

Estudio ficológico de los hábitats rocoso-arenosos del Atlántico Peninsular

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Departamento de Biología Animal, Biología Vexetal e Ecoloxía



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DECLARA:

Que la presente memoria titulada “**Estudio ficológico de los hábitats rocoso-arenosos del Atlántico Peninsular**” presentada por **PILAR DÍAZ TAPIA** para optar el título de Doctora en Biología, ha sido realizada bajo su dirección. Asimismo, considera que dicho trabajo está en condiciones de ser defendido y de optar a la mención “Doctor internacional” debido a que la tesis está escrita en inglés y la citada alumna puede acreditar más de tres meses de estancias de investigación, realizadas en otro país de la Unión Europea.

A Coruña, 27 de febrero de 2013.

Ignacio Bárbara Criado

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Estudio ficológico de los hábitats rocoso-arenosos del Atlántico Peninsular

Resumen

Esta tesis mejora el conocimiento de las especies y comunidades de algas de hábitats rocoso-arenosos del Atlántico Peninsular, abordando diferentes perspectivas: florística, taxonómica, ecológica y conservacionista. El estudio ha sido principalmente llevado a cabo analizando 2525 muestras de diferentes tipos de comunidades algales recogidas en el intermareal e infralitoral superior de 138 localidades, desde 2002 hasta 2011. En la primera parte de esta tesis se presenta un catálogo de 257 especies. Además se incluyen descripciones morfológicas y, en algunos casos, datos moleculares de las 35 especies más características de hábitats rocoso-arenosos, estudiando 13 de ellas en detalle que en su mayoría pertenecen a la familia Rhodomelaceae. Como resultado, se describen dos nuevas especies y las estructuras sexuales de otras cuatro, se llevan a cabo varias propuestas taxonómicas y se proporcionan nuevos datos corológicos para las costas Ibéricas. La segunda parte se centra en el estudio de las comunidades de algas de hábitats rocoso-arenosos: i) se proporciona la descripción de la vegetación de una localidad gallega, ii) se estudia comparativamente la estructura, variabilidad espacial y diversidad de las comunidades de hábitats rocoso-arenosos y hábitats rocosos, iii) se lleva a cabo la monitorización de la estructura, dinámica temporal y fenología de *ErythroGLOSSUM lusitanicum* a lo largo de un año, iv) se analizan las comunidades cespitosas de hábitats rocoso arenosos, describiendo 29 tipos de céspedes algales. Los datos generados en este estudio fueron analizados desde una perspectiva conservacionista (distribución, biodiversidad, endemismos, especies no nativas, amenazas, etc.) en la última parte de esta tesis, y se proponen 20 localidades de interés para la conservación de las comunidades de hábitats rocoso-arenosos.

Palabras clave: Atlántico de la Península Ibérica, biodiversidad, biogeografía, catálogo, céspedes algales, COI-5P, conservación, distribución, estructura de las comunidades, fenología, flora, hábitats rocoso-arenosos, morfología, nueva especie, rbd, sedimento, SSU, taxonomía, variabilidad espacial, vegetación.

Phycological study of sand-covered rocks along the Atlantic Iberian Peninsula

Abstract

This thesis improves the knowledge on algal assemblages and their species from sand-covered rocks along the Atlantic Iberian Peninsula, addressing several perspectives: floristic, taxonomic, ecological and conservational. The study was mainly performed through the analysis of 2525 samples of different types of algal assemblages collected in the intertidal and upper subtidal of 138 sites, from 2002 to 2011. A catalogue of 257 species was provided in the first part of this thesis. Morphological descriptions and, in some cases, molecular data of the 35 most common species from sand-covered rocks were included, studying in detail 13 of them which mostly belong to the family Rhodomelaceae. As a result, two new species were described, as well as the sexual structures of four ones, several taxonomic proposals were performed for other taxa, and new chorological data were added to the Iberian coast. The second part was focused on the study of the algal assemblages from sand-covered rocks: i) providing a description of the vegetation from a Galician locality, ii) comparing the structure, spatial variability and diversity of the assemblages from sand-covered rocks and rocky shores, iii) monitoring the structure, temporal dynamics and phenology of *ErythroglOSSum lusitanicum* through a one-year study, and iv) analyzing the turf assemblages from sand-covered rocks, with the description of 29 types of turfs. In the last part of this thesis, the data generated in this study were analyzed from a conservational perspective (distribution, biodiversity, endemisms, non-native species, threats, etc.) and 20 sites of interest for the conservation of assemblages from sand-covered rocks were proposed.

Keywords: Algal turfs, assemblage structure, Atlantic Iberian Peninsula, biodiversity, biogeography, catalogue, conservation, COI-5P, distribution, flora, morphology, new species, phenology, *rbdL*, sand-covered rocks, sediment, spatial variability, SSU, taxonomy, vegetation.

Estudio ficológico dos hábitats rochoso-areosos do Atlántico Peninsular

Resumo

Esta tese mellora o coñecemento das especies e comunidades de algas de hábitats rochoso-areosos do Atlántico Peninsular, abordando diferentes perspectivas: florística, taxonómica, ecolóxica e conservacionista. O estudo foi realizado principalmente analizando 2525 mostras de diferentes tipos de comunidades algais recollidas no internareal e infralitoral superior de 138 localidades, dende 2002 ata 2011. Na primeira parte desta tese preséntase un catálogo de 257 especies. Ademais inclúense descripcións morfolóxicas e, nalgúns casos, datos moleculares das 35 especies máis características dos hábitats rochoso-areosos, estudando 13 delas en detalle que na súa maioría pertencen á familia Rhodomelacea. Como resultado, se describen dúas especies novas e as estruturas sexuais doutras catro, se levan a cabo varias propostas taxonómicas e se proporcionan novos datos corolóxicos para as costas Ibéricas. A segunda parte céntrase no estudo das comunidades de algas de hábitats rochoso-areosos: i) se proporciona a descripción da vexetación dunha localidade galega, ii) se estuda comparativamente a estrutura, variabilidade espacial e diversidade das comunidades de hábitats rochoso-areosos e hábitats rochosos, iii) se leva a cabo a monitorización da estrutura, dinámica temporal e fenoloxía de *ErythroglOSSum lusitanicum* ó longo dun ano, iv) se analizan as comunidades cespitosas de hábitats rochoso-areosos, describindo 29 tipos de céspedes algais. Os datos xerados neste estudo foron analizados dende unha perspectiva conservacionista (distribución, biodiversidade, endemismos, especies non nativas, ameazas, etc.) na última parte desta tesis, e se propoñen 20 localidades de interés para a conservación das comunidades de hábitats rochoso-areosos.

Palabras chave: Atlántico da Península Ibérica, biodiversidade, bioxeografía, catálogo, céspedes algais, COI-5P, conservación, distribución, estrutura das comunidades, fenoloxía, flora, hábitats rochoso-areosos, morfoloxía, nova especie, *rba*, sedimento, SSU, taxonomía, variabilidade espacial, vexetación.

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Introduction

Introduction

Sand-covered rocks as habitat

Sand-covered rocks is a particular habitat here defined as rocks surrounded and covered by a layer of sand of variable thickness (Fig. 1). This habitat is common both in the boundary and in rocky outcrops of the beaches. Traditionally, ecological studies have been focused on rocky shores or in sandy beaches, completely ignoring mixed systems (Bally *et al.* 1984). Likewise, phycological studies have been mostly aimed on the study of rocky shores, and only occasionally references to sand-covered rocks are mentioned in floristic accounts and descriptions of the vegetation (e.g. Miranda 1931, Ardré 1970, Maggs & Hommersand 1993, Connor 1997). Conversely, rocky shores are not free of sediments and they are influenced by them in different degrees. Indeed, a progressive transition between the rocky coast and the beaches is often observed along the coastline. The extension of the rocky shore affected by adjacent sediment deposits varies depending on the wave exposure of the shore and the movility of the sediments (Bally *et al.* 1984). However, not only transitional zones between beaches and rocks are affected by sediments, but most of rocky shores are impacted by them. Numerous ecological works have highlighted the importance of the presence of sediments in rocky shores (see Airoidi 2003), whose origin derive from a variety of natural processes, including discharges by rivers, erosion of cliffs, and resuspension and transport of sediments.

Sand-covered rocks are worldwide distributed and they have been reported (under different terms) in ecological and floristic studies, such as the British Isles (Cotton 1912, Connor 1997), Atlantic France (Hommeril & Rioult 1962, 1965), South Africa (Bally *et al.* 1984, Anderson *et al.* 2008), New Zealand (Mei & Schiel 2007), Pacific coast of USA (Markham 1973, Littler *et al.* 1983, Stewart 1983, D'Antonio 1986), Atlantic coast of USA (Daly & Mathieson 1977) and Galapagos (Kendrick 1991). In South Africa, it has been estimated that this habitat comprises no less than the 26% of the coastline in certain regions and Bally *et al.* (1984) proposed a classification for mixed shores including 8 categories that range from "pure sandy beaches" to "pure rocky shores", throughout a series of intermediate classes characterized by different predominances of sand and rocks.

It is also important to note that some of the mentioned references describe rocky shores that are seasonally inundated by sand (Stewart 1983, Littler *et al.* 1983, Anderson *et al.* 2008), differing from which we usually observed in sand-covered rocks from the Atlantic Iberian Peninsula. Our studies were focused on rocks that are continuously and throughout the year covered by a layer of sand of variable thickness. Sand is in continuous movement in the beaches, and the general trend consists of sand building up in the spring, and being washed away the subtidal in the autumn (Markham 1973, Stewart 1983, Lobban & Harrison 1997); but a reverse pattern has been also described at particular sites of California (Taylor & Littler 1982).

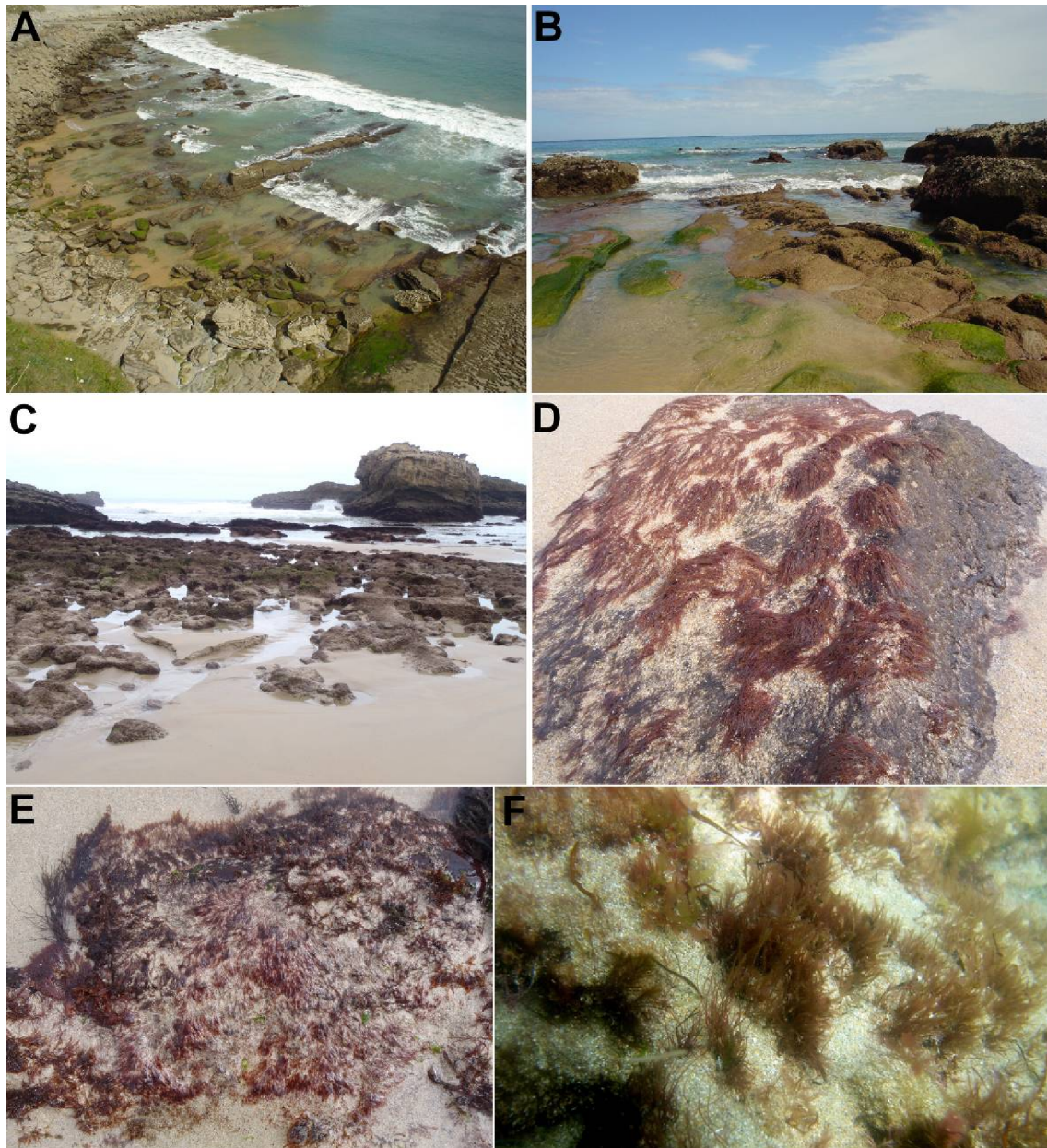


Figure 1. Sand-covered rocks from the Atlantic Iberian peninsula.

This general trend was also observed in beaches of the Atlantic Iberian Peninsula (Fig. 2). We frequently observed, when sites were visited periodically, that rocks emerging in winter were often buried during summer. Our observations show that sand movements can reach several meters in thickness in some cases. But the movement of sand is highly variable depending on a variety of physical factors, such as steepness of waves, angle of wave impact, sand particle size, wind intensity and direction, tidal amplitude and beach slope (Daly & Mathieson 1977). Thus, not only a seasonal pattern can be identified in the Atlantic Iberian Peninsula, while sand deposits of beaches vary month to month, and even week to week depending on the weather conditions. This implies that the thickness of the layer of sand that covers the rocks in the

studied habitat varies time to time, but the habitat here studied was influenced by sediments throughout the year. Indeed, our observations showed that sand deposits are also highly variable in its spatial distribution at a small spatial scale (only a few meters), since local topography also has a strong influence on depositional processes (Daly & Mathieson 1977). All this makes very difficult the monitoring of the time periods that rocks are buried by sand.

Effects of sedimentation on rocky shore assemblages

Sedimentation is one of the most relevant ecological factors that determine the composition, structure and distribution of benthic assemblages from rocky shores (Airoldi 2003). Rocky coasts affected by sediments are extreme environments for benthic species, due to their high stressful physical conditions. Despite this, they are colonized by organisms capable of living in these conditions. Many processes have been proposed as the drivers of the particular species composition of sediment-influenced habitats. These includes the burial and smothering of the organisms, scour and abrasion by moving sediments (Fig. 3), and changes in the physical characteristics of the bottom surface (Deviny & Volse 1978, Mathieson 1982, Kendrick 1991, Airoldi 2003). These processes have negative effects on numerous benthic species which reduce their abundance or disappear under the influence of sediments (Deviny & Volse 1978, Umar *et al.* 1998, Chapman & Fletcher 2002, Eriksson & Johansson 2003, Schiel *et al.* 2006). However, sediment-influenced habitats are colonized by some perennial macroalgae that tolerate or find their optimal habitat on sand-influenced rocks (Markham 1973, Littler *et al.* 1983, D'Antonio 1986) or by opportunistic ephemeral species that develop when the sediment is removed from the habitat (Daly & Mathieson 1977, Littler *et al.* 1983). The first species have been called "psammophytic" or "sand loving" which implies that they are directly favoured by sediments (Daly & Mathieson 1977, Littler *et al.* 1983). However, most of these species are rather "sand tolerant", as they may be negatively affected by sediments but not as severely as other species (Airoldi 2003). The costs imposed by living in sediments-stressed habitats are probably compensated by indirect advantages. Some physical advantages for these species may be that the layer of sand covering the substrate reduces the desiccation stress during low tide and provides protection of the lower portions of plants from the light and temperature stress. In addition, some authors suggested that biotic interactions can be also important determining the particular patterns observed in sediment-influenced habitats. Thereby, the presence of sediments on the rocks may provide to the seaweeds a habitat with less grazers, epiphytes and competitors (D'Antonio 1986, Hay 1981). Thus, effects of sediments on rocky shores may be complex, probably involving both physical direct effects and biotic interactions.



Figure 2. Variations in the level of sand in Ber beach (Galicia) along one year.

A: January 2011.

B: March 2011.

C: September 2011.

D: November 2011.

E: January 2012.

Largest differences were observed in March, when the level of sand was the lowest, and September when it was the highest. Note the difference between January 2011 (A) and 2012 (E).



Figure 3. Algal turfs in sand-covered rocks from the low intertidal subject to scour and abrasion by the movement of sand caused by breaking waves.

Surprisingly, the effects of sedimentation on the structure of assemblages has been scarcely studied compared to other abiotic factors such as wave exposure, intertidal height and depth, seawater temperature or salinity (Stephenson & Stephenson 1949, Underwood 1978, Druehl & Green 1982, McQuaid & Branch 1984, Josselyn & West 1985). Some previous works reported data and observations on the effects of natural sedimentation in rocky shores from different areas (e.g. Daly & Mathieson 1977, Taylor & Littler 1982, Litter *et al.* 1983, Anderson *et al.* 2008) showing that patterns of species abundance are related to sediment dynamics. In addition, in the last 3 decades, numerous studies focused on the effects of the increase of anthropogenic sediment loads in rocky coastal assemblages (e.g. Benedetti-Cecchi *et al.* 2001, Eriksson *et al.* 2002, Airoidi 2003, Gorgula & Connell 2004, Balata *et al.* 2007, Shepherd *et al.* 2009), which is one of the major threat to marine biodiversity at a global scale (United Nations Environmental Programme 1995). Most of these works were performed in Italy, the Baltic Sea and Australia, whereas sand-covered rocks and sediment-affected habitats from the Atlantic Europe are scarce (but see Díez *et al.* 2003, Prathep *et al.* 2003). The general pattern that emerged from these studies is that sedimentation promotes the decrease of the vertical structure of benthic assemblages due to the loss of canopy-forming species, favouring the development of algal turfs (Johansson *et al.* 1998, Eriksson *et al.* 2002, Airoidi 2003, Balata *et al.* 2007, Shepherd *et al.* 2009). In addition, these turfs trap sediments, inhibiting both the recruitment of algae that form the canopies and grazing by herbivores, favouring the prevalence of turfs (Airoidi 2003). Thus, increased sediment loads is a threat in the conservation of marine biodiversity (Airoidi *et al.* 1995, Benedetti-Cecchi *et al.* 2001, Eriksson *et al.* 2002, Pulfrich *et al.* 2003, Airoidi 2003, Gorgula & Connell 2004, Connell 2005, Balata *et al.* 2007).

Conversely, the role of natural sedimentation in the structure of benthic assemblages still remains scarcely studied. In addition, previous works described assemblages from very different sediment depositional conditions. Firstly, it is necessary to distinguish between intertidal and subtidal habitats. Subtidal sedimentation has been studied mostly in relation to enhanced sediment loads as a consequence of human activities (e.g. Airoidi 1996, Erikson & Johansson 2002, Gorgula & Connell 2004, Balata *et al.* 2007). Conversely, works addressed on natural

sedimentation were developed in intertidal habitats (Daly & Mathieson 1977, Taylor & Littler 1982, Littler *et al.* 1983, Schiel *et al.* 2006). Although the effects of sedimentation may be comparable between intertidal and subtidal habitats, there are potentially important differences. An obvious difference is that in intertidal habitats the abrasion and the regime of perturbations must be much higher than in subtidal rocks, due to the movement of the sand by the breaking waves and the tidal movement of water. In addition, within intertidal habitats, it is necessary to distinguish between those permanently influenced by sand or those that are seasonally inundated. Thereby, most of the previous works on intertidal habitats described assemblages seasonally inundated by sand (Taylor & Littler 1982, Littler *et al.* 1983, Anderson *et al.* 2008). By contrast, the number of papers describing assemblages from intertidal habitats permanently influenced by sand are much fewer (but see, Daly & Mathieson 1977, Mei & Schiel 2007).

The two focuses on the study of sedimentation on benthic assemblages (natural *vs* enhanced by human activities) agree in that this environmental factor affects the composition and distribution of rocky coast organisms, but two contrasting views emerge regarding the effects of sedimentation on biodiversity. While the prevalent opinion is that “high” sediment loads related to anthropogenic activities are detrimental to the overall diversity of rocky coast organisms due to the loss of canopy algae (Airoldi 2003 and references therein), other authors support the hypothesis that the natural presence of sediments promotes diversity of species because it increases habitat heterogeneity (Littler *et al.* 1983, Gibbons 1988, McQuaid & Dower 1990). These differences may arise because effects of sediments on rocky coast organisms vary in space and time, depending on the characteristics of the regime of sedimentation and their interactions with variable environmental and biological factors (Airoldi 2003). In addition, it must be also noted that enhanced loads of sediments by human activities are usually accompanied by enhanced nutrient loads (Johansson *et al.* 1998, Gorgula & Connell 2004). Gorgula & Connell (2004) designed experiments to test what component of environmental changes best explains the expansive covers of turf-forming species: increased nutrients in water, increased nutrients in sediments or increased sedimentation. These authors demonstrated that the three treatments had positive effects on the percentage cover of turf-forming species, but increasing nutrients in water had the largest influence in turf-forming algae dominance.

Seaweeds from sediment-influenced habitats: a global perspective

Observations from a variety of sediment-impacted rocky habitats consistently suggest the prevalence of certain morphological, reproductive and physiological attributes of seaweeds. These includes the regeneration of upright portions from remnant bases tolerant to sediment burial and scour, vegetative propagation, apical meristems that maintain dividing cells above sediment, physiological adaptations to withstand darkness or anaerobic conditions and high hydrogen sulphide concentrations (Dahl 1971, Markham 1973, Daly & Mathieson 1977,

Mathieson 1982, Stewart 1983, D'Antonio 1986, Airoidi *et al.* 1995, Díaz-Tapia & Bárbara 2005). The macroalgal species that are somehow favoured by sediments adopted similar morphologies. Two morphological traits have been identified as advantageous in perennial macroalgae from sand-influenced habitats: algal turfs (Hay 1981, Kendrick 1991, Airoidi 1998) and canopy species with very tough thalli (Daly & Mathieson 1977, Littler *et al.* 1983, Johansson *et al.* 1998).

In general, sediments are detrimental to canopy species (Airoidi 2003). By contrast, certain erect species typically grow on sand-covered rocks and are characterized by their very tough thalli. Some examples reported in references are *Neorhodomela larix* (as *Rhodomela larix*), *Laminaria sinclairii*, *Ahnfeltia plicata*, *Phaeostrophion irregulare* in Pacific North America (Markham 1973, Mathieson 1982, D'Antonio 1986), *Sargassum sinicola* in the Gulf of California (Espinoza & Rodriguez 1987), *Mazzaella capensis* and *Gracilariopsis longissima* in South Africa (Stegenga *et al.* 1997, as *Iridaea capensis* and *Gracilaria verrucosa*) or *Caulerpa taxifolia* in Australia and the Mediterranean (Glasby *et al.* 2005, Piazzini *et al.* 2005). This type of species also occurs in sand-covered rocks from the Atlantic Iberian Peninsula where some taxa are typically reported in sand-covered rocks. These are *Ahnfeltia plicata*, *Gracilaria gracilis*, *G. multipartita* and *Halopithys incurva* (Miranda, 1931, Ardre 1957, 1970, Pérez-Cirera & Maldonado 1982, Bárbara 1994, Araújo *et al.* 2005). In addition, other erect species often reported in sand-covered rocks, but also present in other habitats are *Stypocaulon scoparium*, *Cladostephus spongiosus*, *Chondracanthus acicularis* and *C. teedei*.

Algal turfs represent a particular life-form of algae, with a characteristic biological structure and function. They are here defined as assemblages of densely packed, small macroalgae which are often associated with trapped sediment (Airoidi 2001). Conversely, it must be noted that this is the most common interpretation of turfs, but this term has also been widely used in many papers to describe a heterogeneous group of species including from micro algae to large algae (Padilla *et al.* 2000). In addition, this definition is somehow ambiguous regarding the height of the algal turfs. Some authors provided a size in their definitions, but this is variable among works. For example, Gorgula & Connell (2004) consider that turfs are < 5 mm in height, Stuercke & McDermid (2004) that they are < 3 cm and Hay (1981) that they are > 0.5 cm. Probably, the perception of "small" varies in relation to the size of non-turf-forming species typical from different areas. In the Atlantic Iberian Peninsula, where canopy species reach several meters long, our perception is that turfs can reach up to 5 cm height, while they rarely are higher than 3 cm.

Taxonomically, algal turfs are a diverse miscellanea of organisms representing the three macroalgal groups: Rhodophyta, Phaeophyceae and Chlorophyta. In addition, some Cyanophyta are also considered in some studies (Price & Scott 1992). While all these groups are represented in turfs, most works agree in that members of the Rhodophyta are the most common constituents. Indeed, there seems to be a predominance in algal turfs of species of the

order Ceramiales. Thereby, algal turfs from northwestern Italy are dominated by the Rhodomelacean (Ceramiales, Rhodophyta) belonging to genera *Polysiphonia*, *Boergeseniella*, *Lophosiphonia* and *Womersleyella* (Rindi & Cinelli 2000, Airoldi *et al.* 1995); *Pterosiphonia dendroidea* dominates subtidal turfs from California (Miller *et al.* 2009), and two *Polysiphonia* species were reported as dominant in algal turfs from New Zealand (Mei & Schiel 2007). Also, Ceramiales is ca. 80% of species reported in the monograph on the algal turfs of the Great Barrier Reef (Price & Scott 1992). By contrast, other works focused on the composition of algal turfs reported a large list of species belonging to different groups of seaweeds (López *et al.* 2004, Stuercke & McDermid 2004). A number of papers also reported turfs dominated by *Corallina* spp (Stewart 1982, 1989a, b, Kelaher *et al.* 2001, Schmidt & Scheibling 2007, Huff & Jaret 2007). The identification of species that forms algal turfs is in general relatively difficult and feasible only for well-trained phycologists due to the small size of the constituent species and the great morphological similarities among them. This causes in part that numerous species from turfs along the Atlantic Iberian Peninsula remained poorly known despite their widespread distribution (Díaz *et al.* 2009, Díaz Tapia & Bárbara 2011).

The general morphological characteristics of algal turfs include the small size at maturity (variable depending on the work), the slender branches and the often creeping growth habit (Bárbara *et al.* 1995). Turf species possess both prostrate axes that attach to the substratum and upright branches, which are primarily increased by means of vegetative growth (Hay 1981). Considering the morphological forms described by Littler & Littler (1984) and Steneck & Dethier (1994), turf-forming species can be classed as filamentous, calcareous articulated or corticated terete/coarsely branched (Airoldi 2001). While filamentous species are predominant in turfs from the Atlantic Iberian Peninsula, others are also represented in these types of assemblages (Díaz Tapia *et al.* 2011). The success of algal turfs in environments with sediment deposition is related to their capacity to reproduce vegetatively (Norton *et al.* 1982, Airoldi 1998) and the ability to regenerate from basal thallus parts that can resist burial and abrasion (Daly & Mathieson 1977, Stewart 1983, Airoldi & Cinelli 1997, Díaz Tapia & Bárbara 2005a).

Algal turfs often accumulate great amounts of sediment among their densely packed thalli, which is a structural constituent turfs (Stewart 1983, Hommeril & Rioult 1961, 1965, Airoldi & Virgilio 1998). Despite this, only a few studies have analyzed the sediment of turfs, and quantitative data on the amount or dynamics of sediments accumulated are scarce (Airoldi 2003). Available data support that amounts of sediments within turfs are large and variable depending on multiple factors such as species composition, substratum slope or wave exposure (Stewart 1983, Kendrick 1991, Whorff *et al.* 1995, Airoldi & Virgilio 1998). The granulometry of trapped sediment has been studied in turfs assemblages composed by *Rhodothamniella floridula* from Atlantic France (Hommeril & Rioult 1961, 1965) and *Womersleya setacea* from the Mediterranean (Airoldi *et al.* 1996). Turfs dominated by *R. floridula* trap homogeneously only fine

sediment with a diameter similar to the double that of the thallus diameter, being the trapped sand smaller than the present in the surrounding habitat (Hommeril & Rioult 1961, 1965). Studies on *W. setacea*, a species considered invasive in subtidal habitats from Mediterranean Sea, have also demonstrated that turfs trapped only fine sediments (Airoldi *et al.* 1996).

Seaweeds from sand-covered rocks along the Atlantic Iberian Peninsula

Vegetation of intertidal rocky shores from the Atlantic Iberian Peninsula has been previously described in several works. Thereby, Miranda (1931), Hoek & Donze (1966), Seoane (1975), Polo & Seoane-Camba (1978, 1979), Anadón (1979), Fernández & Niell (1971), Anadón (1983), Ibáñez *et al.* (1987), Rallo *et al.* (1988) studied the vegetation from the Cantabrian; Miranda (1934), Seoane-Camba (1958, 1960), Donze (1968), Pérez-Cirera (1974, 1975, 1976), Anadón (1982), Pérez-Cirera & Maldonado (1982), Pérez-Cirera & Pacheco (1985), Bárbara (1994), Bárbara *et al.* (1995), López-Rodríguez *et al.* (1999), Cremades *et al.* (2004) studied the vegetation from Galicia; Ardré (1970), Boaventura *et al.* (2002), Araújo *et al.* (2005, 2006) studied the vegetation from Portugal; and Seoane-Camba (1965) studied the vegetation from Cádiz. However, no previous works were specifically designed to study the species and assemblages from sand-covered rocks, which is surprising considering the particularities of this habitat and that it is widely distributed along the Atlantic Iberian Peninsula (Figs. 4-6). By contrast, most of the mentioned works addressed rocky habitats, while only some of them noted a particular species composition in sand-covered rocks. Thus, some species or assemblages from sand-covered rocks have been reported in works on flora and vegetation from the Atlantic Iberian Peninsula. For example, some of the canopy species previously reported in this habitat are *Ahnfeltia plicata*, *Stypocaulon scoparium*, *Gracilaria gracilis*, *Cladostephus spongiosus*, *Chondracanthus teedei* or *C. acicularis* (Miranda, 1931, Ardré 1957, 1970, Pérez-Cirera & Maldonado 1982, Bárbara 1994, Araújo *et al.* 2005). Regarding turf assemblages, previous works reported the species *Chondria coerulescens*, *Gastroclonium reflexum*, *Gelidium crinale*, *Gymnogongrus griffithsiae*, *Ophidocladus simpliciusculus*, *Polysiphonia fucoides*, *P. stricta*, *P. nigra*, *Pterosiphonia pennata*, *Rhodothamniella floridula* and *Tiffaniella capitata* (Miranda 1931, Ardré 1957, 1976, Pérez-Cirera 1975, 1976, 1980, 1981, Pérez-Cirera & Maldonado 1982, Bárbara 1994, Bárbara *et al.* 1992, 1995). However, the information available in these works mostly consists of lists of species found in sand-covered rocks, while quantitative data are scarce (but see Bárbara 1994, Díaz Tapia & Bárbara 2005a, b).



Figure 4. Sand-covered rocks from the Cantabrian coast. A-B: Zumaia (Guipúzcoa). C-D: Laida (Vizcaya). E: Langre (Cantabria). F: Oyambre (Cantabria). G. Isla: (Asturias. H: Aguilar (Asturias).

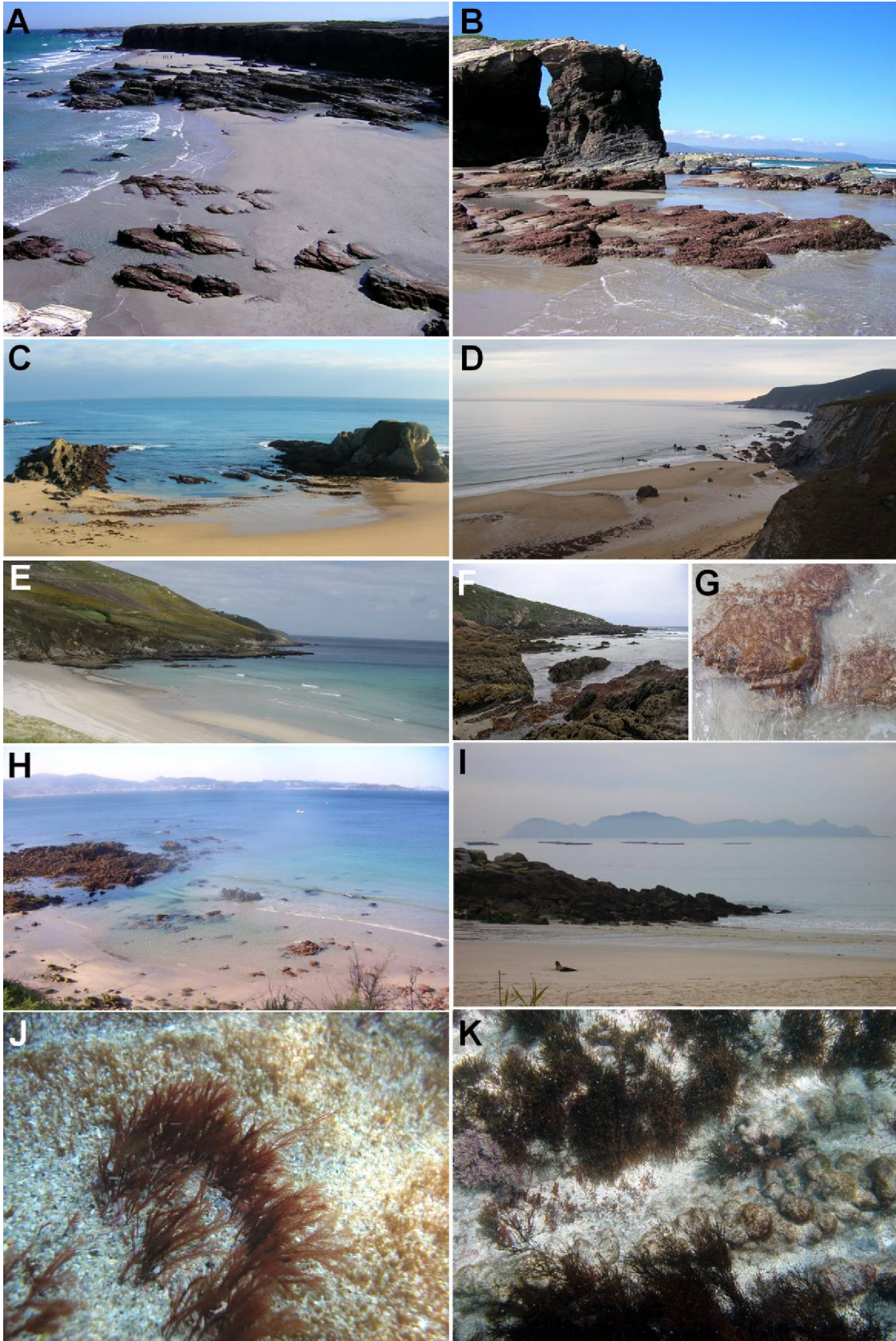


Figure 5. Sand-covered rocks from Galicia. **A-B:** Catedrales (Lugo). **C:** San Román (Lugo). **D:** Picón (A Coruña). **E-G:** Seia (A Coruña). **H:** Agra (Pontevedra). **I:** Nerga (Pontevedra). **J:** Lourido (A Coruña). **K:** Santa Comba (A Coruña).

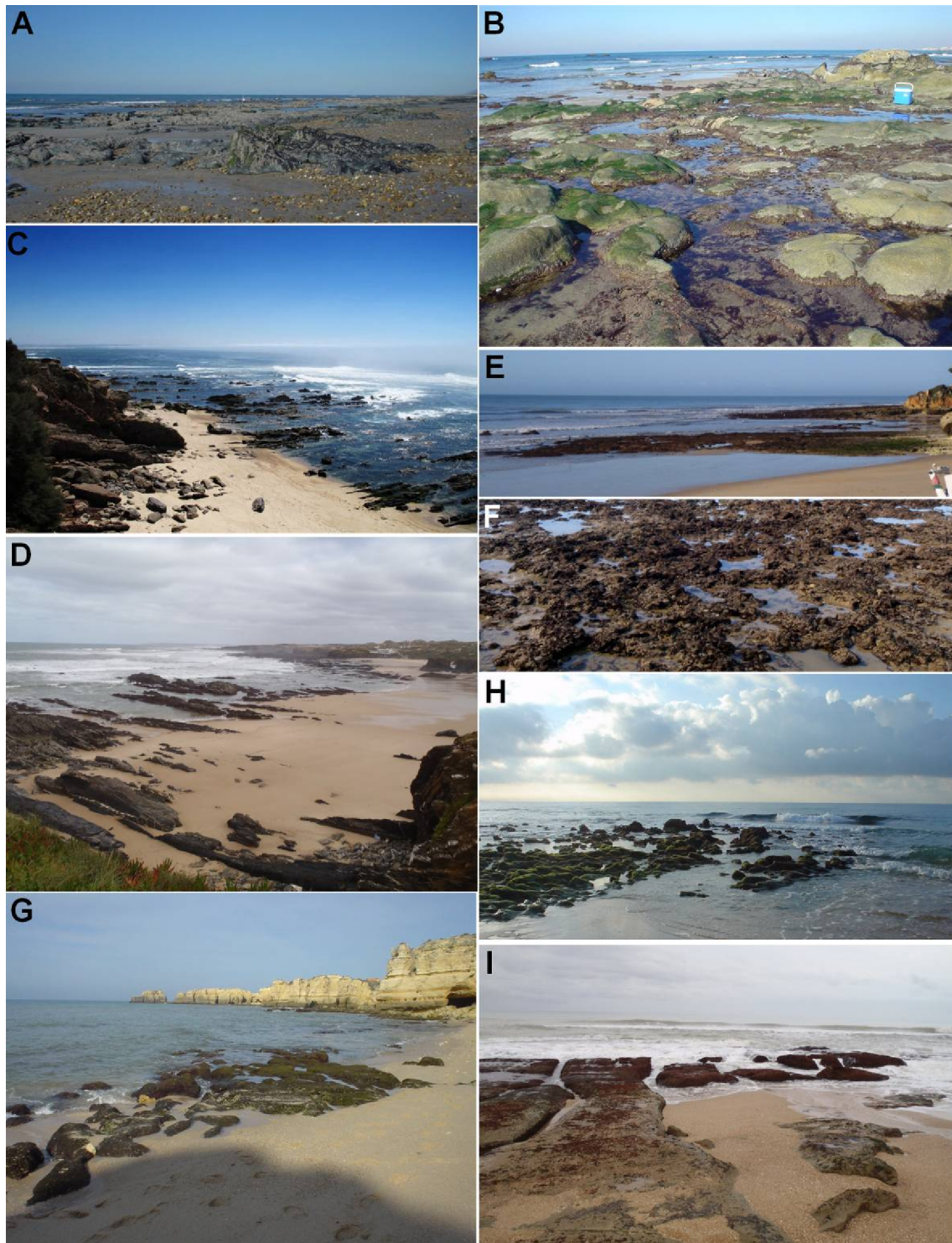


Figure 6. Sand-covered rocks from Portugal and the southern Iberian Peninsula. A: Cegaês (Minho). B: Leça de Palmeira (Douro Litoral). C: Buarcos (Beira Litoral). D: Almogrove (Estremadura). E-F: Olhos d'Água (Algarve). G: Coelho (Algarve). H: Caños de Meca (Cádiz). I: Punta Plata (Cádiz).

Objectives

The aim of this thesis is to improve the knowledge of the sand-covered rocks along the Atlantic Iberian Peninsula from a phycological perspective. This study involves two main parts: a floristic and taxonomic study of the species living in this habitat and a study of the turf assemblages from sand-covered rocks. In addition, another target is to highlight the relevance of the seaweeds from this habitat in the context of the marine floristic diversity from the Atlantic Iberian Peninsula, providing a conservational perspective. The specific objectives of the thesis are listed below:

Part 1. Seaweeds from sand-covered rocks along the Atlantic Iberian Peninsula.

- a) Providing a catalogue of the seaweeds from sand-covered rocks.
- b) Analyzing the relation between the studied sites based on their flora.
- c) Providing descriptions of the morphology, habitat and distribution of the 35 most relevant turf-forming species from sand-covered rocks.
- d) Reassessing the taxonomy of 13 species based on morphological and molecular evidence.

Part 2. Turf assemblages from sand-covered rocks along the Atlantic Iberian Peninsula.

- a) Studying the structure of turf assemblages from sand-covered rocks and describing the different types of turfs.
- b) Comparing the structure, spatial variability and diversity of assemblages from sand-covered and sand-free rocky shores.
- c) Studying the seasonal dynamics and phenology of *ErythroGLOSSUM lusitanicum*.

Part 3. Diversity and conservation of the seaweeds from sand-covered rocks along the Atlantic Iberian Peninsula.

- a) Analyzing the diversity of sand-covered rocks in the context of the marine benthic flora of the Iberian Peninsula.
- b) Comparing the occurrence of turf assemblages in natural and human-impacted rocky shores.
- c) Analyzing the threats and conservation status of sand-covered rocks along the Atlantic Iberian Peninsula and highlighting sites with special interest for their conservation.



General material and methods

General material and methods

Study area

This study was carried out on sand-covered rocks from the Atlantic Iberian Peninsula. This area comprises an extent of about 3800 km of shoreline that shows a wide variety of environmental conditions. In general, two gradients of seawater temperature can be identified. Galicia and Northern Portugal are the coldest regions of the studied area, and seawater temperature increases towards the East, along the Cantabrian coast, and towards the South, along the Portuguese coast. Thus, Cádiz (southern Spain) and the Basque Country (eastern Spain) are the warmest areas of the Atlantic Iberian Peninsula. In addition, the wave exposure is also variable within the study area. It varies from high to extremely high in practically all the studied sites in the Cantabrian, the western Portugal and numerous sites from Galicia, while it is from sheltered to moderately wave-exposed in the southern coast of the Atlantic Iberian Peninsula and some sites from Galicia. In this study, the shoreline was divided in five areas (Fig. 1) that are briefly described below.



Figure 1. Sampling sites along the Atlantic Iberian Peninsula.

The Cantabrian coast consists of a straight and rugged shoreline of about 1000 km with a predominance of high cliffs. This shore is characterized by a gradient that affects both the coast morphology and temperature. The height of the cliffs and surface seawater temperature increase eastward. Monthly mean values range from 13.6 to 22.3 °C in winter and summer, respectively, in Asturias (western) and from 13.4 to 24.1°C in the Basque Country (eastern). In general, beaches are less numerous and shorter than in other regions. All of them are oriented to the North and are, in general, extremely wave-exposed to the prevailing northwest oceanic swell. The maximum wave height registered was 8.29 m, and the annual average for 2011 was 1.38 m. Tidal regime along this shore is semidiurnal with the largest tidal range during spring tides of 3.5-5 m. Along the Cantabrian coast 24 sites were sampled (Fig. 1, Table 1) mostly during March-April and October-November 2006.

The Galician coastline, with 1698 km, is very irregular and is characterized by the alternation of shores open to the sea and its numerous Rías (a series of flooded tectonic valleys where the sea penetrates tens of kilometres inland). This long shoreline of Galicia has numerous beaches of variable extension, as well as medium to high cliffs. Thus, Galicia possesses a great diversity of habitats characterized by variable environmental features such as wave exposure, salinity, substratum, nutrients, etc. The coast of Galicia is exposed to the prevailing northwest oceanic swell, with an annual average height of 2.52 m and a maximum wave height of 11.73 m during 2011. The shores open to the sea are from extremely to moderately wave-exposed, and wave exposure decreases towards the inner of Rías and in sites with southern orientations. Monthly average values of surface seawater temperature range from 13.6 to 20.1°C in winter and summer, respectively, and is lower than in other studied regions, especially considering the summer temperatures. This is in great part due to the positive circulation and upwelling events of Eastern North Atlantic Central Water (ENACW) that occur in the Rías during spring-autumn. This phenomenon causes seawater temperature to remain low during summer months and provides nutrients, making the Rías the most productive zones in the northwest of Spain. Tidal regime along this shore is semidiurnal with the largest tidal range during spring tides of 3.5-4.5 m. Along the Galician coast 39 sites were sampled (Fig. 1, Table 1) in dates from 2002 to 2011.

The northern and central coasts of Portugal are characterized by a straight shoreline of ca. 600 km with long beaches that have large extensions of rocky outcrops in the mid-low intertidal. This region is the one with a more extensive representation of sand-covered rocks of the study area. In this area, the Ría of Aveiro forms a sand barrier of about 90 km length in which natural rocky reefs are absent, and thus this area was not sampled. Portuguese beaches of this region are extremely wave-exposed. The annual average wave height were of ca. 3 m, and the maximum wave height was 13.5 m during 2011. The surface seawater temperature is similar to those of Galicia, and monthly average values range from 13 to 20°C in winter and summer, respectively. Upwelling and downwelling events also occur in the west coast of Portugal. Tide

range is 3.5-4 meters during spring tides. Along this shore 10 sites were sampled (Fig. 1, Table 1) mostly in October-November 2004 in northern Portugal and June 2010 in central Portugal.

The southern Iberian Peninsula is composed of three parts characterized by different environmental conditions: the western coast of Portugal, the southern coast of Portugal and the Atlantic coast of Cádiz. The western coast of Portugal is a straight shoreline of ca. 120 km characterized by a predominance of extensive beaches with numerous rocky outcrops that alternate with cliffs. This coast is extremely wave-exposed to the prevailing northwest oceanic swell, which had annual average values of 2.5 m and a maximum wave height of 11.7 m during 2011. The surface seawater temperature is similar to the northern and central Portugal, with monthly average values ranging from 13.5 to 20 °C in winter and summer, respectively. Tide range is 3.5-4 m during spring tides. Four sites were sampled in May and October 2005 along the southwestern coast of Portugal (Fig. 1, Table 1)

The two regions from the southern coast are separated by a long barrier of sand of about 180 kilometres, that extends from the mid-eastern of southern Portugal to Cádiz, throughout all the coast of Huelva. Natural rocks are absent in the intertidal of this area, and thus sampling was not performed. The southern Portuguese coast is characterized by a rugged shoreline of ca. 100 km length with numerous cliffs and small beaches. The wave exposure in this area is notably lower than in the western coast of Portugal and similar to Cádiz, with prevailing southwestern oceanic swell that reached maximum wave heights of 6 m and annual mean values of ca. 1 m during 2011. The surface seawater temperature was higher than in the west coast, with a monthly mean ranging from 15 to 23 °C in winter and summer, respectively. The tidal regime along this shore is semidiurnal, with the largest tidal range during spring tides of 2.3-3.5 m. Along the southern coast of Portugal, 10 sites were sampled in May and October-November 2005 (Fig. 1, Table 1).

The Atlantic coast of Cádiz is of ca. 190 km length and it is less abrupt than the Algarve, with numerous beaches alternating with rocky shores. The shore of Cádiz has a gradient of wave exposure, from sheltered to moderately wave-exposed, increasing from north to south. The prevailing west oceanic swell had the lowest height of the studied area, with mean annual values of 1.3 m and a maximum wave height of 5.4 m in 2011. Conversely, surface seawater temperature in Cádiz is the highest of the studied area, with monthly averages ranging from 17.4 to 25.5°C in winter and summer, respectively. Tidal regime along this shore is semidiurnal, with the largest tidal range during spring tides of 2.25-3.75 m. Five sites along Cádiz were sampled in November 2005 and January 2011 (Fig. 1, Table 1).

Data on seawater temperature and wave height were included above were obtained for Spain from Puertos del Estado (2013) and for Portugal from Instituto Hidrográfico da Marinha (2013).

Study sites

Sampling sites were selected after inspection of aerial photographs in Planeta (1997, 1998a, b, 1999a, b, 2004), SigPac (2003) and Googlemaps (2003). Sampling sites consisted of beaches with rocky outcrops scattered or forming groups along the beach, as well as in their ends. The extension and size of these outcrops were greatly variable within and between sites. In general, the sites from western Portugal were those that had largest extents of sand-covered rocks because many beaches from this shore have numerous rocks surrounded by sand that emerge during the low tide. The height of the rocky outcrops was also variable. Rocks that reach a low rise over the sand level were colonized mostly by turf assemblages and some canopy species that tolerate the influence of the sand. However, when rocks reached a certain height above the sand level, assemblages become more similar to those from rocky shores. Therefore, in many of the sites the typical assemblages from sand-covered rocks coexist with assemblages similar to those from sand-free rocky shores. While the first type of assemblages colonizes the basal parts of the rocks, which are most directly influenced by sand, the assemblages typical from sand-free rocky shores colonize the upper parts of rocks, which are less influenced by sand. Thus, for example, it is frequent that rocky outcrops have assemblages dominated by *Fucus vesiculosus* var. *compressus*, *Corallina elongata*, *Bifurcaria bifurcata*, *Mytilus galloprovincialis* or *Cystoseira baccata*, which are attached to the upper parts of the rocks surrounded by sand, while below, in the proximity to the sand, algal turfs are the dominant assemblages.

Collection and study of samples

This section intends a general description of the sampling strategy used for the development of a large part of this work, in particular Part 1, Chapter 2.4 and Part 3. By contrast, Chapters 2.1, 2.2 and 2.3 follow a different sampling strategy, which is detailed in their respective sections. A more precise description of materials and methods is given in the respective Chapters.

Field collections

An extensive collection of seaweeds from sand-covered rocks was made in the intertidal of a total of 88 sites from the Atlantic Iberian Peninsula (Fig. 1, Table 1), between 2002-2011. Furthermore, the upper subtidal of some locations was also studied by snorkel or SCUBA. In addition, some samples for floristic and taxonomic studies were also collected in 50 additional sites that were visited with other purposes (Fig. 2, Table 1). Vegetation from sand-covered rocks usually consisted on turf-forming species, but some erect algae were also characteristic from these habitats. This study has been carried out based on samples of turf-forming species and

the erect species *Ahnfeltia plicata*, *Cladostephus spongiosus*, *Chondracanthus acicularis*, *C. teedei*, *Gracilaria gracilis*, *G. multipartita*, *Halopithys incurva* and *Stypocaulon scoparium*.

Each sample consisted of quadrats of 225-400 cm² that were haphazardly selected among the different turfs and erect assemblages visually identified. Subsequently, samples were totally scraped using a jackknife, but a hammer and chisel were also employed to collect encrusting species. The intertidal level and total percent cover of each sampling quadrat was recorded. Samples were transported in labelled bags to the laboratory. They were preserved in 4% formalin in seawater at 4 °C and stored in the dark for later study. In addition, samples of the most representative species collected since 2010 were isolated and preserved in silica gel for molecular analysis. Other parts of the samples were preserved in formalin for morphological studies.



Figure 2. Additional sampling sites along the Atlantic Iberian Peninsula.

Samples identification

In the laboratory, species were studied under the stereomicroscope and optical microscope with the aim to identify them using monographs of the different algal groups. Among the most frequently used works were the several volumes of the Seaweeds of the British Isles, especially the Volume on Ceramiales (Maggs & Hommersand 1993), and monographs on the Rhodomelaceae and Ceramiaceae from the Canary Islands (Sansón Acedo 1991, Rojas González 1997) and the Basque Country (Secilla 2012). Representative specimens were preserved and deposited in the herbarium of the Universidade de Santiago de Compostela (SANT), adding up to a total of about 4800 specimens. Herbarium abbreviations follow Thiers (2013). Furthermore, representative specimens of selected species (those species enough small to fit within a slide, or fragments and cross sections of larger species) were mounted in 20% Karo[®] Syrup (ACH Foods, Memphis, TN, USA) and 80% distilled water. Certain species were previously stained with aniline blue, while others were mounted in a mixture of 1% aniline blue, 1% acetic acid, 50% Karo[®] Syrup and 48% distilled water (Millar & Wynne 1992). Sections for microscopic observations were made by hand using a razor blade. A total of ca. 3400 slides have been mounted and stored in the Seaweeds lab of the University of A Coruña.

Table 1. Sampling sites along the Atlantic Iberian Peninsula ordered from the Northeast to the South. For each site it is provided the region (CA = Cantabrian, GA = Galicia, NP= northern Portugal, CP = Central Portugal, SP = southern Iberian Peninsula), the province (see Fig. 3), the UTM (Datum WGS84, 100 x 100 m) and the geographical coordinates. Symbols represent sampling sites () and additional sampling site ().

Region	Province	Site	UTM	Geographical	
CA	SW Francia	Biarritz	30TPJ162155	43°29'03"N	001°33'46"W
CA	Guipúzcoa	Ondarreta	30TWN808970	43°19'18"N	002°00'11"W
CA	Guipúzcoa	Zumaia	30TWN597946	43°17'59"N	002°15'51"W
CA	Vizcaya	Arrikotartián	30TWN439984	43°20'09"N	002°27'27"W
CA	Vizcaya	Ogeia	30TWP370027	43°22'22"N	003°32'35"W
CA	Vizcaya	Laida	30TWP257064	43°24'28"N	002°40'54"W
CA	Vizcaya	San Juan	30TWP179104	43°26'41"N	002°46'41"W
CA	Vizcaya	La Arena	30TVP844003	43°21'16"N	003°06'53"W
CA	Vizcaya	Kobarón	30TVP893002	43°21'10"N	003°07'54"W
CA	Cantabria	Orión	30TVP737061	43°24'20"N	003°19'34"W
CA	Cantabria	Sonabia	30TVP736070	43°24'51"N	003°19'37"W
CA	Cantabria	Ris	30TVP577160	43°29'38"N	003°31'26"W
CA	Cantabria	Langre	30TVP008142	43°28'37"N	003°41'37"W
CA	Cantabria	Somocueva	30TVP238136	43°28'07"N	003°56'43"W
CA	Cantabria	Virgen del Mar	30TVP293145	43°28'40"N	003°52'31"W
CA	Cantabria	Valdearenas	30TVP222116	43°27'13"N	003°57'37"W

Region	Province	Sites	UTM	Geographical	
CA	Cantabria	Tagle	30TVP125097	43°25'59"N	004°04'50"W
CA	Cantabria	Oyambre	30TUP862062	43°24'02"N	004°20'10"W
CA	Cantabria	Amio	30TUP799054	43°23'42"N	004°28'57"W
CA	Asturias	La Franca	30TUP727060	43°23'39"N	004°34'18"W
CA	Asturias	Isla	30TUP204165	43°28'40"N	005°13'17"W
CA	Asturias	Niembro	30TUP513117	43°26'33"N	004°50'20"W
CA	Asturias	Estaño	30TTP902251	43°32'52"N	005°35'50"W
CA	Asturias	Verdicio	30TTP677345	43°37'30"N	005°52'44"W
CA	Asturias	Aguilar	29TQJ327268	43°33'28"N	006°07'07"W
CA	Asturias	Silencio	29TQJ184273	43°33'58"N	006°17'50"W
CA	Asturias	Serantes	29TPJ637248	43°33'27"N	006°58'39"W
GA	Lugo	Ensenada Cegoñas	29TPJ514241	43°33'18"N	007°07'28"W
GA	Lugo	Catedrales	29TPJ494243	43°33'16"N	007°09'16"W
GA	Lugo	Punta do Castro	29TPJ472249	43°33'47"N	007°10'35"W
GA	Lugo	Llas	29TPJ406266	43°34'47"N	007°15'27"W
GA	Lugo	Peinzás	29TPJ396277	43°35'09"N	007°16'13"W
GA	Lugo	Playa de Peinzás	29TPJ390275	43°35'16"N	007°16'37"W
GA	Lugo	Polas	29TPJ355314	43°37'18"N	007°19'10"W
GA	Lugo	Punta Riomar	29TPJ352316	43°37'31"N	007°19'24"W
GA	Lugo	Linorsa	29TPJ246398	43°41'57"N	007°27'13"W
GA	Lugo	Lago (San Cibrao)	29TPJ227407	43°42'28"N	007°28'32"W
GA	Lugo	San Román	29TPJ104420	43°43'17"N	007°37'39"W
GA	Lugo	Xilloe	29TPJ087446	43°44'41"N	007°39'02"W
GA	Lugo	Cadín	29TPJ068441	43°44'33"N	007°40'24"W
GA	A Coruña	Bares	29TPJ065467	43°46'02"N	007°40'36"W
GA	A Coruña	Picón	29TPJ013444	43°44'45"N	007°44'30"W
GA	A Coruña	Castro	29TNJ997437	43°44'25"N	007°45'44"W
GA	A Coruña	Santa Comba	29TNJ580233	43°33'34"N	008°15'30"W
GA	A Coruña	Doniños	29TNJ550170	43°30'08"N	008°19'17"W
GA	A Coruña	Baleo	29TNJ725332	43°38'50"N	008°06'05"W
GA	A Coruña	Pantín	29TNJ718327	43°38'33"N	008°06'36"W
GA	A Coruña	Chanteiro	29TNJ564108	43°26'46"N	008°18'15"W
GA	A Coruña	Ber	29TNJ639057	43°23'51"N	008°12'44"W
GA	A Coruña	Perbes	29TNJ636029	43°22'33"N	008°12'56"W
GA	A Coruña	Carnoedo	29TNJ597035	43°21'53"N	008°15'02"W
GA	A Coruña	Veigue	29TNJ573037	43°23'04"N	008°17'31"W
GA	A Coruña	Dexo	29TNJ534053	43°25'58"N	008°19'48"W
GA	A Coruña	Canabal	29TNJ532046	43°23'28"N	008°20'40"W

Region	Province	Sites	UTM	Geographical	
GA	A Coruña	Isla Castelo	29TNJ530017	43°21'45"N	008°20'47"W
GA	A Coruña	Santa Cruz	29TNJ527982	43°20'51"N	008°20'58"W
GA	A Coruña	As Lagoas	29TNJ481038	43°23'02"N	008°24'26"W
GA	A Coruña	San Pedro	29TNJ448030	43°22'45"N	008°26'47"W
GA	A Coruña	Bens	29TNJ439013	43°21'36"N	008°27'26"W
GA	A Coruña	Ártabra	29TNJ426005	43°21'12"N	008°28'38"W
GA	A Coruña	Barrañán	29TNH358957	43°18'44"N	008°33'22"W
GA	A Coruña	Leira	29TNH297954	43°18'37"N	008°38'00"W
GA	A Coruña	Sorrizo	29TNH352958	43°18'51"N	008°33'57"W
GA	A Coruña	Cambre	29TNH196940	43°18'01"N	008°45'24"W
GA	A Coruña	Reja	29TNH187942	43°18'01"N	008°46'04"W
GA	A Coruña	Seaia	29TNH143975	43°19'41"N	008°49'34"W
GA	A Coruña	As Garzas, Barizo	29TNH103963	43°19'05"N	008°52'24"W
GA	A Coruña	Barizo	29TNH102958	43°18'48"N	008°52'27"W
GA	A Coruña	Barda	29TNH059924	43°16'58"N	008°55'38"W
GA	A Coruña	Hermida	29TNH038902	43°15'47"N	008°57'10"W
GA	A Coruña	Arou	29TMH915816	43°11'03"N	009°06'46"W
GA	A Coruña	Santa Mariña	29TMH892824	43°11'38"N	009°07'59"W
GA	A Coruña	Lago, Camariñas	29TMH837753	43°07'49"N	009°11'58"W
GA	A Coruña	Lago (Muxía)	29TMH863726	43°05'53"N	009°11'50"W
GA	A Coruña	Lourido	29TMH820713	43°05'28"N	009°13'15"W
GA	A Coruña	Lires	29TMH789616	43°00'04"N	009°15'39"W
GA	A Coruña	Estorde	29TMH823545	42°56'28"N	009°13'04"W
GA	A Coruña	Caldebarcos	29TMH895438	42°50'38"N	009°07'44"W
GA	A Coruña	Mar Lira	29TMH903397	42°48'34"N	009°07'05"W
GA	A Coruña	Lariño	29TMH908341	42°45'32"N	009°06'45"W
GA	A Coruña	Fogareiro	29TMH937336	42°45'08"N	009°04'49"W
GA	A Coruña	Esteiro	29TNH029374	42°47'16"N	008°58'03"W
GA	A Coruña	Arnela	29TMH990288	42°42'35"N	009°00'47"W
GA	A Coruña	Queiruga	29TMH971246	42°40'24"N	009°02'06"W
GA	A Coruña	Caveiro	29TNH006315	42°44'16"N	008°59'28"W
GA	A Coruña	Agueira	29TNH019323	42°44'37"N	008°58'36"W
GA	A Coruña	Basoñas	29TMH956189	42°37'22"N	009°03'10"W
GA	A Coruña	Espiñeirido	29TMH948169	42°36'21"N	009°03'44"W
GA	A Coruña	Aguiño	29TMH993077	42°31'11"N	009°00'33"W
GA	A Coruña	Punta Insuela	29TNH030131	42°34'09"N	008°58'07"W
GA	Pontevedra	Area da Cruz	29TNH077011	42°27'40"N	008°54'37"W
GA	Pontevedra	Playa de Melide	29TNG063933	42°23'27"W	008°55'25"W

Region	Province	Sites	UTM	Geographical	
GA	Pontevedra	Punta Faxilda	29TNG106958	42°24'44"N	008°52'13"W
GA	Pontevedra	Barreiro	29TNG171941	42°23'52"N	008°47'37"W
GA	Pontevedra	Agra	29TNG191937	42°23'38"N	008°46'08"W
GA	Pontevedra	Punta Area Brava	29TNG134825	42°17'29"N	008°50'21"W
GA	Pontevedra	Nerga	29TNG137783	42°15'19"N	008°50'07"W
GA	Pontevedra	Cabo de Mar	29TNG185744	42°13'18"N	008°46'32"W
GA	Pontevedra	Samil	29TNG185739	42°12'55"N	008°46'37"W
GA	Pontevedra	Silleiro	29TNG082621	42°06'42"N	008°54'00"W
GA	Pontevedra	Oia	29TNG098502	42°00'09"N	008°52'48"W
GA	Pontevedra	A Guarda	29TNG103400	41°54'29"N	008°52'36"W
NP	Minho	Ancora	29TNG108296	41°49'07"N	008°52'21"W
NP	Minho	Montedor	29TNG101217	41°44'51"N	008°52'40"W
NP	Minho	Viana do Castelo	29TNG126158	41°41'39"N	008°51'02"W
NP	Minho	Cepaes	29TNG171003	41°33'07"N	008°47'36"W
NP	Douro Litoral	Mindelo	29TNF240728	41°18'33"N	008°44'32"W
NP	Douro Litoral	Leca	29TNF240601	41°12'22"N	008°43'03"W
NP	Douro Litoral	Aguda	29TNF285450	41°03'25"N	008°39'24"W
NP	Beria Litoral	Buarcos	29TNE080480	40°10'58"N	008°54'29"W
CP	Estremadura	Vale Furado	29SMD950927	39°41'04"N	009°03'33"W
CP	Estremadura	Baleal	29SMD713581	39°22'25"N	009°19'56"W
CP	Estremadura	Porto Novo	29SMD689365	39°10'38"N	009°21'27"W
CP	Estremadura	Santa Cruz	29SMD666316	39°07'41"N	009°23'22"W
CP	Estremadura	Playa Azul	29SMD659298	39°06'53"N	009°23'41"W
CP	Estremadura	Guincho	29SMC586863	38°43'29"N	009°28'41"W
SP	Alentejo	Queimado	29SNB184865	37°49'34"N	008°47'34"W
SP	Algarve	Almograve	29SNB176674	37°39'54"N	008°48'04"W
SP	Algarve	Arrifana	29SNB083128	37°17'21"N	008°51'55"W
SP	Algarve	Amado	29SNB085131	37°09'44"N	008°54'22"W
SP	Algarve	Baaleeira	29SNA064966	37°00'45"N	008°55'48"W
SP	Algarve	Martinhal	29SNA066966	37°01'03"N	008°55'31"W
SP	Algarve	Ingrina	29SNA075976	37°02'46"N	008°52'43"W
SP	Algarve	Dona Ana	29SNB296054	37°05'27"N	008°40'08"W
SP	Algarve	Armação de Pêra	29SNB559065	37°06'04"N	008°22'17"W
SP	Algarve	Caneiros	29SNB433068	37°06'14"N	008°30'47"W
SP	Algarve	Coelho	29SNB629035	37°04'22"N	008°17'31"W
SP	Algarve	San Rafael	29SNB639035	37°04'26"N	008°16'51"W
SP	Algarve	Santa Eulalia	29SNB697048	37°05'11"N	008°12'53"W
SP	Algarve	Olhos d'Água	29SNB722053	37°05'20"N	008°11'27"W

Region	Province	Sites	UTM	Geographical	
SP	Cádiz	Chipiona	29SQA293700	36°44'31"N	006°26'09"W
SP	Cádiz	El Puerto	29SQA447520	36°34'48"N	006°15'51"W
SP	Cádiz	Santibañez	29SQA461393	36°28'03"N	006°15'10"W
SP	Cádiz	Encendida	29SSQ555222	36°18'40"N	006°09'12"W
SP	Cádiz	Puerto de Barbate	30STF367083	36°11'04"N	006°55'39"W
SP	Cádiz	Punta Plata	30STE454995	36°06'28"N	005°49'41"W
SP	Cádiz	Caños de Meca	29SQA697085	36°10'55"N	006°00'06"W
SP	Cádiz	Punta Paloma	30STE547943	36°03'44"N	005°43'31"W



Figure 3. Map of the Iberian provinces. Codes of Atlantic provinces: G = Guipúzcoa; Vi = Vizcaya; Cn = Cantabria; As = Asturias; Lu = Lugo; C = A Coruña; Po = Pontevedra; Mi = Minho; DL = Douro Litoral; BL = Beira Litoral; E = Estremadura; BA = Baixo Alentejo; Ag = Algarve; H = Huelva; Ca = Cádiz. Source: Gómez-Garreta *et al.* 2001.



PART 1.

Seaweeds from sand-
covered rocks along the
Atlantic Iberian
Peninsula

PART 1. Seaweeds from sand-covered rocks along the Atlantic Iberian Peninsula.

Introduction

Sand-covered rocks provide for benthic seaweeds a habitat with environmental conditions different to those from purely rocky shores. The sand, together with the wave motion action, causes the abrasion of substratum and the burial of seaweeds (Devinny & Volse 1978; Littler *et al.* 1983; Kendrick 1991; Eriksson & Johansson 2005). These particular stressful conditions greatly influence the composition of the seaweeds, which often includes typical species that are only rarely found in rocky shores. This is proved by floristic accounts from worldwide in which sand-covered rocks are described as the characteristic habitat of certain species (e.g. Ardré 1970, Abbott & Hollenberg 1976, Bárbara 1994, Maggs & Hommersand 1993, Stegenga *et al.* 1997, Womersley 2003, Airoldi 2003). Observations from a variety of sediment-impacted rocky habitats consistently suggest the prevalence of certain morphological attributes in macroalgal species that are somehow favoured by sediments. Thus, two morphological traits have been identified as advantageous in perennial macroalgae from sand-influenced habitats: algal turfs (Hay 1981; Kendrick 1991; Airoldi 1998) and canopy species with very tough thalli (Daly & Mathieson 1977; Littler *et al.* 1983; Johansson *et al.* 1998). While a few robust canopy species are characteristic from sand-covered rocks along the Atlantic Iberian Peninsula, turf-forming species comprise the morphological group that accounts for most of the diversity found in this habitat.

Taxonomically, algal turfs are a diverse miscellanea of organisms representing the three macroalgal groups, but most workers agree that members of the Rhodophyta are the most common constituents. Accordingly, turf-forming species from sand-covered rocks are usually small red seaweeds that share a common outline morphology. This often consists of a system of prostrate axes attached to the substrate by means of rhizoids and from which grow the erect axes that bear, if present, the reproductive structures. Thus, most of the species are very similar between them and their identification in the field, and even in the laboratory, is often difficult without experience. Furthermore, between the most frequent and abundant algal groups of this habitat are several genera of the Rhodomelaceae, including *Polysiphonia sensu lato*. This is among the largest genera within the Rhodophyta in that it currently contains almost 200 recognized species (Guiry and Guiry, 2013). Probably, all these characteristics of the flora from sand-covered rocks contributed to the fact of that a great number of taxa from this habitat remain poorly known, even those that are frequent and abundant along the Atlantic Iberian Peninsula.

Sand-covered rocks are a common and widely represented habitat along the Atlantic Iberian Peninsula, but previous works about the flora and vegetation from the Atlantic Iberian Peninsula

only briefly reported some species from sand-covered rocks such as *Ahnfeltia plicata*, *Gracilaria gracilis*, *Rhodothamniella floridula*, *Ophidocladus simpliciusculus*, *Pterosiphonia pennata*, *Gastroclonium reflexum*, *Chondria coerulescens*, *Gymnogongrus griffithsiae*, *Chaetomorpha aerea*, *Polysiphonia caespitosa*, *Polysiphonia nigra*, *Spermothamnion repens*, *Gelidium crinale*, *Tiffaniella capitata*, etc. (Miranda 1931, Ardré 1970, Pérez-Cirera 1976, 1980, Pérez-Cirera & Maldonado 1982, Pérez-cirera & Pacheco 1985, Bárbara *et al.* 1992, 1995, Bárbara 1994). However, at present, a specific monographic study of this habitat has not been developed. With the aim of filling in this gap in the phycological knowledge of this habitat, we began in 2002 a preliminary study along the Galician coast that was subsequently extended to the Atlantic Iberian Peninsula, and was completed it in the framework of the project “*Céspedes algales de hábitats rocoso-arenosos de la costa Atlántica de la Península Ibérica*” (CGL2009-09495, Ministerio de Ciencia e Innovación partially funded by FEDER).

In the present study, we have sampled 88 sites along the Atlantic Iberian Peninsula (Fig. 1, general material and methods), sometimes on several dates, collecting seaweeds from sand-covered rocks in the intertidal and occasionally, in the upper subtidal. In addition, 50 sites were visited with different purposes and some samples were also taken on them (Fig. 2, general material and methods). This work included a total of about 2200 samples whose study resulted in the finding of 257 species that are listed in the first chapter of this part. In this study we found numerous species with a chorological interest, and numerous new records were published considering the different regions of the Atlantic Iberian Peninsula, as well as the countries Spain, Portugal, and France. Furthermore, we explore the relationships between the studied sites based on the presence/absence of species.

The second chapter of the first part provides morphological descriptions of the most typical turf-forming species from sand-covered rocks. It includes a total of 34 species, of which 29 species proved to be the dominant constituents of the turfs from this habitat according to our study (see Chapter 2.4), as well as other species that, although less abundant, are also frequent or have a special taxonomic interest. During the development of this study we found that several of the characteristic species from sand-covered rocks remained poorly known, including two new species. In consequence, 13 of these species have been studied in depth, preparing detailed morphological descriptions, in some cases developing phylogenetic studies based on molecular data in collaboration to others researchers, and discussing the taxonomic entities related to these species.

The main objectives of this first part are providing: (i) a catalogue of the seaweeds from sand-covered rocks; (ii) a biogeographic analysis of the studied sites based on its floristic composition; (iii) a floristic account including descriptions of the 35 most representative turf-forming species from sand-covered rocks; (iv) taxonomic studies of 13 selected species.

Material and methods

Field collections

An extensive collection of seaweeds from sand-covered rocks was made in the intertidal of 88 sites from the Atlantic Iberian Peninsula, between 2002-2012 (Fig. 1, in general material and methods). Furthermore, the upper subtidal of some locations was also studied, as well as some samples were also collected in 50 additional locations visited with other purposes (Fig. 2, in general material and methods). Vegetation from sand-covered rocks usually consists of turf-forming species, but some erect algae are also characteristic of these habitats. This floristic study has been carried out based on samples of turf-forming species and the erect species *Ahnfeltia plicata*, *Cladostephus spongiosus*, *Chondracanthus acicularis*, *Chondracanthus teedei*, *Gracilaria gracilis*, *G. multipartita*, *Halopithys incurva* and *Stypocaulon scoparium*.

In general, samples consisted of the total scraping of 225-400 cm² quadrats of the different turfs and erect assemblages visually identified in the field. Samples were preserved in 4% formalin in seawater at 4 °C and stored in the dark for later study. In addition, since 2010 samples of the most representative species collected were carefully isolated and preserved in silica gel for their molecular analysis. Other parts of the samples were preserved in formalin for morphological studies.

Samples identification

In the laboratory, species were studied and identified using a stereomicroscope and optical microscope, as well as floras and monographs of the different algal groups. Among the most frequently used works are the several volumes of the Seaweeds of the British Isles, especially the Volume on Ceramiales (Maggs & Hommersand 1993) and the thesis on Rhodomelaceae and Ceramiaceae from the Canary Islands (Sansón Acedo 1991, Rojas González 1997) and the Basque Country (Secilla 2012). Representative specimens were preserved and deposited in the herbarium of the Universidade de Santiago de Compostela (SANT), adding up to a total of about 4800 specimens. Herbarium abbreviations follow Thiers (2013).

Morphological studies

Representative specimens of selected species were mounted in 20% Karo[®] Syrup (ACH Foods, Memphis, TN, USA) and 80% distilled water. Certain species were previously stained with aniline blue, while others were mounted in a mixture of 1% aniline blue, 1% acetic acid, 50% Karo[®] Syrup and 48% distilled water (Millar & Wynne 1992). Sections for microscopic observations were made by hand using a razor blade. Photographs were taken using a Olympus C-5060 digital camera mounted on a Olympus BX50 (Tokyo, Japan) microscope and line drawings using camera lucida.

Molecular analysis of samples

DNA extraction and sequencing. A fragment of about 1 mg of dried thalli was frozen in liquid nitrogen and individually ground into a fine powder using disposable steel beads and a Mini-Bead Beater (Biospec Products, Bartlesville, OK, USA). Immediately afterwards, total DNA was extracted using the Wizard Magnetic 96 DNA Plant System (Promega, USA) kit following the manufacturer's instructions. The extracted DNA was stored at -20°C till amplification of *rbcL*, *cox1* and SSU genes.

Analysis of rbcL, cox1 and SSU regions. Specific primer pairs for the amplification and sequencing reaction of each gene are listed in the Table 1. All PCR amplifications were carried out with a TProfessional Basic thermocycler (Biometra, Germany) using a Taq reaction kit (Sigma Aldrich, USA): a total volume of 25 µL containing 1× Buffer, 2mM MgCl₂, 1nM dNTP mixture, 0.15 mM of each primer, 1 unit of Taq and 1 µL of DNA solution (*rbcL* and/or SSU); and 1× Buffer, 2.5mM MgCl₂, 0.192mM dNTP mixture, 0.1mM of each primer, 1 unit of Taq and 2 µL of DNA solution (COI-5P). PCR was performed with an initial denaturation step at 94°C for 10 min, followed by 35 cycles of 30 s at 90°C, 30s at 50°C, and 2 min at 72°C, with a final 10 min extension cycle at 72°C.

PCR products were purified using a Cycle Pure kit E.Z.N.A. (Omega Bio-Tek, USA). A fewer number of samples were purified using shrimp alkaline phosphatase and exonuclease I enzymes. After removing the excess of primers and nucleotides, fragments were sequenced on an ABI Prism 3730xl DNA Analyzer™ (Perkin-Elmer, USA) using BigDye™ Terminator kit according to manufacturer's recommendations. Sequences were checked, edited, and aligned with CodonCode Aligner software (CodonCode Co., USA) or Geneious Pro 5.6.4 (Biomatters Ltd., New Zealand).

Table 1. Primer sequences utilized in amplification and sequencing reactions of *rbcL*, SSU and COI-5P.

Locus / primer name	Primer sequence	Reference
COI-5P		
Cox1R1	GTATACATATGATGHGCTCAA	Saunders, unpublished
GwsFn	TCAACAAAYCAYAAAGATATYGG	Le Gall & Saunders 2010
GwsLF2	CAAAYCAYAARGATATHGGNAC	Saunders, unpublished
GwsRx	ACTTCTGGRTGICCRARAAYCA	Saunders, unpublished
<i>rbcL</i>		
F7	AACTCTGTAGAACGNACA	Freshwater & Rueness 1994
R753	GCTCTTTCATACATATCTTCC	Freshwater & Rueness 1994
F645	ATGCGTTGGAAAGAAAGATTCT	Lin <i>et al.</i> 2001

Table 1. Continued.

Locus / primer name	Primer sequence	Reference
Rbcs start	TGTGTTGCGGCCCGCCCTTGTGTTAGTCTCAC	Freshwater & Rueness 1994
Frbcl	TGTGTTGTCGACATGTCTAACTCTGTAGAAG	Freshwater & Rueness 1994
R1150+	GCATTTKWCCACARTGDATACC	Choi <i>et al.</i> , unpublished
F993G	GGTACTGTAGTAGGTAACTAGAAAGG	Choi <i>et al.</i> , unpublished
RbcsP	GTCCCTTGTGTTAGTCTCAC	Choi <i>et al.</i> , unpublished
SSU		
G01	CACCTGGTTGATCCTGCCAG	Saunders & Kraft 1994
G14	CCTTGGCAGACGCTTTTCGCAG	Saunders & Kraft 1994
G04	CAGAGGTGAAATTCTTGAT	Saunders & Kraft 1994
G07	AGCTTGATCCTTCTGCAGGTTACCTAC	Saunders & Kraft 1994

Analysis of molecular data

Sequences were obtained for both DNA strands and assembled, corrected and aligned together with sequences downloaded from GenBank using Geneious Pro 5.6.4 (Biomatters Ltd., Auckland, New Zealand). Sequences comparisons were conducted using uncorrected-p distance and the distance analyses were performed using the neighbor-joining. Bootstrap resampling (1000 replicates) was performed to estimate robustness (Felsenstein 1985).

Preparation of the Catalogue

Orders and families were arranged according to Bárbara *et al.* (2005a) and updated according to Algaebase (Guiry & Guiry 2013). Species and genus were named with their nomenclatural authorities and alphabetically arranged. The frequency of the species along all the Atlantic Iberian Peninsula was indicated in the catalogue (IP). Furthermore, the coast was divided in 5 geographical regions (Fig. 1, general materials and methods) grouping the territorial provinces: Cantabrian (CA) including Guipúzcoa, Vizcaya, Santander and Asturias; Galicia (GA), including Lugo, A Coruña and Pontevedra; northern Portugal (NP), including Minho, Douro Litoral and Beira Litoral; central Portugal (CP), including Estremadura; and southern Iberian Peninsula (SP), including Alentejo, Algarve and Cádiz. The number of sites where each species was found per region is also indicated. Furthermore, the habitat of the species was included in the catalogue, considering if the species were found growing in sand-covered rocks (SC) or were epiphyte on other seaweeds (EP); as well as, if they were collected in turf assemblages (T) or in erect ones (E). Those species that are treated in the chapter 1.2 are indicated with asterisks.

Distribution maps

Locations where representative materials of the different species were collected in this study and were housed in SANT are represented in a map for each species. Note that in some cases species were found in more locations than those represented on maps, because materials of the different taxa were not always representative of the species (i.e. young small plants or very scarce material) and herbarium sheets were not mounted for all recorded sites. However, these records were counted for frequencies listed in the catalogue. Therefore, number of points in the maps is frequently lower than the number of records listed in the catalogue. World maps showing the distribution of the species were also provided and were based on available data in Algaebase (Guiry & Guiry 2013).

Analysis of floristic and biogeographic data

With the aim to explore relationships between the 88 sites sampled along the Atlantic Iberian Peninsula, we used a principal coordinate analysis (PCO) and a hierarchical group average agglomerative clustering method. Both were based on a Bray-Curtis dissimilarities matrix (Clarke *et al.* 2006) calculated from presence/absence data of the different species in the studied sites. Significance of groupings in the cluster analysis was tested using the similarity profile test (SIMPROF) on a null hypothesis that a specific sub-cluster can be recreated by permuting the entry species and samples (Clarke & Warwick, 2001). The percentage similarity routine (SIMPER) was employed to quantify the contribution of each species to the dissimilarity between the geographic areas. Multivariate analysis were performed using PRIMER v6 + PERMANOVA (Clarke & Warwick 2001, Clarke & Gorley 2006, Anderson *et al.* 2008).

Chapter 1.1. Catalogue of the seaweeds from sand-covered rocks along the Atlantic Iberian Peninsula

The Catalogue

Table 1 shows the catalogue of the species from sand-covered rocks collected during the development of this study. The frequency of each species in the Atlantic Iberian Peninsula (IP) is indicated, as well as in the 5 regions in which it was divided. Furthermore, the habitat of the species and the type of assemblage where they were collected are also indicated. The catalogue includes 257 species: 182 Rhodophyta, 45 Ochrophyta and 30 Chlorophyta. The number of species and infraspecific taxa and stages is 268: 191 Rhodophyta, 46 Ochrophyta and 30 Chlorophyta. Most species were collected directly attached to sand-covered rocks (125 taxa), while 81 taxa were epiphytes and 62 were found in both types of substrate. In addition, 2 species were parasitic. Most species were found both on turf-forming and erect assemblages (146 taxa), a great number were found only in turfs (79), while only 45 taxa were exclusively collected in erect assemblages.

Table 1. Catalogue of the benthic marine algae from sand-covered rocks along the Atlantic Iberian Peninsula. For each species is indicated its frequency in the Atlantic Iberian Peninsula (IP), as well as in its different regions (from North to South: CA = Cantabrian Sea, GA = Galicia, NP = northern Portugal, CP = Center Portugal, SP = southern Iberian Peninsula; n is indicated between asterisks); and the habitat in which they were collected (Hab.: SC = Sand-covered rocks, EP = epiphyte), as well as, the type of assemblage (Assem.: T = turf assemblages, E= erect assemblages). Asterisks indicate the species that are treated in Chapter 1.2.

	IP (88)	CA (24)	GA (38)	NP (7)	CP (3)	SP (16)	Hab.	Assem.
RHODOPHYTA								
BANGIOPHYCEAE								
STYLONEMATALES								
Stylonemataceae								
Stylonema Reinsch								
<i>Stylonema alsidii</i> (Zanardini) K.M. Drew	8	6	2	0	0	0	T	EP
ERYTHROPELTIDALES								
Erythrotrichiaceae								
Porphyrostromium Trevisan								
<i>Porphyrostromium boryanum</i> (Montagne) P.C. Silva	10	3	7	0	0	0	T	EP
<i>Porphyrostromium cillare</i> (Carmichael) M.J. Wynne	8	2	5	1	0	0	T	EP
Erythrotrichia Areschoug								
<i>Erythrotrichia bertholdii</i> Batters	17	13	4	0	0	0	T	EP
<i>Erythrotrichia carnea</i> (Dillwyn) J. Agardh	23	13	9	0	1	0	T/E	SC
BANGIALES								
Bangiaceae								
Porphyra C. Agardh								
<i>Porphyra umbilicalis</i> Kützting	2	0	2	0	0	0	T/E	EP
Pyropia								
<i>Pyropia leucosticta</i> (Thuret) Neefus & J. Brodie	54	20	27	1	3	3	T	EP

	IP (88)	CA (24)	GA (38)	NP (7)	CP (3)	SP (16)	Hab.	Assem.
FLORIDOPHYCEAE								
COLACONEMATALES								
Colaçonemataceae								
Colaçonema Batters								
<i>Colaçonema daviesii</i> (Dillwyn) Stegenga	50	23	25	1	1	0	T/E	EP
PALMARIALES								
Rhodothamniellaceae								
Rhodothamniella Feldmann								
<i>*Rhodothamniella floridula</i> (Dillwyn) Feldmann	79	23	36	7	3	10	T	SC
AHNFEITIALES								
Ahnfeltiaceae								
Ahnfeltia Fries								
<i>Ahnfeltia plicata</i> (Hudson) Fries	24	4	16	4	0	0	E	SC
NEMALIALES								
Scinaiceae								
Scinaia Bivona-Bernardi								
<i>Scinaia furcellata</i> (Turner) J. Agardh	4	1	1	2	0	0	T/E	SC
GELIDIALES								
Gelidiaceae								
Gelidium J.V. Lamoroux								
<i>Gelidium attenuatum</i> (Turner) Thuret	4	0	1	3	0	0	T/E	SC
<i>*Gelidium crinale</i> (Hare ex Turner) Gaillon	25	5	11	1	2	6	T	SC
<i>Gelidium latifolium</i> Bornet ex Hauck	3	1	2	0	0	0	T/E	SC
<i>Gelidium pusillum</i> (Stackhouse) Le Jolis	36	9	12	5	0	10	T/E	SC
<i>Gelidium pusillum</i> var. <i>pulvinatum</i> (C. Agardh) J. Feldmann	12	3	5	3	0	1	T/E	SC
<i>Gelidium corneum</i> (Hudson) Lamouroux	4	1	2	0	0	1	E	SC/EP
<i>*Gelidium sphaulatum</i> (Kützinger) Bornet	9	6	1	0	0	2	T	SC
Pterocladaceae								
Pterocladia B. Santelices & Hommersand								
<i>Pterocladia capillacea</i> (S.G. Gmelin) Santelices & Hommersand	13	2	9	1	1	0	T/E	SC
<i>*Pterocladia melanoidea</i> (Schousboe ex Bornet) Santelices & Hommersand	32	12	13	5	1	1	T/E	SC
GRACILARIALES								
Gracilariaceae								
Gracilaria Greville								
<i>Gracilaria armata</i> (C. Agardh) Greville	2	0	0	0	0	2	T/E	SC
<i>Gracilaria dendroides</i> Gargiulo, de Masi & Tripodi	1	0	0	0	0	1	E	SC
<i>Gracilaria gracilis</i> (Stackhouse) M. Steentoft, L.M. Irvine & W.F. Farnham	19	4	8	6	0	1	E	SC
<i>Gracilaria multipartita</i> (Clemente) Harvey	5	1	2	1	0	1	E	SC
Pterocladophilaceae								
Holmsella Sturch								
<i>Holmsella pachyderma</i> (Reinsch) Sturch	5	2	3	0	0	0	E	P
BONNEMAISONIALES								
Bonnemaisoniaceae								
Asparagopsis Montagne								
<i>Asparagopsis armata</i> Harvey	17	3	5	0	0	9	T/E	EP
Falkenbergia F. Schmitz								
<i>Falkenbergia rufolanosa</i> (Harvey) F. Schmitz stadium	54	18	27	0	1	8	T	SC
Bonnemaisonia C. Agardh								
<i>Bonnemaisonia hamifera</i> Hariot	4	3	1	0	0	0	E	EP

	IP (88)	CA (24)	GA (38)	NP (7)	CP (3)	SP (16)	Hab.	Assem.
Trailliella Batters								
<i>Trailliella intricata</i> Batters stadium	7	7	0	0	0	0	E	EP
HALYMENIALES								
Halymeniaceae								
<i>Dermocorynus</i> P.L. Crouan & H.M. Crouan								
<i>Dermocorynus dichotoma</i> (J. Agardh) Gargiulo, M. Morabito & Manghisi	3	0	0	3	0	0	T/E	SC
<i>Grateloupia</i> C. Agardh								
<i>Grateloupia filicina</i> (J.V. Lamouroux) C. Agardh	15	4	9	2	0	0	T	SC
<i>Grateloupia turuturu</i> Yamada	1	0	0	1	0	0	E	SC
PEYSSONNELIALES								
Peyssonneliaceae								
<i>Peyssonnelia</i> Decaisne								
<i>Peyssonnelia atropurpurea</i> P.L. Crouan & H.M. Crouan	9	0	5	3	0	1	T/E	SC
<i>Peyssonnelia coriacea</i> Feldmann	1	1	0	0	0	0	T	SC
<i>Peyssonnelia duby</i> P.L. Crouan & H.M. Crouan	16	5	6	2	1	2	T/E	SC
HILDENBRANDIALES								
Hildenbrandiaceae								
<i>Hildenbrandia</i> Nardo								
<i>Hildenbrandia crouaniorum</i> J. Agardh	1	0	1	0	0	0	T	SC
<i>Hildenbrandia rubra</i> (Sommerfelt) Meneghini	41	9	28	2	0	2	T/E	SC
CORALLINALES								
Corallinaceae								
<i>Corallina</i> Linnaeus								
<i>Corallina elongata</i> J. Ellis & Solander	76	20	34	7	3	12	T/E	SC
<i>Corallina officinalis</i> Linnaeus	3	0	0	2	0	1	E	EP
<i>Jania</i> J.V. Lamouroux								
<i>Jania longifurca</i> Zanardini	71	21	29	5	2	14	T/E	SC
<i>Jania rubens</i> (Linnaeus) J.V. Lamouroux	27	13	7	0	0	7	E	EP
<i>Jania rubens</i> var. <i>corniculata</i> (Linnaeus) Yendo	11	6	4	0	0	1	E	EP
<i>Jania squamata</i> (Linnaeus) J.H. Kim, Guiry & H.-G. Choi	1	0	1	0	0	0	E	SC/EP
Lithophylloideae								
<i>Amphiroa</i> J.V. Lamouroux								
<i>Amphiroa beauvoisii</i> J.V. Lamouroux	2	0	0	0	0	2	E	SC
<i>Amphiroa rigida</i> J.V. Lamouroux	1	0	0	0	0	1	E	SC
<i>Lithophyllum</i> Philippi								
<i>Lithophyllum incrustans</i> R.A. Philippi	74	19	34	7	3	11	T/E	SC
<i>Titanoderma</i> Nägeli								
<i>Titanoderma pustulatum</i> (J.V. Lamouroux) Nägeli	2	0	2	0	0	0	E	EP
Hapalidiaceae								
<i>Choreonema</i> F. Schmitz								
<i>Choreonema thuretii</i> (Bornet) F. Schmitz	31	11	16	3	0	1	E	EP
<i>Melobesia</i> J.V. Lamouroux								
<i>Melobesia membranacea</i> (Esper) J.V. Lamouroux	33	14	7	3	0	9	E	EP
<i>Mesophyllum</i> Me. Lemoine								
<i>Mesophyllum lichenoides</i> (J. Ellis) Marie Lemoine	25	9	9	1	0	6	E	EP

	IP (88)	CA (24)	GA (38)	NP (7)	CP (3)	SP (16)	Hab.	Assem.
GIGARTINALES								
Caulacanthaceae								
Catenella Greville								
<i>Catenella caespitosa</i> (Withering) L.M. Irvine	1	0	0	1	0	0	T	SC
Caulacanthus Kützinger								
<i>Caulacanthus ustulatus</i> (Mertens ex Turner) Kützinger	31	8	11	3	1	8	T/E	SC/EP
Cruoriaceae								
Pseudopolyides Gallardo, Bárbara & Cremades								
<i>Pseudopolyides furcellarioides</i> Gallardo, Bárbara & Cremades	1	0	1	0	0	0	T/E	SC/EP
Cystocloniaceae								
Calliblepharis Kützinger								
<i>Calliblepharis jubata</i> (Goodenough & Woodward) Kützinger	5	0	3	2	0	0	E	SC/EP
* <i>Calliblepharis hypneoides</i> Díaz-Tapia, Bárbara & Hommersand	26	9	8	4	1	4	T	SC
Hypnea J.V. Lamouroux								
<i>Hypnea musciiformis</i> (Wulfen) J.V. Lamouroux	7	2	0	0	0	5	E	EP
Gigartinaceae								
Chondracanthus Kützinger								
<i>Chondracanthus acicularis</i> (Roth) Fredericq	49	11	23	5	1	9	T/E	SC
<i>Chondracanthus teedei</i> (Mertens ex Roth) Kützinger	28	1	20	6	1	0	E	SC
<i>Chondracanthus teedei</i> var. <i>lusitanicus</i> (J.E. De Mesquita Rodrigues) Bárbara & Cremades	26	0	2	5	0	0	E	SC
Chondrus Stackhouse								
<i>Chondrus crispus</i> Stackhouse	7	1	3	2	0	1	T/E	SC
<i>Chondrus crispus</i> var. <i>filliformis</i> (Hudson) Lyngbye	2	0	2	0	0	0	E	SC
Gigartina Stackhouse								
<i>Gigartina pistillata</i> (S.G. Gmelin) Stackhouse	30	2	19	5	1	3	T/E	SC
Phylloporaceae								
Ahnfeltiopsis P.C. Silva & De Cew								
<i>Ahnfeltiopsis devoniensis</i> (Greville) P.C. Silva & De Cew	23	3	12	7	0	1	T/E	SC
Gymnogongrus Martius								
<i>Gymnogongrus crenulatus</i> (Turner) J. Agardh	24	3	14	7	0	0	T/E	SC
* <i>Gymnogongrus griffithsiae</i> (Turner) Martius	50	11	23	7	2	7	T/E	SC
Mastocarpus Kützinger								
<i>Mastocarpus stellatus</i> (Stackhouse) Guiry in Guiry, J.A. West, D.-H. Kim & Masuda	15	1	9	4	0	1	T/E	EP
Petrocelis J. Agardh								
<i>Petrocelis cruenta</i> J. Agardh stadium	12	1	8	2	1	0	T/E	SC
Phyllophora Greville								
<i>Phyllophora crispa</i> (Hudson) P.S. Dixon	1	0	1	0	0	0	T	SC
<i>Phyllophora sicula</i> (Kützinger) Guiry & L.M. Irvine	3	2	1	0	0	0	E	SC

	IP (88)	CA (24)	GA (38)	NP (7)	CP (3)	SP (16)	Hab.	Assem.
PLOCAMIALES								
Plocamiaceae								
Plocamium J.V. Lamouroux								
* <i>Plocamium maggsiae</i> G.W. Saunders & K.V. Lehmkuhl	76	22	30	7	3	14	T/E	SC/EP
RHODYMENIALES								
Champiaceae								
Champia Desvaux								
<i>Champia parvula</i> (C. Agardh) Harvey	39	14	14	1	0	10	T/E	EP
Chylocladia Greville								
<i>Chylocladia verticillata</i> (Lightfoot) Bliding	15	7	8	0	0	0	T/E	SC/EP
Gastroclonium Kützing								
<i>Gastroclonium ovatum</i> (Hudson) Papenfuss	27	4	16	1	0	6	T	SC
* <i>Gastroclonium reflexum</i> (Chauvin) Kützing	57	14	22	5	3	13	T/E	SC
Lomentariaceae								
Lomentaria Lyngbye								
<i>Lomentaria articulata</i> (Hudson) Lyngbye	24	3	17	4	0	0	T/E	EP
<i>Lomentaria clavellosa</i> (Turner) Gaillon	18	3	8	0	0	7	T/E	SC/EP
Rhodymeniaceae								
Cordylecladia J. Agardh								
<i>Cordylecladia erecta</i> (Greville) J. Agardh	3	1	2	0	0	0	T/E	SC
Rhodymenia Greville								
<i>Rhodymenia holmesii</i> Ardissonne	1	0	1	0	0	0	E	SC
<i>Rhodymenia pseudopalmata</i> (J.V. Lamouroux) P.C. Silva	1	1	0	0	0	0	T	SC
CERAMIALES								
Callithamniaceae								
Aglaothamnion Feldmann-Mazoyer								
<i>Aglaothamnion bipinnatum</i> (P.L. Crouan & H.M. Crouan) Feldmann & G. Feldmann	1	0	1	0	0	0	T	EP
<i>Aglaothamnion gallicum</i> (Nägeli) Halos <i>ex</i> Ardré	37	14	15	0	1	7	T/E	EP
<i>Aglaothamnion hookeri</i> (Dillwyn) Maggs & Hommersand	35	11	14	3	0	7	T/E	EP
<i>Aglaothamnion pseudobyssoides</i> (P.L. Crouan & H.M. Crouan) Halos	9	4	2	0	0	3	T/E	EP
<i>Aglaothamnion</i> sp.	6	0	0	0	1	5	T/E	SC
<i>Aglaothamnion tenuissimum</i> (Bonnemaison) Feldmann-Mazoyer	22	13	5	0	0	4	T/E	SC/EP
Callithamniella Feldman-Mazoyer								
<i>Callithamniella tingitana</i> (Schousboe <i>ex</i> Bornet) Feldman-Mazoyer	1	0	1	0	0	0	T	EP
Callithamnion Lyngbye								
<i>Callithamnion granulatum</i> (Ducluzeau) C. Agardh	9	4	3	0	0	2	T/E	EP
<i>Callithamnion tetragonum</i> (Withering) S.F.Gray	36	13	15	2	2	4	T/E	EP
<i>Callithamnion tetricum</i> (Dillwyn) S.F.Gray	6	0	5	1	0	0	T/E	SC/EP
Crouania J. Agardh								
<i>Crouania attenuata</i> (C. Agardh) J. Agardh	31	13	6	0	2	10	T/E	EP
Ceramiaceae								
Antithamnion Nägeli								
<i>Antithamnion amphigeneum</i> A.J.K. Millar	3	3	0	0	0	0	T/E	EP
<i>Antithamnion cruciatum</i> (C. Agardh) Nägeli	5	1	1	1	0	2	T/E	SC/EP
<i>Antithamnion villosum</i> (Kützing) Athanasiadis	3	0	2	0	0	1	T/E	SC

	IP (88)	CA (24)	GA (38)	NP (7)	CP (3)	SP (16)	Hab.	Assem.
Antithamnionella Lyle								
<i>Antithamnionella boergesenii</i> (Cormaci & G. Furnari) Athanasiadis	4	4	0	0	0	0	T/E	EP
<i>Antithamnionella multiglandulosa</i> A. Secilla, A. Santolaria, I. Díez & J.M. Gorostiaga	10	5	2	0	1	2	T	EP
<i>Antithamnionella ternifolia</i> (J.D. Hooker & Harvey) Lyle	23	9	12	2	0	0	T/E	EP
Bornetia Thuret								
<i>Bornetia secundiflora</i> (J. Agardh) Thuret	4	3	0	0	0	1	T/E	SC/EP
Centroceras Kützing								
<i>Centroceras clavulatum</i> (C. Agardh) Montagne	21	14	0	0	0	7	T/E	SC/EP
Ceramium Roth								
<i>Ceramium botryocarpum</i> A.W. Griffiths ex Harvey	38	9	13	5	3	8	T	EP
* <i>Ceramium ciliatum</i> (J. Ellis) Ducluzeau	62	21	27	1	0	13	T/E	SC/EP
<i>Ceramium cimbricum</i> H.E. Petersen	2	2	0	0	0	0	E	EP
<i>Ceramium echionotum</i> J. Agardh	45	16	20	4	0	5	T/E	EP
<i>Ceramium gaditanum</i> (Clemente)	10	2	3	5	0	0	T/E	SC/EP
Cremades								
<i>Ceramium pallidum</i> (Nägeli ex Kützing) Maggs & Hommersand	40	9	19	5	3	4	T/E	EP
<i>Ceramium secundatum</i> Lyngbye	62	19	32	6	2	3	T/E	EP
<i>Ceramium siliquosum</i> (Kützing) Maggs & Hommersand	1	0	1	0	0	0	T	EP
<i>Ceramium tenuicorne</i> (Kützing) Waern	6	1	5	0	0	0	T/E	EP
<i>Ceramium virgatum</i> Roth	8	1	2	2	1	2	T	EP
Gayliella T.O. Cho, L.J. McIvor & S.M. Boo								
<i>Gayliella flaccida</i> (Harvey ex Kützing) T.O. Cho & L.J. McIvor	74	23	29	6	2	14	T/E	EP
Scageliopsis E.M. Wollaston								
<i>Scageliopsis patens</i> Wollaston	4	4	0	0	0	0	T/E	EP
Dasyaceae								
Dasya C. Agardh								
<i>Dasya baillouviana</i> (S.G. Gmelin) Montagne	1	0	0	0	0	1	T/E	EP
<i>Dasya hutchinsiae</i> Harvey	41	15	19	0	0	7	T/E	SC/EP
<i>Dasya ocellata</i> (Grateloup) Harvey	6	3	0	0	0	3	T/E	SC/EP
<i>Dasya rigidula</i> (Kützing) Ardissonne	2	0	0	0	0	2	T/E	SC/EP
Heterosiphonia Montagne								
<i>Heterosiphonia crispella</i> (C. Agardh) M.J. Wynne	3	0	0	0	0	3	E	EP
<i>Heterosiphonia plumosa</i> (J. Ellis) Batters	16	2	13	0	0	1	T/E	SC/EP
Delesseriaceae								
Acrosorium Zanardini ex Kützing								
<i>Acrosorium ciliolatum</i> (Harvey) Kylin	33	8	19	2	0	4	T/E	EP
Apoglossum J. Agardh								
<i>Apoglossum ruscifolium</i> (Turner) J. Agardh	9	4	4	1	0	0	T/E	SC/EP
Cryptopleura Kützing								
<i>Cryptopleura ramosa</i> (Hudson) L. Newton	47	14	24	5	0	4	T	SC
Drachiella J. Ernst & Feldmann								
<i>Drachiella minuta</i> (Kylin) Maggs & Hommersand	1	1	0	0	0	0	T/E	SC/EP
Erythroglossum J. Agardh								
* <i>Erythroglossum lusitanicum</i> Ardré	16	2	8	3	0	3	T/E	EP

	IP (88)	CA (24)	GA (38)	NP (7)	CP (3)	SP (16)	Hab.	Assem.
Haraldiophyllum F. Schmitz								
<i>Haraldiophyllum bonnemaisoni</i> (Kylin) A.D. Zinova	1	0	1	0	0	0	E	EP
Hypoglossum Kützing								
* <i>Hypoglossum hypoglossoides</i> (Stackhouse) F.S. Collins & Hervey	72	20	30	6	3	13	T/E	SC/EP
Nitophyllum Greville								
<i>Nitophyllum punctatum</i> (Stackhouse) Greville	5	1	2	0	0	2	E	EP
Taenioma J. Agardh								
<i>Taenioma nanum</i> (Kützing) Papenfuss	2	0	0	0	0	2	T/E	EP
Rhodomelaceae								
Aiolocolax M.A. Pocock								
* <i>Aiolocolax pulchellus</i> M.A. Pocock	46	14	22	3	3	4	T	P
Aphanocladia Falkenberg								
<i>Aphanocladia stichidiosa</i> (Funk) Ardré	5	0	1	0	0	4	T/E	SC/EP
Boergesenella Kylin								
<i>Boergesenella fruticulosa</i> (Wulfen) Kylin	3	2	1	0	0	0	T/E	SC/EP
<i>Boergesenella thuyoides</i> (Harvey) Kylin	39	9	20	3	1	6	T/E	EP
Bostrychia Montagne								
<i>Bostrychia scorpioides</i> (Hudson) Montagne	1	0	0	1	0	0	T	SC
Chondria C. Agardh								
<i>Chondria capillaris</i> (Hudson) M.J. Wynne	5	1	0	0	0	4	T	SC/EP
* <i>Chondria coerulescens</i> (J. Agardh) Falkenberg	67	19	27	5	1	15	T	SC
<i>Chondria dasyphylla</i> (Woodward) C. Agardh	6	4	1	0	0	1	T/E	SC
<i>Chondria scintillans</i> G. Feldmann	25	2	17	2	0	4	T/E	SC
Ctenosiphonia Falkenberg								
* <i>Ctenosiphonia hypnoides</i> (Welwitsch ex J. Agardh) Falkenberg	1	0	1	0	0	0	T/E	SC
Halopithys Kützing								
<i>Halopithys incurva</i> (Hudson) Batters	14	8	0	0	0	6	E	SC
Herposiphonia Nägeli								
<i>Herposiphonia secundaf. secunda</i> (C. Agardh) Falkenberg	9	0	2	1	0	6	T/E	SC/EP
* <i>Herposiphonia cf. secundaf. tenella</i> (C. Agardh) M.J. Wynne	24	8	3	0	1	12	T/E	SC/EP
<i>Herposiphonia</i> sp.	3	1	0	0	0	2	T/E	EP
Laurencia J.V. Lamoroux								
<i>Laurencia cf. chondrioides</i> Børgesen	12	0	0	0	1	11	T/E	SC/EP
<i>Laurencia cf. minuta</i> Vandermeulen, Garbary & Guiry	1	0	0	0	0	1	T	SC
<i>Laurencia pyramidalis</i> Bory de Saint- Vincent ex Kützing	5	4	1	0	0	0	T/E	SC/EP
Leptosiphonia Kylin								
* <i>Leptosiphonia schousboei</i> (Thuret) Kylin	13	0	6	7	0	0	T/E	SC/EP
Lophosiphonia Falkenberg								
* <i>Lophosiphonia reptabunda</i> (Suhr) Kylin	41	17	7	2	0	15	T	SC
* <i>Lophosiphonia</i> sp.	21	11	3	0	0	7	T	SC
Neosiphonia M.S. Kim & I.K. Lee								
<i>Neosiphonia harveyi</i> (J.W. Bailey) M.-S. Kim, H.-G. Choi, Guiry & G.W. Saunders	1	1	0	0	0	0	T	EP
Ophidocladus Falkenberg								
<i>Ophidocladus simpliciusculus</i> (P.L.Crouan & H.M.Crouan) Falkenberg	83	23	35	7	3	15	T	SC

	IP (88)	CA (24)	GA (38)	NP (7)	CP (3)	SP (16)	Hab.	Assem.
Osmundea Stackhouse								
<i>Osmundea hybrida</i> (A.P. de Candolle) K.W.Nam	10	4	5	0	0	1	T/E	SC/EP
<i>Osmundea pinnatifida</i> (Hudson) Stackhouse	59	13	27	7	3	9	T/E	SC
<i>Osmundea truncata</i> (Kützinger) K.W. Nam & Maggs	3	1	2	0	0	0	T/E	SC
Polysiphonia Greville								
<i>Polysiphonia atlantica</i> Kapraun & J.N. Norris	3	1	2	0	0	0	T	SC/EP
<i>Polysiphonia brodiei</i> (Dillwyn) Sprengel	8	0	8	0	0	0	T	SC/EP
* <i>Polysiphonia caespitosa</i> (M.A. Pocock) Hollenberg	84	23	36	7	3	15	T	SC
<i>Polysiphonia ceramiaeformis</i> P.L. Crouan & H.M. Crouan	2	1	0	0	0	1	E	EP
<i>Polysiphonia denudata</i> (Dillwyn) Greville <i>ex</i> Harvey	1	0	0	0	0	1	T	SC
* <i>Polysiphonia devoniensis</i> Maggs & Hommersand	11	9	0	0	0	2	T	SC
<i>Polysiphonia fibrata</i> (Dillwyn) Harvey	12	5	2	0	0	5	T/E	EP
<i>Polysiphonia fibrillosa</i> (Dillwyn) Sprengel	11	2	9	0	0	0	T/E	EP
* <i>Polysiphonia foetidissima</i> Cocks <i>ex</i> Bornet	14	4	4	0	1	5	T	SC/EP
* <i>Polysiphonia fucooides</i> (Hudson) Greville	8	1	7	0	0	0	T	SC
* <i>Polysiphonia nigra</i> (Hudson) Batters	38	8	25	4	0	1	T	SC
<i>Polysiphonia polyspora</i> (C. Agardh) Montagne	6	1	3	2	0	0	T/E	SC
<i>Polysiphonia sertularioides</i> (Grateloup) J. Agardh	8	2	3	0	2	1	T	SC/EP
Polysiphonia sp4 (a)	1	1	0	0	0	0	T	SC/EP
Polysiphonia sp4 (b)	1	1	0	0	0	0	T	SC
Polysiphonia sp5	6	5	0	0	0	1	T	SC/EP
<i>Polysiphonia sphaerocarpa</i> Børgesen	2	0	0	0	0	2	T/E	EP
* <i>Polysiphonia stricta</i> (Dillwyn) Greville	32	10	16	5	0	1	T	SC
* <i>Polysiphonia triplinata</i> J. Agardh	7	0	1	0	1	5	T/E	SC
Pterosiphonia Falkenberg								
* <i>Pterosiphonia ardreana</i> Maggs & Hommersand	52	18	20	7	2	5	T/E	SC
* <i>Pterosiphonia complanata</i> (Clemente) Falkenberg	56	15	28	7	1	5	T/E	SC/EP
* <i>Pterosiphonia parasitica</i> (Hudson) Falkenberg	21	10	10	0	0	1	T/E	SC/EP
* <i>Pterosiphonia pennata</i> (C. Agardh) Sauvageau	79	23	32	7	3	14	T	SC
Streblocladia F. Schmitz								
* <i>Streblocladia collabens</i> (C. Agardh) Falkenberg	72	21	28	7	3	13	T/E	EP
Sarcomeniaceae								
Cottoniella Børgesen								
<i>Cottoniella filamentosa</i> (M.A. Howe) Børgesen	1	0	0	0	0	1	T/E	EP
Wrangeliaceae								
Anotrichium Nägeli								
<i>Anotrichium furcellatum</i> (J. Agardh) Baldock	2	0	0	0	0	2	T/E	SC/EP
Compothamnion (Nägeli) F. Schmitz								
<i>Compothamnion thuyoides</i> (Smith) Nägeli	6	5	1	0	0	0	T/E	SC
Griffithsia C. Agardh								
<i>Griffithsia opuntioides</i> J. Agardh	1	0	0	0	0	1	E	SC

	IP (88)	CA (24)	GA (38)	NP (7)	CP (3)	SP (16)	Hab.	Assem.
Gymnothamnion J. Agardh								
<i>Gymnothamnion elegans</i> (Schousboe ex C. Agardh) J. Agardh	1	0	1	0	0	0	T	SC
Halurus Kützing								
<i>Halurus equisetifolius</i> (Lightfoot) Kützing	25	9	10	3	0	3	T/E	SC/EP
<i>Halurus flosculosus</i> (J. Ellis) Maggs & Hommersand	11	3	5	0	0	3	T/E	SC/EP
Monosporus Solier								
<i>Monosporus pedicellatus</i> (Smith) Solier	19	7	9	0	0	3	T/E	SC/EP
Pleonosporium Nägeli								
<i>Pleonosporium barreri</i> (Smith) Nägeli	2	1	1	0	0	0	T/E	EP
<i>Pleonosporium flexuosum</i> (C. Agardh) Bornet ex De Toni	8	3	2	1	0	2	T/E	SC/EP
Pterothamnion Nägeli								
<i>Pterothamnion crispum</i> (Ducluzeau) Nägeli	8	2	6	0	0	0	T/E	SC/EP
<i>Pterothamnion plumula</i> (J. Ellis) Nägeli	2	0	2	0	0	0	T	SC/EP
Ptilothamnion Thuret								
* <i>Ptilothamnion sphaericum</i> (P.L. Crouan & H.M. Crouan ex J. Agardh) Maggs & Hommersand	45	19	18	4	1	3	T/E	SC
Spermothamnion Areschoug								
* <i>Spermothamnion repens</i> (Dillwyn) Rosenvinge	41	16	17	2	1	5	T/E	SC
Tiffaniella Doty & Meñez								
* <i>Tiffaniella capitata</i> (Schousboe ex Bornet) Doty & Meñez	8	0	6	1	0	1	T	SC
Vickersia Karsakoff								
<i>Vickersia baccata</i> (J. Agardh) Karsakoff	2	0	0	0	0	2	T/E	SC/EP
OCHROPHYTA								
PHAEOPHYCEAE								
SPHACELARIALES								
Cladostephaceae								
Cladostephus C. Agardh								
<i>Cladostephus spongiosus</i> (Hudson) C. Agardh	52	16	24	5	1	6	T	SC
Sphacelariaceae								
Sphacelaria Lyngbye								
<i>Sphacelaria cirrosa</i> (Roth) C. Agardh	56	23	21	4	1	7	T/E	SC
<i>Sphacelaria fusca</i> (Hudson) S.F. Gray	2	1	0	0	0	1	T	EP
<i>Sphacelaria rigidula</i> Kützing	55	18	21	3	2	11	T/E	SC/EP
<i>Sphacelaria tribuloides</i> Meneghini	1	1	0	0	0	0	T	SC
Stypocaulaceae								
Halopteris Kützing								
<i>Halopteris filicina</i> (Grateloup) Kützing	5	4	1	0	0	0	T/E	SC/EP
Stypocaulon Kützing								
<i>Stypocaulon scoparium</i> (Linnaeus) Kützing	63	21	26	4	1	11	T/E	SC
DICTYOTALES								
Dictyotaceae								
Dictyopteris J.V. Lamouroux								
<i>Dictyopteris polypodioides</i> (A.P. De Candolle) J.V. Lamouroux	7	2	3	1	0	1	T	EP
Dictyota J.V. Lamouroux								
<i>Dictyota dichotoma</i> (Hudson) J.V. Lamouroux	50	13	19	7	2	9	E	SC/EP
Taonia J. Agardh								
<i>Taonia atomaria</i> (Woodward) J. Agardh	17	9	7	0	0	1	T/E	SC/EP

	IP (88)	CA (24)	GA (38)	NP (7)	CP (3)	SP (16)	Hab.	Assem.
Padina Adanson								
<i>Padina pavonica</i> (Linnaeus) Thivy	9	3	1	0	0	5	T	SC
ECTOCARPALES								
Acinetoporasceae								
Acinetospora Bornet								
<i>Acinetospora crinita</i> (Carmichael) Kornmann	43	17	21	1	1	3	T	EP
Feldmannia G. Hamel								
<i>Feldmannia irregularis</i> (Kützting) G. Hamel	1	1	0	0	0	0	T	SC
<i>Feldmannia paradoxa</i> (Montagne) G. Hamel	1	0	1	0	0	0	T/E	SC
Hincksia J.E. Gray								
<i>Hincksia granulosa</i> (Smith) P.C. Silva	40	10	24	1	1	4	T/E	EP
<i>Hincksia mitchelliae</i> (Harvey) P.C. Silva	6	3	2	0	1	0	T/E	EP
<i>Hincksia hincksiae</i> (Harvey) P.C. Silva	1	0	1	0	0	0	T	EP
Chordariaceae								
Elachista Duby								
<i>Elachista fucicola</i> (Vellay) Areschoug	1	0	1	0	0	0	T	EP
Leathesia S.F. Gray								
<i>Leathesia marina</i> (Lyngbye) Decaisne	2	0	2	0	0	0	T/E	SC/EP
Myrionema Greville								
<i>Myrionema strangulans</i> Greville	1	1	0	0	0	0	E	EP
Ectocarpaceae								
Ectocarpus Lyngbye								
<i>Ectocarpus fasciculatus</i> Harvey	4	0	4	0	0	0	T/E	EP
<i>Ectocarpus siliculosus</i> (Dillwyn) Lyngbye	1	1	1	0	0	0	E	EP
Pylaiellaceae								
Pylaiella Bory de Saint-Vincent								
<i>Pylaiella littoralis</i> (Linnaeus) Kjellman	1	0	0	0	0	1	T	SC/EP
Scytosiphonaceae								
Colpomenia (Endlicher) Derbès & Solier								
<i>Colpomenia peregrina</i> Sauvageau	21	5	13	0	1	2	T/E	EP
<i>Colpomenia sinuosa</i> (Mertens <i>ex</i> Roth) Derbès & Solier	1	1	0	0	0	0	T/E	EP
Petalonia Derbès & Solier								
<i>Petalonia fascia</i> (O.F. Müller) Kuntze	6	1	5	0	0	0	T/E	SC
Scytosiphon C. Agardh								
<i>Scytosiphon lomentaria</i> (Lyngbye) Link	2	1	1	0	0	0	T	SC
<i>Scytosiphon complanatus</i> (Rosenvinge) Doty	3	0	3	0	0	0	E	SC
RALFSIALES								
Ralfsiaceae								
Ralfsia Berkeley								
<i>Ralfsia verrucosa</i> (Areschoug) Areschoug	10	4	4	0	1	1	T	SC
SCYTOTHAMNALES								
Bachelotiaceae								
Bachelotia (Bornet) Kuckuck <i>ex</i> G. Hamel								
* <i>Bachelotia antillarum</i> (Grunow) Gerloff	4	0	0	0	0	4	T	SC
CUTLERIALES								
Cutleriaceae								
Aglaozonia Zanardini								
<i>Aglaozonia parvula</i> (Greville) Zanardini stadium	1	1	0	0	0	0	T	SC
LAMINARIALES								
Alariaceae								
Undaria Suringar								
<i>Undaria pinnatifida</i> (Harvey) Suringar	1	0	1	0	0	0	T	SC

	IP (88)	CA (24)	GA (38)	NP (7)	CP (3)	SP (16)	Hab.	Assem.
Laminaria J.V. Lamoroux								
<i>Laminaria ochroleuca</i> Bachelot de la Pylaie	3	0	3	0	0	0	E	SC/EP
FUCALES								
Fucaceae								
Fucus Linnaeus								
<i>Fucus chalonii</i> Feldmann	1	1	0	0	0	0	E	SC
<i>Fucus serratus</i> Linnaeus	3	0	3	0	0	0	T	SC
<i>Fucus spiralis</i> Linnaeus (s.l.)	2	0	0	2	0	0	T/E	SC
<i>Fucus vesiculosus</i> Linnaeus	5	1	3	1	0	0	E	SC
<i>Fucus vesiculosus</i> var. <i>compressus</i> Kjellman	3	1	2	0	0	0	E	SC
Pelvetia Decaisne & Thuret								
<i>Pelvetia canaliculata</i> (Linnaeus) Decaisne & Thuret	1	0	0	1	0	0	T	SC
Himanthaliaceae								
Himanthalia Lyngbye								
<i>Himanthalia elongata</i> (Linnaeus) S.F. Gray	9	0	9	0	0	0	T/E	SC
Sargassaceae								
Bifurcaria Stackhouse								
<i>Bifurcaria bifurcata</i> R. Ross	21	6	13	2	0	0	T/E	SC
Cystoseira C. Agardh								
<i>Cystoseira baccata</i> (S.G. Gmelin) P.C. Silva	12	4	8	0	0	0	T/E	SC
<i>Cystoseira tamariscifolia</i> (Hudson) Papenfuss	13	1	4	0	1	7	E	SC
<i>Cystoseira usneoides</i> (Linnaeus) M. Roberts	1	0	0	0	0	1	T	SC
Sargassum C. Agardh								
<i>Sargassum muticum</i> (Yendo) Fensholt	20	4	15	1	0	0	T/E	SC
<i>Sargassum vulgare</i> C. Agardh	3	0	1	0	0	2	T/E	SC
TILOPTERIDALES								
Phyllariaceae								
Saccorhiza								
<i>Saccorhiza polyschides</i> (Lightfoot) Batters	7	0	7	0	0	0	T/E	SC
CHLOROPHYTA								
ULVOPHYCEAE								
ULVALES								
Ulvaceae								
Ulva Linnaeus								
<i>Ulva bifrons</i> Ardré	2	1	1	0	0	0	T/E	SC
<i>Ulva clathrata</i> (Roth) C. Agardh	72	23	31	3	1	14	T/E	SC/EP
<i>Ulva compressa</i> Linnaeus	1	0	1	0	0	0	T	SC/EP
<i>Ulva prolifera</i> O.F. Müller	72	23	34	7	3	5	E	SC
<i>Ulva pseudolinza</i> (R.P.T. Koeman & Hoek) Hayden, Blomster, Maggs, P.C. Silva, M.J. Stanhope & J.R. Waaland	1	0	1	0	0	0	T	EP
<i>Ulva rigida</i> C. Agardh	82	24	35	7	3	12	T/E	SC/EP
Ulvaria Ruprecht								
<i>Ulvaria obscura</i> (Kützinger) P. Gayral ex C. Bliding	55	16	25	7	0	7	T/E	SC/EP
Umbraulva E.H. Bae & I.K. Lee								
<i>Umbraulva olivascens</i> (P.J.L. Dangeard) G. Furnari	1	0	1	0	0	0	T	SC/EP
CTENOCLADALES								
Ulvellaceae								
Ulvella P.L. Crouan & H.M. Crouan								
<i>Ulvella lens</i> P.L. Crouan & H.M. Crouan	1	0	1	0	0	0	T/E	EP

	IP (88)	CA (24)	GA (38)	NP (7)	CP (3)	SP (16)	Hab.	Assem.
CLADOPHORALES								
Cladophoraceae								
Chaetomorpha Kützing								
<i>Chaetomorpha aerea</i> (Dillwyn) Kützing	85	23	37	7	3	15	T/E	SC
<i>Chaetomorpha ligustica</i> (Kützing) Kützing	49	14	24	7	1	3	T/E	EP
<i>Chaetomorpha</i> cf. <i>melagonium</i> (F. Weber & Mohr) Kützing	6	0	0	0	0	6	T/E	SC
Cladophora Kützing								
<i>Cladophora albida</i> (Nees) Kützing	43	17	17	4	2	3	T/E	SC
<i>Cladophora coelothrix</i> Kützing	2	0	0	0	0	2	T/E	SC
<i>Cladophora hutchinsiae</i> (Dillwyn) Kützing	40	13	14	2	2	9	T/E	SC/EP
<i>Cladophora laetevirens</i> (Dillwyn) Kützing	54	20	31	3	2	13	T/E	SC
<i>Cladophora prolifera</i> (Roth) Kützing	15	6	0	0	0	9	T/E	SC
<i>Cladophora rupestris</i> (Linnaeus) Kützing	39	17	11	7	1	3	T	SC
<i>Cladophora sericea</i> (Hudson) Kützing	30	13	12	3	0	2	T/E	SC
BRYOPSISIDOPHYCEAE								
BRYOPSISDALES								
Bryopsidaceae								
Bryopsis J.V. Lamourux								
<i>Bryopsis corymbosa</i> J. Agardh	1	0	0	0	0	1	T/E	EP
<i>Bryopsis cupressoides</i> J. Agardh	1	0	0	0	0	1	E	EP
<i>Bryopsis plumosa</i> (Hudson) C. Agardh	43	18	16	3	1	5	T/E	SC
Codiaceae								
Codium Stackhouse								
<i>Codium adhaerens</i> C. Agardh	1	1	0	0	0	0	T	SC
<i>Codium tomentosum</i> Stackhouse	19	3	9	1	3	3	T	EP
Derbesiaceae								
Derbesia Solier								
<i>Derbesia marina</i> (Lyngbye) Solier	15	8	1	1	2	3	T	SC
<i>Derbesia tenuissima</i> (Moris & De Notaris) P.L. Crouan & H.M. Crouan	5	0	1	2	0	2	T/E	SC/EP
Pedobesia MacRaid & Womersley								
<i>Pedobesia simplex</i> (Meneghini ex Kützing) M.J. Wynne & Leliaert	1	1	0	0	0	0	T	SC
ULOTRICHALES								
Ulotrichaceae								
Ulothrix Kützing								
<i>Ulothrix flacca</i> (Dillwyn) Thuret	1	0	1	0	0	0	T	EP
Acrosiphonia J. Agardh								
<i>Acrosiphonia arcta</i> (Dillwyn) Gain	1	0	1	0	0	0	T	SC
SIPHONOCLADOPHYCEAE								
SIPHONOCLADALES								
Valoniaceae								
Valonia C. Agardh								
<i>Valonia utricularis</i> (Roth) C. Agardh	2	0	0	0	0	2	E	SC/EP

In addition to the species listed in the catalogue, other species occasionally collected in the habitat but that were not found in our samples are *Porphyra dioica* J. Brodie & L.M. Irvine, *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders, *Cystoseira nodicaulis* (Withering) M. Roberts and *Codium effusum* (Rafinesque) Delle Chiaje.

The species listed in the catalogue comprise a good representation of the flora from the Atlantic Iberian Peninsula (Table 2). The number of species is obviously lower than in checklists from this area, as this work has been focused on a particular habitat. Despite this, the catalogued species represent a high percentage (29-41%) of the species recorded in the Iberian Peninsula, as well as in neighboring areas. This fact evidences that sand-covered rocks is a habitat with a great diversity of species. Seaweeds diversity in sand-covered rocks is specially high within the Rhodophyta group, resulting in high values of Feldmann's and Cheney's indexes which are 4 and 4.7, respectively. This values are higher than those found in checklists from the Atlantic Iberian Peninsula and neighboring regions, and they are more similar to values characteristic from warmer areas. This is explained in part by the great representation of the order Ceramiales in sand-covered rocks. While this group was 60% of the total Rhodophyta species in this habitat, the highest values previously recorded in the involved regions are 47% (Asturias and Northern Portugal) and 51% in Morocco (Atlantic). By contrast, Ochrophyta is poorly represented in sand-covered rocks (18% of the total species number), resembling the values found in the warmest areas of the Atlantic Iberian Peninsula (20% in the Basque Country, Andalucia and the Canary Islands). Chlorophyta has a similar representation in sand-covered rocks than in checklists from the regions of the Atlantic Iberian Peninsula.

Table 2. Comparison between the Atlantic continental temperate regions of the number of Rhodophyta, Ochrophyta and Chlorophyta; Feldmann's and Cheney's ratios; and percent of Ceramiales and Rhodomelaceae within Rhodophyta. References: Britain and Ireland (Hardy & Guiry 2003), Atlantic France (Dizerbo & Herpe 2007), Basque coast (Gorostiaga *et al.* 2004), Asturias (Cires Rodríguez & Cuesta Moliner 2010), Galicia (Bárbara *et al.* 2005a), Northern Portugal (Araújo *et al.* 2009), Southern Portugal (Ardré 1970), Portugal (Bereibar 2011), Andalucia (Flores Moya *et al.* 1995 a, b; Conde *et al.* 1996), the Canary Islands (Haroun *et al.* 2002) and Atlantic coast of Morocco (Benhissoune *et al.* 2001, 2002a, b, 2003).

	Sand-covered Rocks Atlantic Iberian Peninsula	British Isles	France Atlantic	Basque Country	Asturias	Galicia	N Portugal	S Portugal	Portugal total	Andalusia	Canary Islands	Morocco (Atlantic)
Rhodophyta	182	341	423	215	239	296	205	227	348	348	385	314
Ochrophyta	45	182	225	65	101	127	67	75	118	108	125	107
Chlorophyta	30	120	153	51	55	77	46	46	83	86	117	83
R/P ratio	4.04	1.87	1.88	3.31	2.36	2.33	3.06	2.87	2.98	3.22	3.08	2.93
R+C/P ratio	4.71	2.53	2.56	4.09	2.91	2.94	3.75	3.48	3.65	4.02	4.02	3.71
Ceramiales (%)	60	38	40	52	47	44	47	50	46	46	40	51
Rhodomelaceae (%)	27	13	13	20	20	16	18	24	16	20	18	19

The 39 most frequent species in sand-covered rocks from the Atlantic Iberian Peninsula are listed in Table 3. Two groups of species can be separated within this list. The first group includes species that are structural (S), i.e. dominant species in turfs from the Atlantic Iberian Peninsula, as for example *Polysiphonia caespitosa*, *Ophidocladus simpliciusculus* or *Rhodothamniella floridula*. The second group includes very common species in turfs from sand-covered rocks, but that usually have low abundance (A). Among them there are species that grow mixed with structural species, such as *Corallina elongata*, *Lithophyllum incrustans*, *Hypoglossum hypoglossoides* or *Streblacladia collabens*, as well as, species that are very frequent and usually consist of small specimens, often epiphitic on the structural species, as for example *Chaetomorpha aerea*, *Ulva* spp, *Sphacelaria* spp or *Pyropia leucosticta*.

Table 3. List of the 39 most frequent species in sand-covered rocks from the Atlantic Iberian Peninsula, arranged according its frequency (IP). The species recorded in more than 44 sites were selected for this table. Species were classified in structural (S) and accompanying (A) considering if they are dominant species in turfs or they are components of turfs that rarely become abundant, respectively.

Species	IP (88)		Species	IP (88)	
<i>Chaetomorpha aerea</i>	85	A	<i>Gastroclonium reflexum</i>	57	S
<i>Polysiphonia caespitosa</i>	84	S	<i>Pterosiphonia complanata</i>	56	A
<i>Ophidocladus simpliciusculus</i>	83	S	<i>Sphacelaria cirrosa</i>	56	A
<i>Ulva rigida</i>	82	A	<i>Sphacelaria rigidula</i>	55	A
<i>Rhodothamniella floridula</i>	79	S	<i>Ulvaria obscura</i>	55	A
<i>Pterosiphonia pennata</i>	79	S	<i>Pyropia leucosticta</i>	54	A
<i>Corallina elongata</i>	76	A	<i>"Falkenbergia rufolanosa" stadium</i>	54	A
<i>Plocamium maggsiae</i>	76	S	<i>Cladophora laetevirens</i>	54	A
<i>Lithophyllum incrustans</i>	74	A	<i>Pterosiphonia ardreana</i>	52	S
<i>Gayliella flaccida</i>	74	A	<i>Cladostephus spongiosus</i>	52	S
<i>Hypoglossum hypoglossoides</i>	72	A	<i>Colaconema daviesii</i>	50	A
<i>Streblacladia collabens</i>	72	A	<i>Gymnogongrus griffithsiae</i>	50	S
<i>Ulva prolifera</i>	72	A	<i>Dictyota dichotoma</i>	50	A
<i>Jania longifurca</i>	71	A	<i>Chondracanthus acicularis</i>	49	A
<i>Ulva clathrata</i>	70	A	<i>Chaetomorpha ligustica</i>	49	A
<i>Chondria coerulescens</i>	67	S	<i>Cryptopleura ramosa</i>	47	A
<i>Stypocaulon scoparium</i>	63	A	<i>Allocolax pulchellus</i>	46	A
<i>Ceramium ciliatum</i>	62	S	<i>Ceramium echionotum</i>	45	A
<i>Ceramium secundatum</i>	62	A	<i>Ptilothamnion sphaericum</i>	45	S
<i>Osmundea pinnatifida</i>	59	A			

The phycological study of sand-covered rocks from the Atlantic Iberian Peninsula resulted in the finding of numerous records (Rhodophyta, Ochrophyta and Chlorophyta) of chorological interest that are showed in Table 4. Moreover, during this study species of Cyanophyta were occasionally identified, and additional samples were collected in other habitats in the visited sites, finding some new records that are also listed in Table 4 and distinguished by an asterisk. Most new records were published in floristic works (Bárbara *et al.* 2003, 2005, 2006, 2008, 2012, Martínez-Gil *et al.* 2007, Díaz *et al.* 2008, Secilla *et al.* 2008, Araújo *et al.* 2009, Bárbara & Díaz Tapia 2012). During the present study a total of 126 species were first or second records for one or several provinces, which accounted a total of 142 new provincial records. More importantly, the species *Microcoleus acutirostris*, *Aiolocolax pulchellus*, *Sphacelaria rigidula*, *Polysiphonia devoniensis* and *P. fibrata* were new records for Portugal, and *ErythroglOSSum lusitanicum* and *Antithamnion hubbsii* were newly reported in France. In addition, two new species have been described in this work, and our preliminary molecular data showed an important cryptic diversity in some species (see Chapter 1.2). Surprisingly, most of the newly recorded species as well as the new ones are very common in sand-covered rocks of the Atlantic Iberian Peninsula. These observations demonstrate that this habitat has a particular flora that remained poorly explored since some typical species were recorded for the first time during this study even in those areas in which the flora is well know (e.g. Vizcaya). Moreover, Asturias, Cantabria and Lugo are the provinces with more new records, showing that the flora of these provinces was in general poorly known. It must be noted that that the number of studied sites in some provinces of Portugal is lower than those studied in other areas.

Table 4. New records of seaweeds from sand-covered rocks found along the Atlantic Iberian Peninsula during the development of the present study, considering first (1) and second records (2). References of publications are indicated between brackets: 1= Bárbara et al. 2003, 2 = Bárbara et al. 2005b, 3 = Bárbara et al. 2006a, 4 = Martínez-Gil et al. 2007, 5 = Bárbara et al. 2008, 6 = Díaz et al. 2008, 7= Secilla et al. 2008, 8 = Araújo et al. 2009, 9 = Bárbara & Díaz Tapia 2012, 10 = Bárbara et al. 2012. Atlantic provinieses, from North to South, are SwFr = Southwest of France, SS = Gupúzcoa, Bi = Vizcaya, S = Cantabria, O = Asturias, Lu = Lugo, C = A Coruña, Po = Pontevedra, Mi = Minho, DL = Douro Litoral, BL = Beira Litoral, Es = Esremadura, BA = Baixo Alentejo, Ag = Algarve, Ca = Cádiz. Asterisks indicate those species that are not included in the catalogue but that were found in additional collections of the sites where sand-covered rocks were sampled, but in different habitats, as well as, the species of Cyanophyta.

	SwFr	SS	Bi	S	O	Lu	C	Po	Mi	DL	BL	Es	BA	Ag	Ca
Cyanophyta															
*Calothrix confervicola (Dillwyn) C. Agardh				2 ⁽⁶⁾											
*Calothrix prolifera Flahault	1 ⁽⁶⁾														
*Chamaecalyx leibleinia (Reinsch) Kómarek & Anagnostidis				1 ⁽⁶⁾	2 ⁽¹⁾	2 ⁽¹⁾									
*Hydrocoleum glutinosum (C. Agardh) Gomont					1 ⁽³⁾										
*Leiblenia baculum (Gomont) Hoffman	1 ⁽⁶⁾	1 ⁽⁶⁾	1 ⁽⁶⁾	1 ⁽⁶⁾	1 ⁽⁶⁾										
*Lynbya confervoides C. Agardh ex Gomont	1 ⁽⁶⁾														
*Microcoleus acutirostris (Crouan) Gomont						1 ⁽¹⁾				1 ⁽⁸⁾					
*Rivularia bullata (Poiret) Berkeley ex Bornet & Falahault	1 ⁽⁶⁾														
*Sirocoleum kurzii (Zeller) Gomont				1 ⁽⁶⁾											
*Symploca atlantica Gomont						1 ⁽¹⁾									
*Xenococcus glykelyae Setchell & Gardner						1 ⁽¹⁾									
Rhodophyta															
Aglaothamnion gallicum	1 ⁽⁶⁾			2 ⁽⁶⁾											
Aglaothamnion pseudobyssoides				2 ⁽⁶⁾											
Aglaothamnion tenuissimum				1 ⁽⁶⁾	2 ⁽¹⁾										
*Aglaothamnion tripinnatum (C. Agardh) Feldmann				1 ⁽⁶⁾											
*Ahnfeltopsis pusilla (Montagne) Silva & DeCew					2 ⁽¹⁰⁾					1 ⁽⁸⁾	1 ⁽⁸⁾	1 ⁽¹⁰⁾	1 ⁽¹⁰⁾	2 ⁽¹⁰⁾	1 ⁽¹⁰⁾
Aiolocolax pulchellus					2 ⁽³⁾										

	SwFr	SS	Bi	S	O	Lu	C	Po	Mi	DL	BL	Es	BA	Ag	Ca
Amphiroa beauvoisii														2 ⁽¹⁰⁾	
*Amphiroa van-bosseae Lemoine					1 ⁽¹⁰⁾								2 ⁽¹⁰⁾		
Antithamnion amphigeneum		2 ⁽¹⁰⁾													
Antithamnion cruciatum						2 ⁽¹⁾			1 ⁽⁸⁾						
*Antithamnion hubbsii Dawson	1 ⁽⁹⁾														
Antithamnionella boergesenii		2 ⁽¹⁰⁾			1 ⁽⁶⁾										
Antithamnionella multiglandulosa		1 ⁽⁶⁾	2 ⁽⁶⁾	1 ⁽⁶⁾	1 ⁽⁶⁾	2 ⁽¹⁰⁾	2 ⁽¹⁰⁾					1 ⁽¹⁰⁾			1 ⁽¹⁰⁾
Antithamnionella ternifolia					1 ⁽¹⁰⁾	2 ⁽⁶⁾			1 ⁽⁸⁾						
Aphanocladia stichidiosa			2 ⁽¹⁰⁾		1 ⁽¹⁰⁾										
Apoglossum ruscifolium											2 ⁽³⁾				
Bonnemaisonia hamifera						1 ⁽¹⁰⁾	1 ⁽¹⁰⁾								
Bornetia secundiflora						1 ⁽¹⁾	2 ⁽¹⁾		1 ⁽⁸⁾						
Callithamniella tingitana															
Centroceras clavulatum		1 ⁽⁶⁾	2 ⁽⁶⁾	1 ⁽⁴⁾											
Ceramium botryocarpum					1 ⁽⁶⁾						1 ⁽⁸⁾				
Ceramium pallidum								2 ⁽⁴⁾							
Ceramium secundatum			1 ⁽⁶⁾		1 ⁽⁶⁾	2 ⁽¹⁾									
Chondria scintillans					2 ⁽³⁾										
Chondrus crispus f. filiformis					2 ⁽⁶⁾										
Choreonema thuretii		1 ⁽⁶⁾		2 ⁽⁴⁾	2 ⁽³⁾										
Colaconema daviesii			2 ⁽⁶⁾											1 ⁽⁸⁾	
Compothamnio thuyoides				2 ⁽⁴⁾											
Cordylecladia erecta					1 ⁽⁶⁾	2 ⁽⁵⁾									
*Cryptonemia lomation (Bertoloni) J. Agardh					2 ⁽⁶⁾										
Dasya hutchinsiae						2 ⁽¹⁾									
*ErythroGLOSSUM laciniatum (Lightfoot) Maggs & Hommersand						2 ⁽¹⁾									2 ⁽¹⁾

	SwFr	SS	Bi	S	O	Lu	C	Po	Mi	DL	BL	Es	BA	Ag	Ca
<i>Erythrogllossum lusitanicum</i>	1 ⁽⁹⁾				2 ⁽⁶⁾	2 ⁽¹⁾									
<i>Erythrotrichia bertholdii</i>		1 ⁽⁶⁾	1 ⁽⁶⁾	1 ⁽⁶⁾											
<i>Gastroclonium reflexum</i>										1 ⁽⁸⁾	1 ⁽⁸⁾				
<i>Gayliella fiaccida</i>										1 ⁽⁸⁾					
<i>Gelidium pusillum</i> var. <i>pulvinatum</i>				2 ⁽⁶⁾											
<i>Gelidium spathulatum</i>		1 ⁽⁶⁾	1 ⁽⁶⁾	1 ⁽⁶⁾	2 ⁽⁶⁾							1 ⁽¹⁰⁾			1 ⁽¹⁰⁾
<i>Gymnogongrus griffithsiae</i>															
* <i>Gymnothamnion elegans</i> (Schousboe ex C. Agardh) J. Agardh						2 ⁽³⁾									
* <i>Haematocelis rubens</i> J. Agardh stadium						2 ⁽¹⁾									
<i>Halarus flosculosus</i>						2 ⁽¹⁾									
<i>Haraidtophyllum bonemaisonii</i>						2 ⁽¹⁾									
* <i>Helminthocladia calvadosii</i> (Lamouroux) Setchell	1 ⁽⁹⁾					2 ⁽²⁾									
<i>Herposiphonia secunda</i>									1 ⁽³⁾						
<i>Hildenbrandia cruaniorum</i>						2 ⁽²⁾									
* <i>Hildenbrandia occidentalis</i> Setchell														2 ⁽¹⁰⁾	
<i>Holmsella pachyderma</i>				1 ⁽⁶⁾	1 ⁽⁶⁾										
<i>Jania longifurca</i>				2 ⁽⁴⁾		2 ⁽¹⁾									
<i>Laurencia pyramidalis</i>					2 ⁽⁶⁾										
<i>Leptosiphonia schousboei</i>				1 ⁽⁶⁾	1 ⁽⁶⁾	2 ⁽¹⁾									
<i>Lomentaria clavellosa</i>				1 ⁽⁶⁾											
<i>Lophosiphonia reptabunda</i>					1 ⁽⁶⁾										
<i>Mastocarpus stellatus</i>															1 ⁽¹⁰⁾
<i>Monosporus pedicellatus</i>				2 ⁽⁴⁾											
<i>Phyllophora sicula</i>						1 ⁽¹⁰⁾		1 ⁽¹⁰⁾							
<i>Peyssonella atropurpurea</i>														1 ⁽⁸⁾	
* <i>Peyssonella harveyana</i> J. Agardh									2 ⁽¹⁰⁾						

	SwFr	SS	Bi	S	O	Lu	C	Po	Mi	DL	BL	Es	BA	Ag	Ca
*Plocamium raphelisianum Dangeard														1 ⁽¹⁰⁾	
Pleonosporium flexuosum											2 ⁽³⁾				
*Polydes rotundus (Hudson) Greville							2 ⁽¹⁰⁾								
Polysiphonia devoniensis	1 ⁽⁶⁾			1 ⁽⁶⁾		1 ⁽¹⁰⁾								1 ⁽¹⁰⁾	1 ⁽¹⁰⁾
Polysiphonia fibrata		2 ⁽¹⁰⁾		1 ⁽⁶⁾	2 ⁽¹⁰⁾	1 ⁽⁵⁾							1 ⁽¹⁰⁾	1 ⁽¹⁰⁾	
Polysiphonia fibrillosa				2 ⁽⁶⁾											
Polysiphonia nigra	1 ⁽¹⁰⁾		1 ⁽⁶⁾	1 ⁽⁴⁾											
Polysiphonia polyspora										1 ⁽⁸⁾					
Polysiphonia scopulorum				1 ⁽⁴⁾	1 ⁽⁶⁾				2 ⁽³⁾	1 ⁽³⁾	1 ⁽³⁾				
Polysiphonia stricta		2 ⁽⁶⁾	2 ⁽⁶⁾	2 ⁽⁶⁾	2 ⁽⁶⁾			2 ⁽³⁾	2 ⁽³⁾						
*Porphyra dioica J. Brodie & L.M. Irvine					1 ⁽¹⁰⁾										
Pyropia leucosticta						2 ⁽¹⁾									
Porphyrostromium boryanum	1 ⁽⁶⁾			1 ⁽⁶⁾											
Porphyrostromium ciliare				1 ⁽⁶⁾		1 ⁽³⁾				1 ⁽⁸⁾					
Pterocladia melanoidea			1 ⁽⁶⁾	1 ⁽⁴⁾	1 ⁽⁶⁾	2 ⁽³⁾			2 ⁽³⁾	2 ⁽³⁾	1 ⁽³⁾				
Pterosiphonia ardreaana	1 ⁽⁶⁾				2 ⁽⁶⁾			2 ⁽³⁾		1 ⁽⁸⁾					
Pterothamnion crispum			1 ⁽⁶⁾	2 ⁽⁶⁾											
Ptilothamnion sphaericum	1 ⁽⁹⁾	1 ⁽⁶⁾	2 ⁽⁶⁾	1 ⁽⁴⁾					2 ⁽³⁾						1 ⁽¹⁰⁾
Rhodothamniella floridula													2 ⁽¹⁰⁾	2 ⁽¹⁰⁾	
Rhodymenia holmesii					2 ⁽⁶⁾										
Scageliopsis patens			1 ⁽⁷⁾	1 ⁽⁷⁾	1 ⁽⁷⁾										
Spermothamnion repens															1 ⁽³⁾
Streblocladia collabens				1 ⁽⁴⁾											
Stylonema alsidii				2 ⁽⁶⁾											
Tiffaniella capitata															2 ⁽¹⁾
"Traiella intricata" stadium				1 ⁽⁴⁾											

	SwFr	SS	Bi	S	O	Lu	C	Po	Mi	DL	BL	Es	BA	Ag	Ca
Ochrophyta															
Acinetospora crinita			1 ⁽⁶⁾	1 ⁽⁴⁾	1 ⁽⁶⁾	1 ⁽³⁾									
Colpomenia peregrina						2 ⁽¹⁾									
Feldmannia irregularis	1 ⁽⁶⁾			2 ⁽⁴⁾											
Hinksia granulosa			1 ⁽⁶⁾	1 ⁽⁶⁾											
Hinksia mitchellae			1 ⁽⁶⁾	1 ⁽⁶⁾											
Leathesia marina			1 ⁽⁶⁾			2 ⁽¹⁾									
Myrionema strangulans															
Petalonia fascia						2 ⁽¹⁾						2 ⁽¹⁰⁾			
*Petrospongium berkeleyi (Greville) Nägeli					2 ⁽³⁾										
*Pliocladus codicola (Setchell & N.L. Gardner) Ardré						2 ⁽²⁾									
*Sargassum flavifolium Kützting															
*Sauvageaugloia divaricata (Clemente) Cremades					2 ⁽³⁾		2 ⁽²⁾								
*Scytosiphon dotyi M.J. Wynne	1 ⁽¹⁰⁾				1 ⁽¹⁰⁾										1 ⁽¹⁰⁾
Sphacelaria rigidula	1 ⁽⁶⁾	2 ⁽⁶⁾			1 ⁽⁶⁾	2 ⁽³⁾			1 ⁽⁸⁾					1 ⁽¹⁰⁾	1 ⁽¹⁰⁾
*Zanardinia typus (Nardo) P.C. Silva													2 ⁽¹⁰⁾		
Chlorophyta															
Chaetomorpha aerea			1 ⁽⁶⁾												
*Chaetomorpha linum (Müller) Kützting						1 ⁽²⁾									
Chaetomorpha ligustica						2 ⁽¹⁾			2 ⁽³⁾						
Cladophora leatevirens															1 ⁽³⁾
*Cladophora pellucida (Hudson) Kützting					1 ⁽⁶⁾										
Cladophora rupestris															
Cladophora sericea			1 ⁽⁶⁾	2 ⁽⁶⁾	2 ⁽⁶⁾										
*Codium fragile subsp. Tomentosoides (Van Goor) P. Silva				2 ⁽⁶⁾		2 ⁽¹⁾									
*Codium vermilara (Olivieri) Delle Chiaje					2 ⁽³⁾										

	SwFr	SS	Bi	S	O	Lu	C	Po	Mi	DL	BL	Es	BA	Ag	Ca
Derbesia marina		1 ⁽⁶⁾	1 ⁽⁶⁾	1 ⁽⁶⁾			2 ⁽³⁾			1 ⁽⁸⁾		1 ⁽¹⁰⁾	1 ⁽¹⁰⁾	1 ⁽¹⁰⁾	
Derbesia tenuissima						1 ⁽³⁾				1 ⁽⁸⁾					
*Pedobesia simplex (Meneghini ex Kützinger) M.J. Wynne & Leliaert												2 ⁽¹⁰⁾			
*Ulva bifrons Ardré	1 ⁽⁹⁾							1 ⁽¹⁰⁾							
*Ulva pseudocurvata Koeman & Hoek									1 ⁽⁸⁾	1 ⁽⁸⁾					
*Ulvella lens P.Crouan & H. Crouan					1 ⁽³⁾										

Biogeographic analysis

This study was based on species records from a particular habitat, sand-covered rocks, whose flora is characterized by a higher representation of Rhodophyta and lower of Ochrorphyta regarding the catalogues that consider all habitats. Despite this, the floristic analysis shows that three regions can be identified. The temperature is the main factor that affects the geographical distribution of marine algae (e.g. Adey & Steneck 2001, Hoek & Breeman 1990), and dissimilarities found between Iberian regions may be related to this factor. In this regard, Galicia-Central Portugal are the colder areas where upwelling events took place during summer months, while the warmer region is the Southern Iberian Peninsula. Finally, the Cantabrian coast has intermediate seawater temperatures.

The PCO ordination (Fig. 1) shows that three overlapping groups can be identified based on presence/absence data of the species in the studied sites. The first group joined most of the sites from Galicia to Central Portugal, the second group joined most of the Cantabrian localities and the third group is composed of the sites from the southern Iberian Peninsula. Interestingly, most sites from the Cantabrian are placed in an intermediate position between sites from Galicia-Central Portugal and the southern Iberian Peninsula.

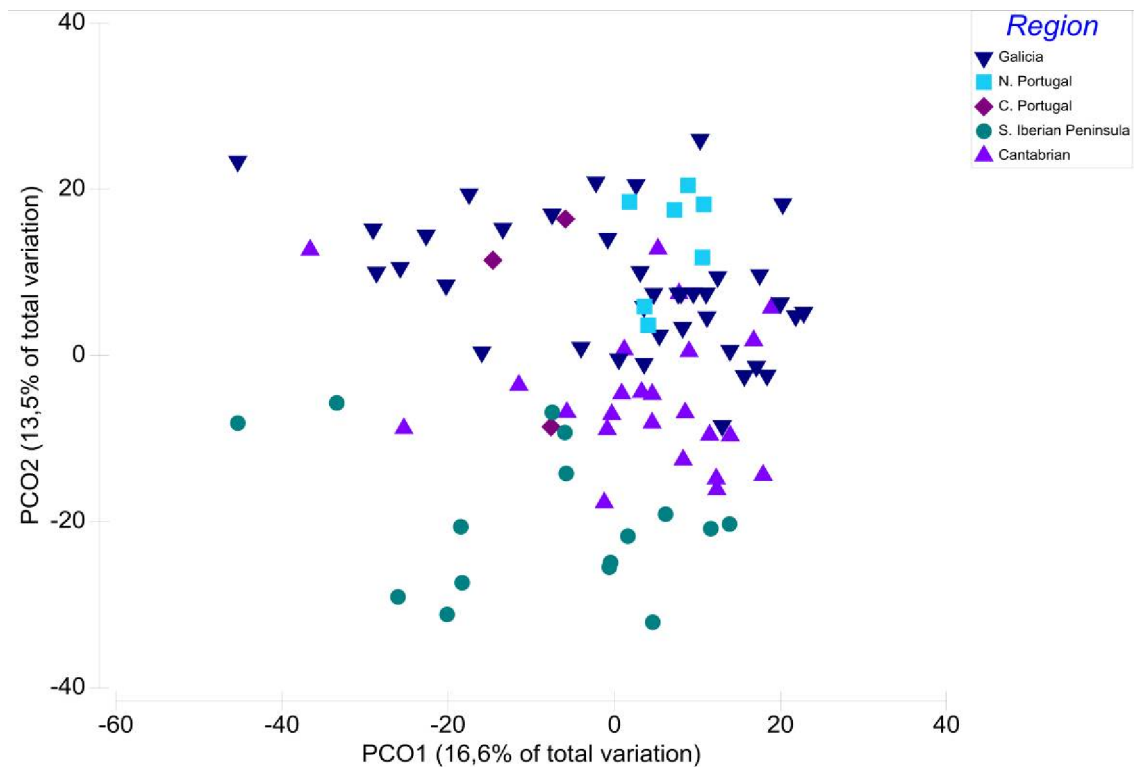


Figure 1. PCO ordination performed on the Bray-Curtis similarity matrix calculated on the presence/absence data of the species in the studied sites. Symbols represent the classification of sites in the five regions in which the Atlantic Iberian Peninsula was divided in this study.

The cluster analysis of the presence/absence data (Fig. 2) shows that most of sites from the Cantabrian and northern Portugal form two respective groups at 58% similarity levels. In addition, most of the sites from the Southern Iberian Peninsula are forming two groups at 50% and 38% similarity levels. Likewise, sites from Galicia and Central Portugal form five groups at different similarity levels ranging from 45-60%. Finally, a few sites from Galicia together with two sites from southern Iberian Peninsula and one site from the Cantabrian form two separate groups with low similarity levels (28 and 35%). Thus, although sites are clustered in groups that in general agree with geographical regions, it is not possible to establish a similarity level to support these groups. In addition, there are 10 sites that disagree in the cluster analysis with the grouping of localities according to their region.

Similarity values within and between the three groups of sites identified in the PCO ordination were calculated and are presented in Table 5. The Cantabrian locations showed the highest values of similarity within groups. By contrast, the lowest ones were found in the Southern Iberian Peninsula, which had the highest heterogeneity in species composition between the studied sites (Table 5, Fig. 1). This is probably related to the largely different environmental conditions existing between sites from the southwestern Portugal, southern Portugal and Cádiz. Comparisons between groups of sites showed that the most similar ones were the Cantabrian and Galicia-Central Portugal, while the Southern Iberian Peninsula and Galicia-Central Portugal had the lowest similarities (Table 5).

Table 5. Matrix of similarity (%) within and between groups of sites belonging to the three regions identified in the PCO ordination, calculated on the Bray-Curtis similarity matrix from the presence/absence data of the species in the studied sites.

	Cantabrian	Galicia+N & C Portugal	S. Iberian Peninsula
Cantabrian	56.77		
Galicia+N & C Portugal	49.65	50.45	
S. Iberian Peninsula	44.98	40.27	46.88

Results of SIMPER procedure showing the most relevant species in the differentiation of the three groups of sites are shown in Table 6. A first group of three species was exclusively recorded in the Cantabrian and, curiously, they were alien species and had low mean frequency. A second group of 23 species, highlighting *Ptilothamnion sphaericum*, *Polysiphonia nigra*, *Pterosiphonia complanata*, *Bifurcaria bifurcata* and *Ahnfeltia plicata*, were more frequently or exclusively found in the Cantabrian and Galicia regarding the Southern Iberian Peninsula. A third group of 11 species, highlighting *Chondracanthus teedei* and *Leptosiphonia schousboei*, were more frequently or exclusively found in Galicia-Central Portugal. Another group of species characterizes the southern Iberian Peninsula regarding the other two regions and includes 10

species among which highlight *Chaetomorpha* cf. *melagonium*, *Bachelotia antillarum*, *Herposiphonia secunda* and *Laurencia* cf. *chondroides*. Finally a group of 15 species distinguishes the Southern Iberian Peninsula and the Cantabrian from Galicia. Some interesting species in this group are *Halopithytis incurva*, *Centroceras clavulatum*, *Lophosiphonia reptabunda*, *Herposiphonia secunda* f. *tenella* or *Cladophora prolifera*, which are Southern-warm species.

Table 6. Results of SIMPER procedure showing the mean frequency of the most relevant species in the differentiation of the three groups of sites: Cantabrian, Galicia-Central Portugal and Southern Iberian Peninsula. Listed species are those that were exclusive of determinate areas, as well as those that showed relevant differences in mean frequency. Species in bold are those that are characteristic from sand-covered rocks, and values in bold are those that are markedly higher than those found in neighboring areas.

	Cantabrian		Galicia – C. Portugal		S. Iberian Peninsula
<i>"Traiella intricata" stadium</i>	0,29	>	0	=	0
<i>Antithamnionella boergensenii</i>	0,17	>	0	=	0
<i>Scagelopsis patens</i>	0,17	>	0	=	0
<i>Polysiphonia</i> sp. 5	0,21	>	0	>	0,06
<i>Ulva prolifera</i>	0,96	~	0,92	>	0,31
<i>Pyropia leucosticta</i>	0,83	>	0,67	>	0,19
<i>Ptilothamnion sphaericum</i>	0,79	>	0,48	>	0,19
<i>Ceramium secundatum</i>	0,79	>	0,83	>	0,19
<i>Acinetospora crinita</i>	0,71	>	0,48	>	0,19
<i>Pterosiphonia complanata</i>	0,63	<	0,75	>	0,31
<i>Chaetomorpha mediterranea</i>	0,58	<	0,67	>	0,19
<i>Hildenbrandia rubra</i>	0,38	<	0,63	>	0,13
<i>Polysiphonia nigra</i>	0,33	>	0,60	>	0,06
<i>Antithamnionella ternifolia</i>	0,38	<	0,29	>	0
<i>Chylocladia verticillata</i>	0,29	>	0,17	>	0
<i>Bifurcaria bifurcata</i>	0,25	<	0,31	>	0
<i>Stylonema alsidii</i>	0,25	>	0,04	~	0
<i>Compsothamnion thuyoides</i>	0,21	>	0,02	~	0
<i>Halopteris filicina</i>	0,17	>	0,02	~	0
<i>Laurencia pyramidalis</i>	0,17	>	0,02	~	0
<i>Apoglossum ruscifolium</i>	0,17	>	0,1	~	0
<i>Cystoseira baccata</i>	0,17	=	0,17	>	0
<i>Grateloupia filicina</i>	0,17	~	0,23	>	0
<i>Sargassum muticum</i>	0,17	>	0,33	>	0
<i>Ahnfeltia plicata</i>	0,17	<	0,42	>	0
<i>Gymnogongrus crenulatus</i>	0,13	<	0,44	>	0
<i>Ceramium gaditanum</i>	0,08	<	0,17	>	0
<i>Polysiphonia fibrillosa</i>	0,08	<	0,19	>	0
<i>Pterocliadiella capillacea</i>	0,08	<	0,23	>	0
<i>Petrocelis cruenta stadium</i>	0,04	<	0,23	>	0
<i>Chondracanthus teedei</i>	0,04	<	0,56	>	0

	Cantabrian		Galicia – C. Portugal		S. Iberian Peninsula
<i>Leptosiphonia schousboei</i>	0	<	0,27	<	0
<i>Chondracanthus teedei</i> var. <i>lusitanicum</i>	0	<	0,15	>	0
<i>Himanthalia elongata</i>	0	<	0,19	>	0
<i>Polysiphonia brodiei</i>	0	<	0,17	>	0
<i>Peyssonella atropurpurea</i>	0	<	0,17	>	0,06
<i>Tiffaniella capitata</i>	0	<	0,15	<	0,06
<i>Aglaothamnion</i> sp.	0	~	0,02	<	0,31
<i>Aphanocladia stichidiosa</i>	0	~	0,02	<	0,25
<i>Polysiphonia tripinnata</i>	0	<	0,02	<	0,31
<i>Herposiphonia secundaf. secunda</i>	0	~	0,06	<	0,38
<i>Laurencia</i> cf. <i>chondroides</i>	0	~	0,02	<	0,69
<i>Polysiphonia sphaerocarpa</i>	0	=	0	<	0,13
<i>Heterosiphonia crispella</i>	0	=	0	<	0,19
<i>Cladophora coelotrix</i>	0	=	0	<	0,13
<i>Bachelotia antillarum</i>	0	=	0	<	0,25
<i>Chaetomorpha</i> cf. <i>melagonium</i>	0	=	0	<	0,38
<i>Chondria capillaris</i>	0,04	~	0	<	0,25
<i>Centroceras clavulatum</i>	0,58	>	0	<	0,44
<i>Polysiphonia devoniensis</i>	0,38	>	0	~	0,13
<i>Halopithys incurva</i>	0,33	>	0	<	0,38
<i>Cladophora prolifera</i>	0,25	>	0	<	0,56
<i>Dasya ocellata</i>	0,13	>	0	<	0,19
<i>Hypnea musciformis</i>	0,08	<	0	>	0,31
<i>Sphacelaria cirrosa</i>	0,96	>	0,44	<	0,96
<i>Lophosiphonia reptabunda</i>	0,71	>	0,19	<	0,94
<i>Melobesia membranacea</i>	0,58	>	0,21	<	0,56
<i>Herposiphonia secundaf. tenella</i>	0,33	>	0,08	<	0,75
<i>Bryopsis plumosa</i>	0,75	>	0,42	>	0,31
<i>Cladophora rupestris</i>	0,71	>	0,4	>	0,19
<i>Spermothamnion repens</i>	0,67	>	0,42	>	0,31
<i>Cladophora sericea</i>	0,54	>	0,31	>	0,13

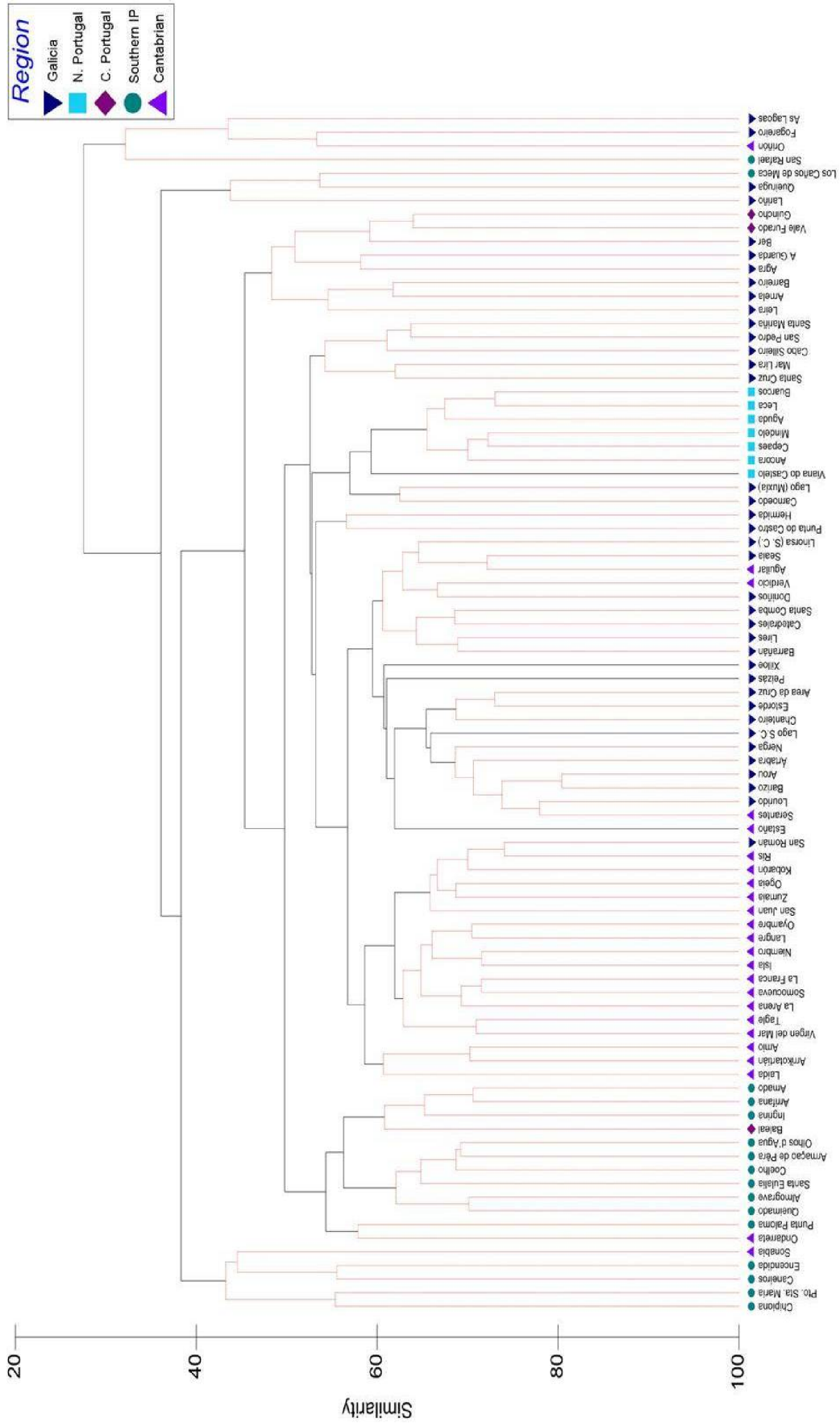


Figure 2. Group-average cluster analysis on Bray-Curtis similarity matrix calculated on the presence/absence data of the species in the studied sites. Black branches indicate significant groups in the SIMPROF test ($p < 0.05$). The y-axis shows Bray-Curtis similarity (%)

Chapter 1.2. Flora of the seaweeds from sand-covered rocks along the Atlantic Iberian Peninsula.

Introduction

This chapter provides a description of the most frequent and abundant species found in sand-covered habitats from the Atlantic Iberian Peninsula. A total of 35 species were included, comprising all those that were identified as dominants in turfs (Chapter 2.4), as well as others having a special taxonomic interest or being characteristics of this habitat. For each species information is provided about the type material, previous references with morphological descriptions, a list of selected specimens studied, a description based on morphological observations, information about their phenology, habitat and distribution, and taxonomic considerations when needed. The species studied in this chapter are arranged systematically, following the catalogue, and alphabetically within each family considered.

During the course of this work we noted that several of the frequent and abundant species from sand-covered rocks remained poorly known, including two species not previously reported that finally proved to be two new species. This motivated us to develop detailed morphological and taxonomic studies on some species from sand-covered rocks which are of particular interest due to different causes. We have specifically studied 13 species, preparing detailed morphological descriptions and discussing the taxonomic entities related to these species. Most of the species studied in detail belong to different genera and tribes of the family Rhodomelaceae (Ceramiales, Rhodophyta). Thus, a brief review of the morphology and classification of the Rhodomelaceae is provided.

In addition, in some cases, we complemented our morphological studies with phylogenetic analyses based on molecular data (study of *Polysiphonia foetidissima* and *Calliblepharis hypneoides*) which were performed in collaboration with other researchers. Furthermore, we have recently started the study of the diversity of the turf-forming species from the Atlantic Iberian Peninsula using molecular assisted identification (COI-5P). Moreover, we have also analyzed *rbcL* and SSU genes of some species. Although our results using molecular data are preliminary and in several cases more sequences and proper phylogenetic analyses are still necessary to reach definitive conclusions, these data inevitably have influenced our taxonomic considerations. Therefore, we considered appropriate to include them here despite new data will be necessary to develop proper phylogenetic studies that support some of the proposed conclusions.

RHODOPYTA
FLORIDEOPHYCEAE
PALMARIALES
RHODOTHAMNIELLACEAE

Rhodothamniella floridula (Dillwyn) Feldmann in T. Christensen

Basionym: *Conferva floridula* Dillwyn

Lectotype: BM

Type locality: Galway, Ireland

Rhodochorton floridulum (Dillwyn) Nägeli

Audouinella floridula (Dillwyn) Woelkerling

References: Knaggs 1965, Stegenga 1978, Coppejans 1995 (as *Rhodochorton floridulum*).
Woelkerling & Womersley 1994, Dixon & Irvine 1977 (as *Audouinella floridula*). Stegenga 1985,
Stegenga *et al.* 1997, Rull Lluch 2002, Rull Lluch & Gómez Garreta 2002 (as *Rhodothamniella floridula*).

Selected specimens collected at 17 sites, from a total of 87 (121 dates): Guipúzcoa: 1) Zumaia (43°17'59"N; 2°15'41"W), 30.iii.2006, SANT-Algae 20273; Vizcaya: 2) San Juan de Gaztelugatxe (43°26'41"N; 2°46'41"W), 29.iii.2006, SANT-Algae 20296; Cantabria: 3) Oriñón (43°24'20"N; 3°19'34"W), 27.iii.2006, SANT-Algae 20978; 4) Langre (43°28'37"N; 3°41'31"W), 6.xi.2010, SANT-Algae 24624; 5) Virgen del Mar (43°28'40"N; 3°52'31"W), 28.iii.2006, SANT-Algae 20396; 6) Tagle (43°25'59"N; 4°04'50"W), 1.iv.2006, SANT-Algae 20339; 7) Amio (43°23'42"N; 4°28'57"W), 17.iii.2006, SANT-Algae 20425; Asturias: 8) Aguilar (43°33'28"N; 6°07'07"W), 17.iv.2007, SANT-Algae 19816; 9) Serantes (43°33'27"N; 6°58'39"W), 2.ii.2006, SANT-Algae 17845 (tetrasporangial plants); Lugo: 10) Linorsa (43°41'56"N; 7°27'14"W), 10.iii.2005, SANT-Algae 23118 (tetrasporangial plants); A Coruña: 11) Chanteiro (43°26'46"N; 8°18'15"W), 17.ix.2005, SANT-Algae 19608; 12) Fogareiro (42°45'08"N; 9°04'49"W), 19.viii.2005, SANT-Algae 22812; 13) Hermida (43°15'47"N; 8°57'10"W), 26.iv.2006, SANT-Algae 24369; 14) Arnela (42°42'35"N; 9°00'47"W), 30.i.2006, SANT-Algae 24349; Pontevedra: 15) Area da Cruz (42°27'40"N; 8°54'37"W), 22.viii.2005, SANT-Algae 25065; 16) Nerga (42°15'19"N; 8°50'07"W), 12-ii-2005, SANT-Algae 22820; Extremadura: 17) Guincho (38°43'29"N; 9°28'41"W), 13.vi.2010, SANT-Algae 24800.

Observations

Vegetative and reproductive morphology

Thalli form dense turfs up to 7 cm high and covering rock surfaces of several meters in extent (Figs. 1A-C), consisting of a thin basal layer of agglomerated prostrate axes from which arise the entangled erect axes that form an upper layer with a variable thickness. The basal layer is white in color while turfs formed by the erect axes are brownish red in color; when axes are observed separately prostrate ones are colorless, while erect axes are pink in color. Turfs are robust, while isolated axes are fragile.

Plants consist of uniseriate filaments, differentiated into prostrate and erect axes, both irregularly branched (Figs. 1D-F). Erect axes sparingly branched in basal parts and more densely branched in upper ones. Cells 17-30 µm in diameter and 40-95 µm long, with 3-8 chloroplasts, sinuate, parietal, each with one pyrenoid (Fig. 1G).

Gametangial plants not observed. Tetrasporangia ovoid, 20-28 μm in diameter, arranged in second series on the upper parts of the erect axes, occurring singly or in clusters of 2-5 sporangia; either sessile or on a single-celled stalk, tetraspores cruciately arranged (Figs. 1H-J).

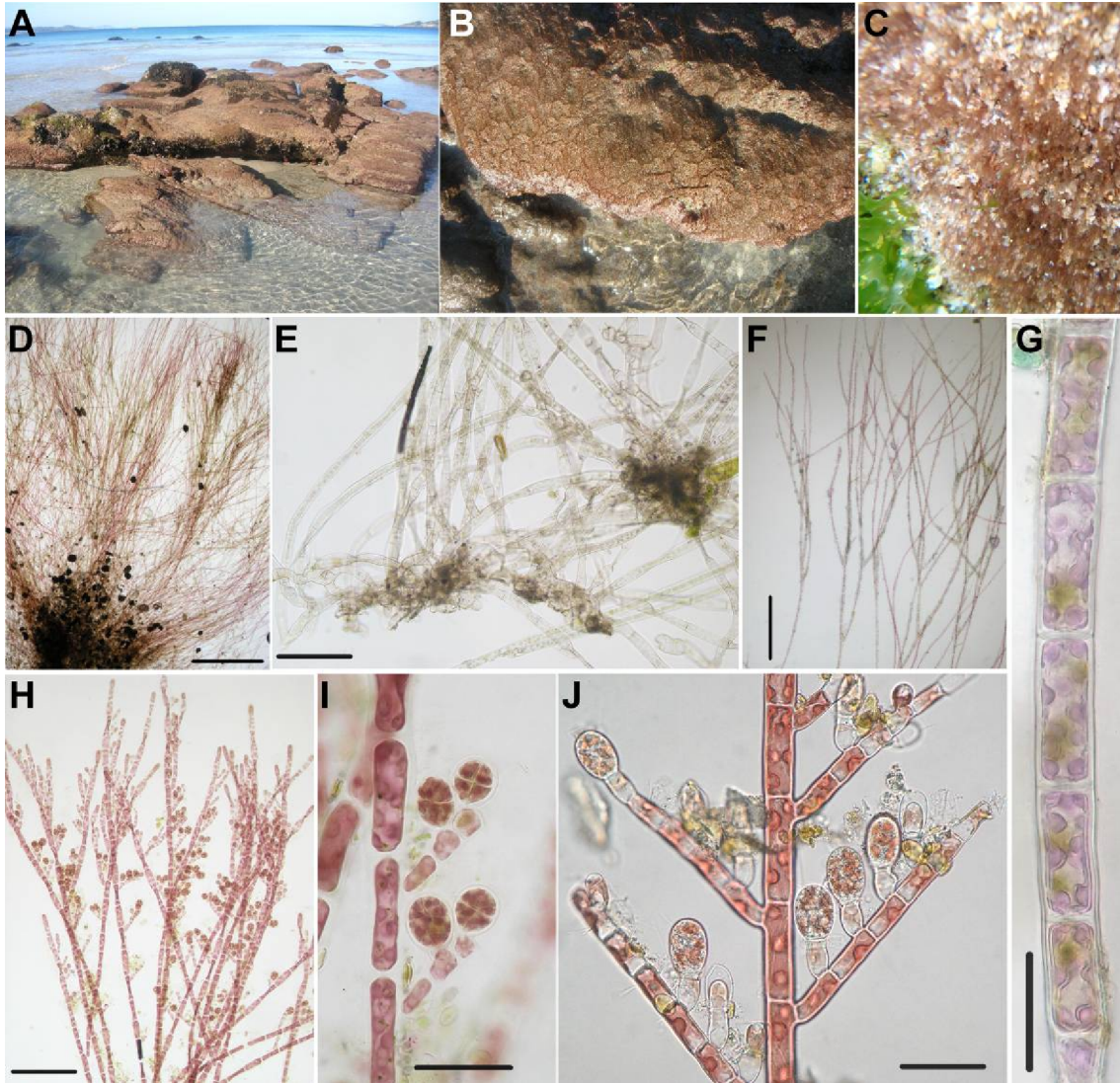


Figure 1. *Rhodothamniella floridula*. Vegetative and reproductive morphology.

A-C: Turfs. **D:** Detail of a turf showing a basal layer of agglomerated prostrate axes from which arise the erect axes. **E:** Prostrate axes consisting of branched colorless filaments. **F:** Upper parts of erect axes irregularly branched. **G:** Cells showing several chloroplasts, each with a pyrenoid. **H:** Upper parts of erect axes bearing tetrasporangia. **I-J:** Tetrasporangia cruciately divided arranged in second series, sessile (I) or with a one-celled stalk (J). Scale bars. D = 2 mm; E, H = 200 μm ; F = 600 μm ; G, I-J = 50 μm .

Phenology

Plants occur throughout the year, and they are probably perennial. Turfs often show a brownish red color during summer months while they are bright red during winter. This seasonal difference in color is due to the developing of epiphytic diatoms during the summer.

Tetrasporangia were rarely recorded, in only 4% of the collections, and they were observed in January, May and October-December. However, it is probable that they be more common but overlooked due to their small size.

Habitat and distribution

Rhodothamniella floridula is one of the most common and abundant species in sand-covered rocks from the Atlantic Iberian Peninsula. It often forms almost monospecific turfs and is also a frequent component of practically all turfs dominated by the different species typical from sand-covered rocks. It grows from the upper intertidal to the upper subtidal, in sites from sheltered to extremely wave-exposed. *Rhodothamniella floridula* traps large amounts of sand among the entangled filaments, and its turfs often remain buried by sand for long periods.

Rhodothamniella floridula is widely distributed along the Atlantic Iberian Peninsula, and it was found in almost all sampled sites (Fig. 2). Although present, its abundance decreases toward the Basque Country (East) and Cádiz (South). *Rhodothamniella floridula* was reported from Europe and the southern coasts of America, Africa and Australia (Fig. 3).

Remarks

Rhodothamniella floridula resembles numerous species of the genera *Audouinella*, *Rhodochorton* and even *Colaçonema*, which often have a similar habit. Nevertheless, *R. floridula* is the only species that forms extensive turfs in sand-covered rocks of the Atlantic Iberian Peninsula, while other species are usually epiphytic. *Rhodochorton purpureum* is the only similar species that also forms turfs, but this species is restricted to the upper littoral in shaded habitats such as caves.

The taxonomic position of *Rhodothamniella floridula* and related species has been largely discussed in literature (e.g. Woelkerling 1983, Lee & Lee 1988, Lee 1993). *Rhodothamniella floridula* was previously placed in the genera *Audouinella* and *Rhodochorton*, which currently belong to the the order Acrochaetiales. Saunders *et al.* (1995) studied phylogenetic relationships of Palmariales and Acrochaetiales, establishing the family Rhodothamniellaceae which represents an early lineage of the order Palmariales.



Figure 2. Distribution of the collections of *Rhodothamniella floridula* along the Atlantic Iberian Peninsula.



Figure 3. World distribution of *Rhodothamniella floridula*. Arrow indicates the type locality.

GELIDIALES
GELIDIACEAE

Gelidium crinale (Hare ex Turner) Gaillon

Basionym: *Fucus crinalis* Hare ex Turner

Lectotype: BM

Lectotype locality: Ilfracombe, Devonshire, England

Gelidium corneum var. *crinale* (Turner) Greville

References: Feldmann & Hamel 1936, Joly 1965, Echegaray & Seoane 1982, Coppejans 1995, Womersley & Guiry 1994, Dawes & Mathieson 2008.

Selected specimens collected at 16 sites, from a total of 32 collections: Cantabria: 1) Langre (43°28'37"N; 3°41'31"W), 6.xi.2010, SANT-Algae 24631; 2) Somocueva (43°28'07"N; 3°56'43"W), 7.x.2006, SANT-Algae 19998 (tetrasporangial plants); Asturias: 3) La Franca (43°23'39"N; 4°34'18"W), 6.x.2006, SANT-Algae 19749 (tetrasporangial plants); A Coruña: 4) Barizo (43°18'48"N; 8°52'27"W), 9.ix.2002, SANT-Algae 24978; 5) Arou (43°11'03"N; 9°06'46"W), 6.iv.2004, SANT-Algae 26390; 6) Estorde (42°56'28"N; 9°13'04"), 11.iii.2005, SANT-Algae 23055 (tetrasporangial plants); 7) Mar de Lira (42°48'34"N; 9°07'05"W), 3.iii.2006, SANT-Algae 22759; Pontevedra: 8) Agra (42°23'38"N; 8°46'08"W), 28.iv.2006, SANT-Algae 25067; 9) Nerga (42°15'19"N; 8°50'07"W), 12-ii-2005, SANT-Algae 22831; Estremadura: 10) Vale Furado (39°41'04"N; 9°03'33"W), 12.vi.2010, SANT-Algae 24812 (female and tetrasporangial plants); 11) Guincho (38°43'29"N; 9°28'41"W), 13.vi.2010, SANT-Algae 24784; Algarve: 12) Martinhal (37°01'03"N; 8°55'31"W), 3.xi.2005, SANT-Algae 26204; 13) Caneiros (37°06'14"N; 8°30'47"W), 18.x.2005, SANT-Algae 26220 (female and tetrasporangial plants); 14) Cádiz: El Puerto (36°34'48"N; 6°15'51"W) 16.xi.2005, SANT-Algae 26075 (tetrasporangial plants); 15) Cala Encendida (36°18'40"N; 6°09'12"W), 18.ii.2011, SANT-Algae 26623 (tetrasporangial plants); 16) Caños de Meca (36°10'55"N; 6°00'06"W), 17.xi.2005, SANT-Algae 26140 (tetrasporangial plants).

Observations

Reproductive and vegetative morphology

Thalli form dense turfs up to 3.5 cm high and covering rock surfaces of ca. 900 cm² in extent. Plants consist of a basal system of prostrate axes irregularly branched, bearing erect slender branches and rhizoids that attach to the substrate (Figs. 4A-E). Turfs dark brownish red in color, with a rigid texture. Erect branches abundant, growing from an apical cell, terete to slightly compressed, up to 550 µm in diameter, from simple to abundantly branched with an irregular pattern (Figs. 4A-C, F-I). Structure uniaxial, differentiating an inner medulla of 3-6 cells across and an outer compact cortex 3-4 cells thick (Fig. 4J).

Cystocarps formed in lateral branchlets, single per ramulus, 220-550 µm long, bilocular, with one ostiole on each side (Figs. 4K-N). Male reproductive structures not observed. Tetrasporangia formed on short lateral branches or on the apex of erect branches, compressed, up to 25 µm long; elongate, furcated or with lateral lobes (Figs. 4O-P). Tetrasporangia ovoid, 25-35 µm in diameter, cruciately divided (Figs. 4Q-R).

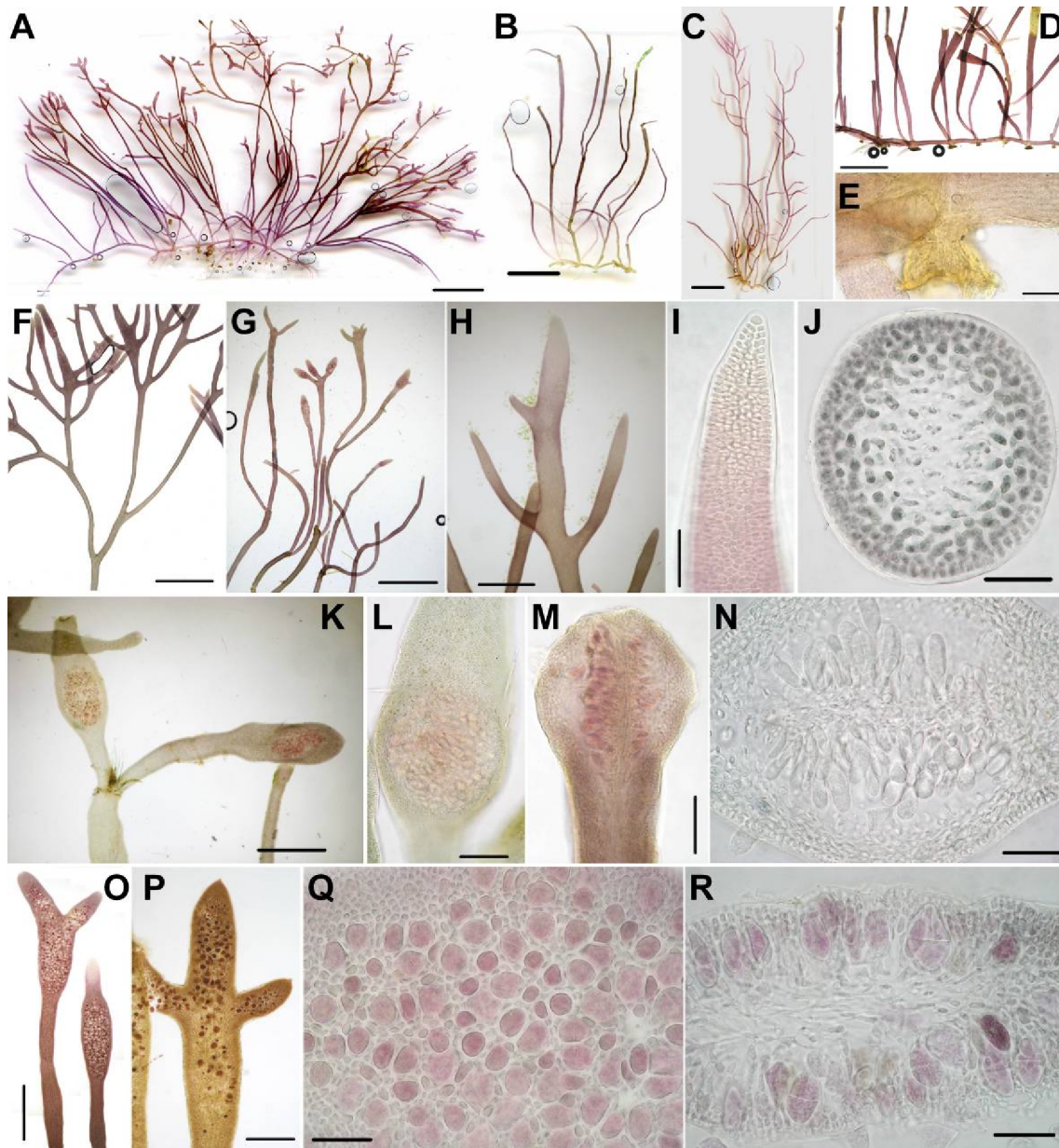


Figure 4. *Gelidium crinale*. Vegetative and reproductive morphology.

A-C: Habit of a tetrasporangial plant (A) and sterile thalli (B-C). **D:** Prostrate system bearing rhizoids and erect branches. **E:** Rhizoid. **F-H:** Erect axes with irregularly arranged branches. **I:** Apical cell of an erect branch. **J:** Cross section of thallus showing an inner medulla and an outer compact cortex. **K:** Branchlets with single cystocarps. **L:** Cystocarp in surface view. **M:** Lateral view of a bilocular cystocarp showing two ostioles. **N:** Cross section of a cystocarp. **O-P:** Tetrasporangia formed on the apical parts of plants or on short lateral branches, elongate, furcated (O) or with lateral lobes (P). **Q:** Tetrasporangia in surface view. **R:** Cross section of a branch with tetrasporangia. Scale bars. A-C = 3 mm; D, F-G = 2 mm; E, L-M = 100 μ m; H, K, O = 600 μ m; I-J, N, Q-R = 50 μ m; P = 200 μ m.

Phenology

Plants occur throughout the year, and they are probably perennial. Tetrasporangia commonly found (46% of the collections), not showing a detectable temporal pattern. Female structures observed twice (6% of the collections), in April and October, both in locations from Portugal.

Habitat and distribution.

Gelidium crinale is a common species in sand-covered rocks from the Atlantic Iberian Peninsula (Fig. 5). *Gelidium crinale* forms almost monospecific tufts that sometimes are up to 1 m² in extent. Sometimes they are mixed with other species, such as *Rhodothamniella floridula*. It is especially common in the mid intertidal, in sites from sheltered to highly wave-exposed. *Gelidium crinale* was widely reported in world temperate coasts (Fig. 6).

Remarks: See remarks about *Gelidium spathulatum* (p. 67).



Figure 5. Distribution of the collections of *Gelidium crinale* along the Atlantic Iberian Peninsula.



Figure 6. World distribution of *Gelidium crinale*. Arrow indicates the type locality.

Gelidium spathulatum (Kützinger) Bornet

Basionym: *Acrocarpus spathulatus* Kützinger

Lectotype: L

Type locality: Adriatic Sea

Gelidium crinale var. *spathulatum* (Kützinger) Hauck

References: Bornet 1892, Feldmann & Hamel 1936, Echeagaray & Seoane 1982.

Selected specimens collected at 4 sites, from a total of 10 (11 dates): Guipúzcoa: 1) Zumaia (43°17'59"N; 2°15'41"W), 30.iii.2006, SANT-Algae 20274 (female and tetrasporangial plants); Cantabria: 2) Oriñón (43°24'20"N; 3°19'34"W), 27.iii.2006, SANT-Algae 20378 (tetrasporangial plants); Algarve: 3) Armação de Pêra (37°06'04"N; 8°22'17"W), 17.10.2005, SANT-Algae 24845 (tetrasporangial plants); Cádiz: 4) Punta Paloma, (36°03'44"N; 5°43'31"W), 18.xi.2005; SANT-Algae 26154.

Observations

Reproductive and vegetative morphology

Thalli form dense turfs up to 2 cm high and covering rock surfaces of ca. 900 cm² in extent, consisting of a basal system of irregularly branched prostrate axes, bearing erect slender branches and rhizoids that attach to the substrate (Figs. 7A-E). Turfs brownish red in color, with a rigid texture. Erect branches abundant, growing from distinct apical cells, upper parts predominantly compressed and narrowing gradually towards basal parts becoming terete, up to 750 µm wide, distichously to irregularly branched (Figs. 7 A-C, F-G).

Cystocarps formed in lateral branchlets, 350-550 µm long, bilocular with one ostiole on each side (Figs. 7H). Male reproductive structures not observed. Tetrasporangia on short laterals or terminal on erect branches, compressed, up to 2 mm long (Figs. 7I-J). Tetrasporangia ovoid, 22-38 µm in diameter, cruciately divided (Figs. 7K).

Phenology

Gelidium spathulatum was collected in different seasons and is probably perennial. Female structures and/or tetrasporangia were present in most of the collections (40% in each case). Cystocarps were collected in March, June and October; tetrasporangia were collected in February, March, June, October and November.

Habitat and distribution

Gelidium spathulatum is a rare species in sand-covered rocks from the Atlantic Iberian Peninsula (Fig. 8), but when present it forms turfs that sometimes are more than 900 cm² in extent. It was collected from the upper to the low intertidal, in sites from sheltered to highly wave-exposed. *Gelidium spathulatum* was reported in southern Europe and northern Africa, as well as in Vietnam (Fig. 9).

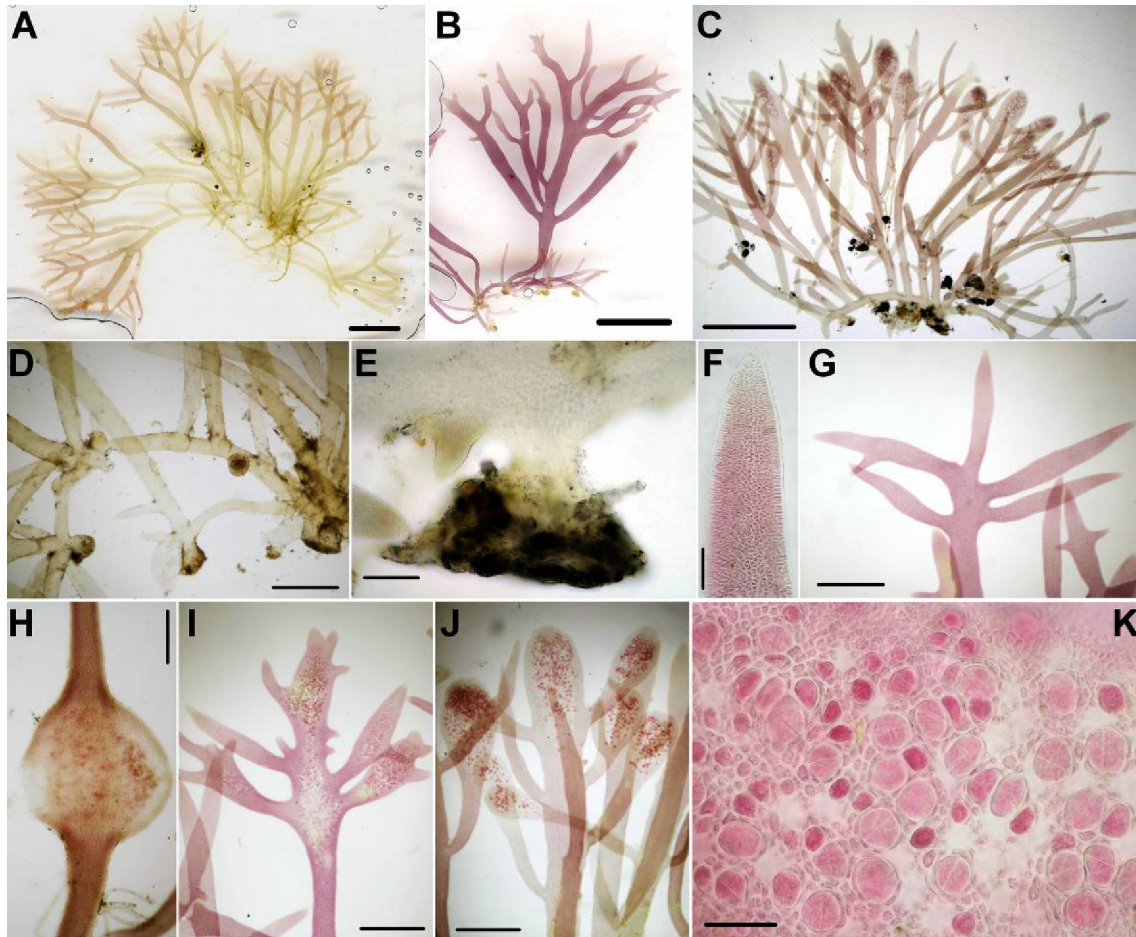


Figure 7. *Gelidium spathulatum*. Vegetative and reproductive morphology.

A-C: Habit of sterile plants (A-B) and a tetrasporangial plant I. D: Prostrate system bearing rhizoids and erect branches. E: Rhizoid. F: Apical cell of an erect branch. G: Erect thallus producing branches irregularly arranged. H: Cystocarp bilocular. I-J: Tetrasporangia on apical parts of axes or on short laterals. K: Tetrasporangia in surface view. Scale bars. A-B = 3 mm; C = 2 mm; D, G, I-J = 600 μ m; E = 100 μ m; F, K = 50 μ m; H = 200 μ m.

Remarks

The separation between *Gelidium spathulatum* and *G. crinale* is doubtful. Bornet (1892) remarked that *G. spathulatum* is probably a form of *G. crinale*, and while some authors considered them synonymous (e.g. Womersley & Guiry 1994), others regarded them as separate species (e.g. Ardré 1970, Feldmann & Hamel 1936). Moreover, Dixon (1966) considered that these two species together with *G. pulchellum* and *G. pusillum* are a single entity that shows morphological variations in relation to the environmental conditions. Recent works involving molecular data clarified that *G. pusillum* is a different species from *G. crinale/pulchellum* and suggested that the last pair of species probably represent a single one (Freshwater & Rueness 1994). With regard to *G. spathulatum* there are no published molecular data, and its morphological differentiation from *G. crinale* is still more complex. In the Atlantic Iberian Peninsula 4 entities can be separated based on their morphology, of which two are

present in sand-covered rocks. Whether these entities correspond to four different species or they are just different forms of a lesser number of taxa surely deserves further research. Our criterion to separate *G. crinale* and *G. spathulatum* is that the former species has erect branches predominantly terete, while they are predominantly compressed in *G. spathulatum*. We recognize that sometimes there are intermediate forms that are assigned to one or another entity with difficulty, but in general both can be separated.



Figure 8. Distribution of the collections of *Gelidium spathulatum* along the Atlantic Iberian Peninsula.



Figure 9. World distribution of *Gelidium spathulatum*. Arrow indicates the type locality.

Pterocladia *melanoidea* (Schousboe *ex* Bornet) Santelices & Hommersand

Basionym: *Gelidium melanoideum* Schousboe *ex* Bornet

Lectotype: PC

Type locality: Tingi, Tanger, Morocco

References: Bornet 1892, Feldmann & Hamel 1936, Fredriksen & Rueness 1990, Bárbara & Díaz-Tapia 2012.

Selected specimens collected at 4 sites, from a total of 28 (39 dates): Asturias: 1) Aguilar (43°33'28"N; 6°07'07"W), 17.iv.2007, SANT-Algae 19795 (tetrasporangial plants); A Coruña: 2) Barizo (43°18'48"N; 8°52'27"W), 9.ix.2002, 5.iv.2004, SANT-Algae 24948, 24949 (female and tetrasporangial plants); 3) Seaia (43°19'41"N; 8°49'34"W), 19.ix.2008, SANT-Algae 24432 (female and tetrasporangial plants); 4) Lourido (43°05'28"N, 9°13'15"W), 1.ii.2006, SANT-Algae 16878, 22600.

Observations

Vegetative and reproductive morphology

Thalli forming tufts up to 3 cm high, consisting of a short system of creeping stoloniferous prostrate axes, irregularly branched, bearing erect slender branches and rhizoids that attach to the substrate (Figs. 10A-G). Tufts bright red in color, with a rigid texture. Erect branches growing from distinct apical cells, predominantly compressed, up to 350 µm wide, but often with terete parts especially at the base, from scarcely to densely and irregularly branched, opposite branches are common (Figs. 10C-E, H). Structure uniaxial, showing in cross section a central row of 7-11 non-pigmented cells, surrounded by medullary cells and a layer of outer cortical cells (Fig. 10J), with hyaline cells intercalated between the cortical ones; rhizines are present in the medulla only in holdfast regions (Fig. 10K). Cortical cells polygonal, longest side is 5-17 µm (Fig. 10I).

Cystocarps intercalary on axes and branches (Fig. 10E), often located above branching points, 350-600 µm long, unilocular with a single ostiole (Figs. 10L-M), gonimoblast attached to the cystocarpic floor (Fig. 10N). Male reproductive structures not observed. Tetrasporangia formed in apical parts of erect axes or on lateral branches, which often reinstated the growth and then tetrasporangia appear on main axes, compressed, up to 1.5 mm long, tetrasporangia forming V-shaped rows, with up to 8 tetrasporangia per row and 20 rows per branch (Figs. 10O-P). Tetrasporangia ovoid, 27-40 µm in diameter, cruciately divided (Figs. 10Q).

Phenology

Pterocladia melanoidea was collected throughout the year, but only rarely during July and August. It is probably perennial. Reproductive structures were common year round. Female structures were found in 18% of the collections and tetrasporangia in 53%.

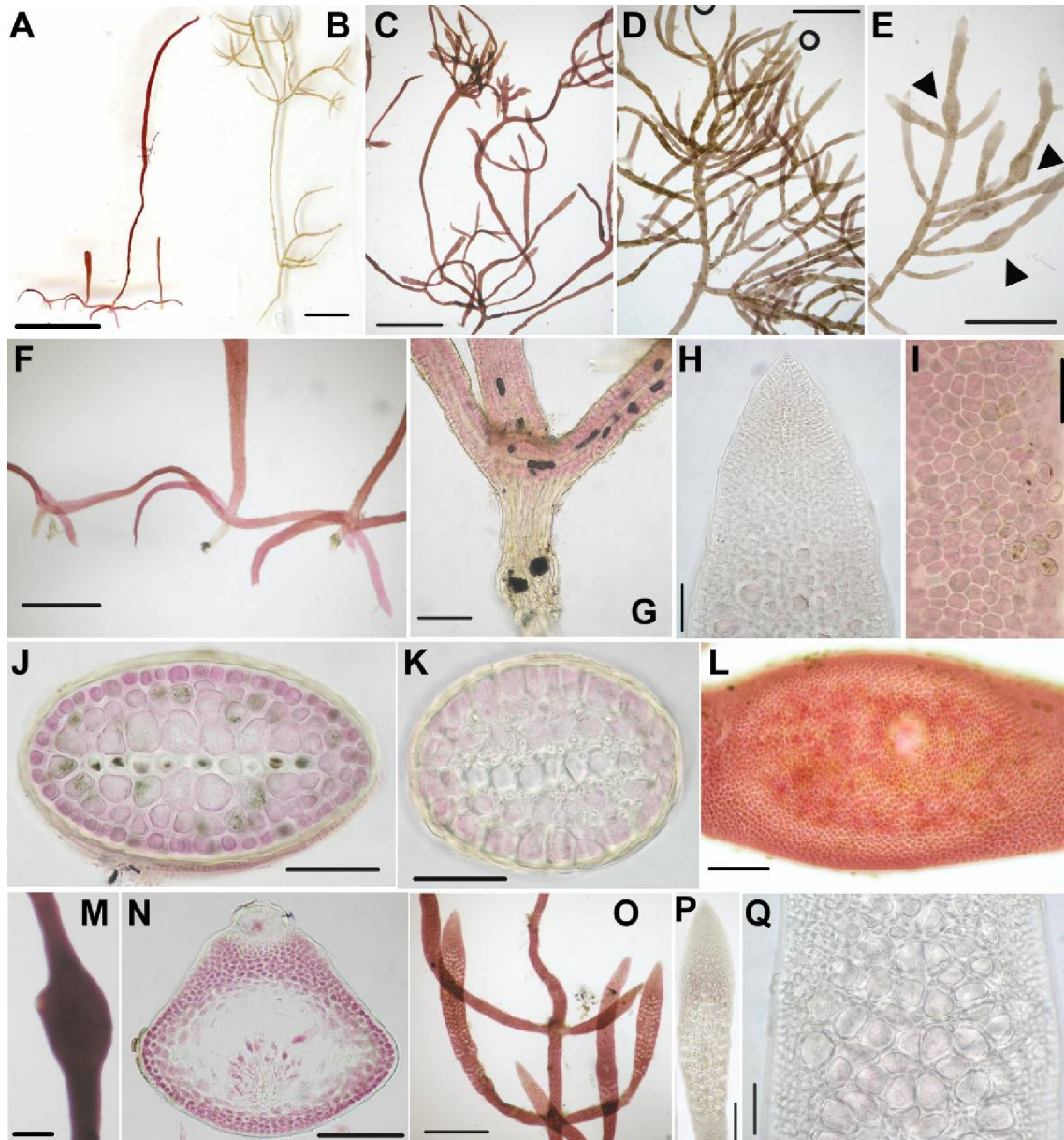


Figure 10. *Pterocliadiella melanoidea*. Vegetative and reproductive morphology.

A-D: Habit of plants from simple (A) to densely and irregularly branched (D). E: Upper branches with cystocarps (arrowheads). F: Prostrate system of stoloniferous axes. G: Rhizoid. H: Apex of a branch with a prominent apical cell. I: Surface view of thallus. J: Cross section of mid part of thallus showing a central row of cells surrounded by medullary cells and an outer layer of cortical cells. K: Cross section of holdfast showing rhizines in the medulla. L: Surface view of a cystocarp showing a prominent ostiole. M: Lateral view of a cystocarp. N: Cross section of a cystocarp. O-P: Lateral branches with tetrasporangia forming V-shaped rows. Q: Tetrasporangia. Scale bars. A-B = 3 mm; C-E = 2 mm; F, M, O = 600 μ m; G, L, N = 100 μ m; H-K, Q = 50 μ m; P = 200 μ m.

Habitat and distribution

Pterocladia melanoidea is frequent in sand-covered rocks from the Atlantic Iberian Peninsula (Fig. 11), but it is commonly found forming small tufts mixed with *Rhodothamniella floridula* or other species typical from the habitat and only rarely forms extensive turfs. *Pterocladia melanoidea* and *Ptilothamnion sphaericum* usually grow together, and both species are especially abundant on vertical rocks that are buried by sand for long periods. This explains the low number of the collections during summer months, when the sand builds up in the beaches. It was collected in the low intertidal, in highly wave-exposed sites. *Pterocladia melanoidea* has been reported from southern Europe and northern Africa, and more recently from northwestern France (Fig. 12).



Figure 11. Distribution of the collections of *Pterocladia melanoidea* along the Atlantic Iberian Peninsula.



Figure 12. World distribution of *Pterocladia melanoidea*. Arrow indicates the type locality.

Remarks

Descriptions of *Pterocladia melanoidea* show a high morphological variability, and two varieties are recognized: *P. melanoidea* var. *filamentosa* (Schousboe ex Bornet) M.J. Wynne and *P. melanoidea* var. *gracile* (Feldmann & Hamel) M.J. Wynne (Bornet 1892, Feldmann & Hamel 1936, Fredriksen & Rueness 1990). All materials here assigned to *P. melanoidea* resemble var. *gracile*, which is distinguished by its larger cortical cells and because it has elongate lateral axes that are mostly unbranched (Feldmann & Hamel 1936, Fredriksen & Rueness 1990, Bárbara & Díaz Tapia 2012). Our material also has large cortical cells, but by contrast, lateral axes are usually branched. The habit of specimens from sand-covered rocks along the Atlantic Iberian Peninsula clearly differs from the typical forms of *P. melanoidea* (Feldmann & Hamel 1936, Fredriksen & Rueness 1990).

This species was originally described as a member of the genus *Gelidium* based on its vegetative features (Bornet 1892). Subsequently, a study of its reproductive structures revealed that this species is better accommodated in the genus *Pterocladia*, since it has unilocular cystocarps that differ from bilocular ones that characterize the genus *Gelidium* (Fredriksen and Rueness 1990). Later, a study of the cystocarps in selected species of the genus *Pterocladia* showed that two types of cystocarps can be distinguished, and the genus *Pterocladia* was segregated including, among other species, *P. melanoidea* (Santelices & Hommersand 1997). Although we have not carried out a detailed study of the female structures in materials here assigned to *P. melanoidea*, our specimens have unilocular cystocarps and young cystocarps apparently with nutritive cells organized in a central core around the axial filament (Fig 10N), which is in agreement with the genus *Pterocladia* (Santelices & Hommersand 1997).

Materials here assigned to *Pterocladia melanoidea* largely resemble *Gelidium calcicola* Maggs & Guiry, which was described from maërl beds of the British Isles and northern France

(Maggs & Guiry 1987), and subsequently reported in Galician maërl beds (Bárbara *et al.* 2004). In Galicia, specimens from the intertidal assigned to *P. melanoidea* and those from maërl beds labelled as *G. calcicola* show great similarity, and we have doubts that both belong to different species (Bárbara & Díaz Tapia 2012). The habitat is practically the only criterion used to separate them. The differentiation of an intertidal and subtidal species in the Atlantic Iberian Peninsula, the assignment of materials either to *G. calcicola* or *P. melanoidea*, and the study of the relations between the different varieties of *P. melanoidea* and *G. calcicola* surely deserves further research.

GIGARTINALES
CYSTOCLONIACEAE

Calliblepharis hypneoides Díaz-Tapia, Bárbara & Hommersand, sp. nov.

Holotype: SANT-Algae

Type locality: Aguilar, Asturias, Spain

A new species is described in the following article. *Calliblepharis hypneoides* has been widely collected in sand-covered rocks along all the Atlantic Iberian Peninsula. Interestingly, this species was initially labelled as *Hypnea* cf. *musciiformis* and later as *Hypnea arbuscula* because its habit resembles this genus. However, molecular and morphological studies of vegetative and reproductive features evidenced that this species is a new taxon belonging to the genus *Calliblepharis*.

Morphology and systematics of *Calliblepharis hypneoides* sp. nov. (Cystocloniaceae, Rhodophyta) from the Atlantic Iberian Peninsula.

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Abstract

Calliblepharis hypneoides Díaz-Tapia, Bárbara et Hommersand, sp. nov. is described based on plants collected in sand-covered rocks from southern France to Portugal. *Calliblepharis hypneoides* is distinguished by a terete thallus, forming an extensive basal system of entangled prostrate axes that bear few irregularly branched upright axes, an inner structure consisting of a central axial filament surrounded by 5-7 filaments of elongated cells, a continuous outer cortex, spermatangial parent cells transformed from outer cortical cells and bearing spermatangial filaments 3-4 cells long, a single gonimoblast initial cut off from the inner side of the auxiliary cell, with the young carposporophyte consisting of a central reticulate network of interconnected cells linked inwardly to a cluster of basal nutritive filaments and forming gonimoblasts outwardly that bear chains of carposporangia in non-ostiolated cystocarps arising on main axes and branches, and with tetrasporangia terminal in sori on ultimate branchlets. These features are characteristic of *Calliblepharis* and the molecular analyses confirm this relationship. In all phylogenetic analyses of *cox1*, *rbcL*, and SSU sequences, *C. hypneoides* was consistently distinct from congeners. In both *rbcL* and SSU trees, its sister relationship to other species was unresolved probably due to missing species or the exclusion of undescribed species. This is the first report on the systematics of *Calliblepharis* using three molecular markers.

Key words: *Calliblepharis*, *cox1*, *Cystocloniaceae*, *Gigartinales*, *Hypnea*, morphology, reproduction, *rbcL*, red algae, SSU.

Introduction

The family Cystocloniaceae, which produces the economically important carbohydrate polymer carrageenan, includes 13 genera and ca. 89 species from cold- to warm-temperate waters (Chiovitti *et al.*, 1998; Guiry and Guiry, 2013). Most genera are monospecific or contain less than five species, except *Hypnea* (ca. 54 species), *Rhodophyllis* (ca. 12 species) and *Craspedocarpus* (ca. 7 species).

Kylin (1930) suggested a close relationship between the genera *Calliblepharis* and *Hypnea*, based primarily on similarities in their procarp structure. At first, Kylin (1930) placed both genera in the Hypneaceae, but he later moved *Calliblepharis* to the Cystocloniaceae (Kylin, 1932, as Rhodophyllidaceae), based on its carposporophyte structure. While only terminal cells of the carposporophyte form carposporangia in *H. musciformis*, several layers of gonimoblast filaments are converted into carposporangia in *Calliblepharis jubata* and the carposporangia are borne terminally in chains. Moreover, the cystocarp of *H. musciformis* contains numerous filaments that link the gonimoblast filaments and the pericarp (Kylin 1930), which are absent in *C. jubata* (Kylin, 1928). In vegetative structure and other reproductive details *Hypnea* is similar to other Cystocloniaceae (Womersley, 1994). Recent molecular phylogenies do not support the recognition of the Hypneaceae as distinct from Cystocloniaceae and the two families are currently merged (Hommersand & Fredericq, 2003; Saunders *et al.*, 2004). While most molecular studies have focused on the large genera, such as *Hypnea* (Yamagishi & Masuda 2000; Geraldino *et al.*, 2009, 2010), the diversity and phylogeny of the smaller genera remain unclear.

Calliblepharis, established upon *C. ciliata* from England (Kützing, 1843; Dixon & Irvine, 1977), is presently a genus that includes 6 species with a continuous distribution from England to Australia. *Calliblepharis ciliata* and *C. jubata* are distributed from the British Isles through the Iberian Peninsula to Mauritania (Dixon & Irvine, 1977; Bárbara *et al.*, 2005; Araújo *et al.*, 2009). *Calliblepharis fimbriata* was originally described from South Africa and the Falkland Islands and has subsequently been recorded from other localities (Silva *et al.*, 1996); *C. planicaulis* and *C. celatospora* occur in Australia (Womersley, 1994; Chiovitti *et al.*, 1998); while *C. jolyi* is recorded from Brazil (Guimarães & Pereira, 1993). The genus *Hypnea* is much more numerous, containing about 53 species from tropical and warm temperate regions (Geraldino *et al.*, 2009). The only species of this genus reported in the Atlantic Iberian Peninsula are *H. musciformis*, widely recorded worldwide from temperate coasts, and *H. coccinea*, a poorly documented species reported only from its type locality (Cádiz, Southern Spain).

During a sampling survey for unravelling algal diversity in sand-covered rocks, we found for the first time in 1997 a terete gigartinean rhodophyte, that could not be identified based on local floristics or monographic references (e.g. Ardré, 1970; Dixon & Irvine, 1977). We extended sampling of this species from the entire Atlantic Iberian Peninsular region up to 2011 and