

**Seaweeds from sand-covered rocks
of the Atlantic Iberian Peninsula.
Part 2. Palmariales, Ceramiales
(excluding Rhodomelaceae), Gelidiales, Gigartinales,
Plocamiales, Rhodymeniales and Scytothamnales**

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Abstract – This work presents a taxonomic, floristic and chorological account of the most representative turf-forming species from sand-covered rocks along the Atlantic Iberian Peninsula, including in this Part 2 species belonging to six orders of the Rhodophyta and one of the Phaeophyceae. For each species are provided morphological descriptions, distribution maps, and/or COI-5P sequences, as well as taxonomic notes. The species studied are: *Rhodothamniella floridula*, *Ceramium ciliatum*, *ErythroGLOSSUM lusitanicum*, *Hypoglossum hypoglossoides*, *Ptilothamnion sphaericum*, *Spermothamnion repens*, *Tiffaniella capitata*, *Gelidium crinale*, *G. spathulatum*, *Pterocladia melanoidea*, *Calliblepharis hypneoides*, *Gymnogongrus griffithsiae*, *Plocamium maggsiae*, *Gastroclonium reflexum* and *Bachelotia antillarum*.

Algal turfs / COI-5P / distribution / morphology / sand-covered rocks / Phaeophyceae / Rhodophyta / taxonomy

INTRODUCTION

Sand-covered rocks provide for benthic seaweeds a habitat with environmental conditions different to those on purely rocky shores. Turf-forming species account for most of the macroalgal diversity in this habitat along the Atlantic Iberian Peninsula (Díaz-Tapia *et al.*, 2011, 2013a; Díaz-Tapia & Bárbara, 2013). The Rhodomelaceae are among the most frequent and abundant taxa encountered in this habitat and 18 species of this family, as well as a parasitic alga of uncertain taxonomic position, were studied in Part 1 (Díaz-Tapia & Bárbara, 2013). Moreover, 15 species belonging to six orders of the Rhodophyta and one order of the Phaeophyceae are also abundant and common in algal turfs over sand-covered rocks along the Atlantic Iberian Peninsula. The aim of this work is to provide morphological descriptions and COI-5P sequences of these 15 taxa, completing the flora of the 34 most typical species from this habitat along the Atlantic Iberian Peninsula.

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MATERIALS AND METHODS

An extensive collection of seaweeds from sand-covered rocks was made in the intertidal of 88 sites from the Atlantic Iberian Peninsula, from 2002-2012. Furthermore, the upper subtidal of some localities was also studied, and some samples were also collected at 50 additional sites, two of them in Atlantic France.

World maps showing the distribution of the species were based on available data in Guiry & Guiry (2013). The taxonomy follows Schneider & Wynne (2007) and Wynne & Schneider (2010). Collection information and GenBank accession numbers for sequences generated in this study are provided in Table 1. Materials and Methods were as described in Díaz-Tapia & Bárbara (2013). Despite our efforts, COI-5P sequences could not be obtained for 5 of the 15 species studied in this work.

Table 1. Sequences of species generated in this study and GenBank accession numbers

<i>Species</i>	<i>Herbarium code; collection site, date and collectors¹</i>	<i>Genbank</i>
<i>Calliblepharis hypneoides</i>	SANT-Algae 25159; Rodeira, Pontevedra, Spain, 5.04.11, IB & VP.	KJ179925
<i>Ceramium ciliatum</i>	SANT-Algae 25151; Zumaia, Guipúzcoa, Spain, 18.03.11, PD & IB. SANT-Algae 25996; Tragove, Pontevedra, Spain, 04.03.11, JC. SANT-Algae 28094; A Toxa, Pontevedra, Spain, 24.04.13, PD, VG & CI.	KJ179928 KJ179929 KJ179931
<i>Gastroclonium reflexum</i>	SANT-Algae 24335; Sarello, Asturias, Spain, 28.07.10, PD. SANT-Algae 24436; Picón, A Coruña, Spain, 12.07.2010, PD & IB. SANT-Algae 24204; Leira, A Coruña, Spain, 25.06.10, PD & IB. SANT-Algae 25432; Biarritz, southern France, 24.03.11, PD & IB.	KJ168046 KJ168048 KJ168050 KJ179926
<i>Gelidium crinale</i>	SANT-Algae 24631; Langre, Santander, Spain, 06.11.10, PD. SANT-Algae 24719; Perbes, A Coruña, Spain, 20.01.11, PD & CP. SANT-Algae 26556; Punta Plata, Cádiz, Spain, 19.02.11, PD & IB. SANT-Algae 25147; Zumaia, Guipúzcoa, Spain, 18.03.11, PD & IB. SANT-Algae 25618; La Franca, Asturias, Spain, 23.03.11, PD & IB. SANT-Algae 28095; A Toxa, Pontevedra, Spain, 24.04.13, PD, VG & CI.	KJ168044 KJ179932 KJ179933 KJ179934 KJ179935 KJ179937
<i>Gymnogongrus griffithsiae</i>	SANT-Algae 24478; Llas, Lugo, Spain, 14.07.10, PD. SANT-Algae 24339; Sarello, Asturias, Spain, 28.07.10, PD. SANT-Algae 25407; Biarritz, southern France, 24.03.11, PD & IB.	KJ168045 KJ168049 KJ179938
<i>Hypoglossum hypoglossoides</i>	SANT-Algae 24329; Catedrais, Lugo, Spain, 26.07.2011, PD & IB. SANT-Algae 25628; La Arena, Vizcaya, Spain, 22.03.11, PD & IB.	KJ168047 KJ179930
<i>Plocamium maggsiae</i>	SANT-Algae 26804; Santa Cruz, Estremadura, Portugal, 16.06.11, IB. SANT-Algae 25597; La Franca, Asturias, Spain, 23.03.11, PD & IB. SANT-Algae 26472; Olhos d'Água, Algarve, Portugal, 20.02.11, PD & IB. SANT-Algae 24754; Barrañán, A Coruña, Spain, 21.01.11, PD & CP. SANT-Algae 24334; Sarello, Asturias, Spain, 28.07.10, PD.	KJ179940 KJ179941 KJ179942 KJ179943 KJ179944
<i>Pterocladia melanoidea</i>	SANT-Algae 26689; Playa Azul, Estremadura, Portugal, 14.06.11, IB.	KJ179936
<i>Ptilothamnion sphaericum</i>	SANT-Algae 26652; Castro, A Coruña, Spain, 27.09.11, PD.	KJ179927
<i>Rhodothamniella floridula</i>	SANT-Algae 25529; Locquemeau, France, 20.03.11, PD & IB.	KJ179939

¹Collectors initials: PD, Pilar Díaz-Tapia; IB, Ignacio Bárbara; CP, Cristina Pardo; CI, Cristina Piñeiro; JC, Javier Cremades; VP, Viviana Peña; VG, Verónica García.

RESULTS AND DISCUSSION

RHODOPHYTA
FLORIDEOPHYCEAE
NEMALIOPHYCIDAE
PALMARIALES

RHODOTHAMNIELLACEAE

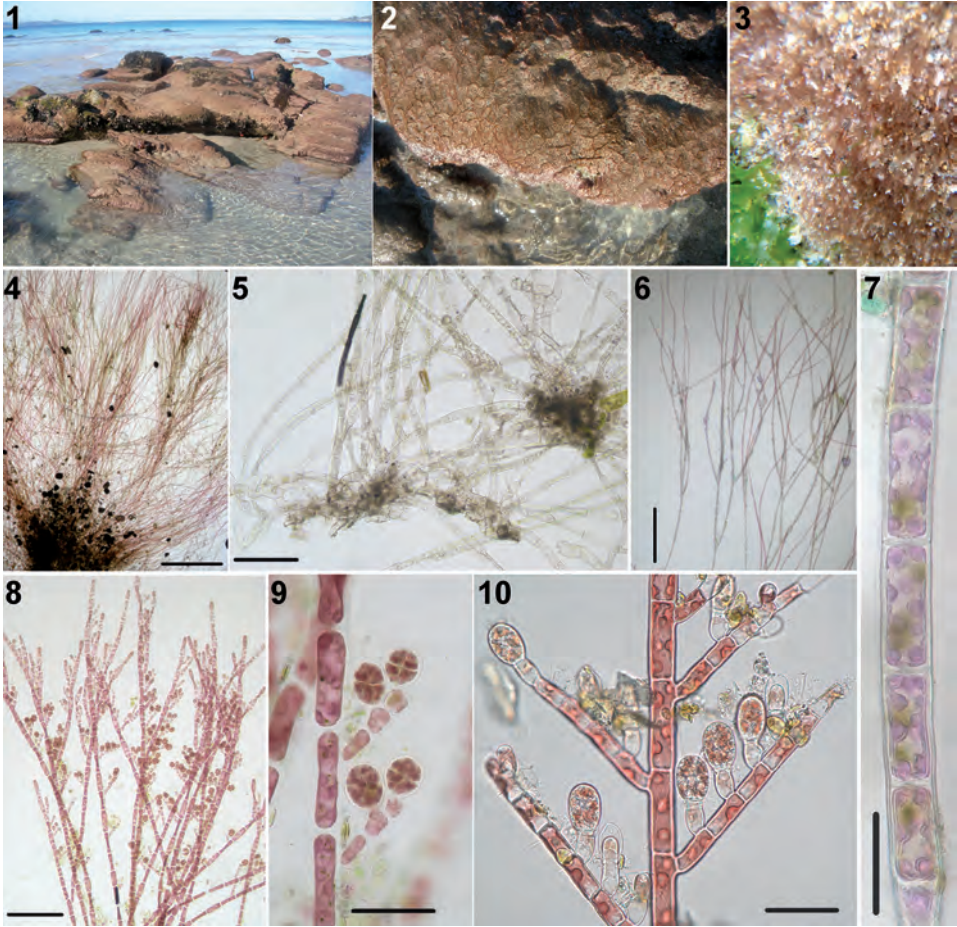
Rhodothamniella floridula (Dillwyn) Feldmann

Figs 1-12

Basionym: *Conferva floridula* Dillwyn.**Lectotype:** NMW (*vide* Woelkerling, 1971).**Lectotype locality:** Galway, Ireland.**Synonyms:** *Rhodochorton floridulum* (Dillwyn) Nägeli; *Audouinella floridula* (Dillwyn) Woelkerling.**References:** Knaggs, 1965; Stegenga, 1978; Coppejans, 1995 (as *Rhodochorton floridulum*). Woelkerling, 1971; Dixon & Irvine, 1977a; Woelkerling & Womersley, 1994; (as *Audouinella floridula*). Stegenga, 1985; Stegenga *et al.*, 1997; Rull Lluch, 2002; Rull Lluch & Gómez Garreta, 2002 (as *Rhodothamniella floridula*).**Molecular voucher:** GenBank accession number KJ179939.**Selected specimens:** 1) Zumaia (43°17'59"N; 2°15'41"W), 30.iii.2006, SANT-Algae 20273; 2) San Juan de Gaztelugatxe (43°26'41"N; 2°46'41"W), 29.iii.2006, SANT-Algae 20296; 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; 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); 10) Linorsa (43°41'56"N; 7°27'14"W), 10.iii.2005, SANT-Algae 23118 (tetrasporangial plants); 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; 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; 17) Guincho (38°43'29"N; 9°28'41"W), 13.vi.2010, SANT-Algae 24800.*Vegetative and reproductive morphology*

Thalli form dense turfs up to 7 cm high covering rock surfaces of several meters in extent (Figs 1-3), consisting of a thin basal layer of agglomerated prostrate filaments from which arise the entangled erect filaments that form an upper layer of variable thickness. The basal layer is white in colour and the upper layer is brownish red in colour; when filaments are observed separately, prostrate filaments are colourless or greenish and erect filaments are pink in colour. Turfs are robust, while isolated filaments are fragile.

Thalli consisting of uniseriate filaments, differentiated into prostrate and erect filaments (Fig. 4). Prostrate filaments irregularly branched, forming erect filaments or further prostrate filaments (Fig. 5). Erect filaments irregularly branched (Fig. 6), branches scarcely divided in basal parts and more densely branched in upper ones. Cells cylindrical, 17-30 µm in diameter and 40-95 µm in length, containing 3-8 chloroplasts, sinuate, parietal, each with one pyrenoid (Fig. 7).



Figs 1-10. *Rhodothamniella floridula*. Vegetative and reproductive morphology. **1-3**. Turfs. **4**. Detail of a turf showing a basal layer of agglomerated prostrate filaments from which arises the erect filaments. **5**. Prostrate filaments irregularly branched. **6**. Upper parts of erect filaments irregularly branched. **7**. Cells showing several chloroplasts, each with a pyrenoid. **8**. Upper parts of erect filaments bearing tetrasporangia. **9-10**. Tetrasporangia cruciately divided, arranged in second series, sessile (9) or with a one-celled stalk (10). Scale bars: 2 mm in Fig. 4; 200 μm in Figs 5 and 8; 600 μm in Fig. 6; 50 μm in Figs 7, 9 and 10.

Gametangial plants not observed. Tetrasporangia formed on the upper parts of the erect filaments (Fig. 8), arranged in adaxial second series, ovoid, 20-28 μm in diameter, either sessile or on a single-celled stalk, cruciately divided (Figs 9-10).

Phenology

Rhodothamniella floridula occurred throughout the year, and turfs are probably perennial. Tetrasporangia were rarely recorded (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.



Figs 11-12. Distribution of *Rhodothamniella floridula*. **11**. Collections along the Atlantic Iberian Peninsula. **12**. World distribution: arrow – type locality.

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 in 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 of time. It is widely distributed along the Atlantic Iberian Peninsula, and it was found in almost all sampled sites (Fig. 11). Although present, its abundance decreases toward the Basque Country (East) and Cádiz (South). *Rhodothamniella floridula* has been reported from Europe and southern coasts of America, Africa and Australia (Fig. 12).

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* (Lightfoot) Rosevinge is the only similar species that also forms turfs, but in the Iberian Peninsula it is restricted rocks from the upper littoral in shaded habitats, such as caves.

The taxonomic position of *Rhodothamniella floridula* and related species has been extensively discussed (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 order Acrochaetales. However, Saunders *et al.* (1995) studied phylogenetic relationships of Palmariales and Acrochaetales, establishing the family Rhodothamniellaceae which represents an early lineage of the order Palmariales.

RHODYMENIOPHYCIDAE CERAMIALES

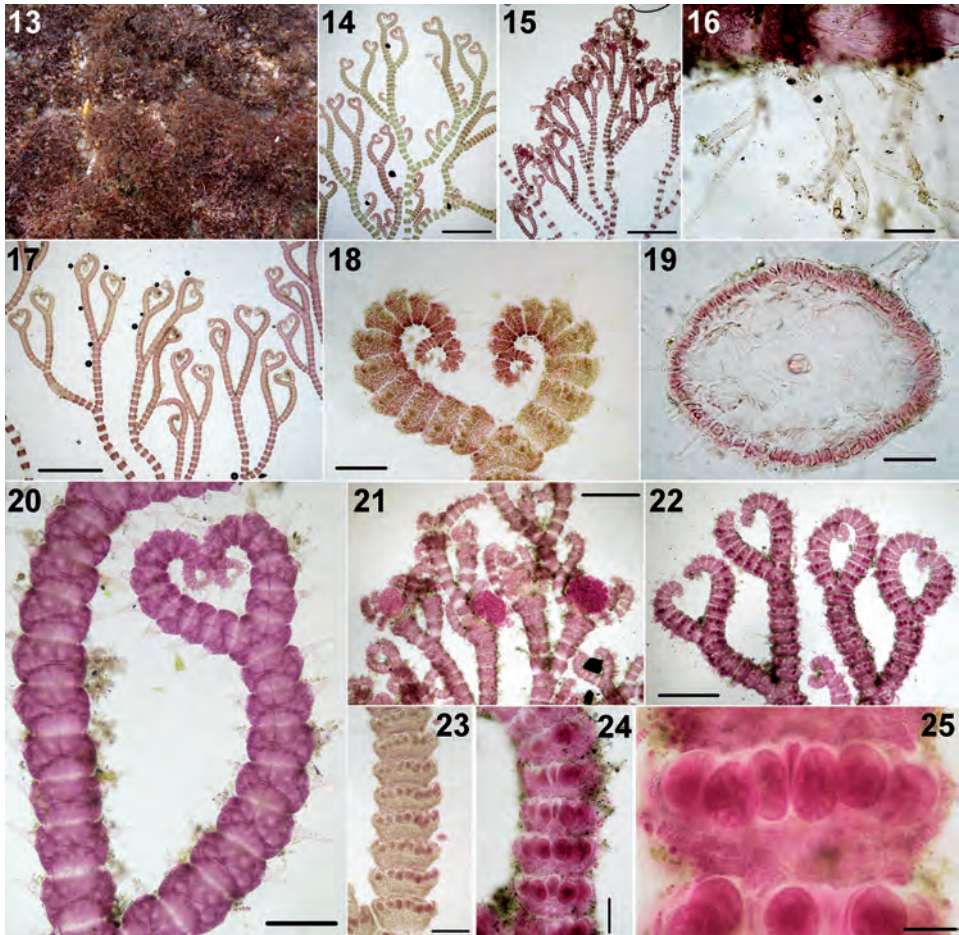
CERAMIACEAE

Ceramium ciliatum (J. Ellis) Ducluzeau

Figs 13-25

Basionym: *Conferva ciliata* J. Ellis.

Lectotype: Ellis (1768), pl. 18 fig. H (Maggs & Hommersand, 1993).



Figs 13-25. *Ceramium ciliatum*. Vegetative and reproductive morphology. **13**. Turf. **14-15**. Upper parts of thalli with pseudodichotomously branched axes. **16**. Multicellular rhizoids. **17**. Upper parts of thallus with inrolled apices. **18**. Apex of an axis with whorls of 3-celled spines around nodes. **19**. Cross section of a node with 6 pericentral cells. **20**. Apex of an axis bearing spines at the nodes. **21**. Gonimocarps located in the upper parts of the thalli. **22-25**. Tetrasporangia forming whorls in the upper parts of the thalli. Scale bars: 2 mm in Figs 14, 15 and 17; 100 μ m in Figs 16 and 24; 200 μ m in Figs 18, 20 and 23; 50 μ m in Figs 19 and 25; 600 μ m in Figs 21 and 22.

Type locality: Unlocalized, ?England.

References: Sansón Acedo, 1991; Maggs & Hommersand, 1993; Secilla, 2012.

Molecular vouchers: GenBank accession numbers KJ179928, KJ179929, KJ179931.

Selected specimens: 1) Ondarreta (43°19'18"N; 2°00'11"W), 30.iii.2006, SANT-Algae 20193; 2) Ogeia (43°22'22"N; 2°32'35"W), 15.iii.2006, SANT-Algae 20320 (female and tetrasporangial plants); 3) Virgen del Mar (43°28'40"N; 3°52'31"W), 7.xi.2010, SANT-Algae 24638; 4) Ártabra (43°21'12"N; 8°28'38"W), 9.ii.2005, SANT-Algae 17860 (tetrasporangial plants); 5) Area da Cruz (42°27'40"N; 8°54'37"W), 22.viii.2005, SANT-Algae 25062 (tetrasporangial plants); 6) Barreiro (42°23'52"N; 8°47'37"W), 28.iv.2006, SANT-Algae 22655 (female and tetrasporangial plants).



Figs 26-27. Distribution of *Ceramium ciliatum*. **26**. Collections along the Atlantic Iberian Peninsula. **27**. World distribution: arrow – type locality.

Vegetative and reproductive morphology

Thallus forming turfs up to 5 cm high (Fig. 13), consisting of interwoven decumbent axes growing as erect axes produce rhizoids at their basal parts, and from which arise the erect axes that are pseudodichotomously branched (Figs 14-15). Plants are rose-pink in colour, rigid and brittle in texture.

Rhizoids abundantly developed from cortical cells of the basal parts, multicellular (Fig. 16). Axes with strongly inrolled apices (Figs 17-18), growing from apical cells ca. 15 μm in diameter, mature axes 180-370 μm in diameter. Axes pseudodichotomously branched at regular intervals of 9-13 axial cells, adventitious branches absent to abundant (Figs 14-15). Nodes consisting of 6-7 periaxial cells (Fig. 19) from which develop descending and ascending cortical filaments. Nodes bearing 3-celled spines in whorls near apices (Fig. 20). Internodes of naked axial cells separating cortical bands, more conspicuous in basal parts of axes (Figs 15, 17).

Gametophytes dioecious. Gonimocarps consisting of 1-3 gonimolobes, 250-470 μm in diameter, surrounded by 4-6 involucre branchlets (Fig. 21). Spermatangia not observed. Tetrasporangia borne on the younger axes forming whorls of 5-12 around the nodes, subspherical, 37-63 μm wide (Figs 22-25).

Phenology

Ceramium ciliatum was collected throughout year, except in December, and collections were more frequent between March and October. Female structures and tetrasporangia were frequent (23% and 20% of the collections, respectively) and observed in March-June and September-October.

Habitat and distribution

Ceramium ciliatum is common on sand-covered rocks along the Atlantic Iberian Peninsula (Fig. 26), where it is epiphytic and sometimes overgrows completely the turfs dominated by other species, especially *Rhodothamiella floridula*. It grows from the mid to the low intertidal, at sites from sheltered to extremely wave-exposed. *Ceramium ciliatum* is widely distributed in southern Europe and northern Africa, as well as it was reported in Australia, Japan and Taiwan (Fig. 27).

Remarks

A recent revision of selected *Ceramium* species from the Atlantic and Mediterranean coasts of Europe revealed that materials from the Venice lagoon

previously assigned to *C. ciliatum* var. *robustum* (J. Agardh) Feldmann-Mazoyer, truly constitute a different species and the name *C. nudiusculum* (Kützinger) Rabenhorst has been reinstated (Wolf *et al.*, 2011). The two species can be distinguished because the Mediterranean one has 4-celled spines that are paired or in a single row, while that of the Atlantic has 3-celled spines forming whorls (Wolf *et al.*, 2011). Specimens of *Ceramium ciliatum* from sand-covered rocks of the Atlantic Iberian Peninsula have 3-celled spines in whorls and agree with those described from the British Isles.

DELESSERIACEAE

Erythrogloussum lusitanicum Ardré

Figs 28-44

Lectotype: PC (Díaz Tapia *et al.*, 2009).

Lectotype locality: Montedor (Portugal).

References: Ardré, 1970; Díaz Tapia *et al.*, 2009; Bárbara & Díaz-Tapia, 2012.

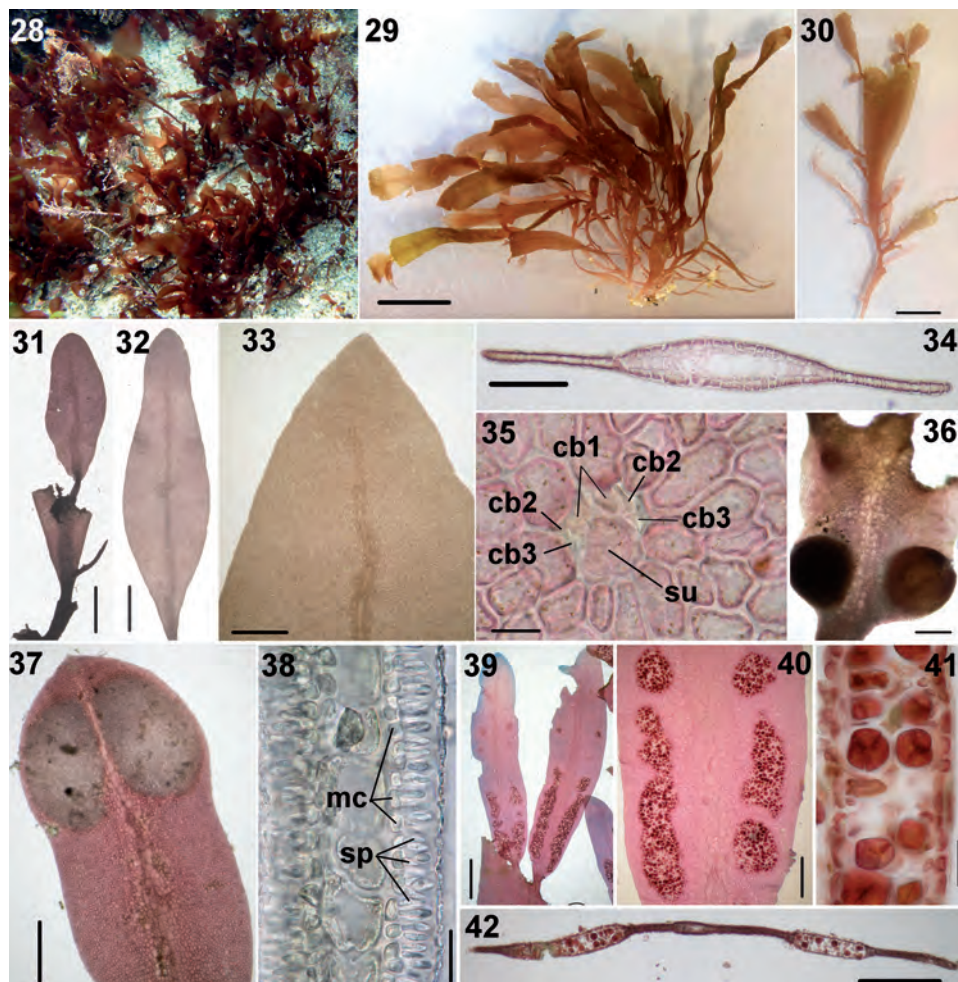
Molecular vouchers: no available COI-5P data.

Selected specimens: 1) Biarritz (43°29'03"N; 1°33'46"W), 19.iii.2011, SANT-Algae 25410; 2) Estaño (43°32'52"N; 5°35'50"W), 18.iv.2007, SANT-Algae 19841; 3) Aguilar (43°33'28"N; 6°07'07"W), 17.iv.2007, SANT-Algae 19830; 4) Sarello (43°33'27"N; 6°58'39"W), 02.ii.2006, SANT-Algae 16843 (tetrasporangial plants), 16844; 5) Catedrais (43°33'16"N; 7°09'16"W), 20.ix.2005, SANT-Algae 16539; 6) Peinzás (43°35'09"N; 7°16'13"W), 26.xii.2007, SANT-Algae 19786; 7) San Román (43°43'17"N; 7°37'39"W), 31.i.2006, SANT-Algae 16869; 20.ii.2008, SANT-Algae 19791 (tetrasporangial plants); 8) Pantín (43°38'33"N; 8°06'36"W), 26.x.2007, SANT-Algae 19531 (male plants); 9) Artabra (43°21'12"N; 8°28'38"), 09.ii.2005, SANT-Algae 17897; 09.iii.2005, SANT-Algae 17285 (tetrasporangial plants); 10) Cambre (43°18'01"N; 8°45'24"W), 18.ii.2008, SANT-Algae 19787; 11) Barizo, 29.ix.2004, SANT-Algae 15252; 12) Camelle (43°11'29"N; 9°05'50"W), 20.iii.2007, SANT-Algae 19007; 13) Lourido (43°05'28"N, 9°13'15"W), 01.ii.2006, SANT-Algae 17008 (tetrasporangial plants); 13.ii.2008, SANT-Algae 19789 (tetrasporangial plants); 14) Ancora (41°49'07"N; 8°52'21"W), 17.ix.2003, SANT-Algae 15583 (female and tetrasporangial plants); 15) Viana do Castelo (41°41'39"N; 8°51'02"W), 28.ix.1999, SANT-Algae 10474; 16) Cepães (41°33'07"N; 8°47'36"W), 14.xi.2004, SANT-Algae 15584 (male and tetrasporangial plants); 17) Leça de Palmeira (41°12'22"N; 8°43'03"W), 16.xi.2004, SANT-Algae 16352 (tetrasporangial plants); 18) Queimado (37°49'34"N; 8°47'34"W), 25.v.2005, SANT-Algae 15732 (female and tetrasporangial plants); 19) Olhos d'Água (37°5'20"N; 8°11'27"W), 06.v.2005, SANT-Algae 15731.

Vegetative and reproductive morphology

Thalli forming turfs (Fig. 28), 3-5 cm long, consisting of a basal discoid holdfast bearing a cylindrical to compressed stipe, from which arise lateral elongate proliferations and erect ovate to oblanceolate blades with a midrib (Figs 29, 32). Old blades bearing young blades irregularly located along margins of basal parts and on broken tips (Figs 30-31). Blades brownish-pink in colour with a fairly rigid texture.

Blades arising from a short stipe, cylindrical to compressed; growing by means of a single apical cell (Figs 31-33). Young blades small and simple, from ovate to oblanceolate (Figs 31-32); older blades oblanceolate (Fig. 29), to 27 mm long and 6 mm wide, usually simple but sometimes dichotomously branched. Tips of old blades usually broken, bearing one to several new blades (Figs 30-31), forming 2-4 orders of successive blades. Margins entire or with short proliferations, sometimes producing new blades or rhizomatous proliferations. Blades monostromatic except in the midrib region (Fig. 34). Monostromatic areas (30-) 40-65 (-100) μm



Figs 28-42. *Erythroglossum lusitanicum*. Vegetative and reproductive morphology. **28.** Turf in sand-covered rocks. **29.** Habit, consisting of a discoid holdfast bearing numerous oblanceolate blades. **30-31.** Old blades bearing young blades at their margins or at broken apices. **32.** Young oblanceolate blade with a midrib. **33.** Apex of a blade. **34.** Cross section of a blade showing a 3-5-celled midrib region and the monostromatic wings. **35.** Immature procarp showing the supporting cell (su) and two opposite carogonial branches (cb1-3). **36.** Cystocarps. **37.** Spermatangial sori located on both sides of the midrib. **38.** Cross section of a male sorus showing the spermatangial mother cells (mc) which bear 2-3 elongate spermatangia (sp). **39-40.** Tetrasporangial sori growing on both sides of the midrib. **41.** Cross section of a tetrasporangial sorus with two rows of tetrasporangia. **42.** Cross section of a blade with tetrasporangial sori located on both sides of the midrib. Scale bars: 1 cm in Fig. 29; 0.5 cm in Fig. 30; 1.5 mm in Figs 31, 32 and 39; 200 μ m in Fig. 33; 300 μ m in Fig. 34; 20 μ m in Figs 35 and 38; 500 μ m in Figs 36, 37, 40 and 42; 50 μ m in Fig. 41.

thick in median parts. Midrib with 3 layers of cells and (35-) 45-100 (-140) μ m thick in the apical parts and up to 7 cells and (50-) 80-180 (-250) μ m thick in basal parts. Microscopic veins or nerves absent. Cells polygonal in surface view.



Figs 43-44. Distribution of *Erythroglossum lusitanicum*. **43.** Collections along the Atlantic Iberian Peninsula. **44.** World distribution: arrow – type locality.

Gametophytes dioecious. Procarps scattered over the monostromatic areas of blades; consisting of a supporting cell, a group of 2-4 sterile cells and two opposite carpogonial branches, each consisting of 4 cells (Fig. 35). Cystocarps scattered over blades (Fig. 36), 275-430 μm in diameter. Male sori located on both sides of the midrib (Fig. 37), oval to elongate, consisting of a layer of spermatangial mother cells, bearing 2 (-3) elongate spermatangia, 5-9 μm long and 2.5-3.5 μm wide (Fig. 38). Tetrasporangial sori located at both sides of the midrib (Figs 39-40, 42), initially oval and usually several per blade (Fig. 40), or becoming confluent acquiring an elongate outline (Figs 39-40). Sorus with two rows of tetrasporangia (each on one side of the blade) (Fig. 41), which are ellipsoid, 22-53 \times 30-63 μm .

Phenology

Erythroglossum lusitanicum was found throughout the year and turfs are perennial. Tetrasporangia were frequently found (35% of the collections), except in summer when they were only occasional. Conversely, sexual structures are rare, as male gametophytes were collected only twice (October and November) and female gametophytes were collected in 5 samples in (February, May and September). A study on the phenology of *E. lusitanicum* was conducted in two sites from Galicia (Díaz-Tapia *et al.*, 2011) showing the maximum size and sporangia production in spring and winter, respectively, and the minimum in summer.

Habitat and distribution

Erythroglossum lusitanicum is common in sand-covered rocks from the Atlantic Iberian Peninsula (Fig. 43). It occurs mainly from the low intertidal to upper subtidal (up to 2 meters depth) on wave-exposed coasts. Turfs are from almost monospecific to mixed with other species typical of this habitat, such as *Pterosiphonia ardreana* Maggs *et* Hommersand, *P. pennata* (C.Agardh) Sauvageau, *Jania longifurca* Zanardini, *Rhodothamniella floridula*, *Hypoglossum hypoglossoides* and *Ptilothamnion sphaericum*. The known distribution of *E. lusitanicum* is restricted to the Atlantic Iberian Peninsula and Morocco (Fig. 44).

Remarks: See remarks on *Hypoglossum hypoglossoides*.

Hypoglossum hypoglossoides* (Stackhouse) F.S. Collins *et* Hervey** **Figs 45-63*Basionym:** *Fucus hypoglossoides* Stackhouse.**Lectotype:** CN (Wynne, 1984).**Lectotype locality:** Polridmouth Cove, Cornwall, England.**Synonyms:** *Hypoglossum woodwardii* Kützinger; *Delesseria hypoglossum* (Woodward) J.V. Lamouroux.**References:** Wynne, 1984; Schneider & Searles, 1991; Maggs & Hommersand, 1993; Littler & Littler, 2000; Dawes & Mathieson, 2008; Littler *et al.*, 2008.**Molecular vouchers:** GenBank accession numbers KJ168047, KJ179930.**Selected specimens:** 1) Tagle (43°25'59"N; 4°04'50"W), 1.iv.2006, SANT-Algae 20346; 2) Playa de Amio (43°23'42"N; 4°28'57"W), 17.iii.2006, SANT-Algae 20438; 3) Linorsa (43°41'56"N; 7°27'14"W), 10.iii.2005, SANT-Algae 23114 (tetrasporangial plants); 4) Santa Comba (43°33'34"N; 8°15'30"W), 26.iv.2005, SANT-Algae 23094 (male and tetrasporangial plants); 5) Doñiños (43°30'08"N; 8°19'17"W), 12.iii.2005, SANT-Algae 24536; 6) Chanteiro (43°26'46"N; 8°18'15"W), 17.ix.2005, SANT-Algae 19596 (tetrasporangial plants), 19602 (female plants); 7) Barizo (43°18'48"N; 8°52'27"W), 15.v.2003, 9.ix.2003, SANT-Algae 24555, 22952 (tetrasporangial plants); 8) Hermida (43°15'47"N; 8°57'10"W), 26.iv.2006, SANT-Algae 24380; 9) Queiruga (42°40'24"N; 9°02'06"W), 30.i.2006, SANT-Algae 24493 (tetrasporangial plants); 10) Nerga (42°15'19"N; 8°50'07"W), 12-ii-2005, SANT-Algae 22829 (female and tetrasporangial plants); 11) Leça de Palmeira (41°12'22"N; 8°43'03"W), 16.xi.2004, SANT-Algae 16355 (male and tetrasporangial plants); 12) Queimado (37°49'34"N; 8°47'34"W), 24.v.2005, SANT-Algae 25254 (tetrasporangial plants); 13) Almogrove (37°39'54"N; 8°48'04"W), 25.v.2005, SANT-Algae 24768; 14) Armação de Pêra (37°06'04"N; 8°22'17"W), 17.10.2005, SANT-Algae 24849; 15) Coelho (37°4'22"N; 8°17'31"W), 7.v.2005, SANT-Algae 25299 (tetrasporangial plants); 16) Caños de Meca (36°10'55"N; 6°00'06"W), 17.xi.2005, SANT-Algae 26144 (female plants), 26147 (tetrasporangial plants).***Vegetative and reproductive morphology***

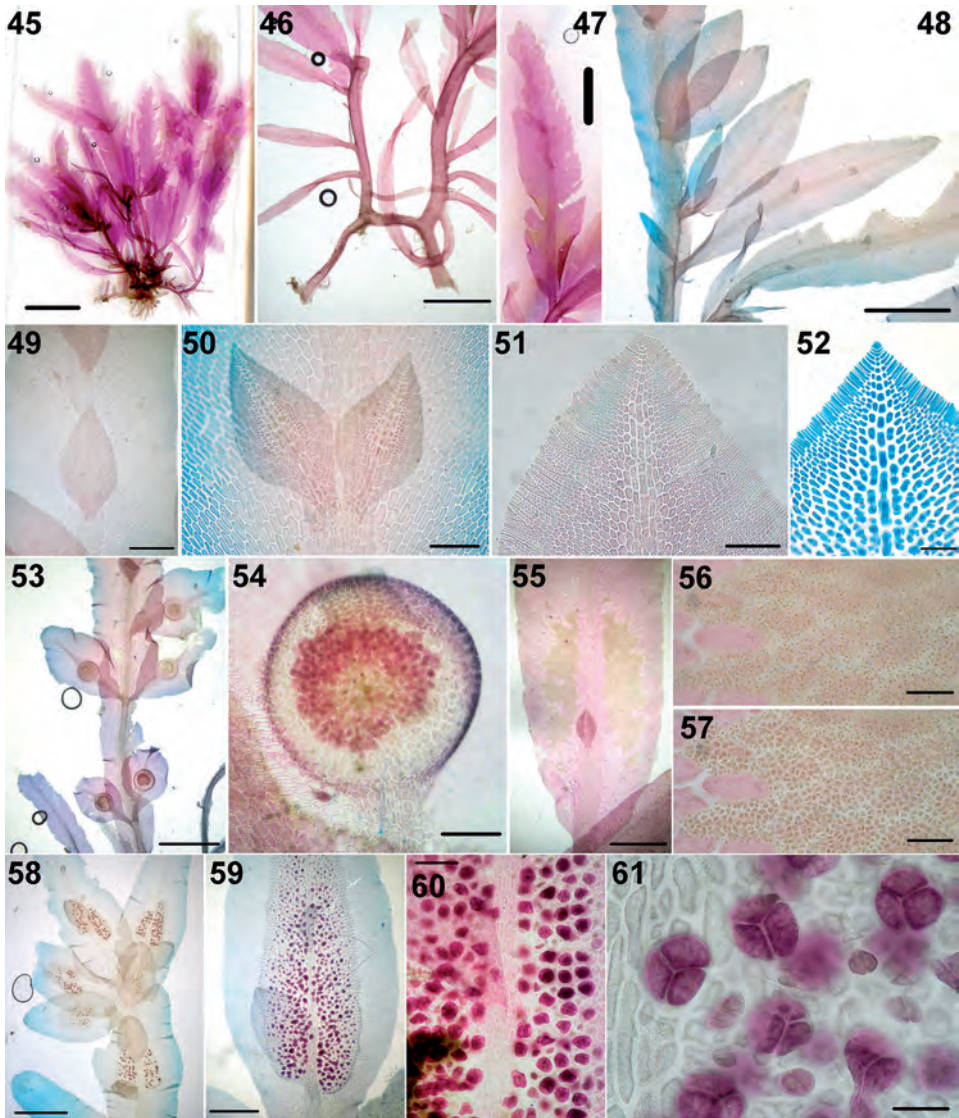
Thalli 5 cm high, consisting of a system of cylindrical or compressed prostrate axes with discoid holdfasts that attach to substrate, bearing numerous oblanceolate blades with a midrib which produce lateral blades (Figs 45-46). Plants pink to dark red in colour, with a flaccid and delicate texture.

Blades arising from a short cylindrical stipe (Figs 46-47), growing by means of a conspicuous apical cell (Figs 51-52). They are ovate when young to oblanceolate when mature, simple, to 4 cm long and 6 mm broad, margins entire (Figs 47-50). Blades with a conspicuous midrib that bears numerous single or grouped lateral blades, producing 1-4 orders of successively smaller blades (Figs 47-50). Blades monostromatic except in the midrib region which is composed by several layers of cells. Microscopic veins or nerves absent. Cells polygonal in surface view.

Gametophytes dioecious. Cystocarps (Figs 53-54) formed singly on lateral blades, hemispherical, 640-1200 µm in diameter, with a protruding ostiole. Male sori located on both sides of the midrib, elongate and with irregular margins (Fig. 55), consisting of a layer of spermatangial mother cells, bearing elongate spermatangia (Figs 56-57). Tetrasporangial sori elongate and located at both sides of the midrib (Figs 58-59). Tetrasporangia spherical, 50-90 µm in diameter (Figs 60-61).

Phenology

Hypoglossum hypoglossoides was found throughout the year, and it is probably perennial. Tetrasporangia were commonly found (49% of the



Figs 45-61. *Hypoglossum hypoglossoides*. Vegetative and reproductive morphology. 45. Habit, consisting of a prostrate axis bearing numerous blades. 46. Prostrate axis. 47. Blade with a basal stipe and a conspicuous midrib. 48-50. Lateral blades growing from the midrib of primary blades. 51-52. Apical organization. 53. Cystocarps growing singly on lateral blades. 54. Detail of a cystocarp. 55. Spermatangial sori growing on either sides of midrib. 56-57. Surface view of spermatangial sori showing spermatangia (56) and spermatangial mother cells (57). 58-59. Tetrasporangial sori growing on either sides of midrib. 60-61. Tetrasporangia. Figs 48-50, 52-54, 58 and 59 specimens stained with aniline blue. Scale bars: 2 mm in Figs 45-48, 53 and 58; 600 μ m in Figs 49, 55 and 59; 200 μ m in Figs 50, 54 and 60; 50 μ m in Figs 51, 52, 56, 57 and 61.



Figs 62-63. Distribution of *Hypoglossum hypoglossoides*. **62.** Collections along the Atlantic Iberian Peninsula. **63.** World distribution: arrow – type locality.

collections) throughout the year; cystocarps were also frequent (10%) and they were collected in January-February, April-May, September and November; while male structures were rarely observed (2%), in samples collected in April and November.

Habitat and distribution

Hypoglossum hypoglossoides is frequent in sand-covered rocks from the Atlantic Iberian Peninsula (Fig. 62). Although not forming monospecific turfs, it is occasionally abundant in turfs dominated by other species such as *Rhodothamniella floridula* or *Ophidocladus simpliciusculus*. *Hypoglossum hypoglossoides* is distributed in northern Europe, northern Africa, southeastern USA, Caribbean and northern Australia (Fig. 63).

Remarks

Hypoglossum hypoglossoides and *Erytroglossum lusitanicum* are similar in habit, and they commonly grow together. The species can be easily separated because *H. hypoglossoides* has lateral blades growing from the midrib of primary blades, which never occurs in *E. lusitanicum*. Conversely, *E. lusitanicum* usually exhibits broken blades, and its apices regenerate new blades. In addition, *H. hypoglossoides* is pink in colour, while *E. lusitanicum* is brownish red. Furthermore, both species can be clearly separated, among other features, by their apical organization, as in *H. hypoglossoides* second and third order initials reach the thallus margin and intercalary divisions are absent in primary cell rows (Figs 51-52), while in *E. lusitanicum* not all third-order initials reach the margin and cells of the primary row undergo intercalary divisions (Fig. 33).

WRANGELIACEAE

Ptilothamnion sphaericum (P.L. Crouan et H.M. Crouan ex J. Agardh)

Maggs et Hommersand

Figs 64-78

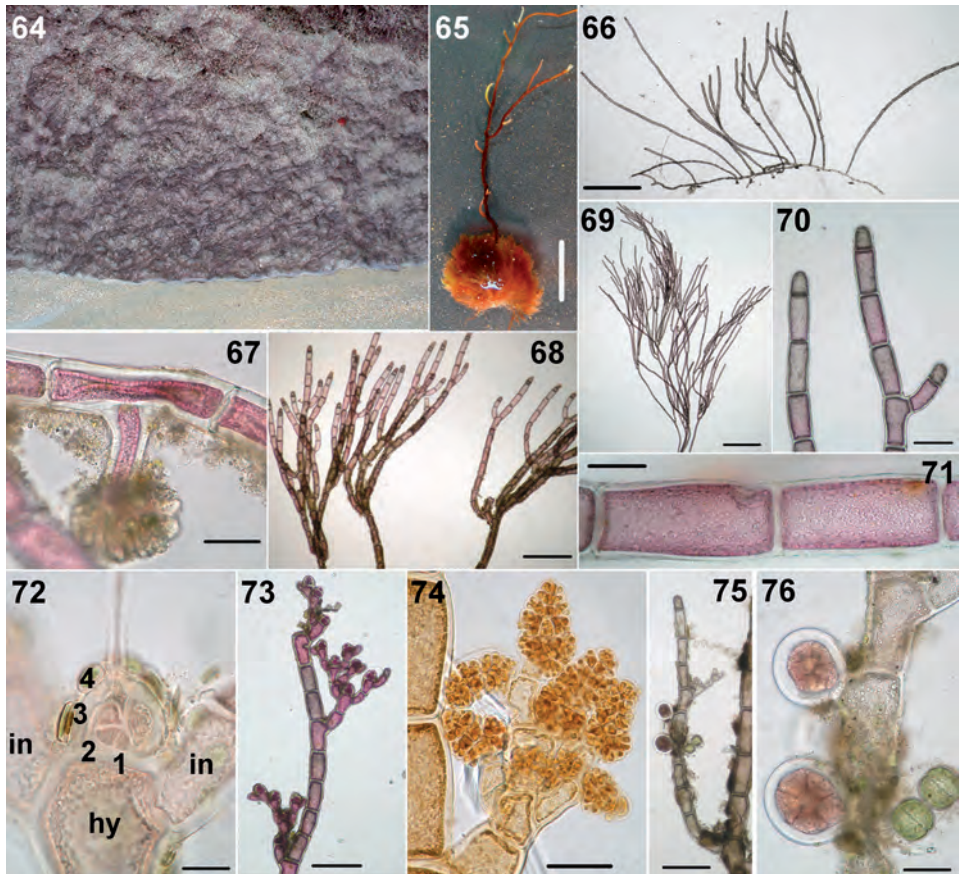
Basionym: *Callithamnion sphaericum* P. Crouan et H. Crouan ex J. Agardh.

Holotype: LD.

Type locality: Anse du Minou, Brest, France.

References: Maggs & Hommersand, 1993; Bárbara et al., 2001; Díaz-Tapia & Bárbara, 2005, 2011; Secilla, 2012.

Molecular voucher: GenBank accession number KJ179927.



Figs 64-76. *Ptilothamnion sphaericum*. Vegetative and reproductive morphology. **64**. Turf in sand-covered rocks. **65**. Epiphytic tuft at the base of *Ahnfeltia plicata*. **66**. Habit of a vegetative specimen consisting of a prostrate axis which bears rhizoids and erect axes. **67**. Rhizoid inserted in the median position of a cell of the prostrate axis. **68-69**. Apical parts of erect axes irregularly branched. **70**. Apexes of erect axes with barrel-shaped cells. **71**. Cells of an erect axis. **72**. Female fertile axis showing the hypogenous cell (hy), the basal cells of two involucrel branches (in) and the 4-celled carpogonial branch (1-4). **73**. Apex of an erect axis bearing female fertile axes. **74**. Branchlet bearing spermatangial heads. **75**. Lateral branch with polysporangia. **76**. Detail of polysporangia. Scale bars: 1 cm in Fig. 65; 15 mm in Figs 66 and 69; 50 μ m in Figs 67, 71, 74 and 76; 500 μ m in Fig. 68; 100 μ m in Fig. 70; 20 μ m in Fig. 72; 200 μ m in Figs 73 and 75.

Selected specimens: 1) Biarritz (43°29'03"N; 1°33'46"W), 19.iii.2011, SANT-Algae 25408; 2) San Juan de Gaztelougatxe (43°26'41"N; 2°46'41"W), 8.ix.2006, SANT-Algae 19731; 3) Oyambre (43°24'02"N; 4°20'10"W), 11.ix.2006, SANT-Algae 21775 (female plants); 4) La Isla (43°28'40"N; 5°13'17"W), 10.x.2006, SANT-Algae 20166 (polysporangial plants), 21773 (male and female plants); 5) Aguilar (43°33'28"N; 6°07'07"W), 17.iv.2007, SANT-Algae 19781 (polysporangial plants); 6) Catedrales (43°33'16"N; 7°09'16"W), 20-ix-2005, SANT-Algae 16554 (polysporangial plants); 7) Castro (43°44'25"N; 7°45'44"W), 27.ix.2011, SANT-Algae 26652; 8) Barrañán (43°18'44"N; 8°33'22"W), 05.xi.2002, SANT-Algae 15124 (polysporangial plants), 21777 (female plants); 9) Reja (43°18'01"N; 8°46'04"W), 27.vi.2009, SANT-Algae 21782; 10) Seasia (43°19'41"N; 8°49'34"W), 27.ii.2002, SANT-Algae 13878 (polysporangial plants); 11) Barizo (43°18'48"N; 8°52'27"W), 5.iv.2004, SANT-Algae 15129



Figs 77-78. Distribution of *Ptilothamnion sphaericum*. **77**. Collections along the Atlantic Iberian Peninsula. **78**. World distribution: arrow – type locality.

(polysporangial plants); 12) Lourido (43°05'28"N, 9°13'15"W), 1.ii.2006, SANT-Algae 21776 (male plants), 22517 (female plants); 13) Nerga (42°15'19"N; 8°50'07"W), 12-ii-2005, SANT-Algae 22833; 14) Leça de Palmeira (41°12'22"N; 8°43'03"W), 16.xi.2004, SANT-Algae 21774 (monoecious plants); 15) Buarcos (37°39'54"N; 8°48'04"W), 15.xi.2004, SANT-Algae 15552; 16) Ingrina (37°02'46"N; 8°52'43"W), 09.v.2005, SANT-Algae 25210; 17) Encendida (36°18'40"N; 6°09'12"W), 18.ii.2011, SANT-Algae 26625 (female plants).

Vegetative and reproductive morphology

Thalli epilithic, forming extensive turfs (Fig. 64) up to 25 mm high, or epiphytic, forming dense tufts (Fig. 65) up to 15 mm high. Plants consisting of a prostrate system of densely entangled axes which bear rhizoids that attach to substrate and numerous erect axes (Fig. 66). They are pink in colour, with a rigid texture.

Axes composed of barrel-shaped cells, 40-110 µm in diameter, with walls 5-10 µm thick and plastids discoid to polygonal (Figs 68, 70, 71). Prostrate axes irregularly branched, forming further prostrate axes or erect ones, and bearing unicellular rhizoids inserted in the median position of cells and terminating in a discoid pad (Fig. 67). Erect axes growing from apical cells ca. 55 µm in diameter with a rounded apex (Fig. 70); from simple to densely branched, especially in the upper parts, branches irregularly arranged, up to 4 orders, often forming second series (Figs 66, 68-69).

Gametophytes dioecious or monoecious. Female fertile axes formed terminally on the upper parts of erect axes (Figs 72-73). They consist of short apical and subapical cells, and a longer hypogynous cell similar to vegetative cells, which bears 1-2 opposite involucrel filaments (Fig. 72). Three periaxial cells arise from the subapical cell, becoming two sterile cells and the supporting cell, which bears a four-celled carpogonial branch (Fig. 72) and produces another single sterile cell. Post-fertilisation development was not observed. Spermatangial heads densely aggregated on upper parts of erect filaments, borne on 3-5-celled lateral branchlets (Fig. 74). Up to three spermatangial heads borne terminally or laterally on each cell of the branchlets. Spermatangial heads ovoid to short cylindrical, (40-) 45-60 (-70) × (30-) 35-45 (-50) µm, consisting of a stalk cell and 3-4 axial cells bearing a dense cluster of spermatangial mother cells that cut-off 1-2 spherical spermatangia 4-5 µm in diameter and enclosed in a mucilage sheath. Polysporangia (Figs 75-76) produced laterally in the upper parts of erect axes, solitary or forming short series, sessile, spherical, 70-100 µm in diameter, containing 8-16 spores. Occasionally, plants bear polysporangia-like anomalous whitish spherical structures, 30-100 µm in diameter, terminally on branches.

Phenology

Ptilothamnion sphaericum was collected throughout the year, and it is probably perennial. Plants cultured in the laboratory survived for 21 months (Díaz-Tapia & Bárbara, 2005). Sexual structures were rare and only found in winter and autumn. Female plants were only observed in 5 collections (5%), male ones in 2 collections (2%) and monoecious plants were observed once. Polysporangia were observed year round and were more frequent (20% of the collections) than sexual structures.

Habitat and distribution

Ptilothamnion sphaericum is common on sand-covered rocks from the Atlantic Iberian Peninsula (Fig. 77). Most collections correspond to small specimens that were found growing intermixed with other turf-forming species typical from the habitat such as *Rhodothamniella floridula* or *Ophidocladus simpliciusculus*; or were collected as epiphytic plants at the basis of *Ahnfeltia plicata* (Hudson) E.M. Fries and *Halopithys incurva* (Hudson) Batters, which usually have their basal parts buried under a layer of sand of several centimeters. More rarely, *P. sphaericum* forms dense turfs almost monospecific growing over rocks that are buried by sand during long periods. Small specimens were collected from the low to the mid intertidal in sites from sheltered to extremely wave-exposed. Monospecific turfs were observed in the low intertidal of highly wave-exposed sites. The distribution of *P. sphaericum* is restricted to the coasts from the British Isles to the Iberian Peninsula (Fig. 78).

Remarks: See remarks on *Spermothamnion repens*.

Spermothamnion repens (Dillwyn) Rosenvinge

Figs 79-98

Basionym: *Conferva repens* Dillwyn.

Lectotype: BM (Maggs & Hommersand, 1993).

Lectotype locality: England, unlocalized.

Synonyms: *Spermothamnion turneri* (Mertens ex Roth) Areschoug, *Spermothamnion roseolum* (C. Agardh) Pringsh.

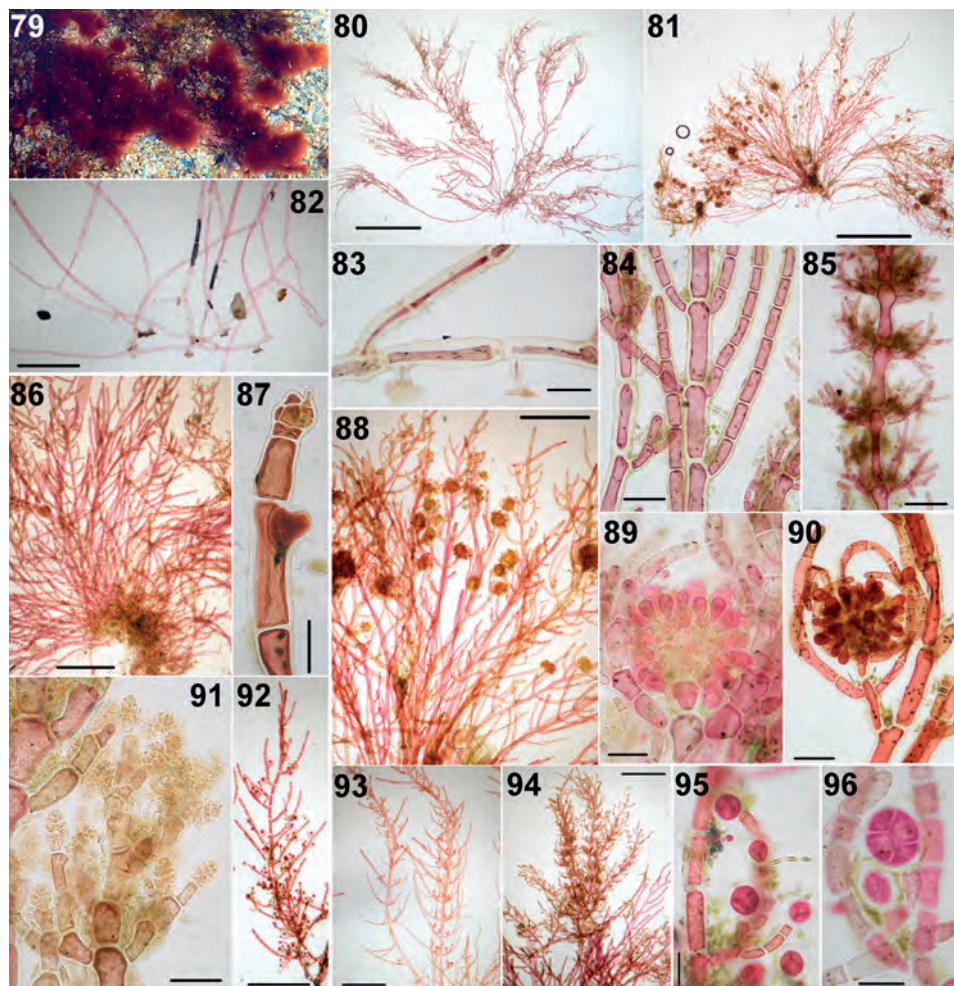
References: Rosenvinge, 1924; Feldmann-Mazoyer, 1941; Lundsteen, 1980; Sansón Acedo, 1991; Bárbara & Cremades, 1993; Maggs & Hommersand, 1993; Coppejans, 1995; Dawes & Mathieson, 2008; Secilla, 2012.

Molecular vouchers: no available COI-5P data.

Selected specimens: 1) Langre (43°28'37"N; 3°41'31"W), 6.xi.2010, SANT-Algae 24625 (female and tetrasporangial plants); 2) Virgen del Mar (43°28'40"N; 3°52'31"W), 28.iii.2006, SANT-Algae 20411, 7.xi.2010, SANT-Algae 24636 (male, female and tetrasporangial plants); 3) Verdicio (43°37'30"N; 5°52'44"W), 19.iv.2007, SANT-Algae 19629 (tetrasporangial plants); 4) Aguilar (43°33'28"N; 6°07'07"W), 17.iv.2007, SANT-Algae 19815; 5) Lourido (43°05'28"N, 9°13'15"W), 1.ii.2006, SANT-Algae 16875 (tetrasporangial plants); 6) Coelho (37°4'22"N; 8°17'31"W), 7.v.2005, SANT-Algae 25311 (female and tetrasporangial plants); 7) Santa Eulalia (37°05'11"N; 8°12'53"W), 19.x.2005; SANT-Algae 26287 (tetrasporangial plants).

Vegetative and reproductive morphology

Thalli epiphytic, forming dense tufts up to 15 mm high (Fig. 79), consisting of a prostrate system of densely entangled axes, bearing numerous erect axes and rhizoids that attach to substrate (Figs 80-81). They are pink in colour, with a flaccid texture.



Figs 79-96. *Spermothamnion repens*. Vegetative and reproductive morphology. **79.** Tufts growing on *Ahnfeltia plicata*. **80-81.** Habit. **82.** Prostrate axes bearing rhizoids and erect axes. **83.** Rhizoids growing at the posterior end of cells. **84.** Erect axes bearing opposite and alternate branches. **85.** Erect axes bearing verticillate branches. **86.** Erect axes growing from densely entangled prostrate axes, irregularly branched. **87.** Female fertile axis. **88.** Erect axes bearing gonimocarps. **89-90.** Gonimocarps surrounded by two whorls of involucre branches. **91.** Spermatangial heads. **92-94.** Erect axes bearing tetrasporangia. **95.** Tetrasporangia. **96.** Octosporangia. Scale bars: 2 mm in Figs 80 and 81; 600 μ m in Figs 82, 86, 88 and 92-94; 100 μ m in Figs 83-85 and 90; 50 μ m in Figs 87, 89, 91, 95 and 96.

Axes composed of cylindrical cells (Figs 83-84), 40-70 μ m in diameter, with walls 5-17.5 μ m thick and plastids discoid to bacilloid. Prostrate axes irregularly branched, forming further prostrate axes or erect ones, which are inserted in the anterior end of cells (Figs 82-83). Rhizoids unicellular, inserted in the posterior end of cells and terminating in a discoid pad (Figs 82-83). Erect axes growing from apical cells ca. 35-47.5 μ m in diameter with a rounded apex; from



Figs 97-98. Distribution of *Spermothamnion repens*. **97.** Collections along the Atlantic Iberian Peninsula. **98.** World distribution: arrow – type locality.

simple to densely branched, especially in the upper parts; branches irregularly arranged, alternate or secund, often paired and sometimes verticillate (Figs 84-86).

Gametophytes dioecious. Female fertile axes formed terminally on lateral branches of erect axes (Fig. 87). Gonimocarps subglobular, 120-250 μm in diameter, with a central fusion cell bearing clusters of gonimoblast cells that produce carposporangia terminally, surrounded by a whorl of 4 post-fertilization involucre branches borne on the subhypogenous cell with a second whorl of branchlets sometimes developing from the cell below this (Figs 88-90). Carposporangia pyriform (Fig. 89), 20-35 \times 32.5-45 μm . Spermatangial heads densely aggregated on branchlets of upper parts of erect axes, formed terminally or laterally, sessile, ovoid to short cylindrical, 27-40 \times 25 μm , enclosed in a mucilage sheath (Fig. 91). Tetrasporangia formed on short branchlets, initially terminal and later in groups as the branchlets grow, subspherical 42-75 μm in diameter (Figs 92-95); octosporangia mixed with tetrasporangia (Fig. 96).

Phenology

Spermothamnion repens was recorded throughout the year and it is probably perennial. Reproductive structures were observed in most of the collections, which were commonly found year-round. Tetrasporangia were observed in 55% of the collections, gonimocarps in 35% and spermatangial heads in 8%.

Habitat and distribution

Spermothamnion repens is a frequent species on sand-covered rocks from the Atlantic Iberian Peninsula (Fig. 97). It is usually an epiphytic species, growing on *Ahnfeltia plicata*, *Halopithys incurva*, *Ophiodcladus simpliciusculus*, etc. In addition, *S. repens* also appears intermixed in turfs dominated by other species typical of the habitat. It was collected from the low to the mid intertidal in sites from sheltered to extremely wave-exposed. Its world distribution includes the coasts of Europe, northern Africa and Atlantic North America (Fig. 98).

Remarks

Spermothamnion repens shows a high degree of variability in branching pattern and tetrasporangial arrangement, and three varieties of the species have been recognized based on this variability: *S. repens* var. *turneri* (Mertens) Rosenvinge, *S. repens* var. *variable* (C. Agardh) Feldmann-Mazoyer and *S. repens*

var. *flabelliferum* (De Notaris) Feldmann-Mazoyer. *Spermothamnion repens* from sand-covered rocks of the Atlantic Iberian Peninsula showed great variability in its features and is not possible to assign our materials to a specific variety.

Spermothamnion repens is commonly considered a monoecious species (Maggs & Hommersand, 1993; Secilla, 2012). Conversely, fertile gametophytes we have studied were dioecious. Other morphological features observed in specimens from sand-covered rocks along the Atlantic Iberian Peninsula agree with previous descriptions of the species.

Spermothamnion repens is similar in habit to *Ptilothamnion sphaericum*, both being very common and usually found sharing the same habitat and even the same turfs. Both species are distinguished by the position of rhizoids and erect axes on the cells from prostrate axes (central in *P. sphaericum* vs distal in *S. repens*); the axes diameter (40-110 μm in *P. sphaericum* vs 40-70 μm in *S. repens*); as well as by the features of the female structures, although these are very rare in *P. sphaericum*. In addition, the arrangement of branches is more irregular in *P. sphaericum*, which furthermore has wider, barrel-shaped, cells. Both species were commonly found epiphytic on *Ahnfeltia plicata* and other erect species from sand-covered rocks. Curiously, *P. sphaericum* is often epiphytic on basal parts of the host alga, which are buried by sand, and *S. repens* grows on upper parts.

Tiffaniella capitata (Schousboe ex Bornet) Doty et Meñez

Figs 99-113

Basionym: *Spermothamnion capitatum* Schousboe ex Bornet.

Type material: No published information.

Type locality: Tanger.

References: Bornet, 1892; Feldmann-Mazoyer, 1941 (as *Spermothamnion capitatum*); Doty & Meñez, 1960; Sansón Acedo, 1991; Bárbara *et al.*, 1992; Secilla, 2012.

Molecular vouchers: no available COI-5P data.

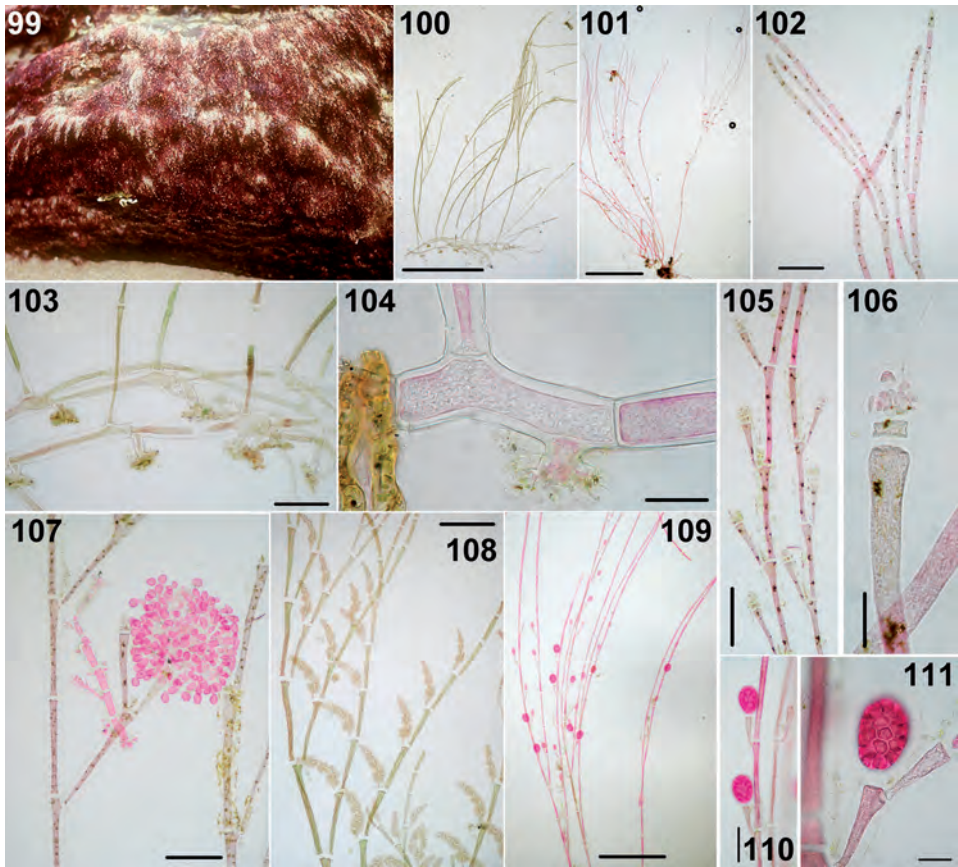
Selected specimens: 1) Xilloe (43°44'41"N; 7°39'02"W), 29.ix.2011, SANT-Algae 26650 (female plants); 2) Area da Cruz (42°27'40"N; 8°54'37"W), 22.viii.2005 (female, male and tetrasporangial plants); 3) Cabo de Mar (42°13'18"N; 8°43'32"W), 23.i.2008, SANT-Algae 21120 (female plants); 4) El Puerto (36°34'48"N; 6°15'51"W) 16.xi.2005, SANT-Algae 26074.

Vegetative and reproductive morphology

Thalli forming turfs (Fig. 99) up to 15 mm high and covering rock surfaces that sometimes exceed 1 m² in extent, consisting of a prostrate system of axes bearing numerous erect axes and rhizoids that attach to substrate (Figs 100-101). Thalli are pink in colour, with a flaccid and very delicate texture.

Axes composed by cylindrical cells (Fig. 102), 40-70 μm in diameter, with walls 7-18 μm thick and plastids discoid to bacilloid. Prostrate axes irregularly branched forming further prostrate axes. Rhizoids unicellular, inserted in the posterior end of cells and terminating in a discoid pad (Figs 103-104). Erect axes formed on each cell of the prostrate axes, inserted in the anterior end of cells (Figs 103-104). Erect axes growing from apical cells 25-35 μm in diameter with a rounded apex (Fig. 102); scarcely branched in basal parts and with abundant branches in upper parts, branches pseudodichotomous or unilateral (Figs 100-102, 108).

Gametophytes dioecious. Female fertile axes terminal on unicellular stalks formed in upper parts of the erect axes (Figs 105-106). Gonimocarps subglobular, 350-400 μm in diameter, with a central fusion cell bearing clusters of gonimoblasts cells that produce carposporangia terminally, lacking involucrel branches (Fig. 107). Carposporangia pyriform, 13-35 \times 30-47.5 μm . Spermatangial



Figs 99-111. *Tiffaniella capitata*. Vegetative and reproductive morphology. **99**. Turf in sand-covered rocks. **100-101**. Habit consisting of prostrate axes with rhizoids, and erect axes. **102**. Apexes of erect axes. **103-104**. Prostrate axes with rhizoids inserted on the posterior end of cells and erect branches on the opposite sides. **105**. Erect axes with female fertile axes. **106**. Female fertile axis. **107**. Gonimocarp. **108**. Spermatangial heads unilaterally arranged. **109-111**. Polysporangia. Scale bars: 2 mm in Figs 100 and 101; 200 μ m in Figs 102, 103, 105, 107 and 108; 50 μ m in Figs 104, 106 and 111; 600 μ m in Fig. 109; 100 μ m in Fig. 110.

heads in long branches of the upper parts of erect axes, unilaterally arranged forming series, one per axial cell, with a cylindrical stalk, cylindrical, 150-250 \times 45-75 μ m (Fig. 108). Polysporangia formed on short branchlets of the upper parts of erect axes, which are arranged in second series, are alternate or opposed; initially terminal and later in groups as the branchlets grow; subspherical 70-95 μ m in diameter (Fig. 109-111).

Phenology

Tiffaniella capitata was recorded throughout the year and it is probably perennial. Most of the collections showed reproductive structures, which were commonly found. Polysporangia were observed in 48% of the collections, gonimocarps in 33% and spermatangial heads in 24%.



Figs 112-113. Distribution of *Tiffaniella capitata*. **112.** Collections along the Atlantic Iberian Peninsula. **113.** World distribution: arrow – type locality.

Habitat and distribution

Tiffaniella capitata was mainly collected in the northwestern Iberian Peninsula, as well as it was also recorded once in the South (Fig. 112). It was found only rarely, and although its chorological distribution has been extended since it was reported for the first time in Galicia (Bárbara *et al.* 1992), it is uncommon. *Tiffaniella capitata* forms dense turfs in sand-covered rocks from the mid to low intertidal of sites from moderately to highly wave-exposed. Turfs occur in almost monospecific growths or are mixed with other species, commonly *Rhodothamniella floridula*. Although most records of this species in the Atlantic Iberian Peninsula come from sand-covered rocky habitats, it was also found at shadow sites with high sedimentation such as harbours. The world distribution of *T. capitata* is restricted to southern Europe and northern Africa (Fig. 113).

GELIDIALES

GELIDIACEAE

Gelidium crinale (Hare *ex* Turner) Gaillon

Figs 114-133

Basionym: *Fucus crinalis* Hare *ex* Turner.

Lectotype: BM (*fide* Dixon & Irvine, 1977b).

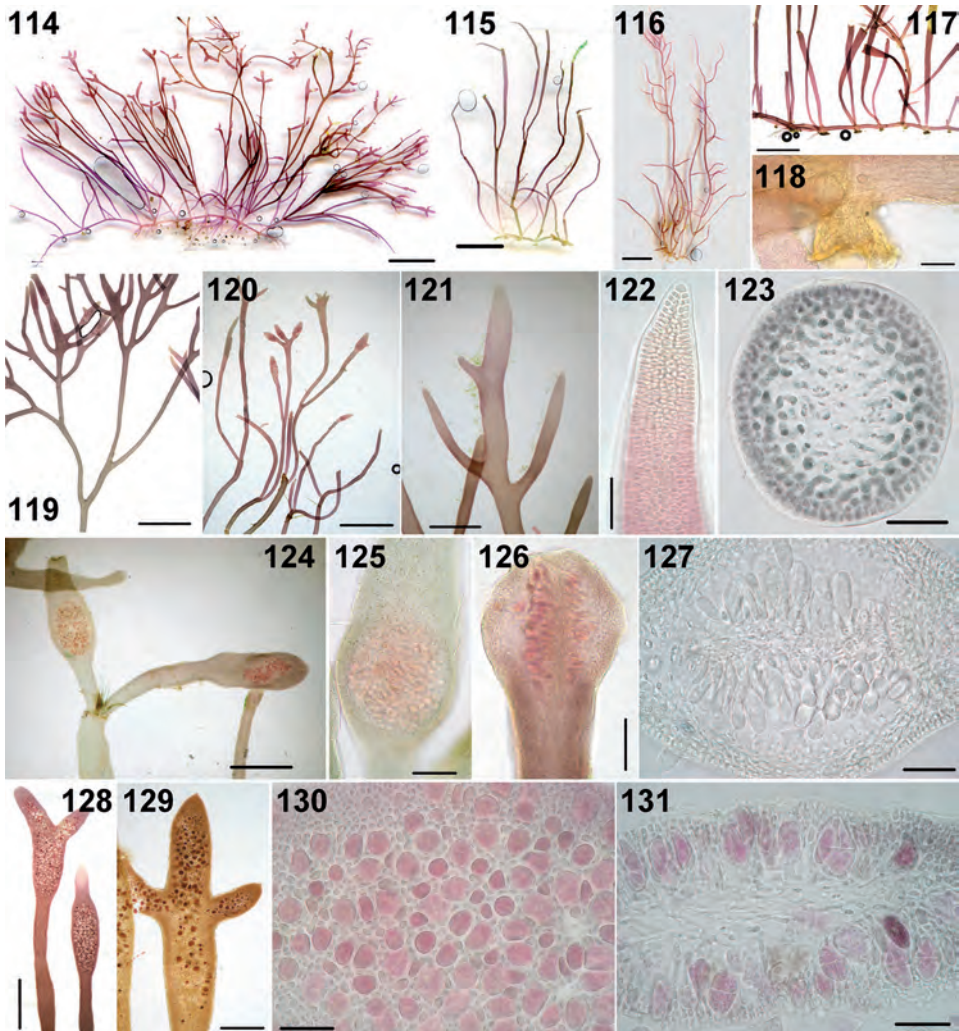
Lectotype locality: Ilfracombe, Devonshire, England.

Synonym: *Gelidium corneum* var. *crinale* (Turner) Greville.

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

Molecular vouchers: GenBank accession numbers KJ168044, KJ179932, KJ179933, KJ179934, KJ179935, KJ179937.

Selected specimens: 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); 3) La Franca (43°23'39"N; 4°34'18"W), 6.x.2006, SANT-Algae 19749 (tetrasporangial plants); 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; 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; 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



Figs 114-131. *Gelidium crinale*. Vegetative and reproductive morphology. **114-116.** Habit of a tetrasporangial plant (114) and sterile thalli (115-116). **117.** Stoloniferous axes bearing discoid holdfasts and erect branches. **118.** Discoid holdfast. **119-121.** Erect axes with irregularly arranged branches. **122.** Apical cell of an erect branch. **123.** Cross section of thallus showing the inner medulla and the outer compact cortex. **124.** Branchlets bearing cystocarps. **125.** Cystocarp in surface view. **126.** Lateral view of a bilocular cystocarp showing two ostioles. **127.** Cross section of a cystocarp. **128-129.** Tetrasporangial sori formed on the apical parts of plants or on compressed short lateral branches, elongate or furcated (128), or with lateral lobes (129). **130.** Tetrasporangia in surface view. **131.** Cross section of a branch with tetrasporangia. Scale bars: 3 mm in Figs 114-116; 2 mm in Figs 117, 119 and 120; 100 μ m in Figs 118, 125 and 126; 600 μ m in Figs 121, 124 and 128; 50 μ m in Figs 122, 123, 127, 130 and 131; 200 μ m in Fig. 129.

24784; 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) 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-



Figs 132-133. Distribution of *Gelidium crinale*. **132.** Collections along the Atlantic Iberian Peninsula. **133.** World distribution: arrow – type locality.

Algae 26623 (tetrasporangial plants); 16) Caños de Meca (36°10'55"N; 6°00'06"W), 17.xi.2005, SANT-Algae 26140 (tetrasporangial plants).

Reproductive and vegetative morphology

Thalli forming dense turfs, up to 3.5 cm high and covering rock surfaces that can exceed 1 m² in extent. Plants consist of a basal system of stoloniferous axes, branched forming further prostrate axes, and bearing erect branches and discoid holdfasts that attach to the substrate (Figs 114-118). Turfs dark brownish red in colour, with a rigid texture; isolated specimens dark purplish red.

Stoloniferous axes terete, 120-220 µm in diameter, producing discoid holdfasts and/or 1-2 erect branches at rather regular intervals of 0.8-1.5 mm (Figs 117-118). Erect branches growing from an apical cell (Fig. 122), up to 550 µm in diameter in mid parts. The basal parts of axes are terete and upper ones are from terete to compressed; from simple to abundantly branched with an irregular pattern (Figs 114-116, 119-122). Structure uniaxial, differentiating in cross section an inner medulla of 3-6 cells and an outer compact cortex 3-4 cells thick (Fig. 123), with rhizines. Cortical cells polygonal in surface view, 5-10 µm length in their longest side.

Cystocarps formed on lateral branchlets, single per ramulus, 220-550 µm long, bilocular, with one ostiole on each side (Figs 124-127). Male reproductive structures not observed. Sori of tetrasporangia up to 25 mm long, formed on compressed short lateral branches or on the apex of erect branches, which are elongate, furcated or with lateral lobes (Figs 128-129). Tetrasporangia ovoid, 25-35 µm in diameter, cruciately divided (Figs 130-131).

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 sites from Portugal.

Habitat and distribution.

Gelidium crinale is a common species in sand-covered rocks from the Atlantic Iberian Peninsula (Fig. 132). It forms almost monospecific tufts; or 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 on temperate coasts of the world (Fig. 133).

Remarks: See remarks on *Gelidium spathulatum*.

Gelidium spathulatum (Kützinger) Bornet**Figs 134-146****Basionym:** *Acrocarpus spathulatus* Kützinger.**Lectotype:** L (Segi, 1963).**Type locality:** Adriatic Sea (Kützinger, 1868).**Synonym:** *Gelidium crinale* var. *spathulatum* (Kützinger) Hauck.**References:** Bornet, 1892; Feldmann & Hamel, 1936; Echegaray & Seoane, 1982.**Molecular vouchers:** no available COI-5P data.**Selected specimens:** 1) Zumaia (43°17'59"N; 2°15'41"W), 30.iii.2006, SANT-Algae 20274 (female and tetrasporangial plants); 2) Oriñón (43°24'20"N; 3°19'34"W), 27.iii.2006, SANT-Algae 20378 (tetrasporangial plants); 3) Armação de Pêra (37°06'04"N; 8°22'17"W), 17.10.2005, SANT-Algae 24845 (tetrasporangial plants); 4) Punta Paloma, (36°03'44"N; 5°43'31"W), 18.xi.2005; SANT-Algae 26154.*Reproductive and vegetative morphology*

Thalli forming dense turfs up to 2 cm high and covering rock surfaces that can exceed 1 m² in extent. Plants consist of a basal system of stoloniferous axes, irregularly branched forming further prostrate axes, and bearing erect branches and discoid holdfasts that attach to the substrate (Figs 134-138). Turfs brownish red in colour, with a rigid texture; isolated specimens dark purplish red.

Stoloniferous axes terete, 130-260 µm in diameter, producing discoid holdfasts and erect branches at irregular intervals (Figs 137-138). Erect branches growing from distinct apical cells (Fig. 139), upper parts predominantly compressed and narrowing gradually towards basal parts becoming terete, up to 750 µm wide, with abundant branches especially in upper parts, alternate, opposite or irregularly arranged, with up to 3 branching orders (Figs 134-136, 140). Structure uniaxial, differentiating in cross section an inner medulla of 3-6 cells and an outer compact cortex 3-4 cells thick, with rhizines. Cortical cells polygonal in surface view, 5-7.5 µm length in their longest side.

Cystocarps formed in lateral branchlets, 350-550 µm long, bilocular with one ostiole on each side (Fig. 141). Male structures not observed. Tetrasporangia forming sori, up to 2 mm long, on compressed short lateral branches or on the apex of erect branches (Figs 142-143). Tetrasporangia ovoid, 22-38 µm in diameter, cruciately divided (Fig. 144).

Phenology

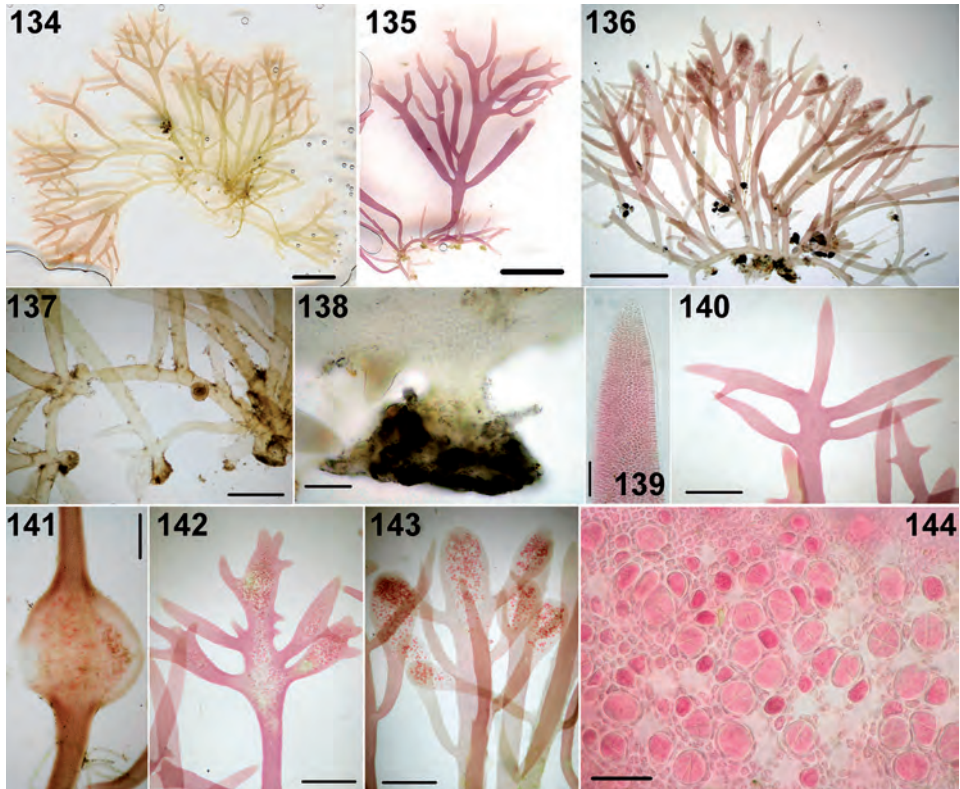
Gelidium spathulatum was collected in different seasons and it is probably perennial. Female structures and/or tetrasporangia were present in most of the collections (40% in each case). Cystocarps were collected in March, June and October; tetrasporangia were collected in February, March, June, October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

Habitat and distribution

Gelidium spathulatum is an uncommon species in sand-covered rocks from the Atlantic Iberian Peninsula (Fig. 145), but when present it forms turfs that sometimes exceed 1m² in extent. It was collected from the upper to the lower intertidal, in sites from sheltered to highly wave-exposed. It was reported in southern Europe and northern Africa, as well as in Vietnam (Fig. 146).

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



Figs 134-144. *Gelidium spathulatum*. Vegetative and reproductive morphology. **134-136**. Habit of sterile plants (134-135) and a tetrasporangial plant (136). **137**. Stoliferous axes bearing discoid holdfasts and erect branches. **138**. Discoid holdfast. **139**. Apical cell of an erect branch. **140**. Erect axes producing branches irregularly arranged. **141**. Cystocarp bilocular formed on apical parts of axes or on short lateral branches. **142-143**. Tetrasporangia formed on apical parts of axes or on short lateral branches. **144**. Tetrasporangia in surface view. Scale bars: 3 mm in Figs 134 and 135; 2 mm in Fig. 136; 600 μ m in Figs 137, 140, 142 and 143; 100 μ m in Fig. 138; 50 μ m in Figs 139 and 144; 200 μ m in Fig. 141.



Figs 145-146. Distribution of *Gelidium spathulatum*. **145**. Collections along the Atlantic Iberian Peninsula. **146**. World distribution: arrow – type locality.

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 & Irvine (1977a) considered that these two species together with *G. pulchellum* (Turner) Kützing and *G. pusillum* (Stackhouse) Le Jolis are a single entity that shows morphological variations in relation to the environmental conditions. Recent studies involving molecular data (Freshwater & Rueness, 1994) 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. With regard to *G. spathulatum*, molecular data have not been published, and its morphological differentiation from *G. crinale* is still more complex. In the Atlantic Iberian Peninsula, four 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.

GELIDIACEAE

Pterocliadiella melanoidea (Schousboe ex Bornet) Santelices et Hommersand
Figs 147-165

Basionym: *Gelidium melanoideum* Schousboe ex Bornet.

Type material: PC (Fredriksen & Rueness, 1990).

Type locality: Tanger, Morocco.

Synonym: *Pterocladia melanoidea* (Schousboe ex Bornet) Dawson.

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

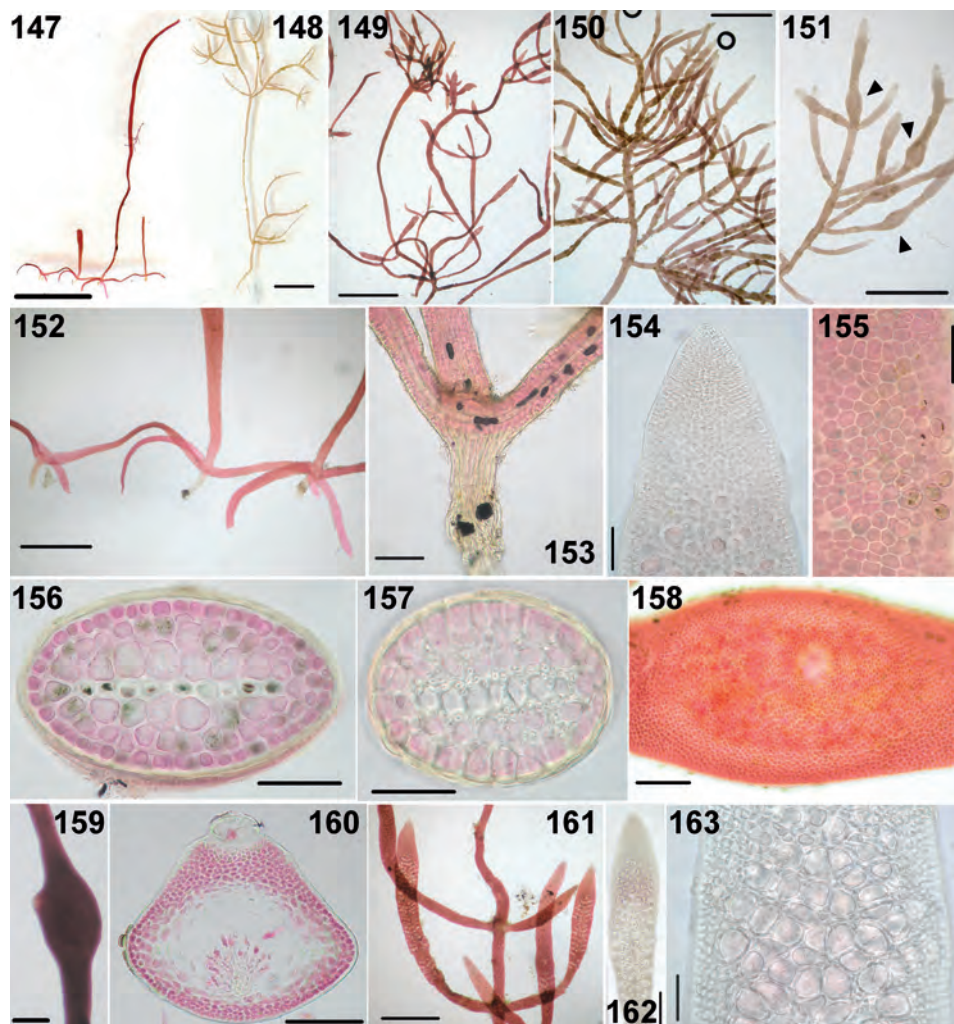
Molecular voucher: GenBank accession number KJ179936.

Selected specimens: 1) Aguilar (43°33'28"N; 6°07'07"W), 17.iv.2007, SANT-Algae 19795 (tetrasporangial plants); 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.

Vegetative and reproductive morphology

Thalli forming turfs up to 3 cm high and covering rock surfaces that can exceed 1 m² in extent, consisting of a short system of stoloniferous axes, irregularly branched forming further prostrate axes, and bearing erect branches and discoid holdfasts that attach to the substrate (Figs 147-151). Tufts bright red in colour, with a rigid and fragile texture.

Stoloniferous axes terete, 110-150 µm in diameter, producing discoid holdfasts and erect branches at irregular intervals (Figs 147, 152-153). Erect branches growing from distinct apical cells (Fig. 154), 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 149-151, 161). Structure uniaxial, showing in cross section a central row of 7-11 small non-pigmented cells, surrounded by medullary cells and a layer of outer cortical cells



Figs 147-163. *Pterocliadiella melanoidea*. Vegetative and reproductive morphology. **147-150**. Habit of plants, with erect branches from simple (147) to densely and irregularly branched (150). **151**. Upper branches with cystocarps (arrowheads). **152**. Stoloniferous axes. **153**. Discoid holdfast. **154**. Apex of a branch with a prominent apical cell. **155**. Surface view of thallus. **156**. Cross section of mid part of thallus showing a central row of cells, surrounded by medullary cells and an outer layer of cortical cells. **157**. Cross section of a holdfast showing rhizines among the medullary cells. **158**. Surface view of a cystocarp showing a prominent ostiole. **159**. Lateral view of a cystocarp. **160**. Cross section of a cystocarp. **161-162**. Lateral branches with tetrasporangia forming V-shaped rows. **163**. Tetrasporangia in surface view. Scale bars: 3 mm in Figs 147 and 148; 2 mm in Figs 149-151; 600 μm in Figs 152, 159 and 161; 100 μm in Figs 153, 158 and 160; 50 μm in Figs 154-157 and 163; 200 μm in Fig. 162.

(Fig. 156), with hyaline cells intercalated between the cortical ones; rhizines are present in the medulla only in holdfast regions (Fig. 157). Cortical cells polygonal in surface view, 5-18 μm length in their longest side (Fig. 155).



Figs 164-165. Distribution of *Pteroclatiella melanoidea*. **164**. Collections along the Atlantic Iberian Peninsula. **165**. World distribution: arrow – type locality.

Cystocarps intercalary on axes and branches (Fig. 151), often located above branching points, 350-600 μm long, unilocular with a single ostiole (Figs 158-159), gonimoblast attached to the cystocarpic floor (Fig. 160). Male structures not observed. Tetrasporangia forming sori up to 1.5 mm long, on compressed apical parts of erect axes or on lateral branches, which often reinstated the growth and then tetrasporangia appear intercalary. Tetrasporangia forming V-shaped rows, with up to 8 tetrasporangia per row and 20 rows per branch (Figs 161-162). Tetrasporangia ovoid, 27-40 μm in diameter, tetrahedrally divided (Fig. 163).

Phenology

Pteroclatiella 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 observed in 18% of the collections and tetrasporangia in 53%.

Habitat and distribution

Pteroclatiella melanoidea is frequent in sand-covered rocks from the Atlantic Iberian Peninsula (Fig. 164), 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. *Pteroclatiella 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. *Pteroclatiella melanoidea* has been reported from southern Europe and northern Africa (Fig. 165).

Remarks

Pteroclatiella melanoidea shows 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 et 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 from 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 & 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 160), which is in agreement with the genus *Pterocladia* (Santelices & Hommersand, 1997).

Materials here assigned to *Pterocladia melanoidea* largely resemble *Gelidiella calcicola* Maggs *et* 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). At the present, 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 *et* Hommersand **Figs 166-183**

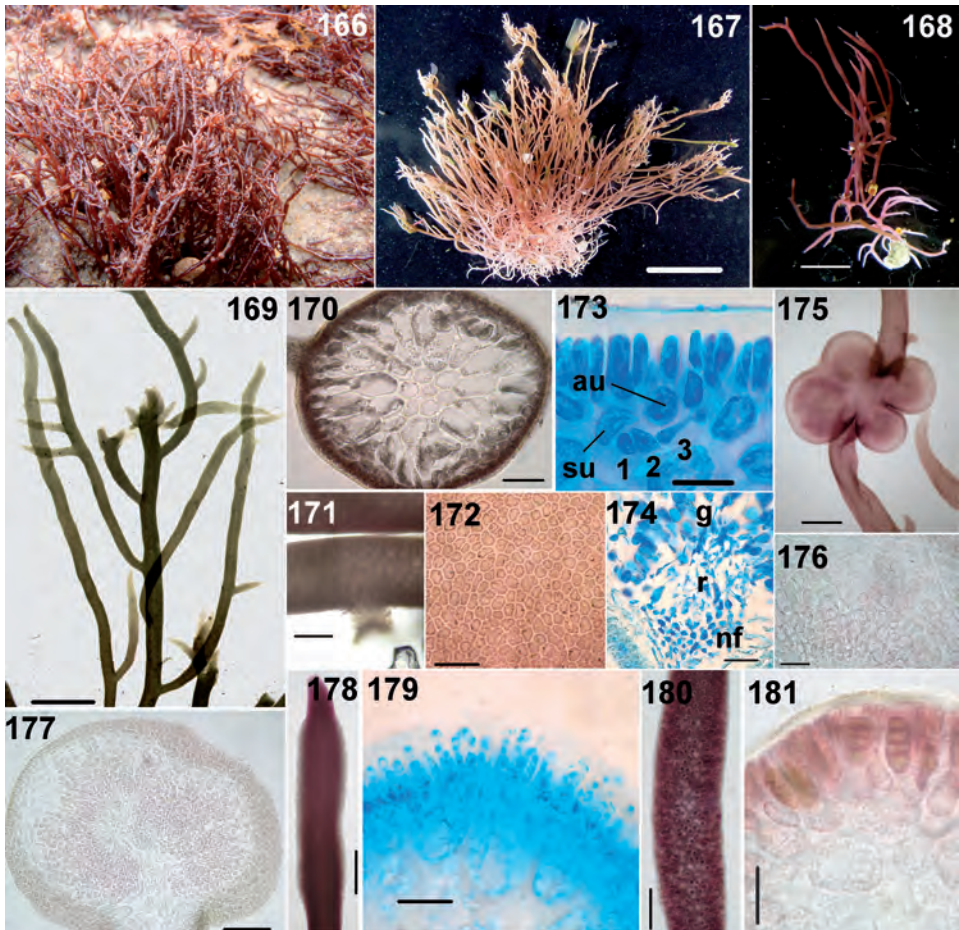
Holotype: SANT.

Type locality: Aguilar, Asturias, Spain.

References: Díaz-Tapia *et al.*, 2013b.

Molecular voucher: GenBank accession number KJ179925.

Selected specimens: 1) Biarritz (43°29'03"N; 1°33'46"W), 19.iii.2011, SANT-Algae 25425; 2) Zumaia (43°17'59"N; 2°15'51"W), 18.iii.2011, SANT-Algae 25138; 3) Laida (43°24'28"N; 2°40'54"W), 31.iii.2006, SANT-Algae 20283; 4) Langre (43°28'37"N; 3°41'37"W), 6.xi.2010, SANT-Algae 24626; 5) Virgen del Mar (43°28'40"N; 3°52'31"W), 7.xi.2010, SANT-Algae 24653; 6) Aguilar (43°33'28"N; 6°07'07"W), 27.v.2010, SANT-Algae 26428; 7) Catedrales (43°33'16"N; 7°09'16"W), 20.ix.2005, SANT-Algae 16555; 8) Bares (43°46'02"N; 7°40'36"W), 31.iii.2010, SANT-Algae 24326; 9) Perbes (43°22'33"N; 8°12'56"W), 29.i.2010, SANT-Algae 24107; 10) Nerga (42°15'19"N; 8°50'07"W), 12.ii.2005, SANT-Algae 22817; 11) Leça de Palmeira (41°12'22"N; 8°43'03"W), 11.vi.2010, SANT-Algae 24225; 12) Buarcos (40°11'58"N; 8°54'29"W), 11.vi.2010, SANT-Algae 24213; 13) Vale Furado (39°41'04"N; 9°03'33"W), 12.vi.2010, SANT-Algae 26598; 14) Olhos d'Água (37°5'20"N; 8°11'27"W), 20.ii.2011, SANT-Algae 26264.



Figs 166-181. *Calliblepharis hypneoides*. Vegetative and reproductive morphology. **166.** Turf in sand-covered rocks. **167-168.** Habit consisting of a basal system of densely entangled creeping branches from which arise the upright axes. **169.** Upright axis irregularly branched. **170.** Cross section of an upright axis showing a central axial cell, surrounded by 6 cells, two layers of medullary cells, a layer of inner cortical cells and a layer of outer cortical cells. **171.** Peg-like projection. **172.** Surface view of an axis showing a continuous layer of outer cortical cells. **173.** Procarp showing a supporting cell (su), bearing a 3-celled carpogonial branch (1-3) and an auxiliary cell (au). **174.** Young carposporophyte showing a basal cushion of nutritive filaments (nf), a central reticulum of interconnected cells (r) and the gonimoblasts (g). **175.** Cystocarps. **176-177.** Cross section of a mature cystocarp with carposporangia in chains. **178.** Spermatangial sorus. **179.** Cross section of a male sorus showing the spermatangial filaments. **180.** Tetrasporangial sorus on a branchlet. **181.** Cross section of a tetrasporangial sorus, with zonately divided tetrasporangia. Figs 173, 174 and 179 specimens stained with aniline blue. Scale bars: 1.5 cm in Fig. 167; 3 mm in Fig. 168; 1.5 mm in Fig. 169; 100 μ m in Figs 170 and 176; 200 μ m in Figs 171, 177, 178 and 180; 50 μ m in Figs 172, 174 and 181; 20 μ m in Figs 173 and 179; 500 μ m in Fig. 175.



Figs 182-183. Distribution of *Calliblepharis hypneoides*. **182.** Collections along the Atlantic Iberian Peninsula. **183.** World distribution: arrow – type locality.

Vegetative and reproductive morphology

Thalli forming turfs (Fig. 166) up to 7 cm high and covering rock surfaces of up to several metres in extent. Thallus consisting of an extensive basal system of densely entangled creeping branches attached to the substratum by means of numerous peg-like projections (Fig. 171), and from which arise the sparsely branched upright axes (Figs 167-169). Thallus cartilaginous; basal axes reddish white and upright axes reddish brown to bright red.

The basal system consists of terete and irregularly branched entangled axes (Figs 167-168), (170-) 200-300 (-350) μm in diameter. Upright axes terete, non-percurrent, (200-) 300-600 (-680) μm in diameter, unbranched or irregularly pseudodichotomously branched (Figs 168-169) or sometimes forming 2-5 whorled branches. Branchlets and spiniform proliferations sometimes present (Fig. 166), especially in upper parts of erect axes. Structure uniaxial, consisting of an axial filament surrounded by 5-7 filaments of elongated cells, two or three layers of large medullary cells, a layer of rounded inner cortical cells and a layer of surface cortical cells (Fig. 170). Cortical cells forming a continuous layer of irregularly polygonal cells, without rosettes (Fig. 172). They usually contain one or two refractive spherical inclusions.

Gametophytes dioecious. Carpogonial branches formed near the apices of main axes and branches. The supporting cell is an inner cortical cell that bears a three-celled carpogonial branch (Fig. 173). 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 (Fig. 174). Mature cystocarps subglobose, (600-) 700-1000 (-1100) μm in diameter, non-ostiolate, often forming dense aggregates on main axes and branches (Figs 175-177). Spermatangia forming sori, girdling the branchlets in the upper parts of the thallus, with initials from outer cortical cells forming chains of 3-4 spermatangia (Figs 178-179). Mature spermatia ovoid and ca. 3 μm in length (Fig. 179). Tetrasporangia forming sori that surround the branchlets or main axes (Fig. 180); ovoid, (40-) 50-65 (-75) μm long and (15-) 20-30 (-40) μm in diameter, zonately divided (Fig. 181).

Phenology

Plants occur throughout the year and they are probably perennial. Reproductive structures were common throughout the year. Tetrasporangia were observed in 55% of the collections, female plants in 22% of collections and male plants were only observed in 10% of the collections.

Habitat and distribution

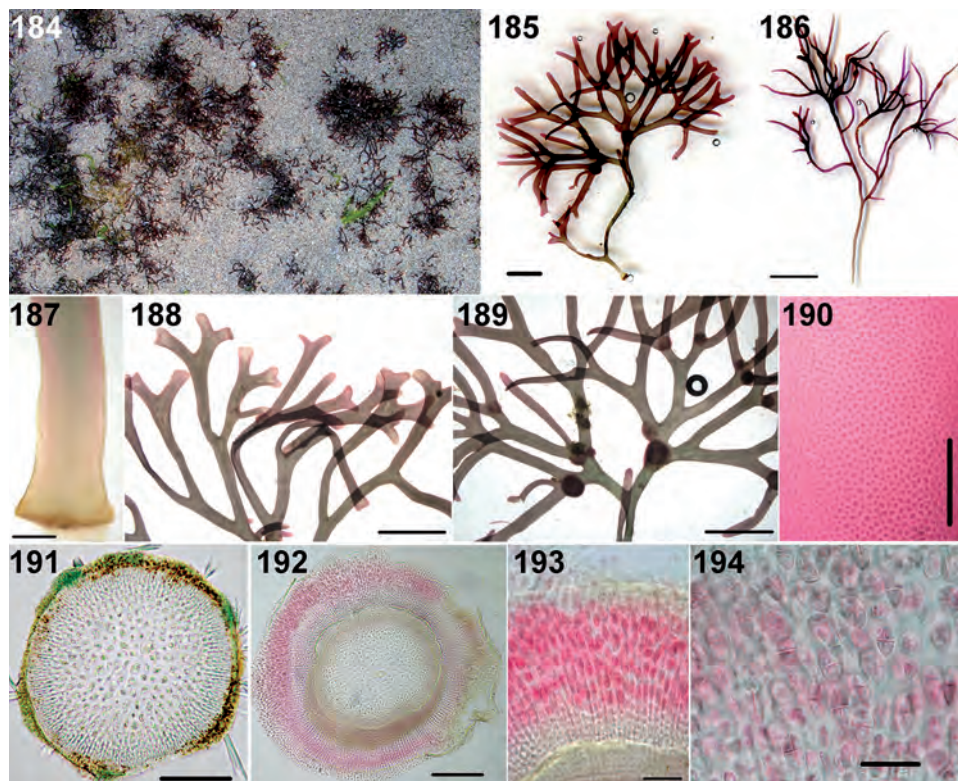
Calliblepharis hypneoides was found throughout the Atlantic Iberian Peninsula (Fig. 182). It was collected forming turfs on sand-covered rocks from the lower intertidal to the upper subtidal of extremely to moderately wave exposed sites. Turfs develop both directly on the sand-covered rocks or overgrowing other turf-forming species, such as *Rhodothamniella floridula* or *Ophidocladus simpliciusculus*. Turfs were often buried by sand, which made observation of the species difficult. *Calliblepharis hypneoides* has been reported exclusively in the Atlantic Iberian Peninsula (Fig. 183), but its distribution is probably wider.

PHYLLOPHORACEAE***Gymnogongrus griffithsiae* (Turner) Martius****Figs 184-196****Basionym:** *Fucus griffithsiae* Turner.**Lectotype:** BM (Dixon & Irvine, 1977a).**Type locality:** Devon, England.**References:** Chemin, 1933; Gregory, 1934; Joly, 1965; Schotter, 1968; Cordeiro-Marino, 1978; Dixon & Irvine, 1977a; Schneider & Searles, 1991; Lewis & Womersley, 1994; Coppejans, 1995; Masuda *et al.*, 1996; Dawes & Mathieson, 2008.**Molecular vouchers:** GenBank accession numbers KJ168045, KJ168049, KJ179938.**Selected specimens:** 1) La Franca (43°23'39"N; 4°34'18"W), 6.x.2006, SANT-Algae 19747 (carpotetrasporangial plants); 2) Barizo (43°18'48"N; 8°52'27"W), 9.ix.2002, 5.iv.2004, SANT-Algae 24973; 3) Estorde (42°56'28"N; 9°13'04"), 11.iii.2005, SANT-Algae 23052; 4) Playa de Arnela (42°42'35"N; 9°00'47"W), 30.i.2006, SANT-Algae 24350 (carpotetrasporangial plants); 5) A Guarda (41°54'29"N; 8°52'36"W), 25.xi.2003, SANT-Algae 24588.*Vegetative and reproductive*

Thallus erect, usually forming tufts (Fig. 184) up to 6 cm high and covering rock surfaces that can exceed 1 m², consisting on dichotomously branched erect fronds attached to the substratum by a basal disc (Fig. 187). Thallus dark purplish brown to black in colour, with a rigid texture.

Erect fronds sometimes completely terete (Fig. 186), most commonly terete in the basal parts of the thallus and compressed or flattened in the upper parts, with the apices flattened and expanded (Figs 185, 188-189); 220-500 µm in diameter in terete parts and 500-600 µm broad in compressed portions, dichotomously branched up to 5 orders (Figs 185-186, 188-189). Structure multiaxial, consisting of inner medullary cells surrounded by radial rows of very small cortical cells ca. 2 µm in diameter in surface view (Figs 190-191).

Spermatangia unknown. Carpotetrasporangial outgrowths are usually formed near dichotomies (Fig. 189) and sometimes girdling entirely the branch; consisting of gonimoblast filaments that produce rows of carpotetrasporangia outwardly (Figs 192-193). Carpotetrasporangia ovoid, 17-30 × 7-13 µm; spores cruciately divided (Fig. 194).



Figs 184-194. *Gymnogongrus griffithsiae*. Vegetative and reproductive morphology. **184.** Turfts with the basal parts buried by sand. **185-186.** Habit consisting of pseudodichotomously branched axes. **187.** Basal disc. **188.** Apices of a thallus, flattened and expanded. **189.** Mid part of the thallus showing dichotomic branches and carpotetrasporangia outgrowths. **190.** Cortical cells in surface view. **191.** Cross section of the thallus showing the inner medullary cells surrounded by rows of small cortical cells. **192.** Cross section of a carpotetrasporangia outgrowth, showing the gonimoblast filaments surrounding the thallus. **193.** Cross section of a carpotetrasporangia outgrowth, showing the gonimoblast filaments that produce rows of carpotetrasporangia outwardly. **194.** Cruciate divided carpotetrasporangia. Scale bars: 2 mm in Figs 185, 188 and 189; 5 mm in Fig. 186; 200 μ m in Figs 187 and 192; 50 μ m in Figs 190 and 193; 100 μ m in Fig. 191; 30 μ m in Fig. 194.



Figs 195-196. Distribution of *Gymnogongrus griffithsiae*. **195.** Collections along the Atlantic Iberian Peninsula. **196.** World distribution: arrow – type locality.

Phenology

Plants occur throughout the year and they are probably perennial. Carpotetrasporangial outgrowths were commonly found (63% of the collections) year-round.

Habitat and distribution

Gymnogongrus griffithsiae is frequent in sand-covered rocks from the Atlantic Iberian Peninsula (Fig. 195). It is a common component of turfs dominated by other species typical from sand-covered rocks, such as *Rhodothamniella floridula*, *Polysiphonia caespitosa* (M.A.Pocock) Hollenberg or *Lophosiphonia reptabunda* (Shur) Kylin. More rarely it forms almost monospecific tufts. *Gymnogongrus griffithsiae* was found from the upper to the mid intertidal, in sites from sheltered to extremely wave-exposed. It has been reported from Europe, northern Africa, America and western Pacific (Fig. 196).

PLOCAMIALES**PLOCAMIACEAE**

Plocamium maggsiae G.W. Saunders *et* K.V. Lehmkuhl

Figs 197-209

Holotype: UNB.

Type locality: St. John's Point, Co. Down, Northern Ireland.

References: Saunders & Lehmkuhl, 2005.

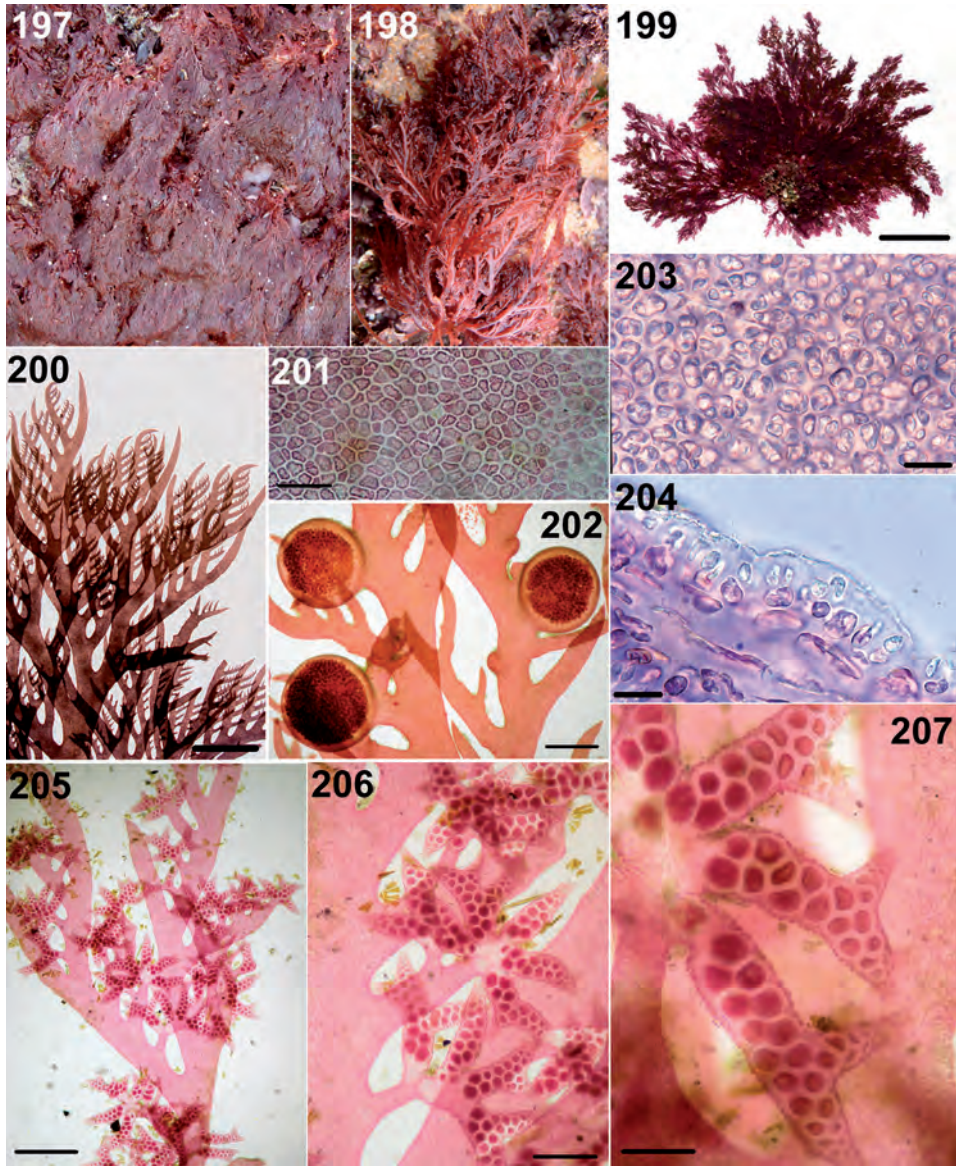
Molecular vouchers: GenBank accession numbers KJ179940, KJ179941, KJ179942, KJ179943, KJ179944.

Selected specimens: 1) Zumaia (43°17'59"N; 2°15'41"W), 30.iii.2006, SANT-Algae 19664 (male, female and tetrasporangial plants); 2) Laida (43°24'28"N; 2°40'54"W), 31.iii.2006, SANT-Algae 20288 (tetrasporangial plants); 3) Virgen del Mar (43°28'40"N; 3°52'31"W), 7.xi.2010, SANT-Algae 24654 (tetrasporangial plants); 4) Aguilar (43°33'28"N; 6°07'07"W), 17.iv.2007, SANT-Algae 19817 (tetrasporangial plants); 5) Linorsa (43°41'56"N; 7°27'14"W), 10.iii.2005, SANT-Algae 23115 (female and tetrasporangial plants); 6) Ártabra (43°21'12"N; 8°28'38"W), 9.iii.2005, SANT-Algae 17903 (female and tetrasporangial plants); 7) Nerga (42°15'19"N; 8°50'07"W), 12-ii-2005, SANT-Algae 22836 (female and tetrasporangial plants); 8) Leça de Palmeira (41°12'22"N; 8°43'03"W), 30.x.2004, SANT-Algae 16391 (female and tetrasporangial plants); 9) Olhos d'Água (37°05'20"N; 8°11'27"W), 20.ii.2011, SANT-Algae 26472 (tetrasporangial plants); 10) Caños de Meca (36°10'55"N; 6°00'06"W), 17.xi.2005, SANT-Algae 26149.

Vegetative and reproductive morphology

Thallus forming turfs up to 9 cm height and covering rock surfaces of up to several meters in extent, consisting of a prostrate system of entangled stolons that attach to substrate, from which arise numerous axes that are terete and narrow at their bases, up to 1 mm in diameter, and complanate at upper branches, up to 2 mm width (Figs 197-199). Thallus dark red to brownish red in colour, with a cartilaginous texture.

Erect fronds abundantly branched from the base, forming repeatedly alternate series of (4) 5-6 (10) ramuli in the axil of the dormant, which is usually long and narrow, up to 0.5 mm width (Fig. 200). Structure uniaxial, consisting on a medulla surrounded by 1-2 layers of cortical cells, which are polygonal in surface view, 5-15 × 11-18 µm (Fig. 201).



Figs 197-207. *Plocamium maggsiae*. Vegetative and reproductive morphology. **197-198.** Turfs in sand-covered rocks. **199.** Herbarium specimen showing the habit, which consists of a basal part of entangled axes bearing numerous erect axes. **200.** Branches of erect fronds, forming alternate series of ramuli in the axil of the dormant. **201.** Cortical cells in surface view. **202.** Cystocarps located in the thallus margins. **203.** Spermatangial sori in surface view. **204.** Cross section of a male sori showing the spermatangia. **205-207.** Furcated stichidia bearing numerous tetrasporangia. Scale bars: 3 cm in Fig. 199; 100 μ m in Figs 200 and 207; 50 μ m in Fig. 201; 500 μ m in Figs 202 and 205; 10 μ m in Fig. 203 and 204; 200 μ m in Fig. 206.



Figs 208-209. Distribution of *Plocamium maggsiae*. **208.** Collections along the Atlantic Iberian Peninsula. **209.** World distribution: arrow – type locality.

Gametophytes dioecious. Cystocarps formed on thallus margins, subglobose, 800-950 μm in diameter (Fig. 202). Spermatangia forming sori covering the surface of apical ramuli (Figs 203-204). Tetrasporangial stichidia with 3-5 furcations, mature ones sometimes branched up to 2 (-3) orders (Figs 205-207). Tetrasporangia subspherical, 37-75 μm broad, zonately divided.

Phenology

Plants occur throughout the year, and they are probably perennial. However, the abundance of the populations decreases in the summer, because large fronds were rarely collected in July-August. Cystocarps and tetrasporangia were frequently found (24% and 46% of the collections, respectively) throughout the year, except in July-August. Spermatangia were only observed twice (2%), in March and May, but most probably due to the fact that they are easily overlooked rather than due to an absence of these structures in our collections.

Habitat and distribution

Plocamium maggsiae is one of the most common and abundant species in sand-covered rocks along the Atlantic Iberian Peninsula (Fig. 208). It forms turfs sometimes covering rock surfaces of several meters in extent, and it is also a common component in turfs dominated by different species typical from sand-covered rocks. It is common from the mid to the low intertidal, in sites from sheltered to extremely wave-exposed. Until recently, *P. maggsiae* was only recorded from Ireland, the country of its type locality (Fig. 209).

Remarks

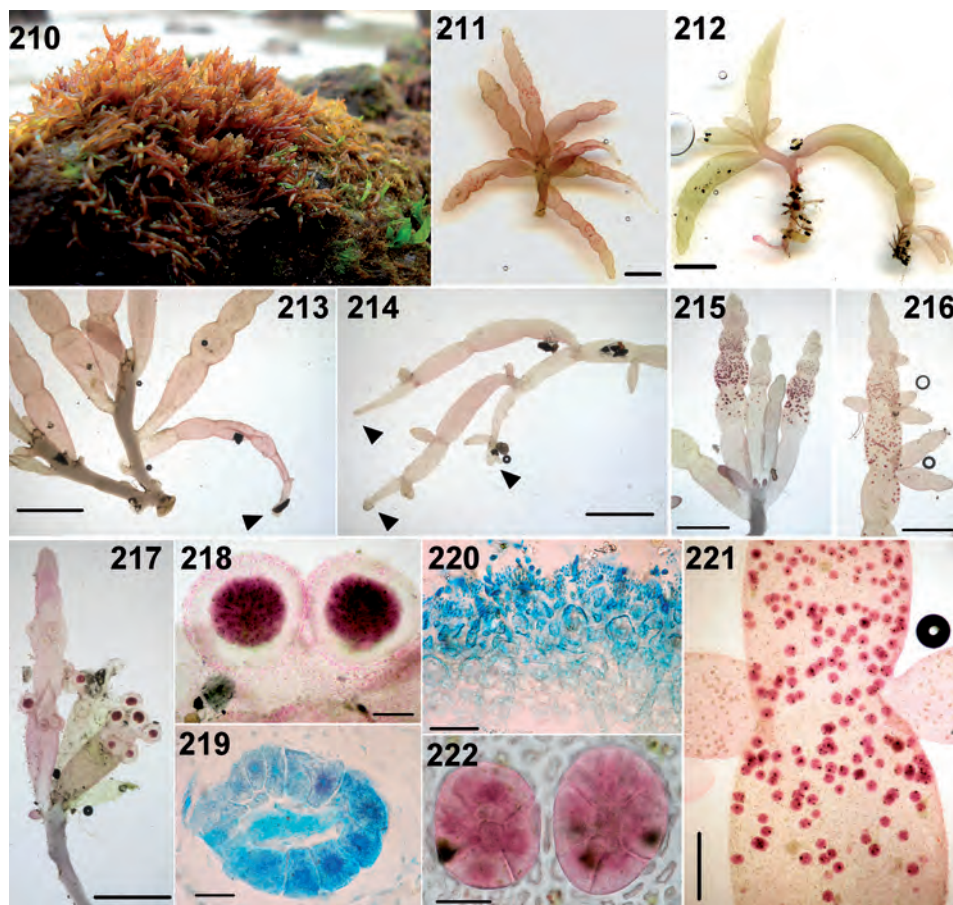
Plocamium maggsiae was recently segregated from *Plocamium cartilagineum* (Linnaeus) P.S.Dixon, after a study based on molecular data which showed an important cryptic diversity under the name of the last species (Saunders & Lehmkuhl, 2005). That is why the distribution of *P. maggsiae* is still restricted to Ireland, and this species has been not reported in the Iberian Peninsula yet. However, Cremades *et al.* (2011) suggested that its distribution may be wider in Europe, as our data support. Furthermore, despite reproductive structures are very common in *P. maggsiae* along the Atlantic Iberian Peninsula, they remained undescribed.

RHODYMENIALES

CHAMPIACEAE

Gastroclonium reflexum (Chauvin) Kützing

Figs 210-224

Basionym: *Lomentaria reflexa* Chauvin.**Lectotype:** CN (Irvine & Guiry, 1983).**Lectotype locality:** Port-en-Bessin, France.**Synonym:** *Chylocladia reflexa* (Chauvin) Zanardini.

Figs 210-222. *Gastroclonium reflexum*: Vegetative and reproductive morphology. **210.** Turf. **211-212.** Habit consisting of a basal disc, bearing a stipe from which arise reflexed branches with a beaded appearance. **213.** Basal part of thallus showing the stipe and a reflexed branch forming a new attachment discs (arrowhead). **214.** Branches forming new attachment discs at the apices (arrowheads). **215-216.** Polysporangial branches simple (215) or with secondary branches (216). **217.** Plant bearing external cystocarps. **218.** Cystocarps. **219.** Cross section of a cystocarp, showing the gonimocarp. **220.** Cross section of a male sorus. **221-222.** Polysporangia. Figs 219 and 220 specimens stained with aniline blue. Scale bars: 2 mm in Figs 211-217; 200 μ m in Fig. 218; 50 μ m in Figs 219, 220 and 222; 600 μ m in Fig. 221.



Figs 223-224. Distribution of *Gastroclonium reflexum*. **223**. Collections along the Atlantic Iberian Peninsula. **224**. World distribution: arrow – type locality.

References: Irvine & Guiry, 1983; Rull Lluch, 2002; Rull Lluch & Gómez Garreta, 2002.

Molecular vouchers: GenBank accession numbers KJ168046, KJ168048, KJ168050, KJ179926.

Selected specimens: 1) San Juan de Gaztelugatxe (43°26'41''N; 2°46'41''W), 29.iii.2006, SANT-Algae 20298; 2) Verdicio (43°37'30''N; 5°52'44''W), 19.iv.2007, SANT-Algae 19630 (male, female and polysporangial plants); 3) Estaño (43°32'52''N; 5°35'50''W), 18.iv.2007, SANT-Algae 19848 (polysporangial plants); 4) Aguilar (43°33'28''N; 6°07'07''W), 27.v.2010, SANT-Algae 24135; 5) Santa Comba (43°33'34''N; 8°15'30''W), 26.iv.2005, SANT-Algae 23103 (polysporangial plants); 6) Estorde (42°56'28''N; 9°13'04''), 11.iii.2005, SANT-Algae 23085.

Vegetative and reproductive morphology

Thallus forming turfs of up to 3 cm high and covering rocks surfaces that can exceed 1 m² in extent (Fig. 210), consisting of a holdfast bearing a short stipe from which arise a tuft of erect branches often reflexed and stolon-like (Figs 211-212). Thallus dark red to yellowish in colour, often with a greenish iridescence, with a mucilaginous and firm texture.

Holdfast discoid or irregularly branched, bearing a short solid stipe up to 6 mm long (Fig. 213). Branches terete, up to 15 mm long and 2.25 mm in diameter, hollow, constricted by septa giving a beaded appearance. They are simple, or bearing secondary short branches that are secund, pseudodichotomous or verticillate (Figs 211-212, 215-216). Reflexed branches often stolon-like and producing new attachment discs at their apices (Figs 212-214). Structure multiaxial; branches with medullary filaments longitudinally arranged along the branches, bearing secretory cells 8-15 µm in diameter; cortex 2-layered, with the outer layer often incomplete; stipe with a compact medulla and a cortex of smaller cells.

Gametophytes dioecious. Cystocarps external, clustered on branches, subspherical, up to 700 (-900) µm broad, without a definite ostiole (Figs 217-219). Spermatangia in superficial sori on the younger segments of branches (Fig. 220). Polysporangia subspherical, 67-110 µm in diameter (Figs 221-222), abundantly formed on branches (Figs 215-216).

Phenology

Gastroclonium reflexum was collected throughout the year and it is probably perennial. Both female structures and tetrasporangia were frequent and were observed in 14 and 32% of the collections, respectively. Male structures were

observed twice (4% of the collections), although they are probably common but easily could go unnoticed.

Habitat and distribution

Gastroclonium reflexum grows in sand-covered rocks along the Atlantic Iberian Peninsula, where it is a common species (Fig. 223). It forms dense turfs, mostly overgrowing turfs of *Rhodothamniella floridula*; although it is also a frequent component of turfs dominated by other species. It was collected from the low to the mid intertidal of sites from moderately to highly wave-exposed. *Gastroclonium reflexum* is distributed along the Atlantic and Mediterranean European coasts, as well as in the Canary and Salvaje Islands and southern Africa (Fig. 224).

PHAEOPHYCEAE SCYTOTHAMNALES

BACHELOTIACEAE

Bachelotia antillarum (Grunow) Gerloff

Figs 225-231

Basionym: *Ectocarpus antillarum* Grunow.

Type: W (?) (Womersley 1987).

Type locality: Guadeloupe, Caribbean.

References: Cardinal, 1964; Womersley, 1987.

Molecular vouchers: no available COI-5P data.

Selected specimens: 1) Armação de Pêra (37°06'04"N; 8°22'17"W), 17.10.2005, SANT-Algae 24842; 2) Olhos d'Água (37°05'20"N; 8°11'27"W), 6.v.2005, SANT-Algae 26200; 3) Punta Paloma, (36°03'44"N; 5°43'31"W), 18.xi.2005; SANT-Algae 26155.

Vegetative morphology

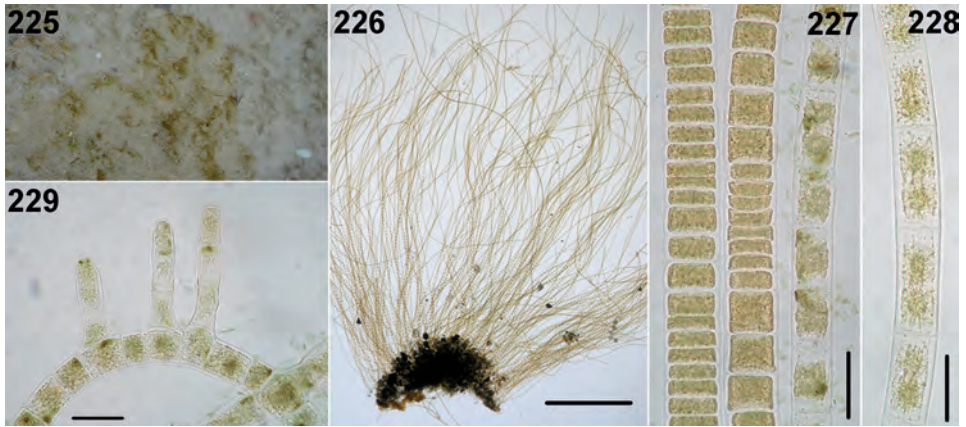
Thallus forming dense turfs up to 1 cm high (Fig. 225), consisting of a basis formed by entangled filaments attached by rhizoids, from which arise the erect filaments (Fig. 226). Erect filaments of similar diameter throughout, 30-40 µm, unbranched or only sparsely branched, sometimes forming clusters of short branches (Fig. 229). Growth diffuse, with prominent meristematic regions scattered through the lower parts of filaments (Fig. 227). Mature cells with 1-2 stellate phaeoplasts (Fig. 228).

Phenology

Bachelotia antillarum was collected in February and October-November. Sporangia were not found.

Habitat and distribution

Bachelotia antillarum was collected in this study only from sites of the southern Atlantic Iberian Peninsula (Fig. 230), where it was found forming almost monospecific turfs in the mid intertidal of sand-covered rocks. However, it was also recorded in other areas from the Atlantic Iberian Peninsula such as Portugal, the Cantabrian and Galicia (e.g. Ardré, 1970; Gorostiaga *et al.*, 2004; Bárbara *et al.*, 2005). *Bachelotia antillarum* was widely reported in world temperate coasts (Fig. 231).



Figs 225-229. *Bachelotia antillarum*. Vegetative morphology. **225**. Turf in sand-covered rocks. **226**. Habit showing a basal layer of entangled filaments from which arise the erect ones. **227**. Filaments with meristematic regions (short cells) between mature cells. **228**. Cells with two stellate phaeoplasts. **229**. Filament forming clusters of short branchlets. Scale bars: 2 mm in Fig. 226; 50 μ m in Figs 227-229.



Figs 230-231. Distribution of *Bachelotia antillarum*. **230**. Collections along the Atlantic Iberian Peninsula. **231**. World distribution: arrow – type locality.

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