachnion ligulatum*) were found only as their sporophyte phases ("*Rhododiscus pulcherrimus*" and "*Cruoria rosea*," respectively). Apart from the crustose red flora, two taxa from the Ochrophyta (*Cutleria adspersa* and *Cutleria chilosa*) were occasionally recorded as their crustose sporophyte phases (*Aglaozonia melanoidea* and *Aglaozonia chilosa*, respectively). Both taxa are reported from the Mediterranean maerl beds, but *A. chilosa* was also associated with Atlantic beds in the Canary Islands (Table 1). We report *Peyssonnelia bornetii* as a new record for Atlantic European coasts; *P. bornetii* was described in the Mediterranean (Boudouresque and Denizot 1973), which is its main center of distribution apart from records from the Pacific Islands (South and Skelton 2003, Guiry and Guiry 2013). This study has also provided the second record of *Contarinia peyssonneliaeformis* in the Atlantic Ocean after the first discovery of this Mediterranean species on the Galician coasts (Peña and Bárbara 2010a). For both of these

species (*C. peyssonneliaeformis* and *P. bornetii*), female and carposporangial structures are reported for the first time. Five taxa ("*Rhododiscus pulcherrimus*" – sporophyte phase of *A. hypnoides*, *C. peyssonneliaeformis*, "*Cruoria rosea*" – sporophyte phase of *Halarachnion ligulatum*, *Peyssonnelia armorica* and "*Aglaozonia chilosa*" – sporophyte phase of *Cutleria chilosa*) constitute new records for Portugal. Three species (*Hildenbrandia crouaniorum*, *Peyssonnelia dubyi* and *P. harveyana*) are new records for the Algarve province; these records extend southward of the distribution ranges previously observed along the Portuguese coast (Ardré 1970), and they also complete the distribution gap observed with southern reports in the Macaronesian region (Guiry and Guiry 2013).

The record of *Peyssonnelia coriacea* associated with Portuguese maerl beds increases the diversity of the European maerl-associated flora. This species is widely reported from other habitats on European coasts (Guiry and Guiry 2013), but it was not previously recorded on maerl. In addition, the diversity of European Atlantic maerl beds has been increased by two species (*P. bornetii* and *P. coriacea*). Two species (*P. bornetii* and *C. peyssonneliaeformis*) have also been reported in the Mediterranean maerl beds; the occurrence of species with Mediterranean distribution pointed out similarities in the crustose flora between both coasts of the Iberian Peninsula.

The European maerl beds harbor 38 crustose taxa of the Rhodophyta and Ochrophyta (29 species in the Atlantic beds, and 20 species in the Mediterranean) (Table 1). The genus *Peyssonnelia* contributes 15 species, indicating the large representation of this genus in subtidal habitats of European coasts. Eleven taxa correspond to the sporophyte phases of heteromorphic species (Rhodophyta: *A. hypnoides*, *Halarachnion ligulatum*, *Mastocarpus stellatus*, *Sphaerococcus coronopifolius*, *Schizymenia dubyi*, *Turnerella pennyi*; Ochrophyta: *Cutlleria chilosa, C. adspersa, C. multifida*, *Scytosiphon lomentaria*, and *Petalonia fascia*). Twenty crustose species were found to be associated only with Atlantic European maerl beds, whereas nine species were reported only from Mediterranean beds. In contrast, 11 taxa, such as *Cruoria cruoriaeformis*, were recorded in both regions; the widespread occurrence of this species contrasts with its restricted habitat distribution, as it is almost totally confined to maerl beds, often overgrowing living maerl (Jacquotte 1962, Cabioc´h 1969, Maggs and Guiry 1989, Soto 1990, Birkett et al. 1998, Peña 2010, Peña and Bárbara 2008, 2010a,b). Based on these observations and its high sensitivity to the disturbance of maerl beds, *C. cruoriaeformis* has been proposed as one of the target species for the monitoring of European maerl beds (Hall-Spencer et al. 2010). The present study confirms the ecological importance of European maerl beds as refuges for crustose species and life history phases of heteromorphic species, which contribute to the later development of erect gametophytes in favorable seasons (Bárbara et al. 2004). Studies of temperate Atlantic maerl beds have shown a marked seasonality of the associated flora with a peak of diversity in spring and summer, but only crustose and a few filamentous species (i.e., *Cladophora rhodolithicola* Leliaert, *Gelidiella calcicola* Maggs *et* Guiry) contributed to the permanent flora throughout the year (Jacquotte 1962, Cabioc´h 1969, Maggs 1983, Bárbara et al. 2004, Peña and Bárbara 2010b).

An identification key is provided here for the 26 crustose taxa (17 Rhodophyta and 9 Ochrophyta) associated with maerl and gravel beds in Atlantic Iberia. The aim of the key is to provide a baseline for further studies of the crustose flora associated with subtidal habitats of European coasts.

1a Red crust not calcified, coriaceous or not, generally with pit connections between cells. 2
1b Brown to olive or yellowish crust. 15
2a Crust coriaceous, sporangial conceptacles containing zonate tetrasporangia.
Hildenbrandia crouaniorum

2b Crust coriaceous, sporangial conceptacles containing irregularly cruciate tetrasporangia.
Hildenbrandia rubra

2c Crust not coriaceous, reproductive cells not formed in conceptacles. 3
3a Thallus of variable thickness, composed of a basal layer, which gives rise to erect filaments. The basal layer could be formed by erect filaments that grow horizontally. Rhizoids absent. Tetrasporangia terminal, lateral or intercalary, zonate, or cruciately arranged. 4
3b Thallus composed of several cell layers, which decrease in size toward the apical part. Rhizoids and gland cells present or absent. 7
4a Tetrasporangia terminal and cruciately arranged. Crust up to 125 μm in thickness (<10 cells), closely adherent, filaments separable under pressure. Erect filaments 8–10 μm in diameter.
***"Rhododiscus pulcherrimus"* (sporophyte phase of *Atractophora hypnoides*)**

4b Tetrasporangia intercalary, cruciately arranged to irregular, thallus thick (up to 1 mm, >15 cells), closely adherent, compact below but loosely held together above. Erect filaments 4–6 μm in diameter.
***"Petrocelis cruenta"* (sporophyte phase of *Mastocarpus stellatus*)**

4c Tetrasporangia lateral, zonate, with or without gland cells among erect filaments. 5

5a Gland cells present. Erect filaments 4–7 µm in diameter sparsely branched. Tetrasporangia 35–40×10–12 µm.
***"Cruoria rosea"* (sporophyte phase of *Halarachnion ligulatum*)**

5b Gland cells absent. Sexual and asexual structures present.
***Cruoria* (6)**

6a Crust thick (up to 1.5 mm). Erect filaments compact below but easily separated above, 7–15 µm in diameter. Tetrasporangia up to 285×65 µm.
Cruoria pellita

6b Crust (up to 300 µm thick) easily squashed under pressure. Erect filaments 5–8 µm in diameter. Tetrasporangia up to 75 µm×20 µm.
Cruoria cruoriaeformis

7a Thallus thick and firm, closely adherent to the substrate, without rhizoids, composed of curved branched filaments at first almost prostrate up to 15 µm in diameter. Tetrasporangia zonately arranged in sori.
***"Haematocelis rubens"* (sporophyte phase of *Schizymenia dubyi*)**

7b Thallus with central filament composed of axial cells with ascending filaments and basal filaments. Gland cells present. Oil globules conspicuous on thallus surface. 8

7c Thallus composed of one to two hypothallial layers (basal layer) and perithallus (ascending filaments). Hypothallus polyflabellate or not, composed of one to two layers. Tetrasporangia cruciate. Gland cells absent.
***Peyssonnelia* (9)**

8a Multicellular rhizoids frequent. Thallus surface not cracked when dried.
Contarinia peyssonneliaeformis

8b Rhizoids absent. Thallus surface cracked when dried.
***"Haematocelis fissurata"* (sporophyte phase of *Sphaerococcus coronopifolius*)**

9a Rhizoids unicellular. Hypothallus as a single layer, polyflabellate, or not. 10

9b Rhizoids multicellular and long. Hypothallus with one to two layers, not polyflabellate. 14

10a Perithallial filaments arise at an angle <30° from hypothallial filaments, not polyflabellate
Peyssonnelia atropurpurea

10b Perithallial filaments arise at an angle >60° from hypothallial filaments, polyflabellate or not. 11

11a Crust closely adherent. Hypothallus polyflabellate. 12

11b Crust closely adherent or with free margins. Hypothallus not polyflabellate. Reproductive structures immersed or not. 13

12a Thallus solid, hypothallial cells boot shaped. Perithallial filaments adjoined, pseudodichotomously branched. Carposporangial sori with chains of two to four carposporangia. Paraphyses unbranched. Tetrasporangia terminal.
Peyssonnelia dubyi

12b Hypothallial cells not boot shaped, perithallial filaments easily separable, sometimes pseudodichotomously branched. Carposporangial sori with branched chains more than eight carposporangia, laterally on perithallial filaments. Paraphyses branched or unbranched.
Peyssonnelia armorica

13a Crust closely adherent, surface with radial striae. Hypothallial cells boot shaped. Rhizoids arise from anterior end of hypothallial cells. Reproductive structures immersed. Tetrasporangia 30–35×10–15 µm.
Peyssonnelia immersa

13b Crust with free margins, surface with radial markings or with concentric bands alternately pale and dark. Rhizoids arise generally from the central part of hypothallial cells, boot shaped. Sori not immersed. Tetrasporangia 75–120×25–45 µm.
Peyssonnelia harveyana

14a Multicellular rhizoids up to 400 µm long, arising from the anterior end of single layer of hypothallial cells.
Peyssonnelia bornetii

14b Multicellular rhizoids up to 300 µm long. Crust with free margins and concentric grooves on the surface. Hypothallus with two layers.
Peyssonnelia coriacea

15a Thallus parenchymatous composed of colorless medullary cells. Crust membranous to sub-coriaceous. Rhizoids multicellular.
***Aglaozonia* (sporophyte phase of *Cutleria* spp.) (16)**

15b Thallus composed of monostromatic to distromatic basal layer, which gives rise to erect filaments. Unilocular and/or plurilocular sporangia present. 17

16a Thallus thick, up to 350 μm (six to eight layers of medullary cells), adherent to the substratum.
***"Aglaozonia melanoidea"* (sporophyte phase of *Cutleria adspersa*)**

16b Thallus thin, up to 125 μm thick (two to three layers of medullary cells), with an entire, rounded margin and overlapping lobes, loosely attached to the substratum with numerous rhizoids.
***"Aglaozonia parvula"* (sporophyte phase of *Cutleria multifida*)**

16c Thallus thin, up to 100 μm thick (two to three layers of medullary cells), branched, loosely attached to the substratum.
***"Aglaozonia chilosa"* (sporophyte phase of *Cutleria chilosa*)**

17a Unilocular sporangia associated with multicellular paraphyses. Plurilocular sporangia, rhizoids, and ascocyst-like cells absent. Texture spongy.
***"Microspongium gelatinosum"* (sporophyte phase of *Scytosiphon lomentaria*)**

17b Unilocular and plurilocular sporangia terminal on filaments. Thallus filaments firmly adjoined or easily separable under pressure. Rhizoids and ascocyst-like cells present or absent. 18

17c Only multiseriate plurilocular sporangia are present, sessile or pedicellated. Unilocular sporangia absent. Thallus filaments, unbranched or branched, firmly adjoined or easily separable under pressure. Rhizoids present or absent. Ascocyst-like cells and hairs present or absent. 19

18a Crust firm, subcoriaceous, filaments firmly united, usually without rhizoids. Unilocular and plurilocular sporangia present, paraphyses associated with sessile unilocular sporangia. Plurilocular sporangia uniseriate or partly biseriate. Ascocyst-like cells absent. Plastid parietal, plate-like.
***"Stragularia clavata"* (sporophyte phase of *Petalonia fascia* according to Fletcher 1987)**

18b Crust gelatinous, filaments easily separable under pressure, multicellular rhizoids present. Unilocular and plurilocular sporangia terminal on filaments, without paraphyses associated with unilocular sporangia, with or without terminal and intercalary ascocyst-like cells. Plastid plate-like, ring shaped.
Petroderma maculiforme

19a Filaments unbranched and firmly adjoined. Colorless ascocyst-like cells are rare, hairs absent. Rhizoids usually absent. Plurilocular sporangia bi- to multiseriate, loculi with straight dividing walls. Plastid discoid, peripheral.
Pseudolithoderma roscoffense

19b Filaments occasionally branched and easily separable under pressure. Rhizoids present or absent. Ascocyst-like cells and hairs common. 20

20a Rhizoids absent. Terminal plurilocular sporangia long (<80 μm), sessile or pedicellate. Crusts (up to 125 μm thick) usually epiphytic. Plastid multilobed.
Phycocelis foecunda

20b Rhizoids present or absent. Terminal plurilocular sporangia short (<40 μm). Plastid single, large.
Symphyocarpus strangulans

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References

Araújo, R., I. Bárbara, M. Tibaldo, E. Berecibar, P. Díaz, R. Pereira, R. Santos and I. Sousa-Pinto. 2009. Checklist of benthic marine algae and cyanobacteria of northern Portugal. *Bot. Mar. 52*: 24–46.

Ardré, F. 1970. Contribution à l'étude des algues marines du Portugal. I. La Flore. *Port. Acta Biol. Sér. B. 10*: 137–555.

Athanasiadis, A. 1987. *A survey of the seaweeds of the Aegean Sea with taxonomic studies on species of the tribe Antithamnieae (Rhodophyta)*. Doctoral Thesis, University of Gothenburg, Gothenburg, Sweden. pp. 174.

Athanasiadis, A. 1996. *Taxonomisk litteratur och biogeografi av Skandinaviska rödalger och brunalger*. Algologia, Göteborg. pp. 280.

Ballesteros, E. 1992. *Els vegetals i la zonació litoral: espècies,comunitats i factors que influeixen en la seve distribució*. Institut d'Estudis Catalans, Barcelona. pp. 616.

Bárbara, I. 1994. *Las comunidades de algas bentónicas marinas en la bahía de La Coruña y ría del Burgo.* Tesis Doctoral. Universidad de Santiago de Compostela. pp. 411.

Bárbara, I., J. Cremades and A.J. Veiga. 2004. A floristic study of a maerl and gravel subtidal bed in the Arousa ría (Galicia, Spain). *Bot. Complutensis 28*: 35–46.

Bárbara, I., J. Cremades, S. Calvo, M.C. López-Rodríguez and J. Dosil. 2005. Checklist of the benthic marine and brackish Galician algae (NW Spain). *Anales Jard. Bot. Madrid 62*: 69–100.

Barberá, C., C. Bordehore, J.A. Borg, M. Glémarec, J. Grall, J.M. Hall-Spencer, Ch. De La Huz, E. Lanfranco, M. Lastra, P.G. Moore, J. Mora, M.E. Pita, A.A. Ramos-Esplá, R. Rizzo, A. Sánchez-Mata, A. Seva, P.J. Schembri and C. Valle. 2003. Conservation and management of northeast Atlantic and Mediterranean maerl beds. *Aquat. Conserv. Mar. Freshw. Ecosyst. 13*: S65–S76.

Belsher, T. and J. Marcot. 1975. Recherches sur le genre *Peyssonnelia* (Rhodophycées). VI. étude d'une population de *Peyssonnelia atropurpurea* de Roscoff. *Cah. Biol. Mar. 16*: 395–413.

Berecibar, E. 2011. *Long-term changes in the phytogeography of the Portuguese continental coast*. Doctoral Thesis. Universidade do Algarve. pp. 266.

Berecibar, E., M. Wynne and R. Santos. 2009. First record of *Contarinia squamariae* (Rhizophyllidaceae, Rhodophyta) from Portugal: description of morphological and reproductive structures. *Bot. Mar. 52*: 15–23.

Birkett, D.A., C.A. Maggs and M.J. Dring. 1998. *Maërl Biotopes (V). An overview of dynamics and sensitivity characteristics for conservation management of marine SACs*. Scottish Association for Marine Science, UK Marine SACs Project. pp. 117.

Børgesen, F. 1929. Marine algae from the Canary Islands especially from Tenerife and Gran Canaria. III. Rhodophyceae. Part II Cryptonemiales, Gigartinales and Rhodymeniales. *Det K. Danske Vidensk Selsk, Biologiske Meddelser 8*: 1–97.

Boudouresque, C.F. and M. Denizot. 1973. Recherches sur le genre *Peyssonnelia* (Rhodophycées). I. *Peyssonnelia rosa-marina* sp. nov. et *Peyssonnelia bornetii* sp. nov. *Giorn. Bot. Ital. 107*: 17–27.

Boudouresque, C.F. and M. Denizot. 1975. Révision du genre *Peyssonnelia* (Rhodophyta) en Méditerranée. *Bull. Mus. Hist. Nat. Marseille 35*: 7–92.

Cabioc´h, J. 1969. Les fonds de maerl de la Baie de Morlaix et leur peuplement végétal. *Cah. Biol. Mar. 10*: 139–161.

Coppejans, E. and C.F. Boudouresque. 1983. Végétation marine de la Corse (Méditerranée). VI. Documents pour la flore des algues. *Bot. Mar. 26*: 457–470.

Denizot, M. 1957. Sur la répartition géographique du *Peyssonnelia coriacea* J. Feldmann. *Rev. Algol. 2*: 274–275.

Denizot, M. 1968. *Les algues floridées encroutants (à l'exclusion des Corallinacées)*. Muséum national d'Histoire Naturelle, Paris. pp. 309.

Dixon, P.S. and L.M. Irvine. 1977. *Seaweeds of the British Isles. Volume 1. Rhodophyta. Part 1 Introduccion, Nemaliales, Gigartinales*. HMSO, London. pp. 252.

Feldmann, J. 1939. Les algues marines de la Côte des Albères. IV. Rhodophycées. *Rev. Algologie 11*: 247–330.

Fletcher, R.L. 1987. *Seaweeds of the British Isles. Volume 3. Part 1. Fucophyceae (Phaeophyceae)*. HMSO, London. pp. 359.

Gil-Rodríguez, M.C., R. Haroun, J. Afonso-Carrillo and W. De la Torre. 1985. Adiciones al catálogo de algas marinas bentónicas para el archipiélago canario. II. *Vieraea 15*: 101–112.

Gorostiaga, J.M., A. Santolaria, A. Secilla, C. Casares and I. Díez. 2004. Check-list of the Basque coast benthic algae (North of Spain). *Anales Jard. Bot. Madrid 61*: 155–180.

Guimarães, S.M.P.B. and M.T. Fujii. 1999. Morphological studies of five species of *Peyssonnelia* (Gigartinales, Rhodophyta) from Southeastern Brazil. *Phycologia 38*: 167–183.

Guiry, M.D. and G.M. Guiry. 2013. *AlgaeBase. World-wide electronic publication*. National University of Ireland, Galway. http://www.algaebase.org.

Hall-Spencer, J.M., J. Kelly and C.A. Maggs. 2010. *Background document for maerl beds*. OSPAR Commission Biodiversity Series 491/2010. pp. 36.

Holmgren P.K., N.H. Holmgren and L.C. Barnett. 1990. *Index herbariorium. Part I: The Herbaria of the World*. New York Botanical Garden, New York. pp. 693.

Irvine, L.M. 1983. *Seaweeds of the British Isles. Volume 1. Rhodophyta. Part 2A Cryptonemiales sensu stricto, Palmariales, Rhodymeniales*. HMSO, London. pp. 113.

Irvine, L.M. and Y.M. Chamberlain. 1994. *Seaweeds of the British Isles. Volume 1. Rhodophyta, Part 2B Corallinales, Hildenbrandiales*. HMSO, London. pp. 276.

Jacquotte, R. 1962. Étude des fonds de maërl de Méditerranée. *Rec. Trav. St. Mar. End. 26*: 141–235.

Kato, A., M. Masuda and H. Kawai. 2005. New records of *Peyssonnelia armorica* and *Peyssonnelia harveyana* (Rhodophyta, Gigartinales) from Japan. *Phycol. Res. 53:* 266–274.

Maggs, C.A. 1983. Seasonal study of seaweed communities on subtidal maerl (unattached coralline algae) in Galway Bay, Ireland. *Prog. Underwater Sci. 9*: 27–40.

Maggs, C.A. 1990. Distribution and evolution of non-coralline crustose red algae in the North Atlantic. *In:* (D.J. Garbary and G.R. South, eds.) *Evolutionary biogeography of the marine algae of the North Atlantic*. Springer-Verlag, Berlin/Heidelberg. pp. 241–264.

Maggs, C.A. and M.D. Guiry. 1982. The life history of *Haematocelis fissurata* Crouan frat. (Rhodophyta: Sphaerococcaceae). *Br. Phycol. J. 17*: 235.

Maggs, C.A. and M.D. Guiry. 1989. A re-evaluation of the crustose red algal genus *Cruoria* and the family Cruoriaceae. *Br. Phycol. J. 24*: 253–269.

Maggs, C.A. and L.M. Irvine. 1983. *Peyssonnelia immersa* sp. nov. (Cryptonemiales, Rhodophyta) from the British Isles and France, with a survey of infrageneric classification. *Br. Phycol. J. 18:* 219–238.

Maggs, C.A., M.D. Guiry and L.M. Irvine. 1983. The life history in culture of an isolate of *Rhododiscus pulcherrimus* (Naccariaceae, Rhodophyta) from Ireland. *Br. Phycol. J. 18:* 206.

Mannino, A.M., Castriota, L., A.M. Beltrano and G. Sunseri. 2002. The epiflora of a rhodolith bed from the Island of Ustica (Southern Tyrrhenian Sea). *Flora Mediterranea 12:* 11–28.

Marcot-Coqueugniot, J. 1980. Recherches sur le genre *Peyssonnelia* (Rhodophyta) XIII. Sur un *Peyssonnelia* du "complexe *Harveyana*". *Bot. Mar. 23*: 35–40.

Marcot-Coqueugniot, J. and C.F. Boudouresque. 1976. Recherches sur le genre *Peyssonnelia* (Rhododphyta). VIII. Ètude du type de *P. harveyana* J. Agardh. *Bull. Mus. Hist. Nat. Marseille 36:* 5–9.

Newton, L. 1931. *A handbook of the British seaweeds*. British Museum (Natural History), London. pp. 478.

Peña, V. 2010. *Estudio ficológico de los fondos de maerl y cascajo en el noroeste de la Península Ibérica*. Tesis Doctoral. Universidade da Coruña. A Coruña. pp. 638.

Peña, V. and I. Bárbara. 2008. Maërl community in the north-western Iberian Peninsula: a review of floristic studies and long-term changes. *Aquat. Conserv. Mar. Freshw. Ecosyst. 18*: 339–366.

Peña, V. and I. Bárbara. 2010a. New records of crustose seaweeds associated with subtidal maërl beds and gravel bottoms in Galicia (NW Spain). *Bot. Mar. 53*: 41–61.

Peña, V. and I. Bárbara. 2010b. Seasonal patterns in the maerl community: case study of shallow subtidal European Atlantic beds. *Eur. J. Phycol. 45*: 327–342.

Peña, V., I. Bárbara, E. Berecibar and R. Santos. 2009. Present distribution of maërl beds in the Atlantic Iberian Peninsula. *Mus. Sci. Nat., volumen speciale*: 46.

Rosenvinge, L.K. 1909. The marine algae of Denmark. Part I, Introduction, Rhodophyceae I (Bangiales and Nemalionales). *Det K. Danske Vidensk. Skr. 7, Mat. Nat. Afd. 7*: 1–151.

Sauvageau, M.C. 1899. Les Cutlériacées et leur alternance de générations. *Ann. Sci. Nat. Ser. 10*: 265–362.

Soto, J. 1990. Vegetación algal sobre sustrato móvil de la zona circalitoral del sureste de la Península Ibérica: una aproximación. *Fol. Bot. Misc. 7*: 43–49.

South, G.R. and P.A. Skelton. 2003. Catalogue of the marine benthic macroalgae of the Fiji Islands, South Pacific. *Aust. Syst. Bot. 16*: 699–758.