GELIDIALES (*RHODOPHYTA*) IN THE CANARY ISLANDS: PREVIOUS STUDIES AND FUTURE PERSPECTIVES

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Abstract

Gelidiales is a red algae order which belongs to the class Florideophyceae and comprises four genetically recognized families: Gelidiaceae, Gelidiellaceae, Pterocladiaceae and Orthogonacladiaceae. It is a copious order characterized in the Canary Islands by 16 species, some of which are endemic and canopy-forming with populations in unforeseen decline over the last four decades. The aim of this article is to examine all previous studies into the Gelidiales in the Canary Islands, in order to synthesize and demonstrate the relevance of these species to the benthic marine communities of the archipelago. This review also identifies those knowledge gaps that need to be addressed to predict future changes in the marine ecosystems and suggest conservation and/or recovery plans for their populations.

Keywords: canopy-forming species, endemism, Gelidiaceae, Gelidiellaceae, phenology, Pterocladiaceae, herbarium.

GELIDIALES (*RHODOPHYTA*) EN LAS ISLAS CANARIAS: ESTUDIOS PREVIOS Y PERSPECTIVAS FUTURAS

Resumen

Gelidiales es un orden de algas rojas perteneciente a la clase Florideophyceae que está constituido por cuatro familias reconocidas genéticamente: Gelidiaceae, Gelidiellaceae, Pterocladiaceae y Orthogonacladiaceae. Es un orden numeroso caracterizado en Canarias por 16 especies, algunas de ellas endémicas, formadoras de hábitats y con poblaciones en marcado declive en las últimas décadas. El objetivo de este trabajo es revisar todos los estudios previos publicados sobre Gelidiales en las islas Canarias con el fin de sintetizar y mostrar su protagonismo en las comunidades bentónicas marinas del archipiélago. Esta síntesis también identifica aquellos vacíos de conocimiento que necesitan ser abordados para predecir cambios futuros en los ecosistemas marinos de Canarias y proponer planes de conservación y/o recuperación de sus poblaciones en las islas.

Palabras clave: endemismo, especies formadoras de hábitat, fenología, Gelidiaceae, Gelidiellaceae, Pterocladiaceae, herbario.

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1. INTRODUCTION

The order Gelidiales Kylin (Florideophyceae, Rhodophyta) is constituted of numerous macroalgal species inhabiting the world's template regions (Guiry and Guiry 2019). Gelidiales stand out due to their economic interest as a natural source of high-quality agar and agarose, which are mainly used in the food, cosmetic and biotechnology industries (Rao and Kaliaperumal 1983, 1987; Santelices 1987a, b; Fredriksen and Rueness 1989; Armisén 1994; Freile-Pelegrin *et al.* 1995; Bouzon *et al.* 2005, 2006; Scariot *et al.* 2012; Simioni *et al.* 2014a, b; Boo *et al.* 2016a; Filipin *et al.* 2016). Nevertheless, the ecological role of the Gelidiales also makes them stand out among other rhodophytes as there are several canopy-forming and dominant species that harbor high biodiversity and provide important ecosystem services (Juanes and Puentes 1993; Melo and Neushul 1993; Scrosati and Servière-Zaragoza 2000; Mercado *et al.* 2001; Bouza *et al.* 2006; Díez *et al.* 2012; Polifrone *et al.* 2012; Borja *et al.* 2013, 2018; Stroobant *et al.* 2014; Quintano *et al.* 2014, 2015, 2017, 2018; Schmidt *et al.* 2015; Alfonso *et al.* 2017a, 2018; Otaíza *et al.* 2018).

Amongst the 7262 documented red algae species, approximately 233 belong to the Gelidiales (Guiry and Guiry 2019). These species share with the entirety of the Rhodophyta a combination of specific attributes that outline them as a distinct eukaryotic monophyletic lineage within the super group of Archaeplastida, together with Glaucophyta and green organisms (green algae and terrestrial plants) (Bhattacharya *et al.* 2004; Adl *et al.* 2005; Yang *et al.* 2005, 2016; Burki 2014; Yoon *et al.* 2010, 2016). The morphological, cytological and reproductive attributes of the Rhodophyta are: (1) accessory pigments named phycobilins [phycoerythrobilin (red) and phycocyanobilin (blue)] that form clusters on the surface of thylakoids; (2) the unstacked thylakoids in the plastid; (3) floridean starch in the cytoplasm; (4) the presence of pit connections (protoplasmic connections) between adjacent cells; (5) triphasic life cycle (gametophyte, sporophyte and carposporophyte) (Figure 1), and (6) complete absence of flagella and centrioles in all life stages (Dixon 1973; Gabrielson *et al.* 1990; Woelkerling 1990; Graham and Wilcox 2000; Yoon *et al.* 2006; Verbruggen *et al.* 2010; Hurd *et al.* 2014; Yang *et al.* 2015). However, the order Gelidiales also display a specific set of morphological characters that enable them to be recognized among other red algae: (1) pseudoparenchymatous uniaxial organization, with the axial filament branched in three planes; (2) agar as component of the cell wall; (3) simple covered pit connections; (4) diplohaplophasic life cycle with isomorphic gametophytes and tetrasporophytes; (5) intercalary carpogonia that originates gonimoblast filaments linking nutritive cells after fertilization; (6) transversally divided spermatangia; and (7) a specific spore germination pattern, so-called "*Gelidium*-type" (Figure 2) (Hommersand and Fredericq 1988).

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Currently, there are four accepted families in the Gelidiales; Gelidiaceae Kützing (7 genera, 158 species), Gelidiellaceae Fan (2 genera, 27 species), Pterocladiaceae Felicini et Perrone (3 genera, 24 species) and Orthogonacladiaceae Boo, Le Gaillon, Miller et Boo (2 genera, 4 species). Boo *et al.* (2016b), combining morphological and molecular studies, described the latest family Orthogonacladiaceae and genetically verified the families previously described (Freshwater and Bailey 1998; Perrone *et al.* 2006; Tronchin and Freshwater 2007). The main attributes used to separate the families are related to carposporophyte development and cystocarp (carposporophyte protected by a pericarp) morphology. Nevertheless, as fertile gametophytes are uncommon in many Gelidiales species, some vegetative diagnostic characters have been proposed owning to the presence of rhizines (internal thick-walled rhizoidal filaments) and the morphology and ontogeny of the attachment system (Perrone *et al.* 2006). In addition, the location of sporangia also helps to identify some genera (Table 1).

TABLE 1. MAIN DIAGNOSTIC MORPHOLOGICAL CHARACTERS OF THE FAMILIES IN GELIDIALES (ADAPTED FROM BOO *et al.* 2016A).

	Gelidiaceae	Gelidiellaceae	Pterocladiaceae	Orthogonacladiaceae
N.º species	167	33	29	4
Branching pattern	Irregular, alternate or pinnate	Irregular, distichous or pinnate	Irregular or pinnate	Irregular or pinnate nearly in right angle with main axis
Rhizines	Present	Absent	Present	Present
Reproductive structures				
Tetrasporangia *Location*	Apical sori	Stichidia	Apical sori	Apical or lateral sori
Organization	Irregularly or in parallel rows	Irregularly, in parallel or in V-like rows	Irregularly, in parallel or in V-like rows	Irregularly or in parallel rows
Espermatangia *Location*	Apical sori	Apical sori or lateral and protrude sori	Apical sori	Apical or lateral sori
Cystocarps	Bilocular	Unknown	Unilocular or ovoid-triangular	Unilocular
Prostrate system				
Rhizoidal filaments	Independent formation. Endogenous	Independent formation. Unicellular and exogenous	Endogenous coalescent within a thick sheath	Extensively branched. Endogenous coalescent within a thick sheath
Haptera	Present	Absent	Present	Present

In relation to the vegetative characters, the branching pattern in Gelidiales is irregularly, alternately, distichously or pinnately branched, with some cases the pinnae and pinnules arising at nearly right angles to the parent branch as occurs in the Orthogonacladiaceae (Boo *et al.* 2016b). Rhizines are only absent in Gelidiellaceae species. Erect axes of all Gelidiales arise from a prostrate system of entangled stolons attached to the substratum, consisting of either independent rhizoidal filaments or complex haptera (Perrone *et al.* 2006). The Gelidiellaceae attachment system consists of independent unicellular rhizoidal filaments arising from stolon superficial cells that remain in open connection with their mother cells. On the contrary, Gelidiaceae, Pterocladiaceae and Orthogonacladiaceae develop a more complex prostrate system with cells of different origin, morphology and function. In these families, rhizoids have an endogenous origin and arise from the cortical cells, whilst the basal cortication of the attachment system originates exogenously and secondarily from superficial cells. Exceptionally, Pterocladiaceae and Orthogonocladiaceae develop a mucilaginous sheath surrounding the rhizoidal filaments (Perrone *et al.* 2006; Boo *et al.* 2016b, c, d).

The reproductive structures in Gelidiellaceae are localized in specialized reproductive branchlets named stichidia (Fan 1961; Rico *et al.* 2002; Perrone *et al.* 2006; Boo *et al.* 2016a). The remaining families display tetrasporangia or bisporangia in apical o lateral sori. Gelidiaceae and Pterocladiaceae develop apical sori, whereas Orthogonacladiaceae and Gelidiellaceae may have apical or lateral sori protruding in the latest family. After fertilization the cystocarps grow bilocular and circular in Gelidiaceae with carposporangia emerging on both surfaces of the fertile branch. Aversely, in Pterocladiaceae and Orthogonocladiaceae the cystocarps are unilocular, ovoid or triangular (Santelices and Hommersand 1997). In Gelidiellaceae, the female reproductive structure is unknown (Santelices 1977; Rico *et al.* 2002; Boo *et al.* 2016a).

In the Canary Islands occurrence of 16 species of Gelidiales is currently accepted (Afonso-Carrillo 2014; Boo *et al.* 2016d; Gallardo *et al.* 2016), some of which are endemic, canopy-forming and with populations that have been declining over the last decades (Sansón *et al.* 2013; Martínez *et al.* 2015; Alfonso *et al.* 2017b). Furthermore, these macroalgae are important primary producers on exposed rocky shores in the islands, so the severe reduction in their populations is of major concern. This article, therefore, aims to highlight the relevance and importance of the Gelidiales to the benthic marine communities in the archipelago by drawing on previous studies into the Gelidiales in the Canary Islands. There exist certain knowledge gaps that will be identified and in combination with conclusions based on previous studies, future changes to the marine ecosystems will be predicted and conservation and recovery plans for their populations suggested.

2. GELIDIALES BIODIVERSITY IN THE CANARY ISLANDS

The number of species documented for the Canary Islands has not significantly changed since the first studies on phytobenthos were carried out on the islands (Montagne 1840; Piccone 1884, 1886; Vickers 1896; Børgesen 1927; Lawson and Norton 1971). Børgesen (1927) had already registered 12 of the species, some of which with recently nomenclatural changes. Nowadays, there are 4 species of Gelidiellaceae, 9 Gelidiaceae and 2 Pterocladiaceae (Afonso-Carrillo and Sansón 1999; Afonso-Carrillo 2014; Guiry and Guiry 2019).

Gelidiellaceae is represented by three genera in these islands, *Millerella* Boo et Boo (*M. tinerfensis*, *M. pannosa*), *Parviphycus* Santelices (*P. antipae*, *P. setaceus*) and *Huismaniella* (*Huismaniella* sp.). Originally, these species were all described as *Gelidiella* or *Echinocaulon* (Afonso-Carrillo and Sansón 1999; Guiry and Guiry 2019), although recent phylogenetic studies have assigned them to the new genera *Millerella*, *Parviphycus* and *Huismaniella* (Boo *et al.* 2016d). *Gelidiella tinerfensis* was first described based on specimens collected at Puerto de la Cruz (Tenerife) by Seoane-Camba (1977) and considered endemic to the Canary Islands. Recently this species was recognized synonymous with *Millerella tinerfensis* (Boo *et al.* 2016d). *Gelidiella tenuissima*, listed for the Canary Islands by Audiffred (1985), Betancort *et al.* (1995), Rico *et al.* (2002) and Gil-Rodríguez *et al.* (2003), was considered synonymous with *Millerella pannosa* (as *Gelidiella pannosa*) by John *et al.* (2004). *Parviphycus antipae* was registered in the archipelago in 1992 (Afonso-Carrillo *et al.* 1992; Sangil *et al.* 2003; as *Gelidiella*), while *P. setaceus* was documented by Afonso-Carrillo *et al.* (2007). More recently, Boo *et al.* (2016d) reported a currently unidentified species of *Huismaniella* from the Canary Islands (Tenerife) as result of their genetic analyses.

Gelidiaceae is represented in the Canary Islands by 9 species of *Gelidium* J.V. Lamouroux: *G. arbuscula*, *G. canariense*, *G. corneum*, *G. crinale*, *G. microdon*, *G. pectinatum*, *G. pusillum*, *G. spathulatum* and *G. spinosum* (Gallardo *et al.* 2016). The first species registered in the islands was *G. arbuscula*. The authority of this species is often attributed to Bory. However, it was Børgesen (1927), who published the combination of *G. arbuscula*, including individuals deposited in the Bory Herbarium collected in Tenerife, which coincided with a specimen named *G. corneum* var. *nereideum* by Montagne (1840). Despite also being cited in northeast Africa, Price *et al.* (1988) and later John *et al.* (2004) agreed on the lack of evidence of that statement, therefore proposing to accept *G. arbuscula* as an endemic species from the Canary Islands.

Gelidium canariense was originally described as *G. cartilagineum* var. *canariensis* by Grunow in Piccone (1884) based on specimens collected at Puerto de la Cruz (Tenerife) (Afonso-Carrillo 2003b). Afterwards, the entity was referred only as *G. cartilagineum* (Lawson and Norton 1971) or as *G. versicolor* (Haroun *et al.* 1984), until the new combination proposed by Seoane-Camba (1979) as a new endemic species to the Canary Islands [*G. canariensis* (Grunow in Piccone) Seoane-Camba]. However, the combination *G. canariensis* was not correctly done in accordance with article 33.3 of the ICBN (Greuter *et al.* 200) hence, Haroun *et al.* (2002) validated the species as *G. canariense* (Grunow in Piccone) Seoane-Camba ex Haroun, Gil-Rodríguez, Díaz de Castro et Prud'homme.

Regarding *G. corneum*, this species was included in the catalogues by Price *et al.* (1988), John *et al.* (2004), Afonso-Carrillo (2014) and Gallardo *et al.* (2016), based on the statement made by Børgesen (1927). Nonetheless, Børgesen (1927) did not observe nor collect any specimen in the Canary Islands, thereupon his reference was based both on Montagne's (1840) study (as *G. corneum* var. *capillaceum*, now *Pterocladiella capillacea*) and also upon the Lyngbye herbarium (Price *et al.* 1988). As a result of this, Børgesen (1927) referred to *G. corneum* as probably rare. No further references are known about the presence of this macroalga in the archipelago, so it is very likely to be a misidentification.

The six remaining species of *Gelidium* were cited in the first phycological studies performed in the Canary Islands. *Gelidium crinale*, *G. pectinatum* and *G. pusillum* were documented by Vickers (1896) from specimens collected in Gran Canaria. *Gelidium pectinatum* was reported from a single specimen and never identified again. Surprisingly, *G. pectinatum* has been omitted from the macroalgae lists of the Canary Islands for several decades, probably due to a nomenclatural problem with *Gelidium bipectinatum* (Furnari *et al.* 1999; Taskin and Wynne 2013; Andersen 2018), so although this species needs confirmation, we include it in the marine flora of the Canary Islands. Subsequently, Sauvageau (1912) mentioned *G. spathulatum* and *G. spinulosum* (now synonymous with *G. microdon*) as collected in Tenerife. Finally, *G. spinosum* was recorded for the first time in the Canary Islands in Price *et al.* (1988). The complex plasticity that characterizes this group of species, together with the seasonal changes, makes difficult to identify correctly based solely on morphological characteristics. Additional morphological, chemical and genetic studies are needed in order to reach a better knowledge of the diversity in this group of macroalgae in the Canary Islands.

Eventually, the family Pterocladiaceae in the Canary Islands is depicted by two species of the genera *Pterocladiella* (Afonso-Carrillo and Sansón 1999). Santelices and Hommersand (1997) created *Pterocladiella* to include the species previously assigned to *Pterocladia* but display cystocarps with nutritive cells around a central axis and carposporangia radially emerging to the cavity. These attributes are absent in *Pterocladia*. The species type *Pterocladiella capillacea* was first mentioned by Børgesen (1927) who stated the citation of *G. corneum var. capillaceum* in Montagne (1840), today synonymous with the aforementioned species. The second species registered in the Canary Islands, *Pterocladiella melanoidea* was recorded for the first time in Tenerife in the 1990s (Elejabeitia *et al.* 1992; Pinedo *et al.* 1992; Reyes *et al.* 1993) (Table 2).

TABLE 2. FAMILIES, GENERA AND GELIDIALES SPECIES DOCUMENTED IN THE CANARY ISLANDS. REFERENCES TO EACH SPECIES ARE INCLUDED

Families and genera	Species	References
Gelidiaceae *Gelidium* J.V. Lamouroux	*G. arbuscula* Bory de Saint-Vincent et Borgesen	Vickers 1896; Sauvageau 1912; Børgesen 1927; Lawson and Norton 1971; Haroun *et al.* 1984; Price *et al.* 1988; Pinedo *et al.* 1992; Afonso-Carrillo and Sansón 1999; Haroun *et al.* 2002; Sangil *et al.* 2003; Gil-Rodríguez *et al.* 2003; John *et al.* 2004; Afonso-Carrillo 2014; Gallardo *et al.* 2016.
	G. canariense (Grunow) Seoane-Camba ex Haroun, Gil-Rodríguez, Díaz de Castro et Prud'home van Reine	Montagne 1840; Piccone 1884; Sauvageau 1912; Børgesen 1927; Lawson and Norton 1971; Seoane-Camba 1979; Haroun *et al.* 1984; Price *et al.* 1988; Pinedo *et al.* 1992; Afonso-Carrillo and Sansón 1999; Haroun *et al.* 2002; Sangil *et al.* 2003; Gil-Rodríguez *et al.* 2003; John *et al.* 2004; Afonso-Carrillo 2014; Gallardo *et al.* 2016.
	G. corneum (Hudson) J.V. Lamouroux	Montagne 1840; Børgesen 1927; Price *et al.* 1988; Afonso-Carrillo and Sansón 1999; John *et al.* 2004; Afonso-Carrillo 2014; Gallardo *et al.* 2016
	G. crinale (Hare ex Turner) Gaillon	Montagne 1840; Vickers 1896; Sauvageau 1912; Børgesen 1927; Price et al 1988; Haroun *et al.* 2002; Gil-Rodríguez *et al.* 2003; John *et al.* 2004; Afonso-Carrillo 2014; Gallardo *et al.* 2016.
	G. microdon Kützing	Montagne 1840; Price *et al.* 1988; Afonso-Carrillo and Sansón 1999; Haroun *et al.* 2002; Gil-Rodríguez *et al.* 2003; John *et al.* 2004; Afonso-Carrillo 2014; Gallardo *et al.* 2016.
	G. pectinatum Montagne	Vickers 1896; Børgesen 1927; Gil-Rodríguez and Afonso-Carrillo 1981; Price et al 1988.
	G. pusillum (Stackhouse) Le Jolis	Vickers 1896; Børgesen 1927; Gil-Rodríguez and Afonso-Carrillo 1981; Delgado *et al.* 1984; Audiffred 1985; Price *et al.* 1988; Pinedo *et al.* 1992; Elejabeitia *et al.* 1992; Reyes *et al.* 1994; González-Ruiz *et al.* 1995 a, b; Guadalupe-González *et al.* 1995; Afonso-Carrillo and Sansón 1999; Haroun *et al.* 2002; Aldanondo-Aristizabal *et al.* 2003; Gil-Rodríguez *et al.* 2003; Sangil *et al.* 2003; Díaz-Villa *et al.* 2004; John *et al.* 2004; Reyes *et al.* 2005; Afonso-Carrillo 2014; Gallardo *et al.* 2016.
	G. spathulatum (Kützing) Bornet	Sauvageau 1912; Børgesen 1927; Price *et al.* 1988; Haroun *et al.* 2002; Gil-Rodríguez *et al.* 2003; John *et al.* 2004; Afonso-Carrillo 2014; Gallardo *et al.* 2016.
	G. spinosum (S.G. Gmelin) P.C. Silva	Price *et al.* 1988; Afonso-Carrillo and Sansón 1999; Haroun *et al.* 2002; Gil-Rodríguez *et al.* 2003; Sangil *et al.* 2003; John *et al.* 2004; Afonso-Carrillo 2014; Gallardo *et al.* 2016.

Gelidiellaceae *Millerella* G.H.Boo et S.M.Boo *Parviphycus* Santelices	*M. pannosa* (Feldmann) G.H. Boo et L.Le Gall	Audiffred 1985; Price *et al.* 1988; Pinedo *et al.* 1992; Elejabeitia *et al.* 1992; Betancort *et al.* 1995; Afonso-Carrillo and Sansón 1999; Haroun *et al.* 2002; Aldanondo-Aristizabal *et al.* 2003; Gil-Rodríguez *et al.* 2003; John *et al.* 2004; Santelices 2004; Afonso-Carrillo 2014; Gallardo *et al.* 2016; Boo *et al.* 2016a.
	M. tinerfensis (Seoane-Camba) S.M. Boo et J.M. Rico	Seoane-Camba 1977; Price *et al.* 1988; Guadalupe-González *et al.* 1995; Afonso-Carrillo and Sansón 1999; Haroun *et al.* 2002; Rico *et al.* 2002; Gil-Rodríguez *et al.* 2003; Sangil *et al.* 2003; John *et al.* 2004; Afonso-Carrillo 2014; Gallardo *et al.* 2016; Boo *et al.* 2016d; Woelkerling *et al.* 2018.
	P. antipae (Celan) B. Santelices	Elejabeitia *et al.* 1992; Afonso-Carrillo and Sansón 1999; Haroun *et al.* 2002; Gil-Rodríguez *et al.* 2003; Sangil *et al.* 2003; John *et al.* 2004; Santelices 2004; Afonso-Carrillo 2014; Gallardo *et al.* 2016.
	P. setaceus (Feldmann) J. Afonso-Carrillo, M. Sansón, C. Sangil et T. Díaz-Villa	Afonso-Carrillo *et al.* 2007; Afonso-Carrillo 2014; Gallardo *et al.* 2016.
Huismaniella G.H. Boo et S.M. Boo	*Huismaniella* sp.	Boo *et al.* 2016d
Pterocladiaceae *Pterocladiella* B.Santelices et Hommersand	*P. capillacea* (S.G.Gmelin) Santelices et Hommersand	Montagne 1840; Piccone 1884, 1886; Vickers 1896; Børgesen 1927; Delgado *et al.* 1984; Pinedo *et al.* 1992; Elejabeitia *et al.* 1992; Reyes *et al.* 1994; Guadalupe-González *et al.* 1995; Lawson *et al.* 1995; Afonso-Carrillo and Sansón 1999; Haroun *et al.* 2002; Gil-Rodríguez *et al.* 2003; Sangil *et al.* 2003; John *et al.* 2004; Afonso-Carrillo 2014; Gallardo *et al.* 2016.
	P. melanoidea (Schousboe ex Bornet) Santelices et Hommersand	Pinedo *et al.* 1992; Elejabeitia *et al.* 1992; Reyes *et al.* 1993; Lawson *et al.* 1995; Afonso-Carrillo and Sansón 1999; Haroun *et al.* 2002; Gil-Rodríguez *et al.* 2003; Sangil *et al.* 2003; John *et al.* 2004; Rancel 2008; Afonso-Carrillo 2014; Gallardo *et al.* 2016.

3. BIOLOGICAL AND MOLECULAR STUDIES OF GELIDIALES IN THE CANARY ISLANDS

The dominant and habitat forming species *Gelidium canariense, G. arbuscula* and *Pterocladiella capillacea* have been the target for most studies performed on the Gelidiales of the Canary Islands due to their important ecological role on the rocky shores. These studies have mainly dealt with the vegetative and reproductive phenology, ecophysiology and genetic diversity of the species (Darias-Rodríguez and Afonso-Carrillo 1986; Sosa and García-Reina 1992, 1993; Sosa *et al.* 1998; García-Jiménez *et al.* 1999; Mercado *et al.* 2001; Bouza, 2002; Rico *et al.* 2005; Bouza *et al.* 2006; Domínguez-Álvarez *et al.* 2011; Polifrone *et al.* 2012). The other Gelidiales species appear primarily as part of cespitose assemblages, albeit little is known about their relevance to the marine communities of the islands (Rico *et al.* 2002; Rancel 2008).

Phenological studies

Gelidiales show a *Polysiphonia*-type life cycle characterized by isomorphic alternation of generations (Figure 1). Diploid sporophytes form sporangia where meiosis occurs to generate haploid spores. After attachment and germination of the spores, they develop into dioecious gametophytes (male and female). Both the sporangia and spermatangia alike are formed in apical or lateral sori. Similarly, carpogonia also arise at terminal ends of branches but they are only evident after fertilization, when they become prominent cystocarps (Chihara and Kamura 1963; Hommersand and Fredericq 1988).

Phenological studies on *Gelidium canariense*, *G. arbuscula* and *Pterocladiella capillacea* show a clear dominance in terms of populations of tetrasporophytes (T) in comparison with female (F) and male (M) gametophytes. In *G. canariense*, ratios of 3:1:1 (T:F:M) (Darias-Rodríguez and Afonso-Carrillo 1986), 12:3:1 (Polifrone *et al.* 2012) and 4:1:1 in Tenerife (Alfonso *et al.* 2017a) and 4:1 (T:F) in Gran Canaria (Lindgren *et al.* 1998) have been found. In *G. arbuscula*, a T:G ratio of 7:1 was detected in Tenerife and Gran Canaria (Sosa and García-Reina 1992) and 33:1 in Tenerife (Polifrone *et al.* 2012), whereas in *P. capillacea* the ratio was 133:1:1 (T:F:M) in Tenerife (Polifrone *et al.* 2012) and 14:1 (T:F) in Gran Canaria (Stroobant *et al.* 2014). These evident differences in tetrasporophyte ratios documented in the literature may be due to changes in temperature and irradiance during the year or site studied. In fact, Stroobant *et al.* (2014) suggest an important effect of these factors on *P. capillacea* tetrasporophyte ratios.

Studies into spatio-temporal variations in populations of the endemic *Gelidium canariense* have agreed on the absence of seasonality of fertile individuals. Thus, all life cycle phases can be found throughout the year (Darias-Rodríguez and Afonso-Carrillo 1986; Lindgren *et al.* 1998; Polifrone *et al.* 2012; Alfonso *et al.* 2017a). In Gran Canaria, Betancort and González (1991) characterized a population with individuals more than 15 cm in length consisting of abundant small individuals (0-5 cm in length), which may suggest a high level of recruitment in the population. More recently, Alfonso *et al.* (2017a) described for the first time the coexistence of two different morphotypes in *G. canariense* populations. One morphotype is characterized by longer branches with a higher number of apices and occur in fertile (tetrasporophytes and gametophytes) individuals, whereas the other corresponds to smaller and less ramified non-fertile individuals. This study widens the available information about the vegetative and reproductive morphology of this endemic species (Piccone 1884; Børgesen 1927; Seoane-Camba 1979; Rico *et al.* 2005).

On the other hand, *Gelidium arbuscula* and *Pterocladiella capillacea* display a clear seasonality in their life cycles. Fertile female gametophytes of *G. arbuscula* only appear in winter in the Tenerife and Gran Canaria populations, while fertile female and male gametophytes of *P. capillacea* can be found in summer and winter respectively. In both species fertile tetrasporophytes can be observed throughout the entire year (Polifrone *et al.* 2012; Stroobant *et al.* 2014). In addition, the cespitose *Pterocladiella melanoidea* develops female gametophytes year-round according to Rancel (2008) and contrary to previous studies (Fredriksen and Rueness 1990).

Physiological studies

Canopy-forming Gelidiales in the Canary Islands have also been the focus of different physiological studies. Cardell *et al.* (1977) studied the annual variation of the agar content in *Gelidium arbuscula* and *G. canariense*. Agar is a phycocolloid used in food, cosmetic and laboratory industries, which is a natural component of the cell walls and intercellular matrix of Gelidiales and cannot be synthetized in laboratory. These authors determined that the agar content of these Gelidiales increase in July and reaches a maximum in November. Furthermore young individuals have an increase of 20% in agar content compared with older specimens.

Mercado *et al.* (2001) studied the effect of dissolved inorganic carbon (DIC) and incident light on the photosynthetic activity of *Gelidium canariense*, *G. arbuscula* and *Pterocladiella capillacea*. Among the different strategies of carbon uptake in macroalgae (Mercado *et al.* 1997, 1998, 2001; Giordano *et al.* 2005), Mercado *et al.* (2001) demonstrated that these species had a low capacity of use HCO_3^- (DIC) actively from the environment and that the light was a limiting factor to their photosynthetic rates. Populations of *G. canariense*, *G. arbuscula* and *P. capillacea* inhabit the northern rocky shores of the islands where clouds tend to accumulate the most (Martín *et al.* 2011), thus, affecting the light incidence to the surface. Furthermore, the northern shores of the islands are characterized by a strong hydrodynamism that allows the water to maintain high CO_2 concentrations independently of the light irradiance level. Hence, the adaptation of these species to their environment would favor the uptake of CO_2 by diffusion rather than by the active uptake of DIC when the light incidence level is low. However, the specific strategy of carbon acquisition in this species needs particular experiments to confirm this.

The photosynthetic inhibition of *Gelidium arbuscula* was studied in the Gran Canaria populations under natural conditions by exposing individuals to incident natural light and filtered ultraviolet (UV) radiation (Häder *et al.* 2001). The photosynthetic ability of macroalgae is determined by the energy associated to UV radiation and photosynthetically active radiation (PAR). However, when this energy exceeds the photochemical demand or dissipation ability of organisms, it is frequently related to photosensitivity, photo-tolerance, photosynthetic damage and photoinhibition (Hanelt and Figueroa 2012; Harb *et al.* 2018). According to Häder *et al.* (2001) the PAR values during the experiment reached 2000 µmol*m^{-2}*s^{-1} in air and 400 µmol*m^{-2}*s^{-1} at a depth of 4-6 m. The results after 30 minutes of continuous exposition to both PAR and filtered UV radiation revealed permanent damage to the algae. When *G. arbuscula* is exposed only 15 minutes, it is able to recover under sheltered conditions, although it never reaches the same photosynthetic levels. This outcome suggests that emersion periods during low tides are crucial to the survival of this species.

Not only is the incident light, but also the desiccation tolerance a key factor in the distribution and survival of the phytobenthos (Häder *et al.* 2011; Hawkins *et al.* 2016). Domínguez-Álvarez *et al.* (2011) studied the tolerance to emersion in *Gelidium canariense, G. arbuscula* and *Pterocladiella capillacea* on the northern shore of Tenerife. The results show a clear effect of desiccation tolerance to vertical distribution of these species. The endemic *G. canariense*, which grows in the upper sublittoral below the other two species, was indeed the most affected after the emersion. In the case of *G. arbuscula*, water loss of the thallus was reduced, although the clumped morphology of this species favors the maintenance of humidity. Lastly, *P. capillacea* demonstrated the fastest rehydration and recovery. This species is distributed worldwide and grows over the other two species in infralittoral pools or in the upper sublittoral, which demonstrates its high adaptability to environmental changes (Domínguez-Álvarez *et al.* 2011). However, little is known about the combined effect of irradiance and temperature on desiccation tolerance or photosynthesis production predicted under the scenario of climate change.

Recent studies have demonstrated the connection of some volatile compounds to the maturation of tetrasporangia in *P. capillacea* (García-Jiménez *et al.* 2013). Various physiological processes related to interspecific competition or reproductive mechanisms in macroalgae imply the emission and/or reception of compounds such as ethylene and dimethyl sulfide (DMS), a biogenic compound with antioxidants and defenses against herbivores (Fink 2007). In *G. arbuscula*, the effect of different light conditions (white light, red light and dark) on the production of these volatile compounds was studied (Alstyne and Puglisi 2007). The result was that there was no clear response or cellular damage to the algae, even though *G. arbuscula* produced high concentrations of dimethyl sulfide under all light conditions. Nevertheless, the authors admitted the need of further studies to assess the particular function of these compounds in the metabolism of this species.

BIOLOGICAL AND EARLY DEVELOPMENT STUDIES

General features of the life cycle of Gelidiales are well known since the first detailed descriptions by Kylin (1923). Yet recently, particular attention has been placed upon certain differences among families or even species (Maggs and Rico 1991; Rico *et al.* 2005; Simioni *et al.* 2014a; Alfonso *et al.* 2018). One example is the formation of different types of sporangia and spores in some Gelidiales, despite the typical cruciate tetrasporangia. Rico *et al.* (2005) described bisporangia along with cruciately, decussately and irregularly divided tetrasporangia in individuals of *Gelidium canariense* deposited in TFC (Herbarium of Universidad de La Laguna). According to Suneson (1982) in some coralline algae and several other rhodophytes, the bisporangia can produce binucleate haploid bispores or uninucleate diploid bispores, whereas the tetrasporangia generate uninucleate tetraspores. Rico *et al.* (2001) found in *G. canariense* mature binucleate spores, which in other species of the genus, usually only appear in immature sporangia (Maggs and Rico 1991).

Attachment and germination of diaspores to the substrate are the most critical and vulnerable stages in the life cycle of benthic macroalgae, with their success threatened by several factors (Fletcher and Callow 1992; Brawley and Johnson 1992; Fierst *et al.* 2005). In Gelidiales, the diaspores are tetraspores and carpospores, and their germination pattern is the so-called *Gelidium*-type, specific to the order (Chihara and Kamura 1963; Hommersand and Fredericq 1988). García-Jiménez *et al.* (1999) developed an axenic cultivation protocol for *G. canariense* from the Canary Islands, so that the species could be exploited as an agar source. After being released, the tetraspores were cultivated in an antibiotic solution for 55 days, after which the formation of rhizoidal filament and the erect axis began. More recently, Alfonso *et al.* (2018) described in detail the initial stages of the tetraspore development in *G. canariense* and *G. arbuscula* and agreed with the *Gelidium*-type germination pattern (Figure 2). Surprisingly, the spore germination in these species began between 2-4 h after release (Alfonso *et al.* 2018), nearly 2 h before other *Gelidium* species (Simioni *et al.* 2014a). This behavior could be an adaptive strategy for species that inhabit shores with strong hydrodynamism. Therefore, the faster attachment and germination of the spore would favor the recruitment of their populations. In addition, Gelidiales species also have modular-clonal growth, with new erect axes arising from the perennial attachment system (Santos and Duarte 1996; Hurd *et al.* 2014). This characteristic, along with the earlier attachment and germination of the spores, would contribute notably to their ability to maintain their populations and even colonize new substrates.

The life history of most of the cespitose Gelidiales is still incomplete. Initially, the absence of gametophytes was considered a diagnostic character in the genus *Gelidiella* until the first description of spermatangial sori in *Gelidiella acerosa* (Santelices 1997). Subsequently, Rico *et al.* (2002) obtained male gametophytes from cultivated tetraspores of *Millerella pannosa* (as *Gelidiella tenuissima*) of Gran Canaria. Only plants cultivated at 20°C developed spermatangial sori which completely covered both surfaces of the fertile branch. To better understand the biological differences among all cespitose Gelidiales species, further studies and cultivation experiments on their life cycles are needed.

GENETIC AND PHYLOGENETIC STUDIES

Genetic studies focusing on Gelidiales of the Canary Islands are scarce. Sosa and García-Reina (1992, 1993) analyzed genetic variability by isoenzyme electrophoresis of female gametophytes and tetrasporophytes of *Gelidium canariense* and *G. arbuscula* from populations in Tenerife and Gran Canaria. Despite being the first contribution to the knowledge of population dynamics of these dominant species, the number of genes used in the haploid subpopulation (gametophytes) were four times greater than those used in the diploid subpopulation (tetrasporophytes), so the authors suggested a possible bias on the results. With this in mind, Sosa *et al.* (1998) re-evaluated the previous data and only used the diploid subpopulation. Their results showed that both species differ in their mating systems and patterns of genetic differentiation. *Gelidium canariense* and *G. arbuscula* had significant differences among populations. However, differences between populations were twice as high in *G. arbuscula* than in *G. canariense*. According to the authors, one possible explanation is that the clonal growth and genetic drift is higher in *G. arbuscula* and therefore displays different allele frequency in haploid and diploid populations. On the contrary, no significant differences were found between tetrasporophytes and gametophytes allele frequencies in *G. canariense*, concluding that sexual reproduction is the main reproductive system in this species.

Bouza (2002) and Bouza *et al.* (2006) also contributed to the study of genetic diversity of natural populations of *Gelidium canariense*. They focus on eight localities of the northern rocky shores of central islands (Tenerife and Gran Canaria) and western islands (La Gomera and La Palma) analyzing random amplified polymorphism DNA (RAPD) marker variation. Their results demonstrated high levels of genetic diversity among populations, contrary to the findings of Sosa and García-Reina (1993), although they do agree on the important role of sexual reproduction to the genetic variability between populations. Furthermore, they established a level of isolation between different islands, albeit only analyzing the genetic variability of female gametophytes. Hence, before stating any conclusions on the population structure and genetic diversity of macroalgae with complex biological cycles, it is important to consider all phases of the life history (Krueger-Hadfield and Hoban 2016).

Several phylogenetic studies of Gelidiales have included species from the Canary Islands. Freshwater *et al.* (1995) and Tronchin *et al.* (2002) include DNA material from *Gelidium canariense* collected in Tenerife and *G. pusillum* collected and cultivated by Rueness and Fredriksen. Results establish that *G. canariense* belongs to the clade of European *Gelidium*, while *G. pusillum* is part of a species-complex together with species of the genera *Onikusa*, *Suhria* and *Gelidium*. At a later date, Boo *et al.* (2014, 2016b) analyzed the molecular phylogeny of Gelidiales, including *G. canariense,* based on five genetic markers. Results indicate that *G. canariense* is closely related to *G. spinosum*, *G. attenuatum* and *G. pulchellum*.

The phylogeny of the Gelidiellaceae was also re-analyzed by Boo *et al.* (2016d), combining morphological and molecular criteria. They proposed a new classification of the family divided into five different groups (*Gelidiella*, *Huismaniella*, *Parviphycus adnatus*, *Millerella* and *Perronella gracilis*). A sample from the Canary Islands is referred as *Huismaniella* sp. exhibiting morphological characteristics very similar to *Parviphycus setaceus* as described by Afonso-Carrillo *et al.* (2007). However, according to the authors, DNA analysis of the type material of *P. setaceus* is required in order to confirm the synonymy. This study also concluded that the genetic sequence analyzed by Rico *et al.* (2002) and identified as *Gelidiella tenuissima* (currently considered as synonym of *Millerella pannosa*), is analogue to that of the endemic *M. tinerfensis*. Additional studies are necessary to clarify this species-complex from this archipelago. Finally, Boo *et al.* (2016d) highlighted the morphological similarity between *Parviphycus antipae* and the species of *Millerella,* although genetic analyses are needed to support this.

4. ECOLOGY, DISTRIBUTION AND CONSERVATION OF GELIDIALES IN THE CANARY ISLANDS

The first studies into the phytobenthos of the Canary Islands had already observed that the macroalgae communities in the northern exposed coasts of central and western islands were dominated by *Gelidium arbuscula* and *G. canariense.*

Sauvageau (1912) and Lawson and Norton (1971) described each of these populations forming a dense belt on the rocky walls just beneath the yellow band of *Treptacantha abies-marina* (as *Cystoseira abies-marina*). According to Sauvageau (1912), the uppermost red-purple belt was characterized by *G. arbuscula*, whereas underneath it developed a thicker and darker band of *G. canariense*, except in abrupt rocky platforms where both species appeared intermingled. Lawson and Norton (1971) also documented this zonation pattern with these species located at the beginning of the sublittoral in northern exposed rocky shores.

The great abundance of *Gelidium arbuscula* and *G. canariense* in the north of Tenerife (Wildpret *et al.* 1987) gave rise to its exploitation as a natural resource of agar (Afonso-Carrillo 2003a). Interestingly, the agar obtained from *Gelidium* is of the highest quality and the only one that can be used in the biotechnology industry to produce culture medium (McHugh 2004; Bixler and Porse 2011; Hurd *et al.* 2014). Since 1950, local fishermen have collected up to 40-50 tons of dry weight of *Gelidium* per year from natural populations that were uprooted by waves. Periodically, this material was air-dried and sent to mainland industries until 1960 when this practice was abandoned since the compilation and transport was not economical (Afonso-Carrillo 2003a, b).

The vertical distribution of macroalgae in Puerto de la Cruz (N of Tenerife) presented by Lawson and Norton (1971) changed after two decades. New studies highlighted a new red belt characterized by *Pterocladiella capillacea*, generally located above *Gelidium arbuscula* or in infralittoral rocky pools (Darias-Rodríguez and Afonso-Carrillo 1986; Betancort and González 1991; Pinedo *et al.* 1992; Pinedo and Afonso-Carrillo 1994). Nowadays, *P. capillacea*, *G. arbuscula* and *G. canariense* are dominant and canopy-forming species of the rocky upper sublittoral at wave-exposed northern shores of La Palma, La Gomera, Tenerife and Gran Canaria (Figure 3) (Wildpret *et al.* 1987; Afonso-Carrillo 2003b; Sangil *et al.* 2004; Rodríguez *et al.* 2008).

Wildpret *et al.* (1987) documented the distribution of *Gelidium arbuscula* and *G. canariense* in the 1980s. This study indicates the location of the most common macroalgae assemblages of the upper sublittoral in the archipelago, including the communities dominated by these Gelidiales, noted as the G1-*G. arbuscula* belt and G2-zonated community *G. arbuscula, G. canariense* and *Treptacantha abies-marina* (as *Cystoseira abies-marina*). Twenty years later, Rodríguez *et al.* (2008a,b) provided data on distribution and population size of *G. arbuscula* and *G. canariense* in different sites of the islands, including a digital cartography of their populations. These studies are of great interest to assess changes occurred throughout the years.

Besides differences in abundance and vertical distribution, recent studies have indicated a reduction in length of *Gelidium* specimens in the last four decades. The greatest decline is described in *G. canariense*, whose individuals have decreased from 30 cm (Seoane-Camba 1979) to less than 20 cm (Polifrone *et al.* 2012; Sansón *et al.* 2013; Alfonso *et al.* 2017b). Børgesen (1927) described individuals of 14 cm in *G. arbuscula*, while those studied by Polifrone *et al.* (2012) were less than 12 cm long. On the contrary, *Pterocladiella capillacea* have exhibited similar length over the years, at 9 to 14 cm (Polifrone *et al.* 2012; Sansón *et al.* 2013; Alfonso *et al.* 2017b). The study of herbarium specimens deposited since 1970 until 2015 in TFC (Dpto. Botánica, Ecología y Fisiología Vegetal; Facultad de Ciencias; ULL) and BCM (Dpto. Biología; Facultad de Ciencias del Mar; ULPGC) have demonstrated a significant decline in the individual length and number of reproductive structures in *G. arbuscula* and *G. canariense*. In addition, this trend also correlates significantly with a significant increase in sea surface temperature over the same period. In contrast, these changes are not detected in *P. capillacea* (Sansón *et al.* 2013; Alfonso *et al.* 2017b). Experimental studies are necessary in order to verify the effects of different environmental variables on the growth of these species, variables that are also changing due to climate change. As a result of these sharp changes in morphology and population abundance, *G. arbuscula* and *G. canariense* have been recently considered as "vulnerable species" in the Listado de Especies Silvestres en Régimen de Protección Especial y *Catálogo Español de Especies Amenazadas* (Orden TEC/596/2019, BOE 2019).

Different studies on intertidal and subtidal communities document several cespitose Gelidiales from the Canary Islands. *Gelidium pusillum* is one of the most common species in the cespitose assemblages across the archipelago (Elejabeitia *et al.* 1992; Pinedo *et al.* 1992; Reyes *et al.* 1994, 2005; González-Ruiz *et al.* 1995a, b; Guadalupe-González *et al.* 1995), whereas *Millerella tinerfensis* or *Pterocladiella melanoidea* have been only occasionally reported (Seoane-Camba 1977; Guadalupe-González *et al.* 1995; Sangil *et al.* 2003; Rancel 2008) and their real distribution and ecological role on the islands needs further research.

5. FUTURE PERSPECTIVES ON GELIDIALES

This review identifies knowledge gaps in the biology and ecology of Gelidiales in the Canary Islands. Certain aspects need further investigation and will help to predict future changes in the diversity, morphology, physiology and ecology of these rhodophytes. This is of grave concern especially with the canopy-forming threatened Gelidiales that are vulnerable to changes, thus, conservation plans and management strategies are necessary in order to recover the populations. The comparison of historical and current data on abundance and distribution of the populations will allow assessment of their conservation status and the extinction risk of the endemic species. The study of the cespitose Gelidiales, of which little is still known, is also important. These overlooked species might play a key role as habitat-forming species in early succession stages when sensitive species decline (Bertolini 2019).

The accurate diversity of Gelidiales species in the Canary Islands is still uncertain. Some species documented to these islands are based on historic and doubtful records (i.e. *Gelidium corneum, G. pectinatum, G. sphatulatum, G. spinulosum, G. spinosum*). The apparent high morphological plasticity characteristic of some species could indicate new cryptic species that will not be detected unless we combine morphological and molecular techniques in further studies on the Gelidiales of the Canary Islands.

Regarding the vegetative and reproductive morphology, additional findings are required particularly in reference to the species of Gelidiellaceae whose female gametophytes are missing and their life cycle is still incomplete. The distribution, vegetative and reproductive phenology, spatio-temporal shifts or successful recruitment rates in many Gelidiales are yet to be discovered. This lack of information makes it difficult to foresee the effects of environmental changes on individual and population levels.

To conclude, it is pivotal to improve our knowledge on Gelidiales species from the Canary Islands owing to the fact that some of them contribute to ecosystem services in the archipelago. Others are endemic and vulnerable species (*Millerella tinerfensis*, *Gelidium canariense*, *G. arbuscula*) or common species on cespitose macroalgae assemblages at the eastern Atlantic (*Gelidium pusillum* and Gelidiellaceae), while there are other introduced species distributed worldwide (*Pterocladiella capillacea*). All these attributes make these species model macroalgae to study and useful tools in order to predict future changes in the marine ecosystems of the Canary Islands.

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FIGURES

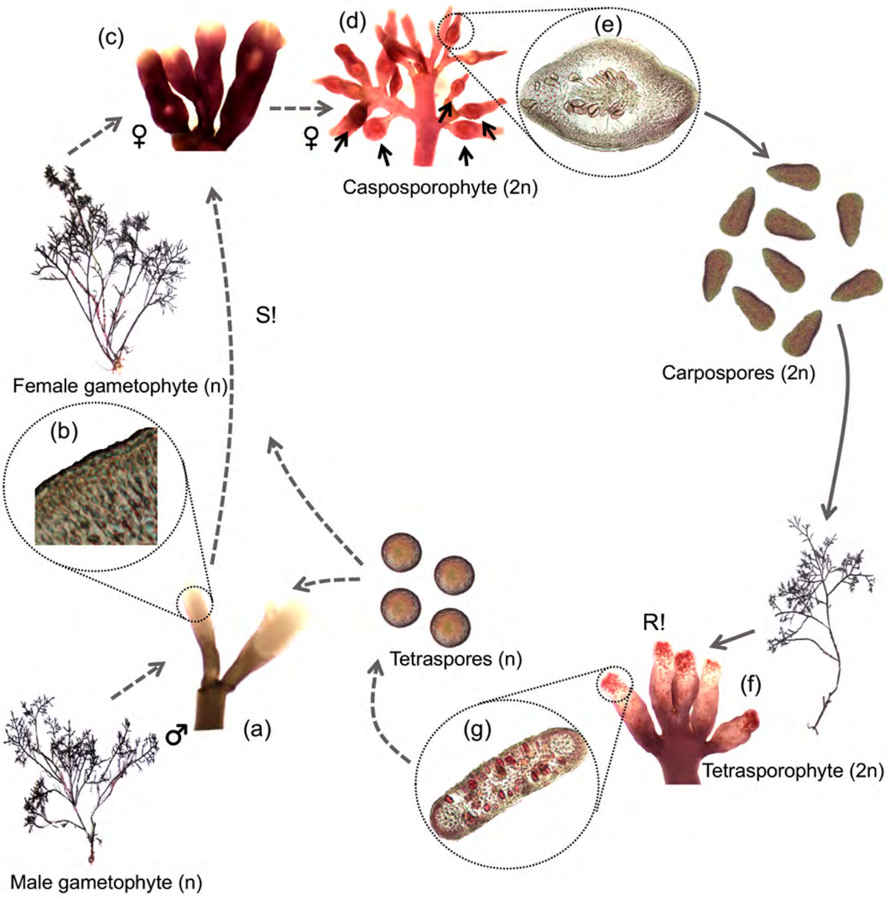

Figure 1. Life cycle of *Gelidium canariense*. Gametophytes are haploid (n) and dioecious. Male gametophytes develop spermatangia merged in whitish sori (a) located in the apical region of lateral branches. In transverse section spermatangia are formed from mother cells originated in the outermost cortical cells (b), each of them release one tiny spermatium. Fertile female gametophytes (c) have a whitish longitudinal line at the terminal region of last order branches. Inside there are several carpogonia and nutritive filaments that constitute a complex procarp. After syngamy (S!) each procarp will develop into a diploid carposporophyte (2n) (arrows). Once carpogonia are fertilized a prominent and bilocular mature cystocarp (e) develops which holds inside multiple carposporangia. Each carposporangium will release a carpospore through the cystocarp ostiole and give rise to a tetrasporophyte. Diploid tetrasporophyte (2n) form tetrasporangia (f) located in sori at ends of last order branches and immerse in the cortex (g). Meiosis (R!) occurs in each tetrasporangium to generate four haploid (n) tetraspores leaving empty cells when release. Dashed line indicates the haploid phases and continuous line indicates diploid phases of the cycle. Images obtained and adapted from Alfonso *et al.* (2017).

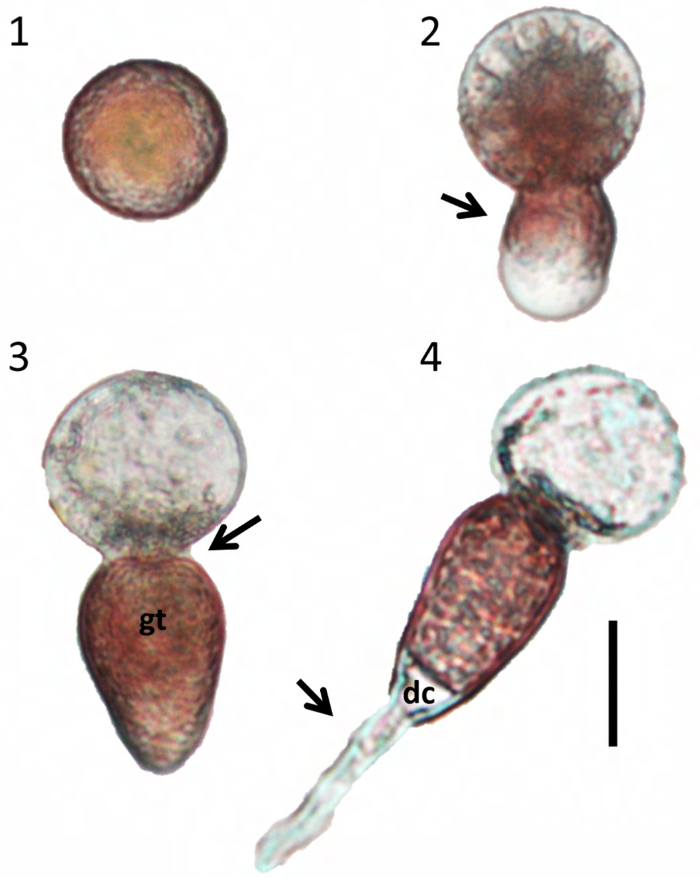

Figure 2. *Gelidium*-type germination pattern. (1) tetraspore immediately after release and settlement still lacking cell wall. (2 and 3) Between 2 to 4 hours after release and attachment of the spore: (2) germination tube begin to develop from the protoplasm content in migration (red color) and germination tube is protrude (arrow); (3) the germination tube is surrounded by a cell wall and separated from the original spore (arrow). (4) 24 hours after tetraspore release. Multicellular organism showing elongate distal cell (dc) and primary rhizoid (arrow). Scale 20 µm. Adapted from Alfonso *et al.* (2018).

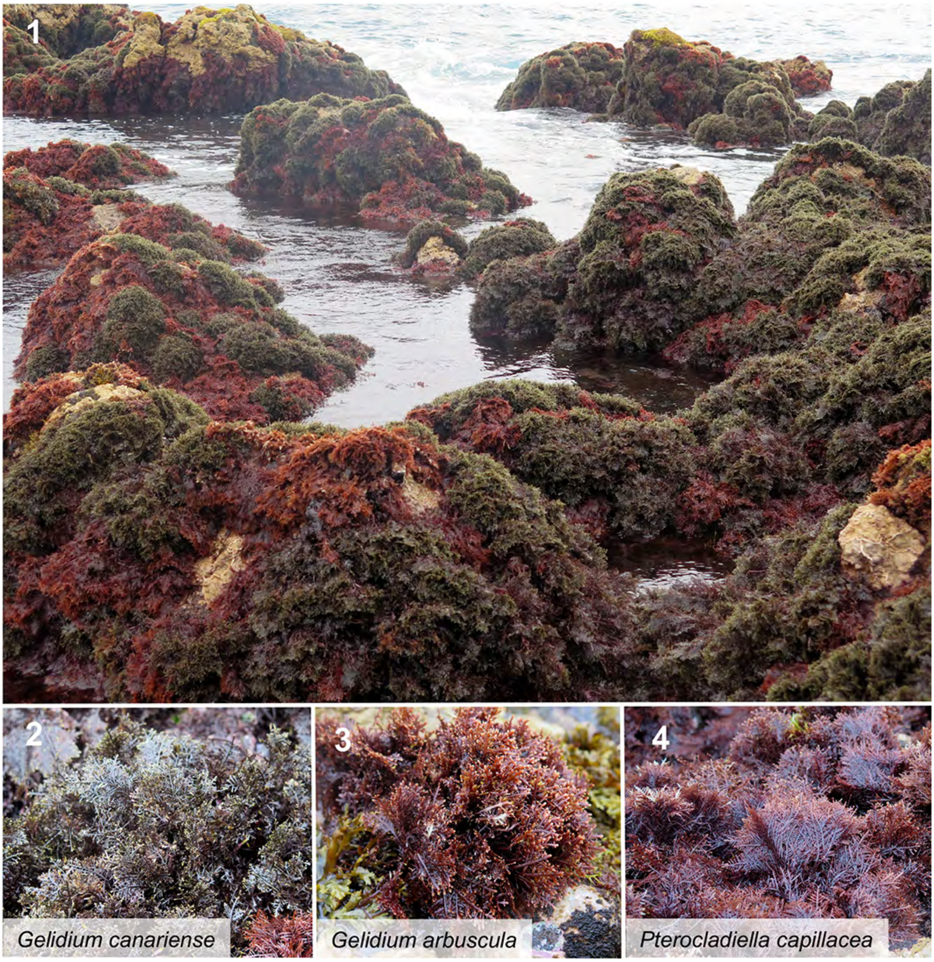

Figure 3. (1) Habitat forming Gelidiales in a mixed community in the north of Tenerife. Below, detail of the species: (2) *Gelidium canariense*, (3) *Gelidium arbuscula* and (4) *Pterocladiella capillacea*.