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Seaweeds from sand-covered rocks of the Atlantic Iberian Peninsula.
Part 1. The Rhodomelaceae (Ceramiales, Rhodophyta)

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Abstract – Sand-covered rocks provide a particular habitat to benthic seaweeds, which must tolerate the stressful conditions imposed by the presence of sediments. Turf assemblages are dominant in this habitat, which is widely distributed along the Atlantic Iberian Peninsula, neverthelss their flora remained poorly known. This work presents a taxonomic, floristic and chorological account of the most representative Rhodomelaceae from sand-covered rocks along the Atlantic Iberian Peninsula. For each species we provided morphological descriptions, distribution maps, and/or COI-5P sequences, as well as taxonomic notes. The species studied are: *Chondria coerulescens, Ctenosiphonia hypnoides, Herposiphonia cf. secunda f. tenella, Leptosiphonia schousboei, Lophosiphonia reptabunda, L. simplicissima sp. nov., Ophidocladus simpliciusculus, Polysiphonia caespitosa, P. devoniensis, P. foetidissima, P. fucoides, P. nigra, P. stricta, P. tripinnata, Pterosiphonia ardreana, P. parasitica, P. pennata* and *Streblocladia collabens*. Among our taxonomical conclusions, we herein proposed a novel species *Lophosiphonia simplicissima* as well as the transfer of *Streblocladia collabens* to the genus *Neosiphonia*: Furthermore, the parasitic species *Aiolocolax pulchellus* is described and its taxonomic position is discussed.

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

INTRODUCTION

Sand-covered rocks provide for benthic seaweeds a habitat with environmental conditions different to those from purely rocky shores. The sand, together with the wave motion action, causes the scour, abrasion and burial of benthic organisms (Devinny & Volse, 1978; Littler *et al.*, 1983; Kendrick, 1991; Eriksson & Johansson, 2005). These stressful conditions greatly influence the seaweeds assemblages, and sand-covered rocks often include typical species that are seldom found over rocky shores. This peculiarity of sand-covered habitats has been reported worldwide (e.g. Ardré, 1970; Abbott & Hollenberg, 1976; Maggs & Hommersand, 1993; Bárbara, 1994; Stegenga *et al.*, 1997; Womersley, 2003). Despite, this habitat is common and widely represented along the Atlantic Iberian Peninsula, previous works about the flora and vegetation from Spain and Portugal only briefly reported some species from this peculiar environment (Miranda, 1931; Ardré, 1970; Pérez-Cirera, 1976, 1980; Pérez-Cirera & Maldonado, 1982; Pérez-Cirera & Pacheco, 1985; Bárbara *et al.*, 1992, 1995; Bárbara, 1994; Díaz Tapia & Bárbara, 2004, 2005 a, b; Díaz *et al.*, 2009).

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Two morphological traits have been identified as advantageous in perennial macroalgae from sand-influenced habitats: algal turfs (Hay, 1981; Kendrick, 1991; Airoldi, 1998) and canopy species which are very tough (Daly & Mathieson, 1977; Littler *et al.*, 1983). Turf-forming species accounts for most of the diversity in this habitat along the Atlantic Iberian Peninsula (Díaz-Tapia *et al.*, 2011; Díaz-Tapia *et al.*, 2013b). Algal turfs are a diverse miscellanea of organisms formed by species of red, brown and green algae, the reds being the most commons (Price & Scott, 1992; Rindi & Cinelli, 2000; Wallenstein *et al.*, 2009). In most cases, turf-forming species from sand-covered rocks share common outline morphology. This often consists of extensive system of prostrate axes attached to the substrate by means of rhizoids and from which grow erect axes bearing, if present, reproductive structures. The Rhodomelaceae are, among the most frequent and abundant taxa encountered in this habitat and the genus *Polysiphonia sensu lato* is very well represented. This genus is among the largest within the Rhodophyta, and currently contains almost 200 recognized species (Guiry & Guiry, 2013). Probably, all these characteristics of the flora from sand-covered rocks contributed to the fact that a great number of taxa from this habitat remain poorly known, even those that are frequent and abundant along the Atlantic Iberian Peninsula.

With the aim of filling the gap in the phycological knowledge of sand-covered rocks we performed this study, which provides morphological descriptions and COI-5P sequences of the most abundant and frequent Rhodomelacean taxa forming algal turfs over sand-covered rocks along the Atlantic Iberian Peninsula, as well as of a small parasitic algae of uncertain taxonomic position. This includes a total of 19 species, of which one is newly described.

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, between 2002-2012. Furthermore, the upper subtidal of some localities was also studied, as well as some samples were also collected in 50 additional sites, one of them in southern France.

Material collected for morphological studies was preserved in 4% formalin in seawater at 4ºC and stored in the dark. Microscope slides were mounted in a mixture of 20% Karo® Syrup (ACH Foods, Memphis, Tennessee, USA) and 80% distilled water. Some specimens were previously stained with aniline blue, while others were mounted in a mixture of 1% aniline blue, 1% acetic acid, 50% Karo® Syrup and 48% distilled water (Millar & Wynne, 1992). Sections for microscopic observations were made by hand using a razor blade. Photographs were taken using an Olympus C-5060 digital camera mounted on an Olympus BX50 (Tokyo, Japan) microscope. Representative specimens were deposited in the herbaria of the Universidade de Santiago de Compostela (SANT). Herbarium abbreviations follow the online *Index Herbariorum* <http://sweetgum.nybg.org/ih/>. The distribution maps of the species along the Atlantic Iberian Peninsula were made using data of specimens generated in this study and housed in SANT. World maps showing the distribution of the species were based on available data in Guiry & Guiry (2013).

Material collected for molecular analysis was dried in silica gel and total genomic DNA was extracted from a fragment of about 1 mg of dried thalli, which was frozen in liquid nitrogen and individually ground into a fine powder using disposable steel beads and a Mini-Bead Beater (Biospec Products, Bartlesville, OK, USA). Immediately afterwards, total DNA was extracted using the Wizard Magnetic 96 DNA Plant System (Promega, USA) kit following the manufacturer's instructions. The extracted DNA was stored at –20ºC.

The mitochondrial marker cytochrome oxidase subunit 1 (COI-5P) was amplified using the pairs of primers GazF1 and GazR1, GWSFn and COX1R1 (Saunders, 2005; Saunders, 2008; Le Gall & Saunders, 2010). All PCR amplifications were carried out with a TProffesional Basic thermocycler (Biometra, Germany) using a Taq reaction kit (Sigma Aldrich, USA): a total volume of 25 µL containing 1 × Buffer, 2mM $MgCl_2$, 1nM dNTP mixture, 0.15 mM of each primer, 1 unit of Taq and 1 µL of DNA solution (*rbc*L and/or SSU); and 1× Buffer, 2.5mM MgCl2, 0.192mM dNTP mixture, 0.1mM of each primer, 1 unit of Taq and 2 µL of DNA solution (COI-5P). PCR was performed with an initial denaturation step at 94ºC for 10 min, followed by 35 cycles of 30 s at 90ºC, 30s at 50ºC, and 2 min at 72ºC, with a final 10 min extension cycle at 72ºC.

PCR products were purified using a Cycle Pure kit E.Z.N.A. (Omega Bio-Tek, USA). After removing the excess of primers and nucleotides, fragments were sequenced on an ABI Prism 3730xl DNA Analyzer™ (Perkin-Elmer, USA) using BigDye™ Terminator kit according to manufacturer's recommendations. Sequences were checked, edited, and aligned with CodonCode Aligner software (CodonCode Co., USA) or Geneious R6 6.0.3 (Biomatters Ltd., New Zealand).

Sequences were obtained for both DNA strands and assembled, corrected and aligned, sometimes together with sequences downloaded from GenBank, using Geneious Pro 5.6.4 (Biomatters Ltd., Auckland, New Zealand). Collection information and GenBank accession numbers for sequences generated in this study are provided in Table 1. Despite our efforts, COI-5P sequences could not be obtained for 3 of the 19 species studied in this work. Sequences comparisons were conducted using uncorrected-p distance and the distance analyses were performed using the neighbor-joining. Bootstrap resampling (1000 replicates) was performed to estimate robustness (Felsenstein, 1985).

RESULTS AND DISCUSSION

Chondria coerulescens (J. Agardh) Falkenberg **Figs 1-20**

Basionym : *Chondriopsis coerulescens* J. Agardh.

Lectotype: LD, "Algues Marines du Finistère", nº 282 (Dixon 1962).

Type locality: Brest, France.

Synonym: *Laurencia coerulescens* P.L. Crouan *et* H.M. Crouan.

References: Maggs & Hommersand, 1993.

Molecular voucher: GenBank accession number KF671147.

Selected specimens: 1) San Juan de Gaztelougatxe (43°26'41"N; 2°46'41"W), 8.ix.2010, SANT-Algae 18931 (tetrasporangial plants); 2) Verdicio (43°37'30"N; 5°52'44"W), 19.iv.2007, SANT-Algae 19615 (male plants); 3) Chanteiro (43°26'46"N; 8°18'15"W), 17.ix.2005, SANT-Algae 19600; 4) San Pedro (43°22'45"N; 8°26'47"W), 22.vii.2004, SANT-Algae 24891; 5) Santa Mariña (43°11'38"N; 9°07'59"W), 23.viii.2005, SANT-Algae 22680; 6) Estorde (42°56'28"N; 9°13'04"), 11.iii.2005, SANT-Algae 23083. 7) Buarcos (37°39'54"N; 8°48'04"W), 13.xi.2004, SANT-Algae 16600 (male, female and tetrasporangial plants).

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

Species	*Herbarium code; collection site, date and collectors[1] / Reference*	*Genbank*
Aiolocolax pullchellus	SANT-Algae 24480; Llas, Lugo, Spain, 14.07.10, PD.	KF671160
Chondria coerulescens	SANT-Algae 24340; Sarello, Asturias, Spain, 28.07.10, PD.	KF671147
Ctenosiphonia hypnoides	SANT-Algae 24410; Cegoñas, Lugo, Spain, 15.07.10, PD & IB.	KF671182
	SANT-Algae 24156; Niembro, Asturias, Spain, 28.05.10, PD & IB.	KF671184
	SANT-Algae 24104; Riomar, Lugo, Spain, 29.03.10, PD.	KF671185
Herposiphonia cf. *secunda* f. *tenella*	SANT-Algae 25620; La Franca, Asturias, Spain, 23.03.11, PD & IB.	KF648513
	SANT-Algae 26526; Punta Plata, Cádiz, Spain, 19.01.11, PD & IB.	KF648516
	SANT-Algae 25480; Ingrina, Algarve, Portugal, 20.02.11, PD & IB.	KF648522
	SANT-Algae 24646; Virgen del Mar, Cantabria, Spain, 07.11.10, PD.	KF671171
	SANT-Algae 24150; Niembro, Asturias, Spain, 28.05.10, PD.	KF671173
	SANT-Algae 24249; Baleal, Estremadura, Portugal, 14.06.10, PD & IB.	KF671179
Leptosiphonia schousboei	SANT-Algae 27303; Peinzás, Lugo, Spain, 25.01.12, PD & IB.	KF648525
	SANT-Algae 24208; Leira, A Coruña, Spain, 25.06.10, PD & IB.	KF671153
	SANT-Algae 24228; Leça, Douro Litoral, Portugal, 11.06.10, PD & IB.	KF671165
	SANT-Algae 24092; Barizo, A Coruña, Spain, 26.07.10, IB.	KF671170
	SANT-Algae 24149; Niembro, Asturias, Spain, 28.05.10, PD & IB.	KF671176
Lophosiphonia reptabunda	SANT-Algae 25139; Zumaia, Guipúzcoa, Spain, 18.03.11, PD & IB.	KF648511
	SANT-Algae 27306; Peinzás, Lugo, Spain, 25.01.12, PD & IB.	KF648519
Ophidocladus simpliciusculus	SANT-Algae 26249; Peinzás, Lugo, Spain, 19.04.11, PD, AS & VP	KF648512
	SANT-Algae 26460; Olhos d´Agua, Algarve, Portugal, 20.02.11, PD & IB.	KF648518
	SANT-Algae 25413; Biarritz, France, 19.03.11, PD & IB.	KF648520
	SANT-Algae 24417; Bares, Lugo, Spain, 13.07.10, PD & IB.	KF671146
	SANT-Algae 24473; Llas, Lugo, Spain, 14.07.10, PD.	KF671148
	SANT-Algae 24445; Valdearenas, Cantabria, Spain, 11.08.10, IB.	KF671150
	SANT-Algae 24422; Catedrales, Lugo, Spain, 15.07.10, PD & IB.	KF671156
	SANT-Algae 24205; Leira, A Coruña, Spain, 25.06.10, PD & IB.	KF671162
	SANT-Algae 24438; Picón, A Coruña, Spain, 12.07.10, PD & IB.	KF671168
	SANT-Algae 24254; Baleal, Estremadura, Portugal, 14.06.10, PD & IB.	KF671169
	SANT-Algae 24333; Sarello, Asturias, Spain, 28.07.10, PD.	KF671180
	SANT-Algae 24619; Langre, Cantabria, Spain, 06.11.10, PD.	KF671183
Polysiphonia caespitosa	SANT-Algae 25144; Zumaia, Guipúzcoa, Spain, 18.03.11, PD & IB.	KF648509
	SANT-Algae 24676; Almograve, Baixo Alentejo, Portugal, 22.02.11, PD & IB.	KF648510
	SANT-Algae 24158; Niembro, Asturias, Spain, 28.05.10, PD & IB.	KF671152
	SANT-Algae 24257; Baleal, Estremadura, Portugal, 14.06.10, PD & IB.	KF671159
	SANT-Algae 24479; Llas, Lugo, Spain, 14.07.10, PD.	KF671161
	SANT-Algae 24343; Sarello, Asturias, Spain, 28.07.10, PD.	KF671163
	SANT-Algae 24212; Guincho, Estremadura, Portugal, 13.06.10, PD & IB.	KF671166
	SANT-Algae 24435; Picón, A Coruña, Spain, 12.07.10, PD & IB.	KF671175
	SANT-Algae 24214; Buarcos, Beira Litoral, Portugal, 11.06.10, PD & IB.	KF671177
	SANT-Algae 24413; Bares, Lugo, Spain, 13.07.10, PD & IB.	KF671178
	SANT-Algae 24420; Catedrales, Lugo, Spain, 15.07.10, PD & IB.	KF671181

Table 1. Sequences of species generated in this study and GenBank accession numbers *(continued)*

Species	*Herbarium code; collection site, date and collectors[1] / Reference*	*Genbank*
Polysiphonia devoniensis	SANT-Algae 24647; Virgen del Mar, Cantabria, Spain, 07.11.10, PD.	KF671149
	SANT-Algae 24630; Langre, Cantabria, Spain, 06.11.10, PD.	KF671186
Polysiphonia nigra	Díaz Tapia *et al.*, 2013a	KC130868
Polysiphonia stricta	SANT-Algae 25613; La Franca, Asturias, Spain, 23.03.11, PD & IB.	KF648514
	SANT-Algae 26261; Montedor, Minho, Portugal, 18.04.11, VP & AS.	KF648515
	SANT-Algae 26186; Arnela, A Coruña, Spain, 18.04.11, PD & IB.	KF648521
Polysiphonia tripinnata	Díaz Tapia *et al.*, 2013a	KC130870
	Díaz Tapia *et al.*, 2013a	KC130871
Pterosiphonia ardreana	SANT-Algae 25132; Zumaia, Guipúzcoa, Spain, 18.03.11, PD & IB.	KF648517
	SANT-Algae 25640; La Arena, Vizcaya, Spain, 22.03.10, PD & IB.	KF648523
	SANT-Algae 24617; Langre, Cantabria, Spain, 06.11.10, PD.	KF671167
	SANT-Algae 24423; Catedrales, Lugo, Spain, 15.07.10, PD & IB.	KF671174
Pterosiphona parasitica	SANT-Algae 25631; La Arena, Vizcaya, Spain, 22.03.10, PD & IB.	KF648524
Pterosiphonia pennata	SANT-Algae 24615; Langre, Cantabria, Spain, 06.11.10, PD.	KF671154
	SANT-Algae 24342; Sarello, Asturias, Spain, 28.07.10, PD.	KF671155
	SANT-Algae 24476; Llas, Lugo, Spain, 14.07.10, PD.	KF671157
	SANT-Algae 24328; Catedrales, Lugo, Spain, 26.07.10, PD & IB.	KF671164
	SANT-Algae 24618; Langre, Cantabria, Spain, 06.11.10, PD.	KF671172
Streblocladia collabens	SANT-Algae 24227; Leça, Douro Litoral, Portugal, 11.06.10, PD & IB.	KF671151
	SANT-Algae 24251; Baleal, Estremadura, Portugal, 14.06.10, PD & IB.	KF671158

1. Collectors initials: PD, Pilar Díaz-Tapia; IB, Ignacio Bárbara; AS, Antonio Secilla; VP, Viviana Peña.

Vegetative and reproductive morphology

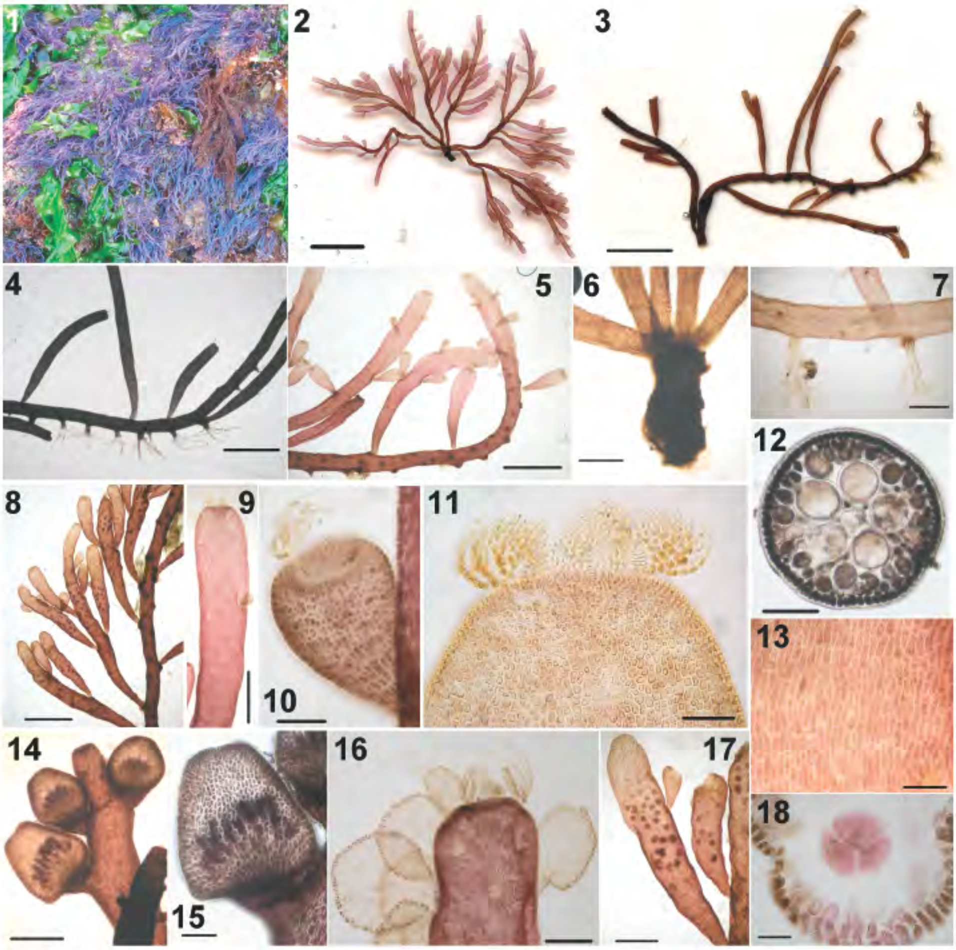
Thalli erect (Fig. 2) or decumbent (Fig. 3), forming turfs up to 5 cm high (Fig. 1), consisting of a discoid holdfast bearing tufted erect axes, some of which curving downwards and reattach by secondary holdfasts that form stolon-like outgrowths (Figs 2-7). Plants dark red in colour with a turquoise iridescence when alive (Fig. 1), flexible and cartilaginous in texture.

Erect axes terete, 400-630 μm in diameter, sparsely branched at irregular intervals in a spiral pattern, branches markedly constricted basally (Figs 8, 9). Apices of erect axes obtuse, ending in a circular depression that sometimes has trichoblasts (Figs 10, 11). Axes consisting of a rounded axial cell and 5 pericentral cells, surrounded by 1-2 layers of subcortical cells and a layer of cortical cells (Fig. 12), which are elongate in surface view (Fig. 13).

Cystocarps subglobular, 650-820 μm in diameter (Figs 14, 15). Spermatangial plates ular, formed on apices of young axes, 350-550 μm in diameter (Fig. 16). Tetrasporangia 135-160 μm in diameter (Figs 17, 18).

Phenology

Chondria coerulescens was collected throughout the year and it is probably perennial. Reproductive structures were rarely found. Tetrasporangia were observed in 10% of the collections, which were carried out in January-February, May-July and September-November. Female structures were only found twice (4%), in May and November; and male ones were found in four collections (7%) in April-June and November.



Figs 1-18. *Chondria coerulescens*. Vegetative and reproductive morphology. **1.** Turf showing the turquoise iridescence. **2-3.** Habit of erect (1) and decumbent (2) plants. **4-5.** Decumbent axes with secondary holdfasts. **6.** Primary holdfast. **7.** Secondary holdfasts. **8.** Erect axes spirally branched. **9.** Apex of erect axes. **10.** Young lateral branch with trichoblasts growing from an apical depression. **11.** Trichoblasts growing at the apex of an axis. **12.** Cross section of an erect axis with an axial cell, 5 pericentral cells, 1-2 layers of subcortical cells and 1 layer of cortical cells. **13.** Cortical cells in surface view. **14-15.** Cystocarps. **16.** Spermatangial plates circular. **17.** Tetrasporangia on young branches. **18.** Cross section of thallus with a tetrasporangium. Scale bars: 5 mm in Figs 2 and 3; 2 mm in Figs 4, 5 and 8; 600 µm in Figs 6, 7, 9, 14 and 17; 100 µm in Figs 10-13; 200 µm in Figs 15 and 16; 50 µm in Fig. 18.

Habitat and distribution

Chondria coerulescens is a common species of the flora from sand-covered rocks along the Atlantic Iberian Peninsula (Fig. 19). It forms dense turfs, mostly overgrowing the turfs of *Rhodothamniella floridula*; and it is also frequent in turfs dominated by other species. It was collected from the low to the mid intertidal of sites from moderately to highly wave-exposed. *Chondria coerulescens* is distributed in southern Europe and northern Africa (Fig. 20).

Figs 19-20. Distribution of *Chondria coerulescens*. **19.** Collections along the Atlantic Iberian Peninsula. **20.** World distribution: arrow - type locality.

Ctenosiphonia hypnoides (Welwitsch *ex* J.Agardh) Falkenberg *in* Schmitz *et* Falkenberg **Figs 21-43**

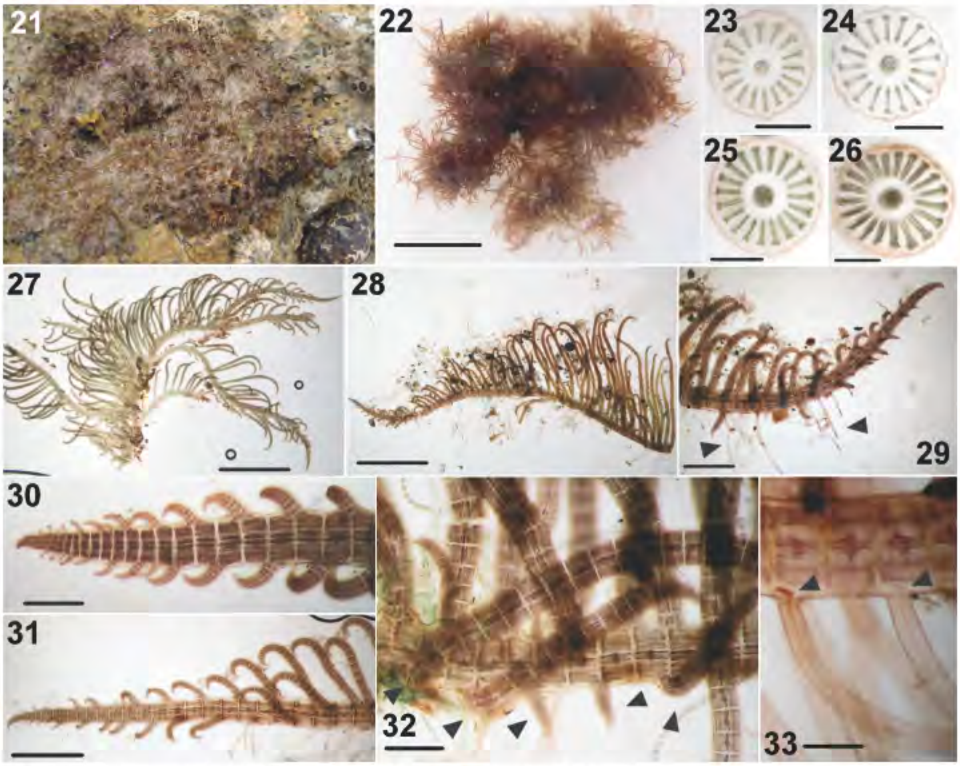
Basionym: *Polysiphonia hypnoides* Welwitsch *ex* J.Agardh.
Holotype: LD, Agardh herbarium n° 39346 (Phycotheca Lusitana n° 292).
Type locality: Arrábida, Portugal.
References: Bornet & Thuret, 1876; Dixon, 1962; Falkenberg, 1901; Rojas-González & Afonso-Carrillo, 2000, 2001a.
Molecular vouchers: GenBank accession numbers KF671182, KF671184, KF671185.

Selected specimens: 1) Niembro (43°26’33”N, 4°50’20”W), 28.v.2010, SANT-Algae 24156 (tetrasporangial plants); 2) Cegoñas (43°33’18”N; 7°07’28”W), 17.x.2004, SANT-Algae 15812; 15.vii.2010, SANT-Algae 24410; 3) Peinzás (43°35’09”N; 7°16’13”W), 1.iii.2002, SANT-Algae 14476; 19.ii.2003, SANT-Algae 17982; 9.ii.2011, SANT-Algae 26002; 4) Riomar (43°37’31”N; 7°19’24”W), 18.x.2004, SANT-Algae 15824; 29.iii.2010, SANT-Algae 24104; 5) Cala Encendida (36°18’40”N; 6°09’12”W), 18.ii.2011, SANT-Algae 26639.

Vegetative and reproductive morphology

Thalli forming dense turfs up to 1 cm high and covering rock surfaces of *ca* 400 cm^2 in extent (Figs 21, 22), often mixed with *Lophosiphonia reptabunda*. Thalli dorsiventral, consisting of an extensive system of indeterminate and interwoven prostrate axes which bears rhizoids ventrally that attach to the substrate, produces dorsally endogenous determinate erect axes on every segment, and branches laterally at irregular intervals to form further prostrate axes (Figs 27-29). Erect axes unbranched or scarcely branched; unilaterally, at irregular intervals. Turfs dark brown in colour, with whitish tufts if trichoblasts are well developed; axes dark brown, with a fairly rigid texture.

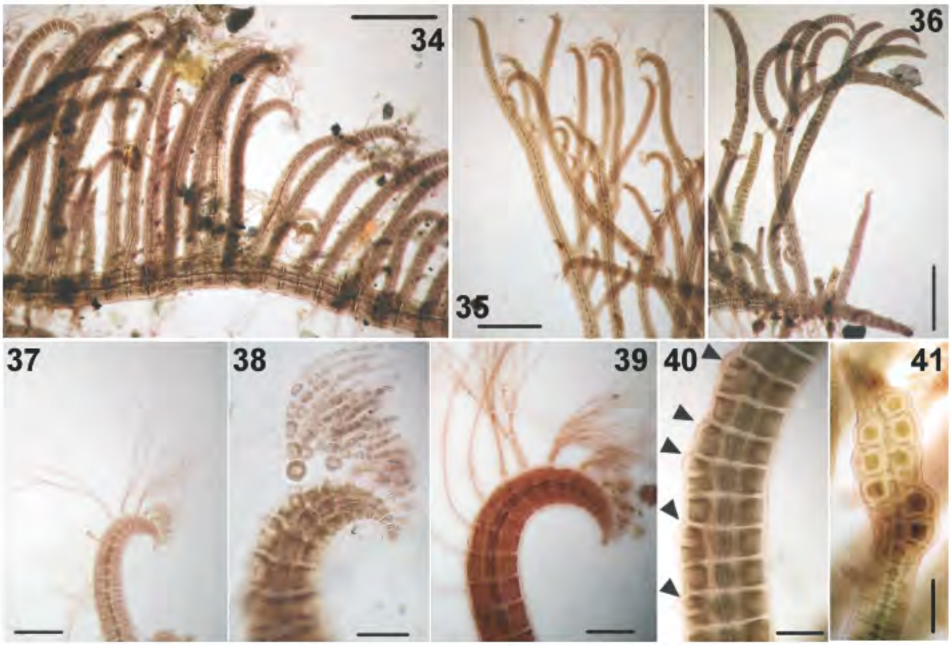
Axes fully ecorticate, consisting of a small axial cell and (15-) 16-19 (-20) pericentral cells (Figs 23-26). Prostrate axes indeterminate and dorsiventral, growing by transverse divisions of large and conspicuous apical cells *ca* 25 µm in diameter; slightly curved downwards at tips, lacking trichoblasts and their scar cells (Fig. 30). Prostrate axes (130-) 160-250 (-280) µm in diameter; composed of segments wider than long, L/D (0.4-) 0.5-0.8 (-1). Prostrate axes endogenously branched in their dorsal side to form erect axes, mostly bearing a branch on every segment, but sometimes each segment bears two branches or none. Branches are mostly arranged in two alternate rows (Figs 30, 31), which are displaced *ca* 6 pericentral cells between successive segments, although sometimes two successive segments are bearing branches in the same flank of the prostrate axes. Branches



Figs 21-33. *Ctenosiphonia hypnoides*. Habit and prostrate axes. **21.** Turf in the mid intertidal. **22.** Turf formed by interwoven prostrate and erect axes. **23-26.** Cross sections of axes with 16 (23), 17 (24), 19 (25) and 20 (26) pericentral cells. **27-28.** Habit consisting of prostrate axes that dorsally produce erect axes (27-28) and laterally form new prostrate axes (27). **29.** Apex of a prostrate axis forming dorsally two tiers of determinate erect axes and ventrally rhizoids: arrowheads - rhizoids. **30-31.** Apex of prostrate axes curved downward and ending in a conspicuous apical cell; producing alternate branches on every segment to form two tiers of erect axes, branches are firstly laterally oriented (30-31) and later they become erect (31). **32.** Old prostrate axis: arrowheads - further prostrate axes formed adventitiously. **33.** Rhizoids cut off from pericentral cells: arrowheads - walls separating the pericentral cells and the rhizoids. Scale bars: 1 cm in Fig. 22; 50 µm in Figs 23-26; 2 mm in Figs 27 and 28; 600 µm in Figs 29 and 31; 200 µm in Figs 30 and 32; 100 µm in Fig. 33.

are firstly laterally oriented and they are curved towards the apex of prostrate axes (Figs 30, 31), and later, at some distance from the apex, branches become erect (Figs 29, 31). Prostrate axes occasionally with adventitious endogenous lateral branches borning at irregular intervals, developing further prostrate axes (Fig. 32). Rhizoids scattered to densely formed in the ventral side of prostrate axes, cut off from pericentral cells (Fig. 33), unicellular, 1-2 (-3) per segment, (20) 30-50 (-60) µm in diameter and up to 1350 µm long, often terminated in digitate haptera.

Erect axes growing from domed apical cells *ca* 23 µm in diameter (Fig. 38). Apices of erect axes curved in the direction to the tip of prostrate axes (Figs 27-29, 34). Erect axes (90-) 100-150 (-170) µm in diameter, composed of segments L/D (0.3) 0.4-0.7 (-1). They are usually unbranched (Fig. 34), but



Figs 34-41. *Ctenosiphonia hypnoides*. Erect axes and tetrasporangia. **34.** Unbranched erect axes. **35-36.** Erect axes with unilateral branches, bearing trichoblasts at their apices, which are sometimes long (35). **37-39.** Apex of erect axes with trichoblasts unilaterally arranged, wich are short near the apices, and sometimes later enlarged (37, 39). **40.** Erect axes: arrowheads - scar cells of trichoblasts. **41.** Erect axes bearing two tetrasporangia per segment. Scale bars: 600 µm in Figs 34-36; 200 µm in Fig. 37; 50 µm in Figs 38 and 40; 100 µm in Figs 39 and 41.

Figs 42-43. Distribution of *Ctenosiphonia hypnoides*. **42.** Collections along the Atlantic Iberian Peninsula. **43.** World distribution: arrow - type locality.

sometimes endogenous branches are formed far from the apex, scattered or in groups unilaterally arranged, with a single branching order (Figs 35, 36). Trichoblasts usually well developed in most of the erect axes, they are rapidly formed in erect axes (Fig. 31), mostly growing on every segment, unilaterally inserted on the convex side of curved apices (Figs 37-39), but sometimes are absent. Young trichoblasts are short (Fig. 38); and later, their cells lengthen, becoming often large, up to 10 mm in length, and with basal cells up to 45 µm in diameter (Figs 37, 39). Thrichoblasts dichotomously branched up to 5 orders, deciduous and leaving conspicuous scar cells (Fig. 40).

Gametophytes not found. Tetrasporangia in upper parts of erect axes, in 2 longitudinal opposite rows (Fig. 41); ovate, *ca* 30-65 µm in diameter, with 2 cover cells similar to pericentral cells.

Phenology

Plants occur throughout the year, and they are probably perennial. Sexual reproductive structures were never found in the Atlantic Iberian Peninsula, and only immature tetrasporangia were once observed in materials collected in May (Niembro, northern Spain).

Habitat and distribution

Ctenosiphonia hypnoides forms extensive turfs almost monospecific or often mixed with *Lophosiphonia reptabunda*. They grow in the mid intertidal of rocky coves in sheltered to extremely wave-exposed coasts. Although these coves are not covered by sand, sedimentation is likely to occur, since turfs from this habitat usually trap sediments.

Ctenosiphonia hypnoides is a rare species along the Atlantic Iberian Peninsula (Fig. 42). We have found three close populations in the northern coast of Galicia, one in Asturias (northern Iberian Peninsula) and one in Cádiz (southern Iberian Peninsula). The world distribution of *C. hypnoides* is restricted to southern Europe, northern Africa and the Macaronesian (Fig. 43).

Remarks

Polysiphonia hypnoides has been originally described based on materials collected by Welwitsch (Agardh, 1863) from Portinho da Arrábida, Portugal in 1951. Subsequently, Falkenberg segregated the species from *Polysiphonia*, creating the monospecific new genus *Ctenosiphonia* (Schmitz & Falkenberg, 1897). *Ctenosiphonia hypnoides* was mostly recorded from the southern France to Morocco, including some of the Macaronesian Islands (e.g. Rojas-González & Afonso-Carrillo, 2001a; Bárbara *et al.*, 2005; Araújo *et al.*, 2009). Curiously, it was also recorded in two locations from Brittany, which are Guernsey (Channel Islands, UK) and Batz (French Brittany) (Ardré *et al.*, 1982). The occurrence of *C. hypnoides* within its distribution range is probably more common than reported because it could be easily overlooked due to its small size. Some detailed descriptions of *C. hypnoides* have been previously provided from Morocco and the Canary Islands (Bornet & Thuret, 1876; Falkenberg, 1901; Rojas-González & Afonso-Carrillo, 2000, 2001a). However, detailed morphological descriptions of the species had not been previously provided for materials from the Atlantic Iberian Peninsula, which is the type locality.

The genus *Ctenosiphonia* is distinctively characterized by its polysiphonous organisation with dorsiventral structure, its characteristic branching pattern of the prostrate axes and the formation of two tetrasporangia per segment (Schmitz & Falkenberg, 1897). The assignment of *Ctenosiphonia* to a tribe or group within the family Rhodomelaceae remains uncertain since Schmitz & Falkenberg (1897) proposed their classification of the Rhodomelaceae. It was firstly placed in the tribe Amansieae (Schmitz & Falkenberg, 1897) and subsequently, Falkenberg (1901) moved it together with *Ophidocladus*, *Lophosiphonia* and *Pleurostichidium* to an unnamed artificial group in which he placed those genera with a pronounced dorsiventral structure that do not meet the other defined groups (Falkenberg, 1901). Later, Kylin (1956) proposed the name *Lophosiphonia* group and he also added the genera *Falkenbergiella*, *Oligocladella* (as *Oligocladus*) and *Stichothamnion*, while he transferred the genus *Pleurostichidium* to the tribe Amansieae. Recent works did not clarify the taxonomic position of the *Lophosiphonia* group within the family Rhodomelaceae. Maggs & Hommersand (1993) amalgamated it with the tribe Herposiphonieae, as they included the genus *Lophosiphonia* in this tribe. However, the tribe Herposiphonieae is characterized by a particular branching pattern that consists of regular sequences of indeterminate and determinate exogenous laterals, differing from the *Lophosiphonia* group which is characterized by having endogenous branches (Hommersand, 1963). Womersley (2003) followed Kylin (1956) and he kept the *Lophosiphonia* group separated, in which he placed the genera *Lophosiphonia* and *Ophidocladus*. Another recent work, focusing on a species of the *Lophosiphonia* group, was carried out on *Pleurostichidium* using molecular data (Phillips, 2000), and leaded to the elevation of this genus to the tribal level, following the proposition previously suggested by Hommersand (1963). In relation to the other genera placed in the *Lophosiphonia* group by Falkenberg (1901) and Kylin (1956), some of them remain poorly known or their phylogenetic affinities have not been specifically studied using molecular data (i.e. *Oligocladella*, *Stichothamnion, Ctenosiphonia*). Finally, with regard to *Falkenbergiella,* all species are currently placed in *Lophosiphonia* or *Polysiphonia* (Hollenberg, 1968a; Norris, 1992). Therefore, the genus *Ctenosiphonia* and other five genera (Table 2) are currently included in the *Lophosiphonia* group, which is probably polyphyletic (Falkenberg, 1901; Hommersand, 1963) and requires a revision of the taxonomic position of their members.

The distinctive features found in *Ctenosiphonia hypnoides* regarding other species and genera of the family Rhodomelaceae are: 1) dorsiventral structure consisting of a extensive system of prostrate indeterminate axes that bears determinate erect axes, 2) all branches are endogenous, 3) the branching pattern of prostrate axes to produce erect ones, which consists of two alternate rows of

Table 2. Comparison of selected features of the genera belonging to the *Lophosiphonia* group

	Stichothamnion	*Oliga*	*Ctenosiphonia*	*Lophosiphonia*	*Falkenbergiella*	*Ophidocladus*
N° of species	2	3	1	10	Currently 0	1
Branches origin	Exo/endo-	Endo-	Endo-	Endo-	Endo-	Endo-
Branching of prostrate axes	Dorsal	Dorsal	Aternate	Dorsal	Dorsal	Dorsal
Trichoblasts arrangement / branches	Spiral / Unbranched	–	Unilateral / Branched	Unilateral, spiral / Branched	Absent / Branched	Alternate / Branched
Tetrasporangia per segment	1	2	2	1	1	2
Spermatangial branches	Cylindrical	–	On the second dichotomy of trichoblasts / Four furcations	Bifurcated	Cylindrical	On the first dichotomy of branched trichoblasts/ Four furcations when young, globose at maturity
References	Børgesen 1930, Vroman 1967, Rojas-González 2001a	Weber van Bosse 1911, 1913	Rojas-González 2001a, this work.	Falkenberg 1901, this work	Pocock 1951, Kylin 1956	Falkenberg 1901, this work

branches arising on every segment, firstly laterally oriented and later becoming erect, 4) the trichoblasts are arranged unilaterally at the convex side of the apices of erect axes, 5) the tetrasporangia are formed in two longitudinal opposite rows. Although sexual structures were not found in our study, they were described based on materials from the Canary Islands (Rojas-González & Afonso-Carrillo, 2000, 2001a). They are unilaterally inserted; procarps have 4-celled carpogonial branches; and spermatangial branches are formed on the second dichotomy of modified trichoblasts, bearing a spermatangial branch each one of the four branches of the trichoblast and lacking sterile apical cells.

Our description of *Ctenosiphonia hypnoides* from the Atlantic Iberian Peninsula is consistent with those previously provided by Bornet & Thuret (1876), Falkenberg (1901) and Rojas-González & Afonso-Carrillo (2000, 2001a), as well as with the type material of the species. *Ctenosiphonia hypnoides* is very similar to *Lophosiphonia reptabunda* in outline morphology, and they usually share the same habitat when *C. hypnoides* is present. The characteristic arrangement of branches through prostrate axes, which is especially noticeably at their apices, and the trichoblasts unilaterally inserted at erect axes of *C. hypnoides* allow a ready separation of the two species.

Ctenosiphonia hypnoides has a combination of features unique within the *Lophosiphonia* group (Table 2) and the Rhodomelaceae. It shares with *Ophidocladus* having a dorsiventral thallus, the endogenous branching and the formation of two tetrasporangia per segment (see the discussion on these features in remarks on *O. simpliciusculus*). However, both genera can be clearly separated, among others, by the branching pattern of prostrate axes and the trichoblasts arrangement.

The characteristic branching pattern of the prostrate axes in *Ctenosiphonia* is unique within the *Lophosiphonia* group, whose other members have erect axes arising in the dorsal side of the prostrate axes forming a unique row of branches (Table 2). Within the family Rhodomelaceae, a tendency to shift the spiral pattern of branches is common, and some examples of pairs of nearly identical genera differentiated by spiral *vs.* alternate branching are *Polysiphonia* and *Pterosiphonia* or *Rhodomela* and *Odonthalia* (Hommersand, 1963). By contrast, alternate branches are not formed on every segment in *Pterosiphonia* and *Odonthalia*, but branches are formed one or several segments apart. Alternate branches borne on every segment, as shows *Ctenosiphonia,* were described only in some members of the tribes Lophothalieae (*Picconiella*, *Ardissonula* and *Sporoglossum*) and Herposiphonieae (Kylin, 1956; Hommersand, 1963; Womersley, 2003). Curiously, in *Ctenosiphonia* this alternate branching pattern is observed in prostrate axes, while erect axes are usually unbranched or sometimes have unilaterally inserted branches.

The unilaterally inserted trichoblasts is also a peculiar feature of *Ctenosiphonia*. Within the *Lophosiphonia* group, this characteristic is shared only by *Lophosiphonia cristata* Falkenberg, while other species of this genus have the trichoblasts spirally arranged (Table 3). Within the family Rhodomelaceae, unilaterally inserted trichoblasts is a feature characteristic of the tribe Amansieae, while other members have usually spirally arranged trichoblasts (Hommersand, 1963).

Finally, sexual reproductive structures in *Ctenosiphonia* are formed on the convex side of apices of erect axes, showing the same pattern than the trichoblasts. This arrangement of sexual structures is typical of the tribe Amansieae (Falkenberg, 1901). Furthermore, the morphology of spermatangial branches in *Ctenosiphonia* is virtually unique within the Rhodomelaceae. They resemble the paired spermatangial axes of *Lophosiphonia reptabunda*, which are formed on the two

Table 3. Comparison of selected features among the species currently placed in the genus *Lophosiphonia*

	Pericentral cells	*Rhizoids*	*Erect axes*	*Trichoblasts*	*Tetrasporangia*	*Type locality; Distribution*	*References*
Lophosiphonia adhaerens Pilger	6-8	Cut off	Pseudodichotomous	–	–	Annobon Island; w. Africa	Pilger 1920
Lophosiphonia bermudensis F.S. Collins *et* Hervey	4	–	Short branches	–	Straight	Bermudas; Micronesia	Collins & Hervey 1917
Lophosiphonia capensis (Kylin) R.E. Norris	4	In open connection	Unbranched or few adaxial laterals	Spiral	Straight	False Bay (Southafrica); Southafrica	Norris 1992, Stegenga *et al.* 1997
Lophosiphonia cristata Falkenberg	9-11	In open connection	Unbranched	Unilateral	Spiral	Napoles (Italy); Medtierrranean Sea, Atlantic Is., eastern Central and South America, Australia, Philipines and Pacific Is.	Falkenberg 1901; Rojas-González & Afonso-Carrillo 2002; Coppejans 1983
Lophosiphonia hayashii Segawa	8	–	–	–	–	Japan	Yoshida 1998
Lophosiphonia macra (Harvey) Falkenberg	4	–	Subsimple	–	–	New Zealand	Harvey 1855; Falkenberg 1901
Lophosiphonia mexicana E.Y. Dawson	6 in narrower parts; 12 in wider ones	Cut off	–	Spiral	Spiral	Angel de la Guardia Island (W. Mexico)	Dawson 1944
Lophosiphonia obscura (C. Agard) Falkenberg	6	In open connection	Irregular	Spiral	–	Cádiz (S. Spain); Mediterranean Sea, Portugal, Atlantic Is., eastern Central and South America, SW Asia, Australia, Pacific Is.	Falkenberg 1901, Coppejans 1983, this work
Lophosiphonia prostrata (Harvey) Falkenberg	4	In open connection	Irregular	Spiral	–	Fremantle (W. Australia); Australia, Japan, Vietnam, Hawaii	Womersley 2003; Abbott 1999
Lophosiphonia reptabunda (Suhr) Kylin	13-23	Cut off	Irregular	Spiral	Spiral	Biarritz (SW France) ; see Fig. 130	Maggs & Hommersand 1993; Rojas-González & Afonso-Carrillo 2002, this work.
Lophosiphonia simplicissima	7	In open connection	Irregular	Spiral	Straight, slightly spiral	Niembro (N. Spain) ; Atlantic Iberian Peninsula	This work

branches of the first dichotomy of trichoblasts, but in *Ctenosiphonia* spermatangial branches arise on the four branches of the second dichotomy of trichoblasts.

In conclusion, *Ctenosiphonia hypnoides* exhibit a particular combination morphological characteristics which could indicate a relation of this species to several tribes or groups of the Rhodomelaceae. Further research is pending to clarify its phylogenetic relationships to other members or the family.

Herposiphonia **cf.** ***secunda*** **f.** ***tenella*** (C. Agardh) M.J. Wynne **Figs 44-63**

Basionym: *Hutchinsia tenella* C. Agardh.
Type locality: Sicily.
Type material: No published information.
Synonyms: *Polysiphonia tenella* (C. Agardh) Moris *et* De Notaris ; *Herposiphonia tenella* (C. Agardh) Ambronn.
References: Falkenberg, 1901; Coppejans, 1983; Rojas-González, 1997.
Molecular vouchers: GenBank accession numbers KF648513, KF648516, KF648522, KF671171, KF671173, KF671179.

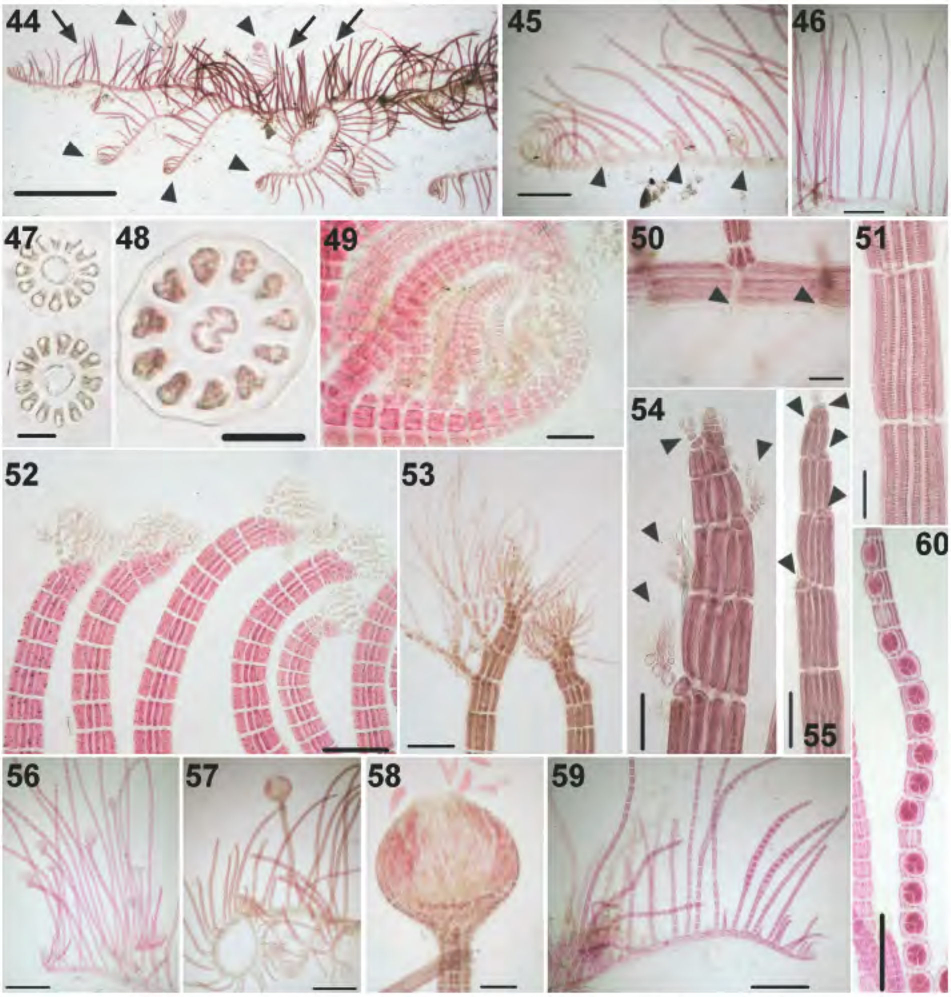
Selected specimens: 1) Virgen del Mar (43°28’40”N; 3°52’31”W), 7.xi.2010, SANT-Algae 24646; 2) La Franca (43°23’39”N; 4°34’18”W), 6.x.2006, SANT-Algae 19751; 3) Niembro (43°26’33”N, 4°50’20”W), 28.v.2010, SANT-Algae 24150; 4) Baleal (39°22’25”N, 9°19’56”W), 14.vi.2010, SANT-Algae 24249 (tetrasporangial plants); 5) Queimado (37°49’34”N; 8°47’34”W), 24.v.2005, SANT-Algae 25240; 6) Almograve (37°39’54”N; 8°48’04”W), 25.v.2005, SANT-Algae 24760; 7) Arrifana (37°09’44”N; 8°54’22”W), 20.x.2005, SANT-Algae 26320 (tetrasporangial plants);8) Martinhal (37º01’03”N; 8°55’31”W), 3.xi.2005, SANT-Algae 26203; 9) Ingrina (37°02’46”N; 8°52’43”W), 20.ii.2011, SANT-Algae 25480; 10) Armaçao de Pêra (37°06’04”N; 8°22’17”W), 17.10.2005, SANT-Algae 24846 (tetrasporangial plants); 11) Caneiros (37°06’14”N; 8°30’47”W), 18.x.2005 (female plants); 12) Santa Eulalia (37°05’11”N; 8°12’53”W), 19.x.2005; 13) Olhos d’Agua (37°05’20”N; 8°11’27”W), 6.v.2005, SANT-Algae 25765; 14) Punta Plata (36°06’28”N; 5°49’41”W), 19.i.2011, SANT-Algae 26529; 15) Punta Paloma, (36°03’44”N; 5°43’31”W), 18.xi.2005; (tetrasporangial plants).

Vegetative and reproductive morphology

Thalli forming dense turfs up to 5 mm high and covering rock surfaces of up to 400 cm^2 in extent. Thallus dorsiventral, consisting of an extensive system of indeterminate and interwoven prostrate axes which bear ventrally numerous rhizoids that attach to the substrate and produce dorsally exogenous erect branches on every segment, bearing three axes of determinate growth and one axis of indeterminate growth in a regular pattern; axes of determinate growth unbranched (Figs 44-46). Axes pink in colour, with a soft texture.

Axes fully ecorticate, consisting of a central axial cell and 11-14 (-15) pericentral cells (Figs 47, 48). Prostrate axes indeterminate and dorsiventral, growing by transverse divisions of conspicuous apical cells; apices curved upwards, without trichoblasts nor scar cells (Fig. 49). Prostrate axes 80-150 µm in diameter. Rhizoids cut off from the pericentral cells, unicellular (Fig. 50). Erect axes of determinate growth, unbranched (Figs 45, 46), 50-80 µm in diameter. Pericentral cells in surface view showing chromatophores forming transverse bands (Fig. 51). Young determinate branches bearing 4-6 trichoblasts in the apices, spirally arranged on every segment, deciduous and leaving conspicuous scar cells (Figs 52-55).

Cystocarps are formed at the apices of determinate branches. The young cystocarps are placed 3 segments below the apices (Fig. 56), while they are terminal when mature (Figs. 57, 58). Cystocarps are globose (Fig. 58), 230-380 µm high and 210-350 µm in diameter. Spermatangial axes not found. Tetrasporangia



Figs 44-60. *Herposiphonia* cf. *secunda* f. *tenella*. Vegetative and reproductive morphology. **44:** Habit consisting of dorsiventral prostrate axes of indeterminate growth that bear branches of determinate and indeterminate growth: arrowheads – branches of indeterminate growth; arrows – branches of determinate growth. **45.** Prostrate axis bearing a branch of indeterminate growth every three determinate branches: arrowheads – branches of indeterminate growth. **46.** Axes of determinate growth unbranched. **47-48.** Cross section of axes with 11 (48), 12 and 13 (47) pericentral cells. **49.** Apex of a prostrate axis upward incurved. **50.** Prostrate axis bearing ventrally rhizoids which are cut off from pericentral cells: arrowheads - walls separating the pericentral cells and the rhizoids. **51.** Surface view of pericentral cells showing chromatophores in transverse bands. **52.** Apices of branches of determinate growth with short trichoblasts. **53.** Apices of erect axes with long trichoblasts. **54.** Apices of determinate branches bearing 4 mature trichoblasts spirally arranged on every segment; arrowheads - trichoblasts. **55.** Apices of determinate branches bearing 5 scar cells of trichoblasts spirally arranged on every segment: arrowheads – scar cells. **56.** Female gametophyte with young cystocarps arising three segments below the apex of determinate branches. **57.** Female gametophyte with a terminal mature cystocarp. **58.** Detail of a cystocarp. **59.** Tetrasporangia formed on determinate branches. **60.** Determinate branch bearing tetrasporangia forming slightly spiral series. Scale bars: 2 mm in Fig. 44; 600 µm in Figs 45 and 46; 25 µm in Figs 47 and 48; 50 µm in Figs 49-51 and 54; 100 µm in Figs 52, 53, 55 and 58; 600 µm in Figs 56, 57 and 59; 200 µm in Fig. 60.

Figs 61-62. Distribution of *Herposiphonia* cf. *secunda* f. *tenella*. **61.** Collections of *Herposiphonia* cf. *secunda* f. *tenella* along the Atlantic Iberian Peninsula. **62.** World distribution: arrow - type locality.

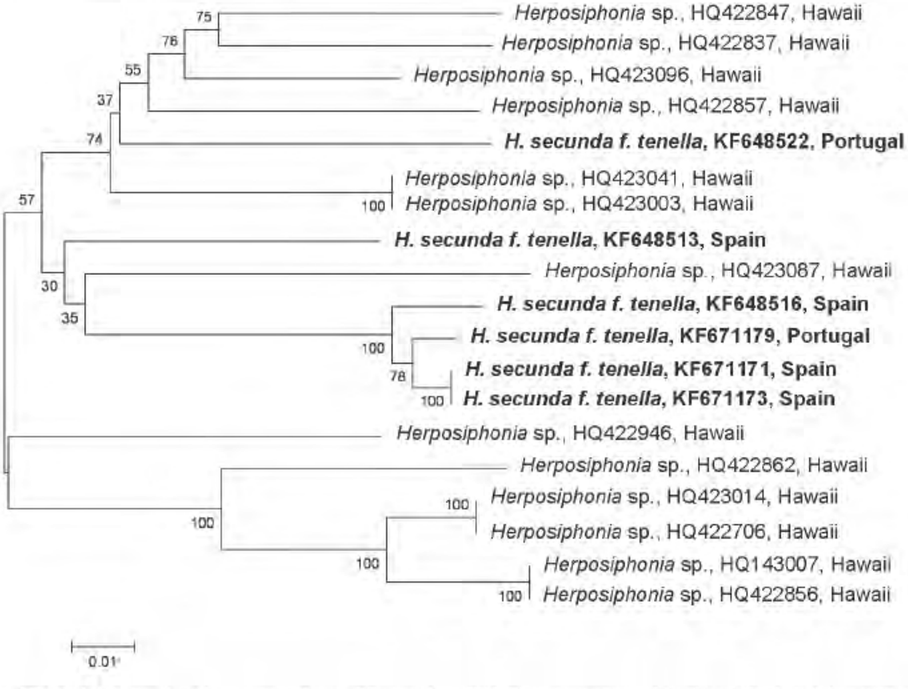


Fig. 63. Neighbour-joining tree inferred from the COI-5P sequences showing relationships among the 19 specimens of *Herposiphonia* spp. included in the present analysis. Six sequences corresponding to specimens morphologically identified as *Herposiphonia secunda* f. *tenella* were generated in this study (in bold), while the other 13 sequences correspond to unidentified specimens of this genus from Hawaii (Sherwood *et al.*, 2010).

formed on determinate branches in slightly spiral series (Figs 59, 60). They are ovate, 42-58 µm in diameter, with 2 cover cells similar to pericentral cells.

Phenology

Plants were collected practically throughout the year and they are probably perennial. Reproductive structures are rare, especially sexual ones, which were observed only in materials from southern locations. Tetrasporangia were found in five collections (20%) and cystocarps in two collections (7%), while male structures were not found.

Habitat and distribution

This species is common in sand-covered rocks from the Atlantic Iberian Peninsula especially in the warmer areas (Fig. 61). *Herposiphonia* cf. *secunda* f. *tenella* forms almost monospecific turfs only in the South, while in the other regions this species is mixed with other typical species from this habitat or it grows epiphytic on other algae, such as *Stypocaulon scoparium* or *Halopithys incurva*. In the South, turfs of *H.* cf. *secunda* f. *tenella* grow from the mid to the upper intertidal of moderately to extremely wave-exposed sites. *Herposiphonia secunda* f. *tenella* has been widely reported in world temperate and warm coasts (Fig. 62).

Remarks

The materials here labelled as *Herposiphonia* cf. *secunda* f. *tenella* share regular branching pattern of prostrate axes, which consists of three axes of determinate growth followed by one axis of indeterminate growth. However, they correspond to a mix of species, according to our molecular data, which surprisingly revealed that the six sequenced specimens were resolved in three distinct clades (Fig. 63). This result suggests that this genus likely encompass an important cryptic diversity along the Atlantic Iberian Peninsula.

Herposiphonia secunda f. *tenella* was originally described from the Mediterranean Sea, however the only detailed descriptions of materials from this area were provided by Schmitz & Falkenberg (1897, as *H. tenella*) and Falkenberg (1901, as *H. tenella*). Our material apparently differs from the Mediterranean one, because the latter have a smaller number of pericentral cells (8-12) and apparently exhibits an irregular branching pattern (Falkenberg, 1901; Kützing, 1863; Coppejans, 1983). Therefore, our specific assignment of the specimens from the Atlantic Iberian Peninsula is tenuous and the absence of updated and detailed descriptions of the species from areas close from the type locality makes it difficult to establish reliable morphological comparisons.

On the other hand, *Herposiphonia secunda* f. *tenella* was reported with a wide distribution, including the shores of the Atlantic, Pacific and Indian Ocean (Guiry & Guiry, 2013) and numerous descriptions were provided from distant locations. Most of them were congruent in describing a regular pattern consisting of one indeterminate branch followed by three determinate branches (e.g. Oliveira Filho, 1969; Hollenberg, 1968b; Masuda & Kogame, 2000), but differed in many features that are often considered diagnostic, as for example the number of pericentral cells, the number of trichoblasts or the number of segments that form the determinate branches. This likely indicates that more than a single species has been assigned this taxonomic name.

One of the three species here labelled as *Herposiphonia* cf. *secunda* f. *tenella* may correspond to *H. parca* Setchell, which was recently introduced in the Mediterranean Sea from the Asiatic shores (Verlaque, 2001). *Herposiphonia parca* and *H. secunda* f. *tenella* are distinguished by the position of the cystocarps, which are terminal in the first species while they are laterally inserted and constituted of several segments below the apex in the second one (Schmitz & Falkenberg, 1987; Segi, 1954, as *H. terminalis*; Hollenberg, 1968b; Rojas-González, 1997). This feature seem to be clear for distinguishing this pair of species, nevertheless cystocarps were rarely observed in materials from the Iberian Peninsula and they were terminal at maturity, in agreement to *H. parca.* Conversely, other features as for example the position of young cystocarps, the number of pericentral cells or the number of trichoblasts differ in materials from the Atlantic Iberian Peninsula and *H. parca* from the Pacific coasts (Segi, 1954, as *H. terminalis*; Hollenberg, 1968b). Furthermore, sequences from Iberian materials were aligned with 13 sequences of *Herposiphonia* spp. from Hawaii (Sherwood *et al.*, 2010). Interestingly, no coincidences were found among them (Fig. 63), despite *H. parca* was reported as a common species of the Hawaiian flora (Hollenberg, 1968b; Abbott, 1999). Therefore, available morphological and molecular data are not enough to conclude whether any of the materials from the Atlantic Iberian Peninsula correspond to *H. parca* and further work is needed to clarify the diversity of species of the genus *Herposiphonia* in the Atlantic Iberian Peninsula, to identify them and to establish their morphological delineation.

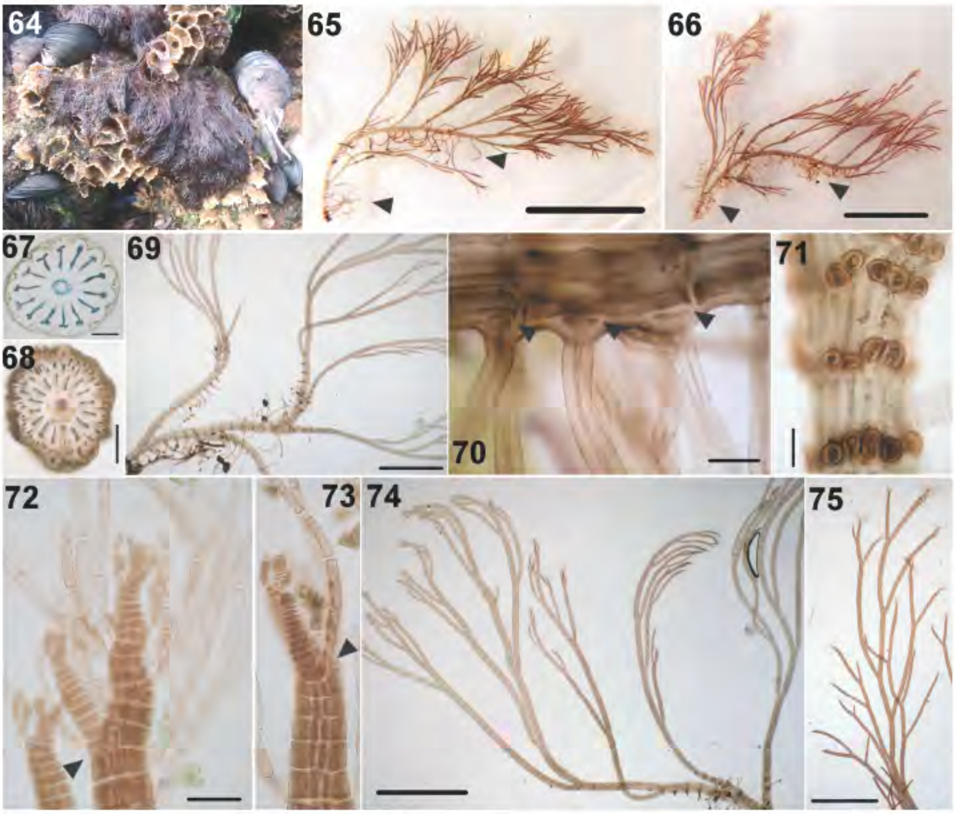
Leptosiphonia schousboei (Thuret) Kylin **Figs 64-90**

Basionym: *Polysiphonia schousboei* Thuret *in* Bornet & Thuret.
Syntypes: PC.
Syntype localities: Biarritz (Southwest of France) and Tanger (Morocco).
Synonym: *Ophidocladus schousboei* (Thuret) Falkenberg.
References: Bornet & Thuret, 1876 (as *Polysiphonia schousboei*); Falkenberg, 1901 (as *Ophidocladus schousboei*).
Molecular vouchers: GenBank accession numbers KF648525, KF671153, KF671165, KF671170, KF671176.
Selected specimens: 1) Playa de Amio (43°23’42”N; 4°28’57”), 17.iii.2006, SANT-Algae 20445; 2) Niembro (43°26’33”N, 4°50’20”W), 28.v.2010, SANT-Algae 24151 (tetrasporangial plants); 3) Linorsa (43°41’56”N; 7°27’14”W), 25.iv.2005, SANT-Algae 15580 (male plants); 4) Perbes (43°22’34”N; 8°12’55”), 5.iii.2011, SANT-Algae 25717 (male plants); 5) Leira (43°18’37”N; 8°38’00”W), 25.vi.2010, SANT-Algae 24208 (male and female plants); 6) Silleiro (42°06’42”N; 8°54’00”W), 8.iii.2004, SANT-Algae-23428; 7) Leça de Palmeira (41°12’22”N; 8°43’03”W), 11.vi.2010, SANT-Algae 24228 (male, female and tetrasporangial plants, mixed phases bearing tetrasporangia and cystocarps); 8) Buarcos (37°39’54”N; 8°48’04”W), 15.xi.2004, SANT-Algae 15872 (male, female and tetrasporangial plants); 9) Baleal (39°22’25”N, 9°19’56”W), 14.vi.2010, SANT-Algae 24252 (male, female and tetrasporangial plants); 10) Almograve (37°39’54”N; 8°48’04”W), 25.v.2005, SANT-Algae 24674 (male, female and tetrasporangial plants).

Vegetative and reproductive morphology

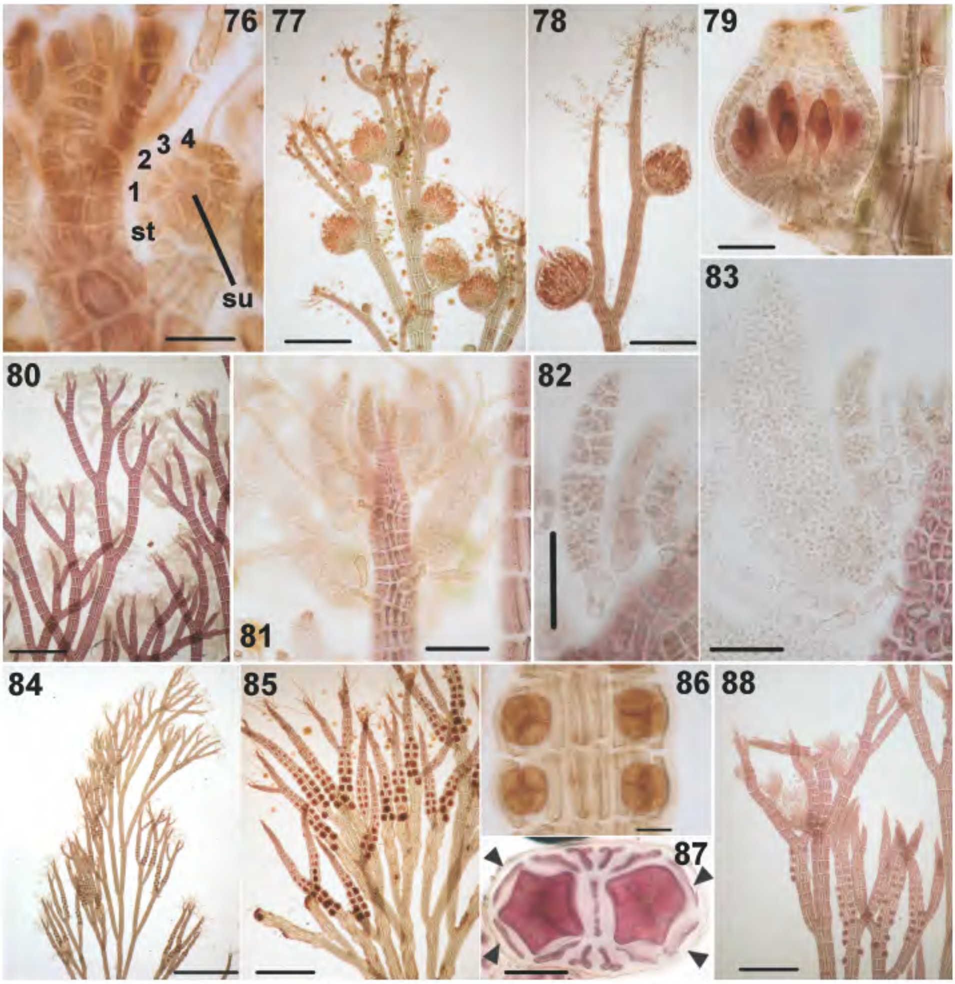
Thalli forming dense tufts up to 6 cm high and covering rock surfaces up to 900 cm^2 in extent (Fig. 64). Thallus radially organized growing from indeterminate erect axes that become decumbent when developing rhizoids at their basal parts, forming a system of prostrate interwoven axes that bears rhizoids which attach to the substrate (Figs 65, 66). Erect axes alternately or unilaterally branched at irregular intervals, up to 4 (-5) orders. Tufts dark brown in colour; axes dark brown, with a fairly rigid texture.

Axes formed by a small axial cell and (12-) 13-14 (-16) pericentral cells, ecorticate or sometimes developing a slight cortication at the base that only occasionally become dense (Figs 67, 68). Prostrate axes growing when the rhizoids develop at basal parts of erect axes (Fig. 69). Prostrate axes (130-) 200-350 (-700) µm in diameter; composed of segments L/D (0.47-) 0.55-1.2 (-1.4). Adventitious branches are only occasional in old parts of prostrate axes. Rhizoids cut off from pericentral cells, unicellular, abundantly developed, usually several per segment, up to 5, 30-70 (-110) µm in diameter and up to 1700 µm long, sometimes terminated in digitate haptera (Figs 70, 71).



Figs 64-75. *Leptosiphonia schousboei*. Vegetative morphology. **64.** Tufts growing on *Sabellaria alveolata* tubes. **65-66.** Habit consisting of erect axes that develop rhizoids at their basal parts becoming decumbent and forming prostrate axes: arrowheads- rhizoids. **67-68.** Cross section of axes showing 14 pericentral cells of an ecorticate part of the thallus (67) and 16 pericentral cells in a corticate basal part of the thallus (68). **69.** Prostrate axes with numerous rhizoids. **70.** Rhizoids cut off from pericentral cells: arrowheads - walls separating the pericentral cells and the rhizoids. **71.** Prostrate axis showing up to 5 rhizoids initials per segment. **72-73.** Apices of erect axes with branches formed in the axils of trichoblasts; trichoblasts are from well (72) to scarcely developed (73): arrowheads – branches in the axils of trichoblasts. **74.** Erect axes showing unilateral and irregularly arranged branches. **75.** Erect axes with alternate branches. Scale bars: 5 mm in Figs 65 and 66, 50 µm in Figs 67, 72 and 73; 200 µm in Fig. 68; 2 mm in Figs 69, 74 and 75; 100 µm in Figs 70 and 71.

Erect axes growing from domed apical cells 15-25 µm in diameter (Figs 72-73). Erect axes (90-) 120-300 (-400) µm in diameter, composed of segments L/D (0.36-) 0.6-1.4 (-1.8). Branches formed exogenously at the apices of erect axes, arising on the axils of trichoblasts (Figs 72, 73). Branches sometimes alternate or arranged in secund series, at irregular intervals, up to 4 (-5) branching orders (Figs 74, 75). Adventitious endogenous branches only rarely present in basal parts of erect axes. Trichoblasts usually present, from scarce to abundant (Figs 72-73), usually short and dichotomously branched 1-2 (-3) orders. When they are abundant, they arise on every segment mostly in a 1/5 spiral; when they are scarce they arise spirally at irregular intervals. They are deciduous, leaving conspicuous scar cells.



Figs 76-88. *Leptosiphonia schousboei*. Reproductive morphology. **76.** Procarp formed on a fertile trichoblast, showing the supporting cell (su) that bears the 4-celled carpogonial branch (1-4) and a basal sterile cell (st). **77-79.** Cystocarps. **80.** Spermatangial branches arising in the upper parts of erect axes. **81.** Spermatangial branches spirally arranged along thallus. **82.** Young spermatangial branch formed in one of the two branches of the first dichotomy of a trichoblast. **83.** Mature spermatangial branch. **84.** Tetrasporangia formed in branches of the upper parts of erect axes. **85.** Tetrasporangia formed in two longitudinal rows. **86.** Detail of tetrasporangia in surface view. **87.** Cross section of a branch with two opposite mature tetrasporangia: arrowheads - two cover cells per tetrasporangia. **88.** Mixed phases bearing cystocarps and tetrasporangia. Scale bars: 25 µm in Fig. 76; 600 µm in Figs 77, 78, 80, 85 and 88; 100 µm in Figs 79 and 81; 50 µm in Figs 82, 83, 86 and 87; 2 mm in Fig. 84.

Gametophytes dioecious. Procarps are formed in suprabasal cells of modified trichoblasts in upper parts of erect axes; and they consist of a four-celled carpogonial branch, a basal sterile cell (Fig. 76) and a group of two lateral sterile cells borne on the supporting cell. Cystocarps (Figs 77-79) globular when mature, (250-) 300-550 (-600) µm high and (190-) 250-500 (-600) µm in diameter, with

Figs 89-90. Distribution of *Leptosiphonia schousboei*. **89.** Collections along the Atlantic Iberian Peninsula. **90.** World distribution: arrows – syntype localities.

an ostiole (20-) 40-80 (-100) µm wide. Carposporangia clavate, (55-) 70-125 (-140) × (15-) 25-40 (-48) µm.

Spermatangial axes located at the apices of main axes and lateral branches of erect axes, arising spirally on every segment or several segments apart (Figs 80, 81). Spermatangial axes are formed on one of the two basal branches of the first dichotomy of modified trichoblasts, leaving the other branch of the trichoblast at maturity (Figs 82, 83). Spermatangial axes are cylindrical and slightly curved, (160-) 200-300 (-350) µm long and (38-) 50-75 (-112) µm in diameter, without sterile apical cells at maturity.

Tetrasporangia in upper branches (Fig. 84), in 2 longitudinal opposite rows (Figs 85-87) with up to 12 segments bearing mature tetrasporangia; ovate, (30-) 40-70 (-88) µm in diameter, with 2 cover cells similar to pericentral cells (Fig. 87). Mixed phases with tetrasporangia and cystocarps were observed (Fig. 88).

Phenology

Plants occur throughout the year, and they are probably perennial. Reproductive structures were frequently observed year-round: tetrasporangia in 53% of the collections, male structures in 50% and female ones in 40% of the collections. Mixed phases were observed once, in June 2010 in Leça de Palmeira (northern Portugal).

Leptosiphonia schousboei shows relatively small morphological variations, both between sites and seasons. However, our observations reveal that plants are usually greatly developed in spring-summer, while during the winter plants are usually shorter. Furthermore the presence of cortication in the basal parts of the plant is variable, being usually absent, sometimes scarce and more rarely dense.

Habitat and distribution

Leptosiphonia schousboei grows in the mid intertidal of moderately to extremely wave-exposed shores, typically on edges of pools, overgrowing on *Corallina elongata* or on sand tubes constructed by the reef-forming polychaete *Sabellaria alveolata*. It tolerates the presence of sand and is common in rocks of beaches, however, it also grows on sand-free rocky shores.

In the Atlantic Iberian Peninsula, *Leptosiphonia schousboei* is especially frequent between Galicia and the centre of Portugal, while it becomes rare towards the western (along the Cantabrian Sea), as well as towards the South

(Fig. 89). It has a world distribution restricted to the coasts between the Iberian Peninsula and Cape Verde (Fig. 90).

Remarks

Leptosiphonia schousboei was originally described by Bornet & Thuret (1876, as *Polysiphonia schousboei*) based on materials from Biarritz (southwestern France) and Tanger (Morocco). The known distribution of *L. schousboei* is restricted to the coasts ranging from southern France to Morocco, and also includes the Canary and Cape Verde Islands (e.g. Ardré, 1970; Benhissoune *et al.*, 2003; Bárbara *et al.*, 2005; Araújo *et al.*, 2009). However, based on our surveys, its distribution could be currently narrower. The herbarium materials collected in Biarritz was dated from 1868-1894, but we did not detect plants of *L. schousboei* during our sampling in this site in March 2011. Furthermore, it was never recorded to date in the Basque Country (Gorostiaga *et al.*, 2004) and the north easternmost site in which it was reported in Spain is Playa de Amio in Cantabria (Díaz *et al.*, 2008). This may indicate a regression of the distribution of the species towards the west throughout the North of the Iberian Peninsula. With regard to the South of the Peninsula, this species was never recorded in the Algarve (Ardré, 1970) or Cádiz (Conde *et al.*, 1996); and was not found in our surveys in this area. Therefore, the collection from Almograve (Baixo Alentejo, South of Portugal) is our southernmost record of the species along the Iberian Peninsula. The Algarve and Basque Country are characterized by warmer temperatures than the other regions of the Atlantic Iberian Peninsula in which upwelling events take place.

The only available descriptions of *Leptosiphonia schousboei* were provided by Bornet & Thuret (1876) and Falkenberg (1901). The most distinctive features found in *L. schousboei* from the Atlantic Iberian Peninsula are: 1) thallus radially organized, growing from indeterminate erect axes which become decumbent when rhizoids are developed at their basal parts, forming an extensive prostrate system, 2) branches mostly exogenous, arising in the axils of trichoblasts, 3) axes with 12-15 pericentral cells, usually ecorticate or sometimes from slightly to densely corticate in basal parts, 4) rhizoids cut off from pericentral cells, 5) trichoblasts usually present in erect axes spirally arranged at irregular intervals, 6) 4-celled carpogonial branches, 7) spermatangial axes growing on a basal branch of trichoblasts, without sterile apical cells, 8) two tetrasporangia per segment.

Falkenberg (1901) included *Polysiphonia schousboei* in the genus *Ophidocladus,* because both taxa share the formation of two tetrasporangia per segment. However, he remarked that this generic assignment was tentative because tetrasporangia is the only feature that differentiates the species from *Polysiphonia.* According to Falkenberg (1901), *Leptosiphonia schousboei* differed from *O. simpliciusculus* because the latter is characterized by dorsiventrally organized thallus and the exclusive formation of endogenous branches. Subsequently, Kylin (1956) created the genus *Leptosiphonia*, which remains as a monotypic genus since then. In addition to the features proposed by Falkenberg (1901) to separate both species, *O. simpliciusculus* is different from *L. schousboei* because, among others, the first genus has trichoblasts arranged in two opposite rows while they are spirally arranged in *L. schousboei* and spermatangial branches in *L. schousboei* are formed on one of the basal branches of trichoblasts, while they are formed on the two basal dichotomies of trichoblasts in *O. simpliciusculus*. Thus, although *Ophidocladus* and *Leptosiphonia* share the formation of two tetrasporangia per segment, they are largely different in other morphological features.

Despite having two tetrasporangia per segment arranged in two longitudinal rows, *Leptosiphonia schousboei* is largely similar to other members of the Polysiphonieae, the tribe in which Kylin (1956) placed this genus. Furthermore, *Leptosiphonia* is not the only genus of the tribe with this feature, the recently described genus *Perrinia* has also two tetrasporangia per segment (Womersley, 2003). This feature is rare in the tribe Polysiphonieae, while it is characteristic of the tribes Rhodomeleae and Amansieae, and some genera of the tribes Pterosiphonieae, Lophothalieae and the *Lophosiphonia* group (e.g. Hommersand, 1963; Womersley, 2003).

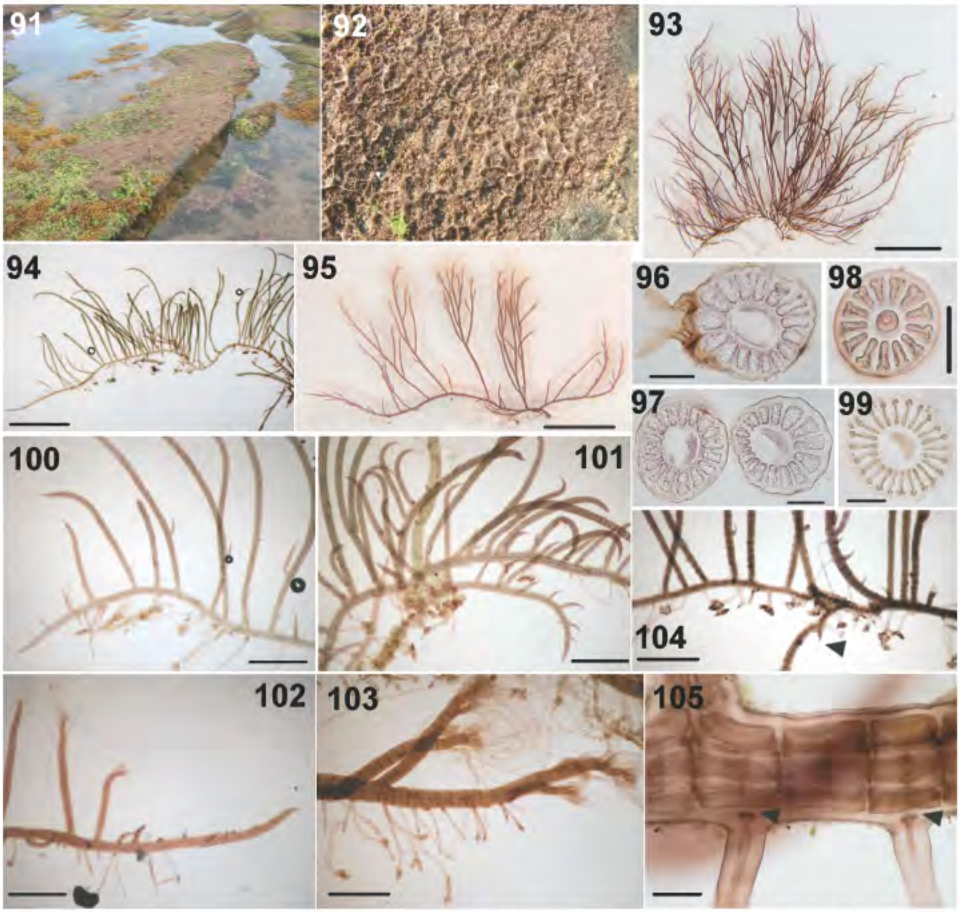
Lophosiphonia reptabunda (Suhr) Kylin **Figs 91-130**

Basionym: *Hutchinsia reptabunda* Suhr.
Holotype: No published information (Silva *et al.* 1996).
Type locality: Biarritz, Pyrénées-Atlantiques, France.
Synonyms: *Polysiphonia reptabunda* (Suhr) Kützing; *Polysiphonia obscura* sensu J. Agardh, non *Hutchinsia obscura* C. Agardh; *Polysiphonia adunca* Kützing.
References: Maggs & Hommersand, 1993; Rojas-González & Afonso-Carrillo, 2002.
Molecular vouchers: GenBank accession numbers KF648511, KF648519.
Selected specimens: 1) Ogeia (43°22’22’’N; 2°32’35’’W), 15.iii.2006, SANT-Algae 20322 (male and female plants); 2) Kobarón (43°21’10’’N; 3°07’54’’W), 12.ix.2006, SANT-Algae 19882 (male, female and tetrasporangial plants); 3) Sonabia (43°24’51’’N; 3°19’37’’W), 27.iii.2006, SANT-Algae 20376; 4) Virgen del Mar (43°28’40’’N; 3°52’31’’W), 7.xi.2010, SANT-Algae 24635; 5) Tagle (43°25’59’’N; 4°04’50’’W), 1.iv.2006, SANT-Algae 20341; 6) Oyambre (43°24’02’’N; 4°20’10’’W), 11.ix.2006, SANT-Algae 20141 (male, female and tetrasporangial plants); 7) Niembro (43°26’33’’N, 4°50’20’’W), 28.v.2010, SANT-Algae 24151 (male, female and tetrasporangial plants); 8) Cegoñas (43°33’18’’N; 7°07’28’’W), 15.vii.2010, SANT-Algae 24409 (tetrasporangial plants); 9) Riomar (43°37’31’’N; 7°19’24’’W), 29.iii.2010, SANT-Algae 24103 (tetrasporangial plants); 10) Barda (43°16’58’’N; 8°55’38’’W), 1.vii.2008, SANT-Algae 21107 (tetrasporangial plants); 11) Almograve (37°39’54’’N; 8°48’04’’W), 25.v.2005, SANT-Algae 24762 (male, female and tetrasporangial plants); 12) Arrifana (37°09’44’’N; 8°54’22’’W), 20.x.2005, SANT-Algae 26317 (female and tetrasporangial plants); 13) Martinhal (37°01’03’’N; 8°55’31’’W), 3.xi.2005, SANT-Algae 26202 (female and tetrasporangial plants); 14) Ingrina (37°02’46’’N; 8°52’43’’W), 9.v.2005, SANT-Algae 25226; 15) Coelho (37°4’22’’N; 8°17’31’’W), 7.v.2005, SANT-Algae 25284 (tetrasporangial plants); 16) Olhos d´Agua (37°05’20’’N; 8°11’27’’W), 20.ii.2011, SANT-Algae 25770; 17) Caños de Meca (36°10’55’’N; 6°00’06’’W), 17.xi.2005, SANT-Algae 26142 (tetrasporangial plants); 18) Encendida (36°18’40’’N; 6°09’12’’W), 18.ii.2011, SANT-Algae 26630 (male and female plants).

Vegetative and reproductive morphology

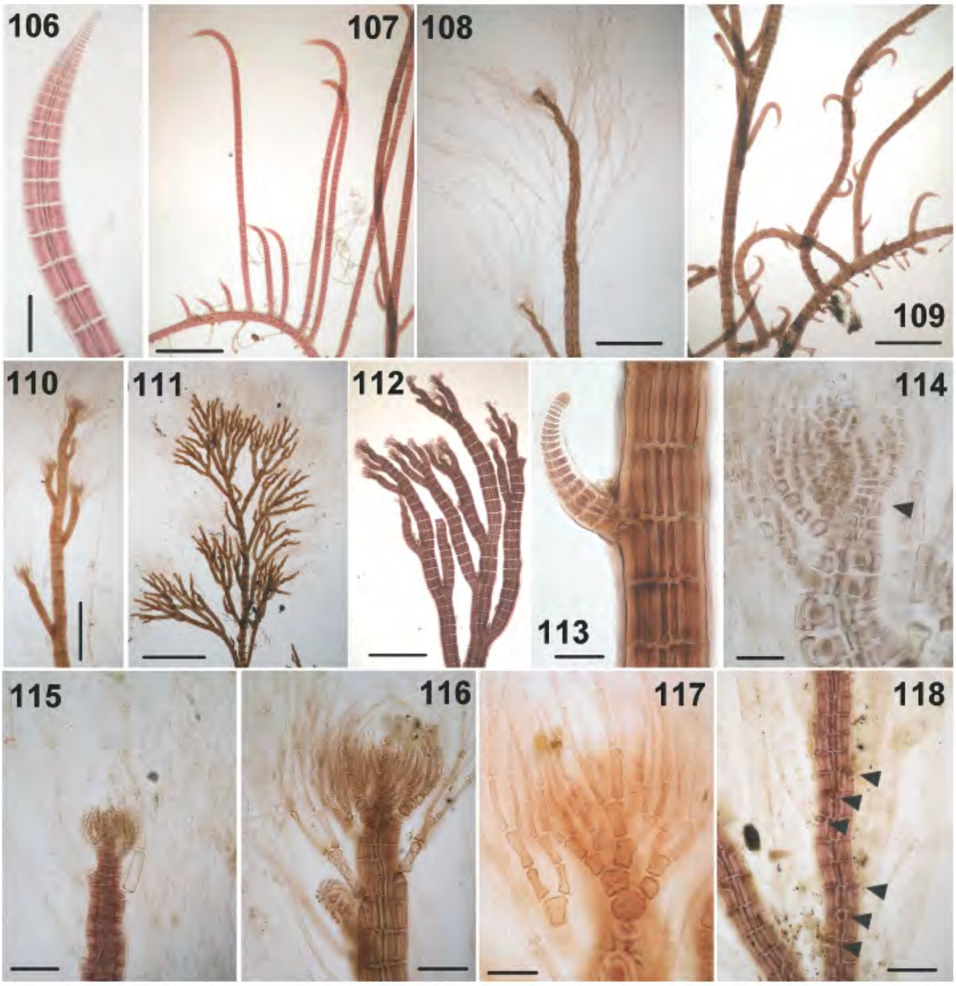
Thalli forming dense turfs up to 2 cm high and covering rocky surfaces of several meters in extent (Figs 91, 92). Thallus dorsiventral, consisting of an extensive system of indeterminate and interwoven prostrate axes which ventrally bear rhizoids that attach to the substrate, dorsally produce endogenous determinate erect axes, and laterally branch to form further prostrate axes (Figs 93-95). Erect axes unbranched when young, and scarcely to densely branched when mature; alternately or unilaterally, at irregular intervals, up to 4 orders. Turfs dark brown in colour, with whitish tufts if the trichoblasts are well developed (Fig. 92); axes dark brown, with a fairly rigid texture.

Axes fully ecorticate, consisting of an axial cell and 13-23 pericentral cells (Figs 96-99). Prostrate axes indeterminate and dorsiventral, growing by transverse divisions of large and conspicuous apical cells *ca* 25 µm in diameter; slightly



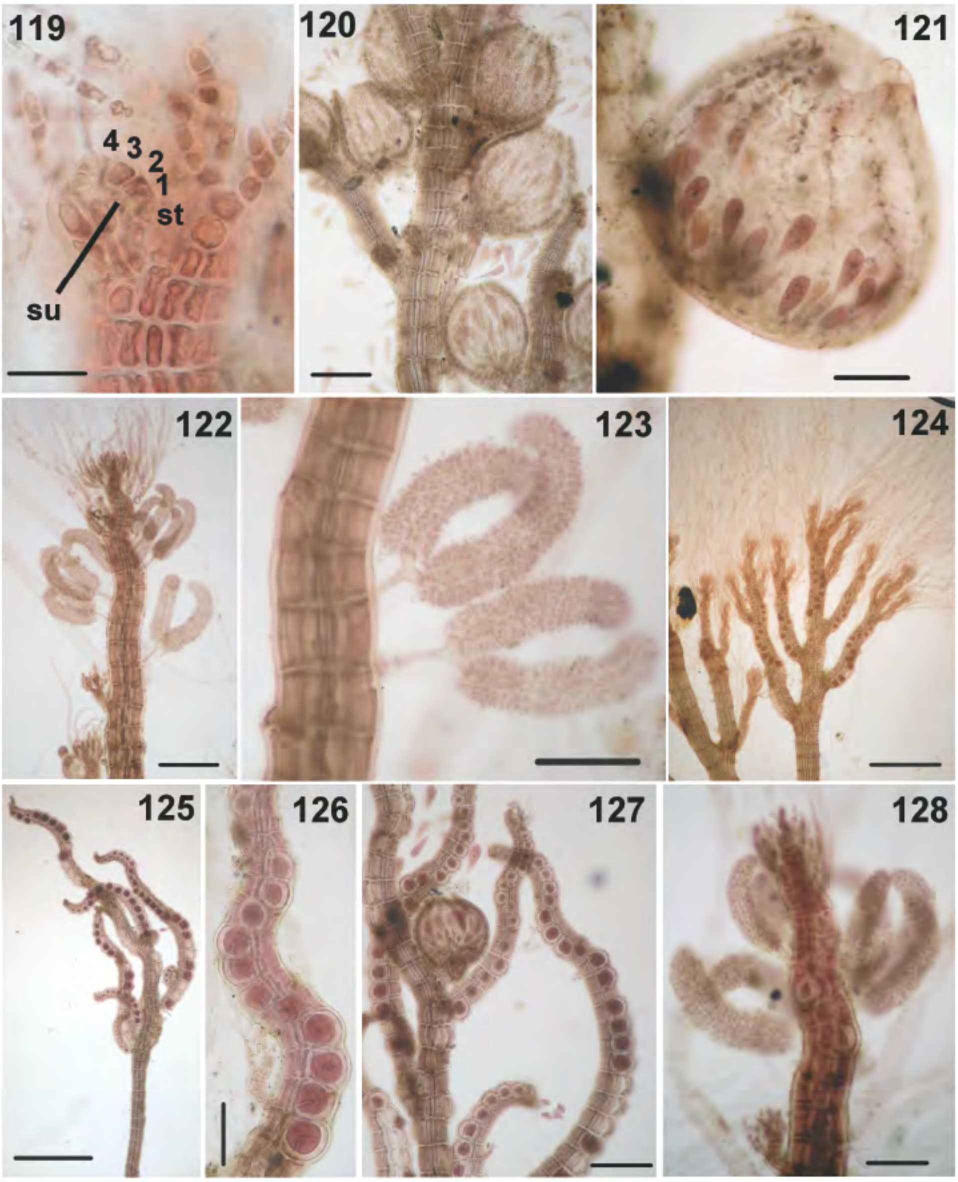
Figs 91-105. *Lophosiphonia reptabunda*. Habit and prostrate axes. **91-92.** Turfs, showing a brown whitish colour when the trichoblasts are well developed (92). **93-95.** Habit consisting of a extensive prostrate axes bearing dorsally erect axes, which are from simple (94) to densely branched (93). **96-99.** Cross section of prostrate (96, 97) and erect axes (98, 99) showing from 13 to 23 pericentral cells. **100-102.** Apex of prostrate axes growing from prominent apical cells, from which arise endogenous branches dorsally and rhizoids ventrally. **103.** Apex of a decumbent erect axis showing apical trichoblasts. **104.** Mature prostrate axis: arrowhead – lateral branch forming further prostrate axes. **105.** Rhizoids cut off from pericentral cells: arrowheads - walls separating the pericentral cells and the rhizoids. Scale bars: 5 mm in Figs 93 and 95; 200 µm in Fig. 94; 50 µm in Figs 96-99 and 105; 600 µm in Figs 100-104.

curved downwards at tips, without trichoblasts nor scar cells (Figs 100-102). Occasionally, the erect axes of the largest specimens develop rhizoids at their basal parts and they become decumbent; then, prostrate axes have trichoblasts at their apices (Fig. 103). Prostrate axes (70-) 90-200 (-260) µm in diameter; composed of segments L/D (0.4-) 0.6-1.2 (-1.6). Prostrate axes dorsally branched bearing endogenous erect axes at irregular intervals, sometimes adventitious branches are formed in old parts (Fig. 104). Prostrate axes often with short lateral endogenous branches that borne at irregular intervals, developing further



Figs 106-118. *Lophosiphonia reptabunda*. Erect axes. **106.** Apex of an erect axis showing a prominent apical cell. **107.** Young erect axes curved in the direction of the apical cell of prostrate axes. **108.** Apical part of an erect axis, unbranched and with abundant large trichoblasts. **109.** Basal parts of erect axes forming inrolled endogenous branches. **110-111.** Apical parts of erect axes alternately branched and with well developed trichoblasts. **112.** Apical part of an erect axis irregularly branched and with short trichoblasts. **113.** Surface view of the basal part of an erect axis bearing a young endogenous branch. **114.** Apex of erect axe with numerous trichoblasts and a young exogenous branch: arrowhead- branch formed in the axil of a trichoblast. **115-116.** Apex of an erect axis with short trichoblasts at the apex and large trichoblasts some segments below of it. **117.** Detail of a short trichoblast. **118.** Trichoblasts formed in a 1/5 spiral: arrowheads - basal cells of trichoblasts. Scale bars: 100 µm in Figs 106, 115, 116 and 118; 600 µm in Figs 107-110 and 112; 2 mm in Fig. 111; 50 µm in Figs 113, 114 and 117.

prostrate axes (Figs 101, 104). Rhizoids scattered, formed in the ventral side of the prostrate axes, cut off from pericentral cells (Fig. 105), unicellular, mostly one per segment but sometimes two, (20-) 30-50 (-60) µm in diameter and up to 1300 µm long, often terminated in digitate haptera.



Figs 119-128. *Lophosiphonia reptabunda*. Reproductive morphology. **119.** Procarp formed in the suprabasal cell of a fertile trichoblast showing the supporting cell (su) that bears the 4-celled carpogonial branch (1-4) and a basal sterile cell (st). **120-121.** Cystocarps. **122.** Spermatangial branches arising in the upper parts of erect axes. **123.** Furcated spermatangial branches. **124-125.** Tetrasporangia arranged in long spiral series in upper parts of erect axes. **126.** Detail of tetrasporangia. **127.** Mixed phases bearing a cystocarp and tetrasporangia. **128.** Mixed phases bearing spermatangial branches and young tetrasporangia. Scale bars: 25 µm in Fig. 119; 200 µm in Figs 120, 127 and 128; 100 µm in Figs 121, 123 and 126; 600 µm in Figs 122, 124 and 125.

Figs 129-130. Distribution of *Lophosiphonia reptabunda*. **129.** Collections along the Atlantic Iberian Peninsula. **130.** World distribution: arrow – type locality.

Erect axes growing from domed apical cells *ca* 25 µm in diameter (Fig. 106). Young erect axes with apices curved in the direction to the tip of prostrate axes (Figs 101, 107), apices of mature erect axes are straight or sinusoidal (Fig. 108). Erect axes 60-150 (-210) µm in diameter, composed of segments L/D (0.4) 0.6-1.4 (-1.5). They are unbranched when young (Fig. 107) and often rapidly develop scarce to abundant endogenous branches in basal parts, which are usually inrolled when young (Fig. 109). Later, erect axes usually develop lateral branches irregularly arranged in upper parts, sometimes secund or alternate, which are from scarce to abundant, up to 4 branching orders (Figs 110-112). Adventitious branches often present especially in basal parts of erect axes (Fig. 113) and on upper parts bearing reproductive structures. Branches from upper parts of erect axes are mostly endogenous, but exogenous branches are occasionally present in reproductive plants, borne in the axils of trichoblasts (Fig. 114). Trichoblasts absent in young erect axes (Figs 100, 101, 107), but later usually present from scarcely (Fig. 112) to extraordinarily developed (Figs 108, 110, 111, 114-118). Trichoblasts are firstly short (Figs 115-117); later, their cells enlarge, becoming large, up to 3.25 mm in length, and with basal cells up to 50 µm in diameter (Figs 108, 110, 111, 115, 116, 118). When present, trichoblasts borne on every segment mostly in a 1/5 spiral (Fig. 118); dichotomously branched up to 5 orders, deciduous and leaving conspicuous scar cells.

Gametophytes dioecious. Procarps are formed on suprabasal cells of modified trichoblasts, in the apices of erect axes. They consist of a 4-celled carpogonial branch, a basal sterile cell (Fig. 119) and a 2-celled lateral group of sterile cells borne on the supporting cell. Cystocarps globular to ovoid when mature (Figs 120, 121), (240-) 300-450 (-550) µm high and (200-) 250-400 (-550) µm in diameter, with an ostiole 20-50 (-75) µm wide. Carposporangia clavate, (50-) 65-110 (-125) × (15-) 20-30 (-38) µm.

Spermatangial axes located at the apices of erect axes, spirally arranged on every segment (Figs 122, 123). They are formed on the two basal branches of the first dichotomy of fertile trichoblasts, bearing each trichoblast two spermatangial branches that replace completely the trichoblasts. Each spermatangial branch is cylindrical, usually with curved tips, without sterile apical cells, (135-) 175-300 (-375) µm long and 35-60 (-75) µm in diameter (Fig. 123).

Tetrasporangia formed in upper parts of erect axes (Figs 124, 125), both in main axes and lateral branches, which are often abundantly developed in the tetrasporophytes; axes bearing tetrasporangia often acquire a sinusoidal outline (Figs 125, 126). Tetrasporangia arranged in long spiral series with up to 15 mature tetrasporangia (Figs 124-126). They are ovate, (30-) 50-60 (-75) µm in diameter, with 2 cover cells similar to pericentral cells.

Mixed phases bearing tetrasporangia and female structures were observed (Fig. 127), as well as specimens bearing tetrasporangia and spermatangial branches (Fig. 128).

Phenology

Plants occur throughout the year, and they are probably perennial. Reproductive structures were frequently observed year-round; tetrasporangia were observed in 30% of the collections and male and female gametophytes were found in 19 and 13 % of the collections, respectively. Mixed phases bearing tetrasporangia and female structures were found once in Arrifana (southern Portugal) and those bearing tetrasporangia and male structures were also found once, in Niembro (northern Spain).

Lophosiphonia reptabunda shows a relatively great morphological variability, mostly related to the thallus size and the abundance of branches and trichoblasts. Some specimens are short and thin, scarcely branched and the trichoblasts, if present, are usually short. By contrast, other specimens are larger and more robust, often with abundant branches, and usually with trichoblasts. These specimens have either only short trichoblasts restricted to the apical segments, or long trichoblasts formed by large cells located below the short ones. This variability has been observed even between specimens collected at the same site and date.

Habitat and Distribution

Lophosiphonia reptabunda forms extensive turfs in sand-covered rocks from the mid to the low intertidal of moderately to extremely wave-exposed sites in the northeastern and southern Atlantic Iberian Peninsula. In these areas, it forms monospecific turfs or mixed ones with other species typical from this habitat, such as *Polysiphonia caespitosa* or *Herposiphonia* cf. *secunda* f. *tenella*. By contrast, along the western Iberian Peninsula the presence of *L. reptabunda* in sand-covered rocks is restricted to shelter to moderately wave-exposed shores. Furthermore, in western Iberian Peninsula, *L. reptabunda* grows not only on sand-covered rocks, but also in rocky coves located in sheltered to moderately wave-exposed coasts where it forms extensive turfs sometimes mixed with *Ctenosiphonia hypnoides*. Although these coves are not covered by sand, sedimentation likely happen since turfs from this habitat usually traps sediments.

Lophosiphonia reptabunda is one of the most frequent and abundant species in sand-covered rocks of the northeastern and the southern Atlantic Iberian Peninsula (Fig. 129), while its abundance and frequency decreased towards west. Its distribution range includes the eastern Atlantic from the British Isles to Namibia, as well as several countries from the Indian and Pacific coasts (Fig. 130).

Remarks

The taxonomy of *Lophosiphonia reptabunda* is complex owing to the still unresolved confusion between this species and *L. obscura*, which is the type of the genus.

The type species of the genus Lophosiphonia

The correct name of the type species of the genus *Lophosiphonia* is historically problematic, as it has been commented in several works and reviewed in Silva *et al.* (1996), in which the following notes are largely based. Falkenberg established the species *L. obscura* (C. Agardh) Falkenberg as the type species of the genus (Schmitz & Falkenberg, 1897). The problem lies in knowing which species to apply C. Agardh´s name. This problem involves two species, one of them with 6 pericentral cells and the other with 12-18. In this work they were tentatively assigned to *L. obscura* C. Agardh and *L. reptabunda* (Suhr) Kylin, respectively.

The number of pericentral cells was not specified either in the original description of the species *Lophosiphonia obscura* (C. Agardh, 1828, as *Hutchinsia obscura*) or in the original description of the genus *Lophosiphonia* (Schmitz & Falkenberg, 1897). In later studies, J. Agardh (1842) described *Polysiphonia obscura* (C. Agardh) J. Agardh as having 5-7 pericentral cells, while the same author later contradicted himself describing the same species as having 12 pericentral cells (J. Agardh, 1863). On the other hand, Falkenberg (1901) described the species *L. obscura* (C. Agardh) Falkenberg as having 12-18 pericentral cells, while he used the name *L. subadunca* (Kützing) Falkenberg for the species with 6 pericentral cells based on *Polysiphonia subadunca* Kützing (1843). Kylin (1956) adopted the name *L. reptabunda* (Suhr) Kylin for the species with a larger number of pericentral cells, based on *Hutchinsia reptabunda* Suhr (1831) from Biarritz (France), while he used the name *L. obscura* for the species with 6 pericentral cells. Therefore, while Falkenberg (1901) named *L. obscura* for the species with a larger number of pericentral cells, Kylin (1956) adopted the same name for the species with 6 pericentral cells. Rueness (1971) later studied the type material of *L. obscura* and he found that all eight herbarium specimens studied uniformly had about 12 pericentral cells, and accordingly he followed Falkenberg (1901). In spite of largely discussed, the problem of what should be considered the type species of the genus *Lophosiphonia* is still unresolved.

In the Atlantic Iberian Peninsula, we have found three species related to the genus *Lophosiphonia*: one with 6 pericentral cells, another with 13-23 pericentral cells and a third species with 7 pericentral cells. Although aware of all nomenclatural problems regarding the involved taxa, we have provisionally followed Kylin's (1956) treatment for these species and we used the name *L. obscura* (C. Agardh) Falkenberg for the species with 6 pericentral cells, and the name *L. reptabunda* (Shur) Kylin for the species with 13-23 pericentral cells. The species with 7 pericentral cells is below proposed as a new species.

The species Lophosiphonia reptabunda

Hutchinsia reptabunda was originally described by Suhr (1831) based on materials from Biarritz, Atlantic France (Silva *et al.*, 1996). Later, Kützing (1843) transferred it to the genus *Polysiphonia*, and subsequently Kylin (1956) placed it in *Lophosiphonia*. Since then, the species has been widely reported in the Atlantic and Mediterranean coasts of Europe and Africa, as well as in scattered locations along the shores of the Pacific and Indian oceans. In spite of the relatively high number of records of this species, it remains poorly known because most of them came from checklists. To our knowledge, descriptions of *L. reptabunda* were provided only by Cribb (1956), Maggs & Hommersand (1993) and Rojas-González & Afonso-Carrillo (2002), based on materials from Australia, the British Isles and the Canary Islands, respectively. *Lophosiphonia reptabunda* is a turf-forming species widely distributed along the Atlantic Iberian Peninsula (e.g. Gorostiaga *et al.*, 2004; Bárbara *et al.*, 2005; Araújo *et al.*, 2009). In spite of its abundance, there are no available descriptions of the species from this area.

The most distinctive features found in *Lophosiphonia reptabunda* from the Atlantic Iberian Peninsula are: 1) dorsiventral structure with an extensive system of prostrate axes, 2) branches mostly endogenous, but exogenous ones are occasionally formed at the apices of erect axes in the axils of trichoblasts, 3) axes ecorticate with 13-23 pericentral cells, 4) rhizoids cut off from pericentral cells, 5) trichoblasts sometimes absent in young erect axes, but usually present in mature ones which have from poorly to extraordinarily developed trichoblasts formed on every segment, 6) 4-celled carpogonial branches, 7) bifurcated spermatangial axes without sterile apical cells, 8) one tetrasporangium per segment, formed in long spiral rows.

The features described for *Lophosiphonia reptabunda* from the Atlantic Iberian Peninsula are, in general, consistent with previous descriptions of the species from the eastern Atlantic coasts (Maggs & Hommersand, 1993; Rojas-González & Afonso-Carrillo, 2002). The only detected morphological differences lie in that specimens from the Atlantic Iberian Peninsula are often larger and have trichoblasts spirally arranged, while previous descriptions indicate that trichoblasts are initially abaxial and later spiral (Maggs & Hommersand, 1993; Rojas-González & Afonso-Carrillo, 2002). Concerning the records of *L. reptabunda* from the Pacific and Indian coasts, the information on its morphology is scarce. The only data that we found come from Australia (Cribb, 1956) and are in agreement with our description of the vegetative morphology, but Cribb did not provide data on the reproductive structures. With regard to materials from western coasts of America, they differ from the entity described here because they apparently have exogenous branches independent from trichoblasts and only 11 pericentral cells (Dawson, 1962, fig. 126c-d). Conversely, *L. reptabunda* in the Atlantic Iberian Peninsula has a higher number of pericentral cells and its branches are usually endogenous, while exogenous branches arise only occasionally and in the axils of trichoblasts. Finally, there are several records under the name *L. obscura* from the eastern central America which correspond to materials with 8-13 pericentral cells and unilaterally inserted trichoblasts (Taylor, 1960 as *L. subadunca*; Littler & Littler, 2000; Cetz-Navarro *et al.*, 2008; Dawes & Mathieson, 2008). These materials are apparently not in agreement either with *L. obscura* which has 6 pericentral cells (Falkenberg, 1901, Coppejans, 1983), or with *L. reptabunda* which has a higher number of pericentral cells. Furthermore, another distinctive feature is that these two species have spirally arranged trichoblasts (Falkenberg, 1901). A detailed comparative study of the morphology of specimens reported in the-different areas is necessary in order to clarify their specific assignment.

The characteristics of *Lophosiphonia reptabunda* are related to the genera *Lophosiphonia* and *Polysiphonia sensu lato*. The genus *Lophosiphonia* was created by Falkenberg (1901) for grouping those species previously placed in *Polysiphonia* which are characterized by dorsiventral structure, chiefly prostrate habit, endogenous origin of branches and formation of one tetrasporangium per segment. *Lophosiphoina reptabunda* is in agreement with the features proposed by Falkenberg (1901) for the genus. The only discrepancy is that we have occasionally observed exogenous branches, while endogenous branches are the most common ones in *L. reptabunda* from the Atlantic Iberian Peninsula. However, the features proposed by Falkenberg (1901) are apparently not enough to separate this genus from *Polysiphonia sensu lato* (Hollenberg, 1942). The latter genus has a high number of species, and although they are mostly erect with predominantly exogenous branches radially arranged (Maggs & Hommersand, 1993), several species have extensive prostrate axes with a dorsiventral structure and mostly endogenous branches. Hollenberg (1942) noted these problems regarding the separation between *Lophosiphonia* and *Polysiphonia* when he studied *L. villum* (currently *P. scopulorum* var. *villum*). Then, he added a new feature to delineate this genus, which is "*the dorsiventral or bilateral apex of all branches, evidenced by unilateral origin of either lateral branches or trichoblasts on the erect branches, or both*" (Hollenberg, 1968c). Accordingly, Hollenberg (1968c) considered that *Lophosiphonia villum (as L. scopulorum* var. *villum)* would be better accommodated in *Polysiphonia,* where it is currently placed. Therefore, following Hollenberg's criteria *L. reptabunda* would be also better placed in *Polysiphonia* because it has alternate or irregular branches and trichoblasts in spiral. However, the validity of this feature is questionable since *L. obscura,* which is the type species of the genus, seems to have trichoblasts and branches of erect axes arranged in spiral (Falkenberg, 1901; Rueness, 1971, both as *L. subadunca*; Coppejans, 1983; pers. obs.), and thus, the additional feature proposed by Hollenberg (1968c) to delineate the genus *Lophosiphonia* is apparently not present in the type species.

In agreement with Hollenberg (1942), our observations in several species of the tribe Polysiphonieae and the *Lophosiphonia* group show that the features proposed by Falkenberg (1901) seem to be insufficient to retain *Lophosiphonia* as a separate genus from *Polysiphonia sensu lato*, at least considering the current circumscription of the first genus. While these features are usually more obviously developed in *Lophosiphonia* than in *Polysiphonia sensu lato*, numerous species of the second taxon show a rather similar structure. For example, *P. atlantica*, *P. scopulorum* or *P. caespitosa* also have an extensive system of dorsiventral prostrate axes and a predominance of endogenous branches, although occasionally they also have exogenous branches (Maggs & Hommersand, 1993; Womersley, 2003; pers. obs.). In our opinion, the predominance of endogenous branches in some species might contribute to the morphological delineation of certain groups of species within *Polysiphonia sensu lato*, as Falkenberg (1901) and Kylin (1956) previously considered. Conversely, it is necessary to carry out a revaluation of their significance, considering species currently assigned to both *Lophosiphonia* and *Polysiphonia sensu lato*.

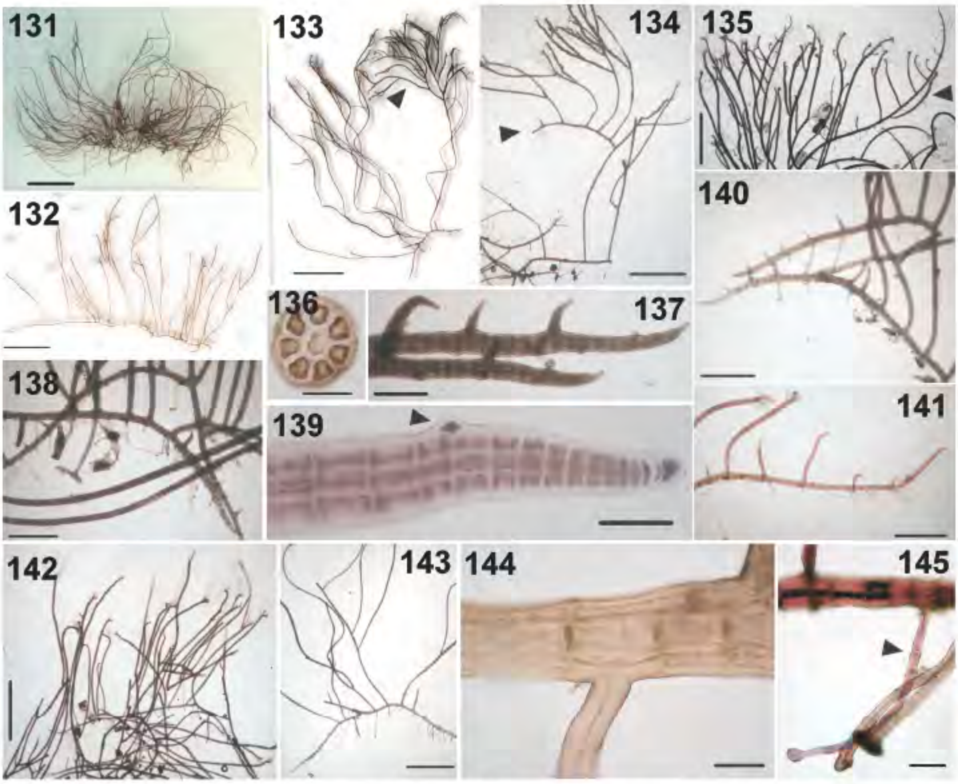
Likewise, other morphological features found in *Lophosiphonia reptabunda* are more similar to *Polysiphonia* than to other species currently assigned to *Lophosiphonia*. The number of pericentral cells is considerably lower in the other species of the genus (Table 3), while there are species with a similar number in *Polysiphonia* (e.g. Maggs & Hommersand, 1993). Rhizoids in *L. reptabunda* are cut off from pericentral cells, which differ from *L. obscura* and vary between species within *Lophosiphonia* (Table 3). According to the two mentioned features and considering also the 4-celled carpogonial branches found in *L. reptabunda*, this species is apparently similar to those placed the "multipericentral group" within *Polysiphonia sensu lato* (Choi *et al.*, 2001).

Lophosiphonia reptabunda is particularly characterized by its extraordinary development of trichoblasts and the furcated spermatangial axes. These features are similar to other species of the genus *Lophosiphonia*. Proportionally long trichoblasts were also reported in *L. cristata* and *L. obscura* (Coppejans, 1983; Rojas-González & Afonso-Carrillo, 2002). With regard to spermatangial branches, these were not detailed in most *Lophosiphonia* species, but furcated ones were also described in *L. obscura* (Falkenberg, 1901, as *L. subadunca*). By contrast, *Polysiphonia sensu lato* has usually simple spermatangial axes, while in some species and only occasionally furcated spermatangial branches are formed between the simple ones, such as in *P. foetidissima* (Kapraun, 1977, as *P. tepida*; Díaz-Tapia *et al.*, 2013c).

The genus *Lophosiphonia* needs a revision that initially should include a reappraisal of *L. obscura*, the type species of the genus, whose identity remains doubtful. In addition, the genus *Lophosiphonia* currently includes 10 species, most of which have been rarely recorded and remain poorly known. These species share the features proposed by Falkenberg (1901) to delineate the genus *Lophosiphonia*, but they show a great morphological variability in other traits that might be also relevant at the generic level (Table 3). Therefore, the generic assignment of most species to *Lophosiphonia* is doubtful. One of these important features lies in the rhizoids, which are in open connection to pericentral cells in four species of *Lophosiphonia* while they are cut off from pericentral cells in the three other taxa. Within the genus *Polysiphonia*, rhizoids cut off from pericentral cells are almost exclusive of *Polysiphonia sensu stricto*, while they are in open connection to pericentral cells in most of the other species (Choi *et al.*, 2001). Interestingly, this is one of the features delineating groups within *Polysiphonia sensu lato* that is showing a highest reliability. If the species placed in *Lophosiphonia* follow a similar pattern, this feature might indicate that at least two groups of species may be expected within the genus. Furthermore, other variable features among the species of the genus *Lophosiphonia* are the number of pericentral cells, the tetrasporangial arrangement (straight *vs.* spiral) and the arrangement of the trichoblasts (unilateral in *L. cristata vs.* spiral). These first two characteristics are also currently considered relevant in the separation of groups/ genera within *Polysiphonia sensu lato* (Choi *et al.*, 2001). Thus, *Lophosiphonia* nowadays includes species with a mixture of characteristics that might be indicating important differences between the species that belong to this genus and which are in part related to different groups of *Polysiphonia sensu lato*. Indeed, some species which were previously assigned to *Lophosiphonia* are currently included both in *Neosiphonia* and *Polysiphonia sensu stricto*: *Neosiphonia sacchorhiza* (F.S. Collins & Hervey) J.M.C. Nunes & S.M. Guimarães, *N. sparsa* (Setchell) I.A. Abbott and *P. scopulorum* (Hollenberg, 1968c; Creed *et al.*, 2010; Choi *et al.*, 2001; Abbott *et al.*, 2002). This suggests that not only the *Lophosiphonia* group is likely polyphyletic (Falkenberg, 1901; Hommersand, 1963), but the genus *Lophosiphonia* could also be polyphyletic.

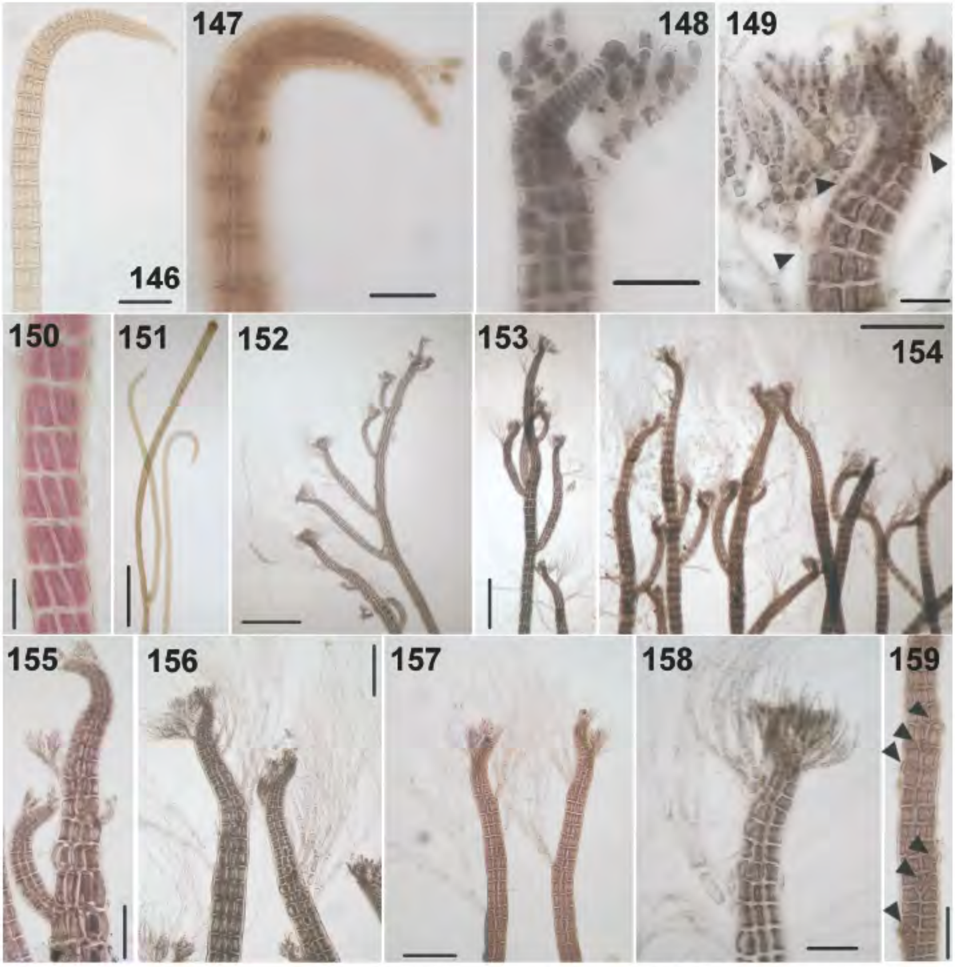
Lophosiphonia simplicissima* Díaz-Tapia, *sp. nov. **Figs 131-167**

Diagnosis: Thalli forming turfs up to 3 cm high, consisting of a dorsiventral extensive system of prostrate axes producing erect axes and rhizoids in open connection to pericentral cells, mostly unicellular but sometimes multicellular. Branches exclusively endogenous, those formed in erect axes often producing rhizoids and becoming prostrate; adventitious branches frequent. Axes ecorticate, with 7 pericentral cells, 50-140 μm in diameter. Trichoblasts from absent to largely developed spirally arranged every 1-3 segments. Spermatangial axes with 1-2 cylindrical bifurcations, replacing trichoblasts. Tetrasporangia forming straight or slightly spiral series, one per segment.
Type locality: Niembro, northern Spain (43°26'33"N, 4°50'20"W).
Holotype: SANT-Algae 24157, collected on 28.v.2010.
Etymology: from the Latin adjective "simplicissima", referring to the common absence or scarcity of branches in erect axes of sterile plants.
Molecular vouchers: no available COI-5P data.
Selected specimens: 1) Ondarreta (43°19'18"N; 2°00'11"W), 30.iii.2006, SANT-Algae 20195; 2) Ogeia (43°22'22"N; 2°32'35"W), 15.iii.2006 SANT-Algae 20330, 9.x.2006, SANT-Algae 19916; 3) Laida (43°24'28"N; 2°40'54"W), 31.iii.2006, SANT-Algae 20289; 4) Kobarón (43°21'10"N; 3°07'54"W), 12.ix.2006, SANT-Algae 19880 (tetrasporangial plants); 5) Ris



Figs 131-145. *Lophosiphonia simplicissima*. Habit and prostrate axes. **131.** Turf formed by entangled prostate and erect axes. **132.** Thallus consisting of a prostrate axes bearing scarcely branched erect axes. **133.** Thallus consisting of a prostrate axis bearing erect axes whose apical branches bear rhizoids: arrowhead – apical branch with rhizoids. **134.** Habit showing a prostrate axis growing from a branch of an erect axis: arrowhead – branch with rhizoids. **135.** Apex of erect axes becoming prostrate by developing rhizoids: arrowhead – erect axis with rhizoids. **136.** Cross section of an axis with 7 pericentral cells. **137.** Apex of prostrate axes with young erect axes. **138.** Old prostrate axes. **139.** Apex of a prostrate axis with a prominent apical cell: arrowhead – initial of an endogenous branch. **140-141.** Apex of prostrate axes with young erect axes curved towards the tip. **142-143.** Prostrate axes irregularly branched bearing further prostrate axes and erect ones. **144.** Rhizoid in open connection to the pericentral cell. **145.** Multicellular rhizoid between unicellular ones: arrowhead – cell wall dividing the two cells of the rhizoid. Scale bars: 5mm in Figs 131-133; 2 mm in Figs 134, 135, 137, 142 and 143; 50 µm in Figs 136, 139, 144 and 145; 600 µm in Figs 138, 140 and 141.

(43°29'38"N; 3°31'26"W), 16.iii.2006, SANT-Algae 18976; 6) Langre (43°28'37"N; 3°41'31"W), 6.xi.2010, SANT-Algae 24629; 7) Virgen del Mar (43°28'40"N; 3°52'31"W), 28.iii.2006, SANT-Algae 20402, 7.xi.2010, SANT-Algae 24637, 24649; 8) Somocueva (43°28'07"N; 3°56'43"W), 7.x.2006, SANT-Algae 20037 (male and female plants); 9) Oyambre (43°24'02"N; 4°20'10"W), 11.ix.2006, SANT-Algae 20134 (tetrasporangial plants); 10) Amio (43°23'42"N; 4°28'57"), 17.iii.2006, SANT-Algae 20423; 11) Niembro (43°26'33"N, 4°50'20"W), 8.x.2006, SANT-Algae 20095 (tetrasporangial plants), 28.v.2010, SANT-Algae 24155, 24157; 12) Llas (43°34'47"N; 7°15'27"W), 19.iv.2011; 13) Lago, San Cibrao (43°42'28"N; 7°28'32"W), 7.iv.2005, SANT-Algae 24505; 14) San Román (43°43'17"N; 7°37'39"W), 31.i.2006, SANT-Algae 17680; 15) Santa Cruz (43°20'51"N;



Figs 146-159. *Lophosiphonia simplicissima*. Erect axes. **146.** Apical cell of an erect axis. **147-148.** Apex of erect axes forming trichoblasts. **149.** Apex of an erect axis with several trichoblasts spirally arranged every two segments: arrowheads – basal cell of trichoblasts. **150.** Surface view of an axis showing twisted pericentral cells. **151.** Erect axes scarcely branched. **152.** Erect axis unilaterally branched. **153-154.** Erect axes alternately branched with abundant long trichoblasts. **155.** Apex of an erect axis with scattered short trichoblasts. **156-158.** Apex of erect axes with abundant trichoblasts, short when young and enlarged when mature. **159.** Scar cells of trichoblasts spirally arranged every 1-3 segments: arrowheads – scar cells. Scale bars: 100 µm in Figs 146, 155, 158 and 159; 50 µm in Figs 147-150; 600 µm in Figs 151, 152 and 154; 200 µm in Figs 153, 156 and 157.

8°20'58"W), 21.i.2004, SANT-Algae 25017; 16) Ártabra (43°21'12"N; 8°28'38"), 14.v.2010, SANT-Algae 24433; 17) Cabo de Mar (42°13'18"N; 8°43'32"W), 23.i.2008, SANT-Algae 21122; 18) Armaçao de Pêra (37°06'04"N; 8°22'17"W), 17.10.2005, SANT-Algae 24832; 19) Caneiros (37°06'14"N; 8°30'47"W), 18.x.2005, SANT-Algae 26218; 20) Coelho (37°4'22"N; 8°17'31"W), 7.v.2005, SANT-Algae 25292; 21) Santa Eulalia (37°05'11"N; 8°12'53"W), 19.x.2005, SANT-Algae 26300 (tetrasporangial plants); 22) Olhos d'Agua (37°05'20"N; 8°11'27"W), 6.v.2005, SANT-Algae 25771, 20.1ii.2011, SANT-Algae 26465

Figs 160-166. *Lophosiphonia simplicissima*. Reproductive morphology. **160.** Erect axis with immature cystocarps: arrowheads – immature cystocarps. **161.** Erect axes with spermatangial branches on branchlets: arrowheads – spermatangial axes. **162.** Immature spermatangial axes covering 2-3 branches of modified trichoblasts, with a furcated appearance. **163.** Apex of an erect axis with tetrasporangia forming rows on branches and main axes. **164.** Erect axis with tetrasporangia on branches. **165.** Tetrasporangia forming long slightly spiral series. **166.** Detail of tetrasporangia. Scale bars: 200 µm in Figs 160 and 165; 600 µm in Figs 161, 163 and 164; 50 µm in Figs 162 and 166.

(tetrasporangial plants); 23) El Puerto (36°34'48"N; 6°15'51"W) 16.xi.2005, SANT-Algae 26072; 24) Santibañez (36°28'03"N; 6°15'10"W), 18.ii.2011, SANT-Algae 26609 25) Caños de Meca (36°10'55"N; 6°00'06"W), 17.xi.2005, SANT-Algae 26146.

Vegetative and reproductive morphology

Thalli forming dense turfs up to 3 cm high (Fig. 131) and covering rock surfaces of up to *ca* 900 cm^2 in extent. Thallus dorsiventral, consisting of an extensive system of indeterminate and interwoven prostrate axes, ventrally bearing rhizoids that attach to the substrate, dorsally producing endogenous erect

Fig. 167. Distribution of *Lophosiphonia simplicissima* along the Atlantic Iberian Peninsula.

axes, and laterally branching to form further prostrate axes (Figs 132, 133). Erect axes unbranched or scarcely branched up to 3 orders; alternately or unilaterally arranged at irregular intervals (Figs 132-135). Erect axes often produce prostrate axes, both through the development of rhizoids in distal parts, as well as by producing branches from which arise rhizoids, chiefly in basal parts (Figs 133-135). Resulting thallus showing an irregular outline, with erect axes growing from prostrate ones and *vice versa*. Turfs dark brown; axes dark red or brown, with a fairly rigid texture. Blue-green pigmented spots were frequently observed in the walls of some cells.

Axes ecorticate, consisting of an axial cell and 7 pericentral cells (Fig. 136). Prostrate axes indeterminate and dorsiventral, growing by transverse divisions of a conspicuous apical cells *ca* 20 µm in diameter; tips slightly curved upwards or straight, without trichoblasts or scar cells (Figs 137-141). Prostrate axes (70-) 80-120 (-130) µm in diameter; composed of segments L/D (0.4-) 0.6-1.1 (-1.6). Prostrate axes dorsally branched bearing endogenous erect axes at irregular intervals (Figs 140-143), adventitious branches often formed in old parts. Prostrate axes bearing lateral endogenous branches at irregular intervals, developing further prostrate axes (Fig. 138). Rhizoids scattered, in open connection to pericentral cells, unicellular or rarely multicellular (Figs 143-145), mostly one per segment but sometimes two, (15-) 70-110 (-140) µm in diameter and up to 1200 µm long, sometimes terminated in digitate haptera.

Erect axes growing from domed apical cells *ca* 20 µm in diameter (Figs 146-148). Erect axes with apices curved towards the tip of prostrate axes or showing a sinusoidal outline if they bear trichoblasts (Figs 151, 156). Erect axes (50-) 70-110 (-140) µm in diameter, composed of segments L/D (0.3-) 0.6-1.2 (-1.6), pericentral cells often spirally-twisted in surface view (Fig. 150). Sterile plants with erect axes unbranched or forming scarce and scattered endogenous branches irregularly arranged. Plants bearing reproductive structures producing endogenous branches in apical parts, forming short lateral branches alternately or unilaterally arranged at irregular intervals (Figs 152-155). Adventitious branches often present, especially in basal parts of erect axes and on upper parts of plants bearing reproductive structures (Fig. 155). Trichoblasts absent (Fig. 146) or present from scarcely (Figs 147, 148) to well developed (Fig. 149). Trichoblasts are firstly short (Figs 148, 149); later, their cells enlarge, becoming long, up to 1.2 mm in length, and with basal cells up to 50 µm in diameter (Figs 152-154, 156-158). When they are well developed, trichoblasts arise every 1-3 segments mostly in a 1/7 spiral or they are spirally arranged at irregular intervals; dichotomously branched up to 5 orders, deciduous and leaving conspicuous scar cells (Fig. 159).

Gametophytes dioecious. Female structures formed in apical parts of erect axes. Only one specimen bearing immature cystocarps was observed (Fig. 160) and thus details on female structures cannot be described.

Spermatangial axes located at the apices of erect axes, both in main axes and lateral branches, spirally arranged every two segments (Fig. 161, 162). They grow on the suprabasal cell of modified trichoblasts, covering the two branches of the first dichotomy of trichoblasts and acquiring a bifurcated outline; or growing on the second dichotomy of trichoblasts and then forming two furcations. Each furcation is cylindrical, 110-175 µm long and 32-50 µm in diameter (Fig. 162).

Tetrasporangia formed in upper parts of erect axes (Figs 163, 164), both in main axes and lateral branches; axes bearing tetrasporangia often acquire a sinusoidal outline (Figs 164, 165). Tetrasporangia forming straight or slightly spiral series, which are sometimes long, with up to 12 mature tetrasporangia (Fig. 165). They are ovate, (40-) 50-70 (-85) µm in diameter, with 2 cover cells similar to pericentral cells (Fig. 166).

Phenology

Plants occur throughout the year, and they are probably perennial. Reproductive structures were rarely observed. Tetrasporangia were found in 20% of the collections, in samples taken in February and September-October. Male and female structures were found only once (3% of the collections), in October. *Lophosiphonia simplicissima* is highly variable in morphology. Numerous collections consisted of small specimens with erect axes sparsely branched and poorly developed trichoblasts when present (Fig. 132). Other collections consisted of larger specimens with more branched erect axes and abundantly developed trichoblasts (Figs 133-135).

Habitat and distribution

Lophosiphonia simplicissima grows forming turfs in sand-covered rocks from the mid to low intertidal, in sheltered to extremely wave-exposed shores. Turfs are rarely monospecific, while they are most commonly mixed with other species typical of this habitat such as *L. reptabunda* or *Rhodothamniella floridula*.

Lophosiphonia simplicissima is a common constituent of turf-forming assemblages from sand-covered rocks along the southern and northeastern of the Atlantic Iberian Peninsula (Fig. 167). With regard to other areas of this shore, *Lophosiphonia simplicissima* was found only in 5 sites from Galicia, where it was collected in moderately wave-exposed locations. The distribution of this species in Galicia probably might be expanded if more sheltered locations were sampled. It was not collected on the west coast of Portugal, which is in general highly to extremely wave-exposed.

Remarks

The most distinctive features of *Lophosiphonia simplicissima* are: 1) extensive system of prostrate axes with a dorsiventral structure, 2) branches exclusively endogenous, 3) axes ecorticate with 7 pericentral cells, 4) rhizoids in open connection to pericentral cells, occasionally multicellular, 5) trichoblasts sometimes absent in young erect axes, but usually present in reproductive ones which have from poorly to well developed trichoblasts formed every 1-3 segments, 6) spermatangial axes with 1-2 cylindrical bifurcations, 7) one tetrasporangium per segment, formed in straight or slightly spiral series. This combination of features distinguishes *L. simplicissima* from other species of *Lophosiphonia* (Table 3), as well as from other species of *Polysiphonia sensu lato* and, accordingly, it is proposed as a new species.

Lophosiphonia simplicissima always has 7 pericentral cells, while most species of *Lophosiphonia* and *Polysiphonia* with more than 4 pericentral cells usually show an interval. This peculiarity, among others, distinguishes *Lophosiphonia simplicissima* from their congeners, as well as from the other 12 species of *Polysiphonia sensu lato* with a similar number of pericentral cells that we found in literature in our attempt to assign our materials to a previously described species. The only two species of *Polysiphonia* that also have 7 pericentral cells are *P. constricta* Womersley and *P. decipiens* Montagne, both with type localities in Australia. They can be separated from *Lophosiphonia simplicissima* mainly because the two Australian species have rhizoids cut off from pericentral cells and branches arising from the basal cell of trichoblasts (Womersley, 1979, 2003).

Lophosiphonia simplicissima is similar to *L. obscura* (C. Agardh) Falkenberg, *Polysiphonia boldii* M.J. Wynne *et* P. Edwards and *P. hemisphaerica* Areschoug (Table 5), whose type localities are in Cádiz (southern Spain), Texas (U.S.A.) and Koster (Sweden), respectively. The only relevant morphological difference found among these species is the number of pericentral cells, which is 7 in *Lophosiphonia simplicissima* and 6 in *L. obscura, P. hemisphaerica* and *P. boldii* (Wynne & Edwards, 1970; Rueness, 1971; pers. obs.). In addition, these three species also differ from *L. simplicissima* by their habitat. While *L. simplicissima* was collected in sand-covered rocks of moderately to wave-exposed sites open to the sea, *L. obscura, P. boldii* and *P. hemisphaerica* are characteristic from sheltered sites where, at least in some cases, low salinities were registered (Wynne & Edwards, 1970; Rueness, 1971; pers. obs.). Interestingly, Rueness (1971) described blue-green pigmented spots in the cells walls of *P. hemisphaerica*, which were also frequently observed in *L. simplicissima*. He discussed that this spots could be minute endophytic cyanophyceans but any cell structure could not be found on them. Their origin remains uncertain.

Lophosiphonia simplicissima agrees with the concept of the genus *Lophosiphonia* delineated by Falkenberg (1901), since it has a dorsiventral thallus, chiefly prostrate habit, endogenous origin of branches and it forms one tetrasporangium per segment. By contrast, these features are not enough to keep this genus separated from *Polysiphonia sensu lato* (see remarks about *L. reptabunda*). However, considering morphological affinities between *L. simplicissima* and *L. obscura* we provisionally included the new species in the genus *Lophosiphonia*. However, it is noteworthy that we assume that *L. obscura* with 6 pericentral cells is the type species of the genus, despite the fact that circumscription of the type species of the genus *Lophosiphonia* remains to be resolved (see remarks on *L. reptabunda*).

In addition to the features proposed by Falkenberg (1901) to characterize the genus *Lophosiphonia*, *L. simplicissima* and *L. obscura,* share the peculiarity of having more than 4 pericentral cells and rhizoids in open connection to pericentral cells. Likewise, this combination of features is also present in *P. hemisphaerica* and *P. boldii*, whose close relationships between them and with *L. obscura* with 6 pericentral cells has been commented by Rueness (1971, 2010). Rhizoids in *Polysiphonia sensu lato* are either in open connection or cut off from pericentral cells. This feature was not evaluated by classical authors (e.g. Falkenberg, 1901; Kylin, 1956), however, later this character was widely used for the delineation of species (e.g. Maggs & Hommersand, 1993; Womersley, 2003). Recent studies have shown that all studied species with 4 pericentral cells and rhizoids in open connection to pericentral cells are placed in *Polysiphonia sensu stricto* in phylogenetic trees, while none of the species with these two features were to date placed outside this group (Choi *et al.*, 2001; Mamoozadeh & Freshwater, 2011, 2012; Bárbara *et al.*, 2013). Therefore, apparently the anatomy of rhizoids has a high taxonomic relevance, not only at the level of species delineation, but also for the separation of groups of species. While rhizoids in open connection are frequent in species with 4 pericentral cells, this feature is relatively rare among the species of *Polysiphonia sensu lato* with a higher number of pericentral cells. We could find only six species of *Polysiphonia sensu lato* with these two features (listed in Table 4), a combination that is present in only three species of *Lophosiphonia* (Table 3). Therefore, this is a rare combination of features and further researches are necessary to understand their significance and its possible usefulness as additional features to those proposed by Falkenberg (1901) in the delineation of the genus *Lophosiphonia.*

The bifurcated (often twice) spermatangial branches of *Lophosiphonia simplicissima* is another peculiarity characterizing this species, and it also could be useful in the delineation of the genus *Lophosiphonia*. Although we could not study fertile material of *L. obscura*, Falkenberg (1901) described similar spermatangial branches in *L. subadunca*, which is here tentatively considered a taxonomic synonym of *L. obscura*. Likewise the related species *P. boldii* and *P. hemisphaerica* also have similar spermatangial branches (Table 4). Conversely, bifurcated spermatangial branches also characterize the genus *Ctenosiphonia* (Rojas-González & Afonso-Carrillo, 2000) and were sometimes observed in some species of *Polysiphonia sensu lato* among the simple ones (e.g. *Polysiphonia foetidissima*, Díaz-Tapia *et al.*, 2013c).

Ophidocladus simpliciusculus (P.L. Crouan *et* H.M. Crouan) Falkenberg **Figs 168-197**

Basionym: *Polysiphonia simpliciuscula* P.L. Crouan *et* H.M. Crouan.

Holotype (?): CO (Womersley 2003).

Type locality: Anse du Minou, Finistère, France.

Synonyms: *Ophidocladus herposiphonioides* Joly *et* Cordeiro; *Rhodosiphonia californica* Hollenberg; *Ophidocladus californicus* (Hollenberg) Kylin.

References: Gayral, 1958; Dawson, 1963; Joly *et al.*, 1963; Saenger, 1971; Abbott & Hollenberg, 1976; Wynne, 1995; Rojas-González & Afonso-Carrillo, 2001a; Rull Lluch, 2002; Womersley, 2003.

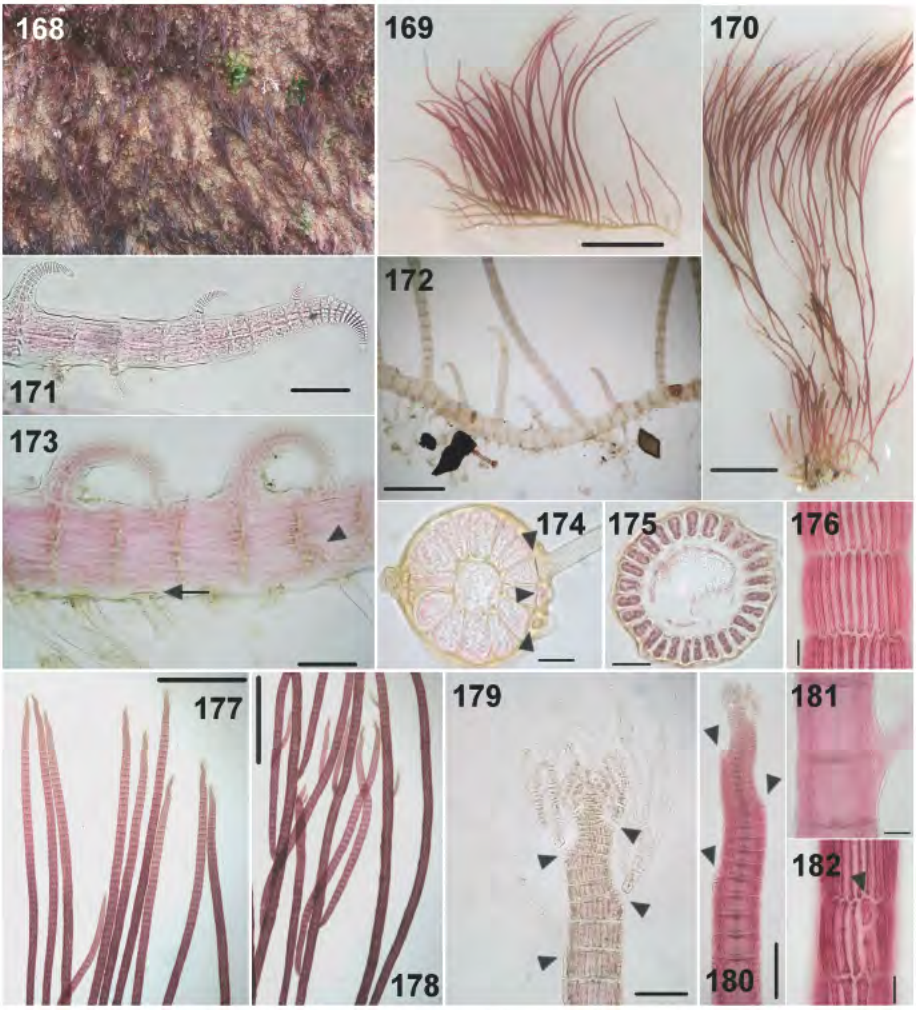
Molecular vouchers: GenBank accession numbers KF648512, KF648518, KF648520, KF671146, KF671148, KF671150, KF671156, KF671162, KF671168, KF671169, KF671180, KF671183.

Selected specimens: 1) Biarritz (43°29’03”N; 1°33’46”W), 19.iii.2011, SANT-Algae 25413; 2) Zumaia (43°17’59”N; 2°15’41”W), 9.ix.2006, SANT-Algae 19666 (tetrasporangial

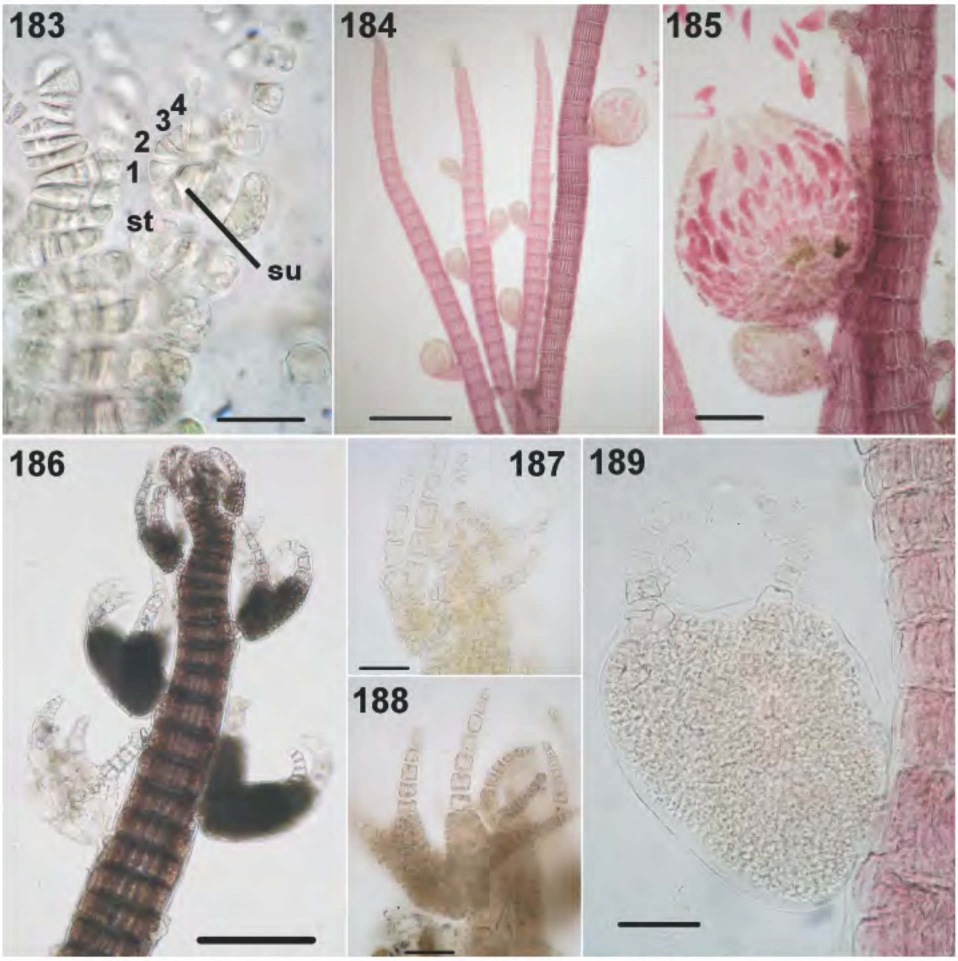
Table 4. Comparison of selected morphological features among species of *Lophosiphonia* and *Polysiphonia sensu lato* with more than 4 pericentral cells and rhizoids in open connection to pericentral cells

	Thallus	*Pericentral cells*	*Branches origin*	*Branches in erect axes*	*Tetra-sporangia*	*Spermatangial branches*	*References*
Lophosiphonia cristata Falkenberg	Dorsiventral	9-11	Endogenous	Unbranched	Spiral	Replacing trichoblasts; bifurcated	Falkenberg 1901, Rojas-González & Afonso-Carrillo 2002
Lophosiphonia obscura (C. Agardh) Falkenberg	Dorsiventral	6	Endogenous	Independent from trichoblasts	–	Replacing trichoblasts; bifurcated	Falkenberg 1901, Coppejans 1983, pers. obs.
Lophosiphonia simplicissima	Dorsiventral	7	Endogenous	Independent from trichoblasts	Slightly spiral	Replacing trichoblasts; bifurcated	This work
Polysiphonia adamsiae Womersley	Dorsiventral	8-12	–	Independent from trichoblasts	Gently spiral	Replacing trichoblasts; simple	Womersley 1979, 2003; Adams 1991, 1994
Polysiphonia aterrima J.D. Hooker *et* Harvey	Erect	9-12	–	Independent from trichoblasts	Spiral	On a branch of trichoblasts; bifurcated	Adams 1991, 1994
Polysiphonia boldii M.J. Wynne *et* P. Edwards	Dorsiventral	6	Endogenous	Independent from trichoblasts	Straight	Replacing trichoblasts; bifurcated	Wynne & Edwards 1970
Polysiphonia dotyi Hollenberg	Decumbent (with scar cells in prostrate axes)	8-10	–	In association with trichoblasts	Spiral	On a branch of trichoblasts; simple	Hollenberg 1968d
Polysiphonia hemisphaerica Areschoug	Dorsiventral	6	Endogenous	Independent from trichoblasts	Slightly spiral	Replacing trichoblasts; bifurcated	Rueness 1971
Polysiphonia teges Womersley	Dorsiventral	6	Endogenous	Independent from trichoblasts	Spiral	Unknown	Womersley 1979, 2003

plants); 9.ix.2006, SANT-Algae 27323 (mixed phases bearing male structures and tetrasporangia); 3) Ogeia (43°22'22''N; 2°32'35''W), 9.x.2006, SANT-Algae 27320 (mixed phases bearing male structures and tetrasporangia); 4) Laida (43°24'28''N; 2°40'54''W), 31.iii.2006, SANT-Algae 20280; 5) Virgen del Mar (43°28'40''N; 3°52'31''W), 7.xi.2010, SANT-Algae 24651 (female and tetrasporangial plants); 6) Somocueva (43°28'07''N; 3°56'43''W), 7.x.2006, SANT-Algae 20001 (mixed phases bearing male structures and tetrasporangia plants); SANT-Algae 27326 (female plants); 7) Valdearenas (43°27'13''N; 3°57'37''W), 11.viii.2010, SANT-Algae 24445 (male and female plants); 8) Aguilar (43°33'28''N; 6°07'07''W), 17.iv.2007, SANT-Algae 19819; 9) Serantes (43°33'27''N; 6°58'39''W), 28.vii.2010, SANT-Algae 27324 (female and male plants); 10) Catedrales (43°33'16''N; 7°09'16''W), 20-ix-2005, SANT-Algae 16551 (tetrasporangial plants); SANT-Algae 16558 (mixed phases bearing male structures and tetrasporangia); 11) Pantín (43°38'29''N; 8°06'37''W), 26.vi.2007, SANT-Algae 19832; 12) Chanteiro (43°26'46''N; 8°18'15''W), 17.ix.2005, SANT-Algae 19609 (tetrasporangial); SANT-Algae 27321 (mixed phases bearing male structures and tetrasporangia); 13) Playa de Barrañán (43°18'44''N; 8°33'22''W), 11.ix.2002, SANT-Algae 15175 (tetrasporangial plants); 5.xii.2002, SANT-Algae 27325 (mixed phases bearing male structures and tetrasporangia); 14) Leira

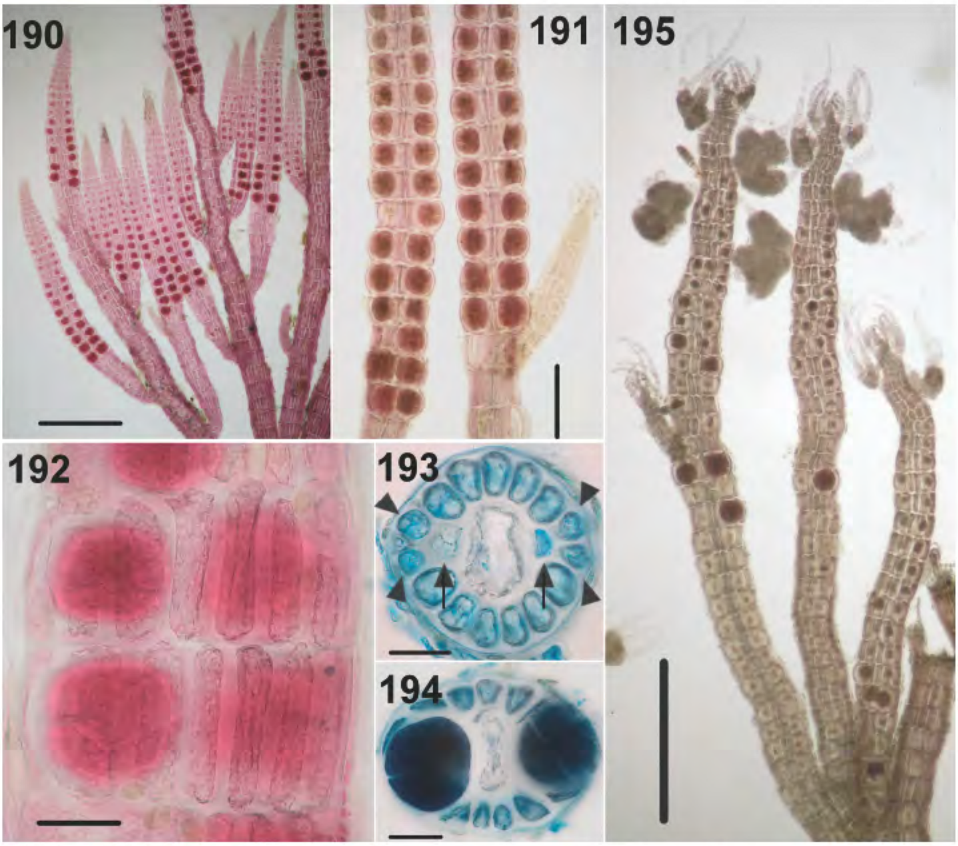


Figs 168-182. *Ophidocladus simpliciusculus*. Vegetative morphology. **168.** Turf in sand-covered rocks. **169-170.** Habit consisting of prostrate axes bearing dorsally erect axes and laterally branches that form further prostrate axes. **171.** Apex of a prostrate axis with a prominent apical cell, forming dorsally endogenous determinate axes and ventrally rhizoids. **172.** Mature prostrate axis forming adventitious erect axes between the oldest ones. **173.** Prostrate axis bearing ventrally rhizoids cut off from pericentral cells, laterally developing indeterminate axes and dorsally bearing young erect axes curved to the apex of prostrate axis: arrow - wall separating the pericentral cell and the rhizoid, arrowhead – young lateral indeterminate branch. **174.** Cross section of a prostrate axis with 13 pericentral cells, showing the origin of three rhizoids cut off from pericentral cells: arrowheads - walls separating the pericentral cells and the rhizoids. **175.** Cross section of an erect axis showing 27 pericentral cells and a large axial cell. **176.** Surface view of an erect axis. **177.** Erect axes with straight apices. **178.** Medium portion of erect axes with branches alternately to irregularly arranged. **179.** Apex of an erect axis with well developed trichoblasts arranged in two opposite rows and several segments apart: arrowheads – basal cells of trichoblasts. **180.** Apex of an erect axis with scar cells of trichoblasts several segments apart – arrowheads: scar cells. **181.** Optical section of an erect axis showing the large axial cell and bearing a young endogenous branch. **182.** Surface view of an erect axis: arrowhead - scar cell of a trichoblast. Scale bars: 5 mm in Figs 169 and 170; 100 µm in Figs 171, 173, 179 and 180; 600 µm in Fig. 172; 50 µm in Figs 174-176, 181 and 182; 2 mm in Figs 177 and 178.



Figs 183-189. *Ophidocladus simpliciusculus*. Sexual structures. **183.** Procarp formed in a modified trichoblast showing the supporting cell (su) bearing the 4-celled carpogonial branch (1-4) and a basal sterile cell (st). **184.** Erect axes with cystocarps bilaterally arranged. **185.** Detail of a mature cystocarp. **186.** Spermatangial branches bilaterally arranged in the apical parts of an erect axis. **187.** Early stage in the formation of a spermatangial branch on a 2-orders branched trichoblast. **188.** Development of a spermatangial branch, showing two conspicuous furcations, each of them in turn divided in other two furcations, each lobule has in the apex a sterile filament. **189.** Mature spermatangial branch, globose and with four sterile filaments in the tips. Scale bars: 25 µm in Fig. 183; 600 µm in Fig. 184; 200 µm in Figs 185, 186; 50 µm in Figs 187-189.

(43°18'37''N; 8°38'00''W), 4.xii.2002, SANT-Algae 18024 (tetrasporangial plants); 15) Barizo (43°18'48''N; 8°52'27''W), 5.iv.2004, SANT-Algae 24952; 16) Arou (43°11'03''N; 9°06'46''W); 6.iv.2004, SANT-Algae 26408; 17) Lariño (42°45'50''N; 9°07'04''W), 19.viii.2005, SANT-Algae 22779 (tetrasporangial plants); 18) Playa de Arnela (42°42'35''N; 9°00'47''W), 30.i.2006, SANT-Algae 24354 (mixed phases bearing male structures and tetrasporangia); 19) Area da Cruz (42°27'40''N; 8°54'37''W), 22.viii.2005, SANT-Algae 25062; 20) Nerga (42°15'19''N; 8°50'07''W), 12-ii-2005, SANT-Algae 22825; 21) Leça de Palmeira (41°12'22''N; 8°43'03''W), 26.x.2004, SANT-Algae 16255; SANT-Algae 27322



Figs 190-195. *Ophidocladus simpliciusculus*. Tetrasporangia. **190-191.** Tetrasporangia formed in two longitudinal rows on the upper parts of erect axes and lateral branches. **192.** Surface view of segments bearing tetrasporangia. **193.** Cross section of a tetrasporangial branch: arrows opposite initial cells of tetrasporangia, arrowheads - cover cells. **194.** Cross section of a branch with mature tetrasporangia. **195.** Erect axes bearing spermatangial branches and tetrasporangia. Scale bars: 600 µm in Figs 190 and 195; 200 µm in Fig. 191; 50 µm in Figs 192-194.

Figs 196-197. Distribution of *Ophidocladus simpliciusculus*. **196.** Collections along the Atlantic Iberian Peninsula. **197.** World distribution: arrow – type locality.

(mixed phases bearing male structures and tetrasporangia); 22) Buarcos (40°10’58”N; 8°54’29”W), 15.xi.2004, SANT-Algae 16246 (mixed phases bearing male structures and tetrasporangia); SANT-Algae 15890 (tetrasporangial plants); 23) Vale Furado (39°41’04”N; 9°03’33”W), 12.vi.2010, SANT-Algae 24811 (male and female plants); 24) Baleal (39°22’25”N, 9°19’56”W), 14.vi.2010, SANT-Algae 24254; 25) Guincho (38°43’29”N; 9°28’41”W), 13.vi.2010, SANT-Algae 24795 (male and female plants); 26) Queimado (37°49’34”N; 8°47’34”W), 24.v.2005, SANT-Algae 25251; 27) Almograve (37°39’54”N; 8°48’04”W), 25.v.2005, SANT-Algae 24772; 28) Ingrina (37°02’46”N; 8°52’43”W), 9.v.2005, SANT-Algae 25212; 29) Coelho (37°4’22”N; 8°17’31”W), 7.v.2005, SANT-Algae 25302 (tetrasporangial plants); 30) Cala Encendida (36°18’40”N; 6°09’12”W), 18.ii.2011, SANT-Algae 26629.

Vegetative and reproductive morphology

Thalli forming dense turfs up to 5 cm high and covering rock surfaces of up to several meters in extent (Fig. 168). Thallus dorsiventral, consisting of an extensive system of indeterminate and interwoven prostrate axes which bear ventrally numerous rhizoids that attach to the substrate, dorsally produces endogenous erect axes, and laterally branches to form further prostrate axes (Figs 169, 170). Erect axes unbranched or scarcely branched, alternate or irregular, up to 3 orders. Erect axes dark pink-red in colour, and prostrate ones light pink to almost white, with a fairly rigid texture.

Axes fully ecorticate. Prostrate axes indeterminate and dorsiventral, growing by transverse divisions of conspicuous apical cells which are 12-18 µm in diameter; apices curved downwards, without trichoblasts nor scar cells (Fig. 171). Prostrate axes (150-) 170-250 (-270) µm in diameter when mature; composed of segments L/D (0.35-) 0.5-0.9 (-1); that consist of an axial cell (42.5-) 55-80 (-100) µm broad and (11-) 12-14 (-15) pericentral cells (42.5-) 55-75 (-90) µm broad (Fig. 174). Prostrate axes scarcely, and irregularly branched laterally to form further prostrate axes, with a narrow angle forming parallel prostrate axes (Figs 169, 173). Prostrate axes bearing dorsally erect ones at intervals of 3-5 segments, sometimes adventitiously in old parts of prostrate axes (Figs 171-173). Both lateral and dorsal branches are formed endogenously. Rhizoids cut off from the pericentral cells, unicellular, abundantly developed up to 3 per segment, (25-) 30-40 µm in diameter and up to 450 µm long, occasionally terminated in digitate haptera (Figs 172-174).

Erect axes growing from domed apical cells which are 12-18 µm in diameter. Young erect axes have apices curved in the direction to the apical cell of the prostrate axes (Figs 171, 173); while the apices of mature erect axes are straight (Fig. 177). Erect axes (130-) 150-230 (-270) µm in diameter, composed of segments L/D (0.4-) 0.6-0.9 (-1); that consist of axial cells (35-) 40-110 (-120) µm broad which are surrounded by (16-) 19-25 (-28) pericentral cells (15-) 25-50 µm broad (Figs 175, 181). In surface view, pericentral cells are displaced between successive segments (Fig. 176). Erect axes of sterile and gametophytic plants scarcely branched endogenously (Fig. 178), up to 3 orders; erect axes bearing tetrasporangia usually develop abundant lateral branches in upper parts; adventitious branches present. Trichoblasts usually numerous (Fig. 179), but sometimes are short (Fig. 180), arising alternately and forming two opposite rows, mostly every 3-5 segments; dichotomously branched up to 4 orders; deciduous and leaving conspicuous scar cells (Fig. 182).

Gametophytes dioecious. Procarps are formed on suprabasal cells of modified trichoblasts in the upper parts of erect axes; and they consist of a four-celled carpogonial branch, a basal sterile cell (Fig. 183) and a group of two sterile cells borne on the supporting cell. Cystocarps (Figs 184, 185) globular when mature, (300-) 350-600 (-650) µm high and (300-) 330-500 (-550) µm in diameter, with an ostiole (50-) 70-150 (-250) µm. Carposporangia clavate, (20-) 25-40 (-50) × (80-) 90-130 (-150) µm.

Spermatangial branches located at the apices of main axes and lateral branches, mostly arising every 3-5 segments (Fig. 186). Spermatangial axes formed on the suprabasal cell of modified trichoblasts, which are branched up to 2 (-3)-orders; spermatangia develop from the basal parts toward the apices, covering the 2 (-3) branching orders of trichoblasts (Figs 187, 188). Young spermatangial branches acquire a lobate appearance in several planes, usually formed by two basal furcations bearing each of them in turn other two furcations (Fig. 188). A sterile filament of 5-7 cells remains at the apex of each lobule. Later, spermatangial axes enlarge, resulting in a globose structure with slightly marked lobes (Fig. 189); apical sterile filaments sometimes break remaining only 1-2 sterile apical cells per filament at maturity. Spermatangial axes (140-) 180-250 (-280) µm long and (140-) 180-260 (-290) µm wide.

Tetrasporangia in upper branches (Fig. 190), formed in 2 longitudinal opposite rows with up to 12 mature tetrasporangia (Fig. 191); ovate, (35-) 45-70 (-80) µm in diameter, with 2 cover cells similar to pericentral cells (Figs 192-194). Mixed phases bearing tetrasporangia and spermatangial branches were observed (Fig. 195).

Phenology

Plants occur throughout the year, and they are probably perennial. Tetrasporangia were frequently observed year-round and they were found in 30% of the collections. By contrast, sexual structures are rare. Until 2010, female structures were only found once and only in a few erect axes bearing procarps and immature cystocarps; while mixed phases bearing spermatangial branches and tetrasporophytes were observed in 8% of the collections. Curiously, in 2010 female gametophytes were frequently observed. During this year 12 collections of the species were carried out, and 42% of them bore female gametophytes; and one of these collections also had male gametophytes (without tetrasporangia). Thus, sexual structures in *Ophidocladus simpliciusculus* are rare along the Atlantic Iberian Peninsula, but their occurrence seems to depend on the timing. Interestingly, the production of female structures was observed at wide scale during 2010, as female plants were found at locations up to 1000 km apart.

Habitat and distribution

Ophidocladus simpliciusculus forms extensive turfs in sand-covered rocks from the mid intertidal to upper subtidal of moderately to extremely wave-exposed sites. Turfs are monospecific or mixed with other species, chiefly *Pterosiphonia pennata*. Another common constituent in these turfs is *Polysiphonia nigra,* whose habit in the field is similar to that of *O. simpliciusculus*. Both can be separated in the field by the extensive prostrate system of *O. simpliciusculus*, which is almost white in colour; while *P. nigra* has a shorter prostrate system almost black in colour. Both species are easily distinguishable by their morphological details, such as the number of pericentral cells, the trichoblasts arrangement or the number of tetrasporangia per segment.

Ophidocladus simpliciusculus is one of the most frequent and abundant species in sand-covered rocks of the Atlantic Iberian Peninsula (Fig. 196). Although it was found along all the studied area (Fig. 196), it was more frequent and abundant in Galicia and western Portugal (the colder areas), while abundance and frequency decreased towards the East and the South of the Iberian Peninsula. *Ophidocladus simpliciusculus* was recorded in southern Europe and northern Africa, southern Africa, Brazil, Pacific North America and Australia (Fig. 197).

Remarks

Polysiphonia simpliciuscula was originally described from the French Brittany in 1852 (Crouan & Crouan, 1852). After that, Falkenberg separated the species from *Polysiphonia* creating a new genus: *Ophidocladus* (Schmitz & Falkenberg, 1897). It is distinctively characterized by a polysiphonous architecture with dorsiventral structure and the formation of two tetrasporangia per segment (Schmitz & Falkenberg, 1897). The genus *Ophidocladus* was firstly placed in the tribe Herposiphonieae (Schmitz & Falkenberg, 1897), and subsequently Falkenberg (1901) moved it, together with other genera, to a group that was later named by Kylin (1956) as "*Lophosiphonia* group". However, it is probably polyphyletic (Falkenberg, 1901; Hommersand, 1963) and a revision is necessary to ascertain the taxonomic position of members of the *Lophosiphonia* group (see remarks on *Ctenosiphonia hypnoides*).

Ophidocladus simpliciusculus was reported in numerous locations of world temperate coasts and descriptions of the species were provided from Morocco (Gayral, 1958), the Canary Islands (Rojas-González & Afonso-Carrillo, 2001a), South Africa (Saenger, 1971), Namibia (Rull Lluch, 2002), Brazil (Joly *et al.*, 1963), Pacific North America (Abbott & Hollenberg, 1976; Dawson, 1963) and Australia (Womersley, 2003). Conversely, an updated detailed description of materials from the European coasts, where the type locality is from, was not provided to date. *Ophidocladus simpliciusculus* is widely distributed along the Atlantic Iberian Peninsula (e.g. Bárbara *et al.*, 2005; Gorostiaga *et al.*, 2004; Araújo *et al.*, 2009), where it is one of the most frequent and abundant turf-forming species in sand-covered rocks.

We visited the type locality of *Ophidocladus simpliciusculus* in 2011 (Anse du Minou, Brittany, France) with the aim to collect new materials. Unfortunately and although the habitat of this site was similar to those where the species grows in the Atlantic Iberian Peninsula, we could not find any specimen. The current northernmost population of *O. simpliciusculus* that we could detect is in Biarritz (southern France). However, it must be noted that J. Cabioch has collected this species in October 1980 and February 1982 in the Bay of Morlaix (pers. com.).

The world distribution of *Ophidocladus simpliciusculus* is rather peculiar in that it was reported in scattered and distant locations in world temperate areas. Curiously, despite the distance, sand-covered rocks are mentioned in most descriptions as the typical habitat for *O. simpliciusculus* (Hollenberg, 1943; Oliveira-Filho, 1969; Saenger, 1971; Rojas-González & Afonso-Carrillo, 2001a). Schmitz & Falkenberg (1987) pointed out that materials from Australia (as New Holland) probably belong to a different species. On the other hand, materials from California and Brazil were described as *O. californicus* (Hollenberg) Kylin and *O. herposiphonioides* Joly *et* Cordeiro (Hollenberg, 1943 as *Rhodosiphonia californica*; Joly *et al.*, 1963), respectively; but later both species were synonymized with *O. simpliciusculus* (Saenger, 1971). Although detailed descriptions were provided in the floras from the different areas, the comparative study of them and the features of materials from the Atlantic Iberian Peninsula did not show enough relevant morphological differences to consider separate species. The only detected differences are related to the size of axes and the number of pericentral cells. *Ophidocladus simpliciusculus* from Brazil (Joly *et al.*, 1963) and Namibia (Rull Lluch, 2002) are similar to specimens from the Atlantic Iberian Peninsula (*ca* 12-28 pericentral cells and up to 290 µm in diameter). Materials from the Canary Islands (Rojas-González & Afonso-Carrillo, 2001a) and South Africa (Saenger, 1971) have a similar number of pericentral cells (12-25), but are narrower (up to 200 µm). By contrast, materials from Pacific North America and Australia have fewer pericentral cells and are narrower than those from the Iberian Peninsula (10-22 pericentral cells and up to 200 µm in diameter). Despite that these differences seem not relevant to separate species, in our opinion the distant and isolated locations in which *O. simpliciusculus* was reported, might host a cryptic species diversity that is difficult to delineate based exclusively on morphological features. Molecular analysis of materials from these areas would be desirable in order to assess whether all those collections belong to a single species.

The most distinctive features of *Ophidocladus simpliciusculus* from the Atlantic Iberian Peninsula are: 1) extensive system of prostrate axes with a dorsiventral structure, 2) branches exclusively endogenous, 3) axes ecorticate, with 12-14 and 19-25 pericentral cells in prostrate and erect axes, respectively, 4) rhizoids cut off from pericentral cells, 5) trichoblasts alternately arranged every 3-5 segments, 6) spermatangial axes globose at maturity, with 4 terminating filaments, 7) two tetrasporangia per segment.

A dorsiventral structure that is similar to that showed by *Ophidocladus simpliciusculus* is found only in the tribe Herposiphonieae, and the other four genera currently assigned to the *Lophosiphonia* group (Falkenberg, 1901; Kylin, 1956). Furthermore, some species of *Polysiphonia sensu lato* share with the *Lophosiphonia* group a similar dorsiventral structure, such as *P. scopulorum* Harvey (Womersley, 2003). By contrast, *O. simpliciusculus* is apparently the only species in which prostrate and erect branches have a different structure in cross section. The number of pericentral cells is considerably higher in erect axes than in prostrate ones. Furthermore, the erect axes in *O. simpliciusculus* have an axial cell much larger than pericentral ones, which is apparently unlike any other Rhodomelaceae. Conversely, prostrate axes have an axial cell with a more similar size to pericentral ones. Thus, secondary dorsiventrality in *O. simpliciusculus* not only involves the fact that prostrate and erect axes can be clearly differentiated, but also involves that both have a different structure in cross section.

The number of pericentral cells in *O. simpliciusculus* is the highest reported in the family Rhodomelaceae. The range of pericentral cells often described for the family is 4-24 (Maggs & Hommersand, 1993; Womersley, 2003), but it can be even slightly higher in *O. simpliciusculus* (up to 28). A comparatively similar high number of pericentral cells is reported only in some members of the Polysiphonieae, Pterosiphonieae and the *Lophosiphonia* group (Maggs & Hommersand, 1993).

The exclusive formation of endogenous polysiphonous branches in *Ophidocladus simpliciusculus* is shared with the other members of the *Lophosiphonia* group (Table 2) with the only exception of *Stichothamnion*, which has endogenous and exogenous branches (Børgesen, 1930). Other members of the Rhodomelaceae have only endogenous branches, as is the case of the tribe Rhodomeleae; or the origin of branches is exclusively exogenous, as in Pterosiphonieae; or both kinds of branches are present, as in Polysiphonieae (Maggs & Hommersand, 1993; Womersley, 2003). The interrelationship and distribution of the various types of lateral branches may be of taxonomic significance as they vary between genera and even species (Scagel, 1953).

Trichoblasts in *Ophidocladus simpliciusculus* are formed in two opposite rows in an alternate-distichous pattern. This feature differs from all the other genera of the *Lophosiphonia* group (Table 2) and, again, this is unusual within the Rhodomelaceae. Trichoblasts, when present, are often spirally arranged; or they are unilaterally inserted as in Amansieae, *Ctenosiphonia* and some members of the genus *Lophosiphonia* (Falkenberg, 1901; Hommersand, 1963; Rojas-González, 2001a). Alternate-distichous pattern of lateral branches is typical of some groups of the Rhodomelaceae as for example in *Pterosiphonia*, but even within this genus, the spermatangial axes replacing trichoblasts, arise spirally (Hommersand, 1963; Díaz-Tapia & Bárbara, 2011).

Spermatangial axes in *Ophidocladus simpliciusculus* show an unusual morphology. Superficially, similar male structures are found in the tribe Amansieae and Pleurostichidiae, which are characterized by globose spermatangial axes. By contrast, the spermatangial axes in Pleurostichidiae are not formed on trichoblasts, but they arise adventitiously from surface cortical cells and many spermatangial branches are formed per segment (Phillips, 2000). With regard to the tribe Amansieae, spermatangial axes are formed on modified trichoblasts, but replacing the whole trichoblasts, or on polysiphonous processes on the blades; and sterile apical cells are absent (Maggs & Hommersand, 1993; Womersley, 2003). By contrast, in *O. simpliciusculus* spermatangial axes are formed on the suprabasal cell of modified trichoblasts, two-orders branched, and four apical sterile filaments are present in the mature globose structure. The formation of bifurcated spermatangial axes has been reported in some species of *Polysiphonia* (e.g. *P. tepida*, *P. scopulorum*; Kapraun, 1977; Womersley, 2003), but in these species spermatangial axes are usually simple and cylindrical, and only occasionally bifurcated spermatangial axes are formed between the simple ones, maintaining this appearance at maturity. *Ctenosiphonia* also has spermatangial axes with four furcations, but they are formed on the second dichotomy of a modified trichoblasts and remain as four cylindrical branches at maturity (Rojas-González & Afonso Carrillo, 2000). By contrast in *O. simpliciusculus*, spermatangial axes are formed on the first dichotomy of trichoblasts and acquire a globose appearance at maturity.

Tetrasporangia in *Ophidocladus simpliciusculus* are formed in two opposite longitudinal rows, while most members of the Rhodomelaceae have a single tetrasporangium per segment. This feature is not exclusive of *Ophidocladus* and other members of the family that characteristically have two tetrasporangia per segment are the tribes Sonderelleae (Phillips, 2001), Rhodomeleae (Maggs & Hommersand, 1993) and Amansieae (Womersley, 2003); some members of the Lophothalieae and, more rarely, of the Polysiphonieae (*Leptosiphonia, Perrinia*). Within the *Lophosiphonia* group (Table 2), this feature is also characteristic of the genera *Oligocladella* (Weber-Van Bosse, 1913) and *Ctenosiphonia* (Rojas-González, 2001a).

In summary, *Ophidocladus simpliciusculus* has a combination of features that clearly distinguish it from the other members of the Rhodomelaceae. Indeed, some of these features are virtually unique within the family. Falkenberg (1901) considered that *O. simpliciusculus* has features typical from the Amansieae, Herposiphonieae and Polyzonieae; but at the same time, it differs from these groups. The *Lophosiphonia* group is artificial (Falkenberg, 1901), and thus probably the genera currently assigned to it would be better accommodated in other tribes, both in previously described taxa as well as in new tribes. This has previously occurred in *Pleurostichidium* which has been segregated as a monotypic tribe, firstly based on morphological features and later confirmed by molecular data (Hommersand, 1963; Phillips, 2000). The genus *Ophidocladus* has enough peculiar morphological features to be distinguished from others members of the

Lophosiphonia group, as well as, from other taxa from the Rhodomelaceae. Phylogenetic studies using molecular characters are required to clarify the taxonomic position of this peculiar genus.

Polysiphonia caespitosa (M.A. Pocock) Hollenberg **Figs 198-224**

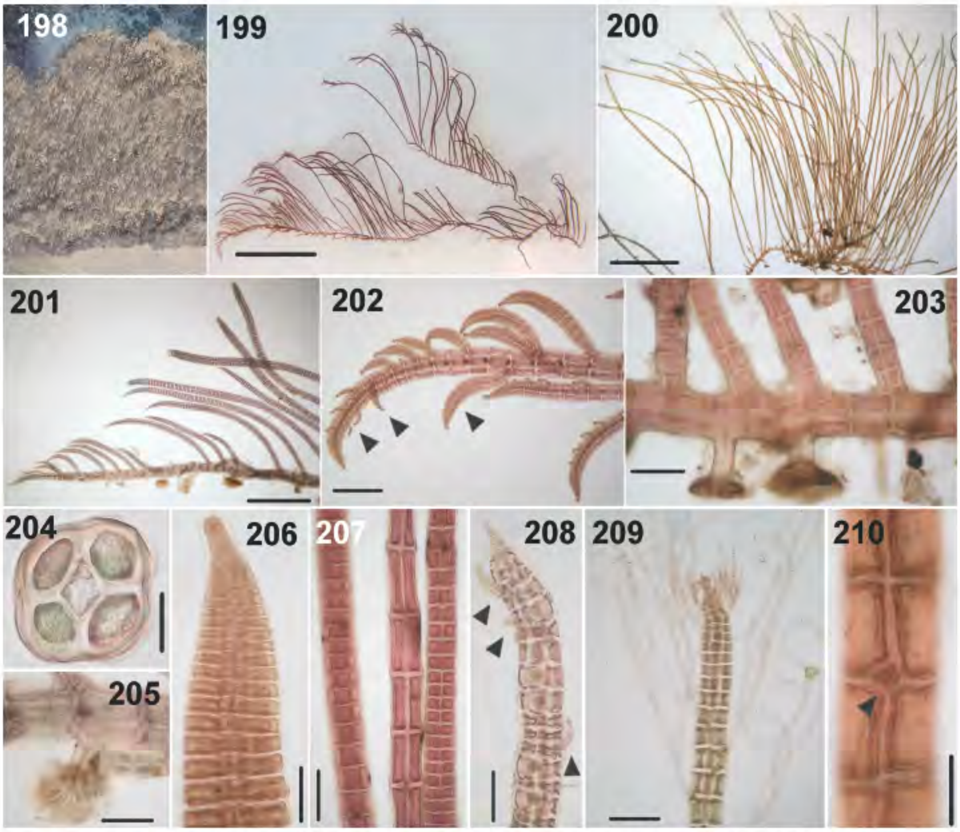
Basionym: *Falkenbergiella caespitosa* M.A. Pocock.
Type material: No published information.
Type locality: Muizenberg, False Bay, Cape Province, South Africa.
References: Pocock, 1953; Pérez-Cirera *et al.*, 1989.
Molecular vouchers: GenBank accession numbers KF648509, KF648510, KF671152, KF671159, KF671161, KF671163, KF671166, KF671175, KF671177, KF671178, KF671181.

Selected specimens: 1) Zumaia (43°17’59”N; 2°15’51”W), 30.iii.2006, SANT-Algae 20266 (male, female and tetrasporangial plants); 2) Laida (43°24’28”N; 2°40’54”W), 31.iii.2006, SANT-Algae 20281 (male and tetrasporangial plants); 3) Oriñón (43°24’20”N; 3°19’34”W), 27.iii.2006, SANT-Algae 20379 (male plants); 4) La Isla (43°28’40”N, 5°13’17”W), 10.x.2006, SANT-Algae 20161 (female and tetrasporangial plants); 5) Catedrales (43°33’16”N; 7°09’16”W), 4.xii.2002, SANT-Algae 15171; 15.vii.2010, SANT-Algae 24420; 6) Linorsa (43°41’56”N; 7°27’14”W), 18.x.2004, SANT-Algae 15579 (male, female and tetrasporangial plants); 25.iv.2005, SANT-Algae 22613; 7) Seaia (43°19’41”N; 8°49’34”W), 22.viii.2002, SANT-Algae 26088 (tetrasporangial plants); 25.iv.2006, SANT-Algae 24512; 8) Barizo (43°18’48”N; 8°52’27”W), 5.iv.2004, SANT-Algae 24955 (tetrasporangial plants); 15.v.2003, SANT-Algae 24557 (male and female plants); 9) Hermida (43°15’47”N; 8°57’10”W), 26.iv.2006, SANT-Algae 24367 (tetrasporangial plants); 10) Lourido (43°05’28”N, 9°13’15”W), 1.ii.2006, SANT-Algae 22596; 11) Fogareiro (42°45’08”N; 9°04’49”W), 19.viii.2005, SANT-Algae 22810 (female and tetrasporangial plants); 12) Arnela (42°42’35”N; 9°00’47”W), 30.i.2006, SANT-Algae 24358 (male, female and tetrasporangial plants); 13) Area da Cruz (42°27’40”N; 8°54’37”W), 22.viii.2005, SANT-Algae 25063 (female and tetrasporangial plants); 14) Agra (42°23’38”N; 8°46’08”W), 28.iv.2006, SANT-Algae 25076 (tetrasporangial plants); 15) Cepaes (41°33’07”N; 8°47’36”W), 28.x.2004, SANT-Algae 16272; 16) Leça de Palmeira (41°12’22”N; 8°43’03”W), 26.x.2004, SANT-Algae 16251; 17) Buarcos (40°10’58”N; 8°54’29”W), 15.xi.2004, SANT-Algae 16245 (male, female and tetrasporangial plants); 18) Baleal (39°22’25”N, 9°19’56”W), 14.vi.2010, SANT-Algae 24257 (male, female and tetrasporangial plants); 19) Guincho (38°43’29”N; 9°28’41”W), 13.vi.2010, SANT-Algae 24785 (male and female plants); 20) San Rafael (37°04’26”N; 8°16’51”W), 2.xi.2005, SANT-Algae 26313; 21) Encendida (36°18’40”N; 6°09’12”W), 18.ii.2011, SANT-Algae 26642 (tetrasporangial plants).

Vegetative and reproductive morphology

Thalli forming dense turfs up to 2 cm high and covering rock surfaces of up to 1 m^2 in extent (Fig. 198). Thallus dorsiventral, consisting of an extensive system of indeterminate and interwoven prostrate axes which ventrally bear rhizoids that attach to the substrate, dorsally produce endogenous erect axes, and laterally branch to form further prostrate axes (Fig. 199). Erect axes unbranched or scarcely branched in sterile plants (Fig. 200), while fertile ones are from scarcely to densely branched in upper parts, in an alternate or irregular pattern, up to 3 orders. Turfs black in colour, axes dark pink-red, with a fairly rigid texture.

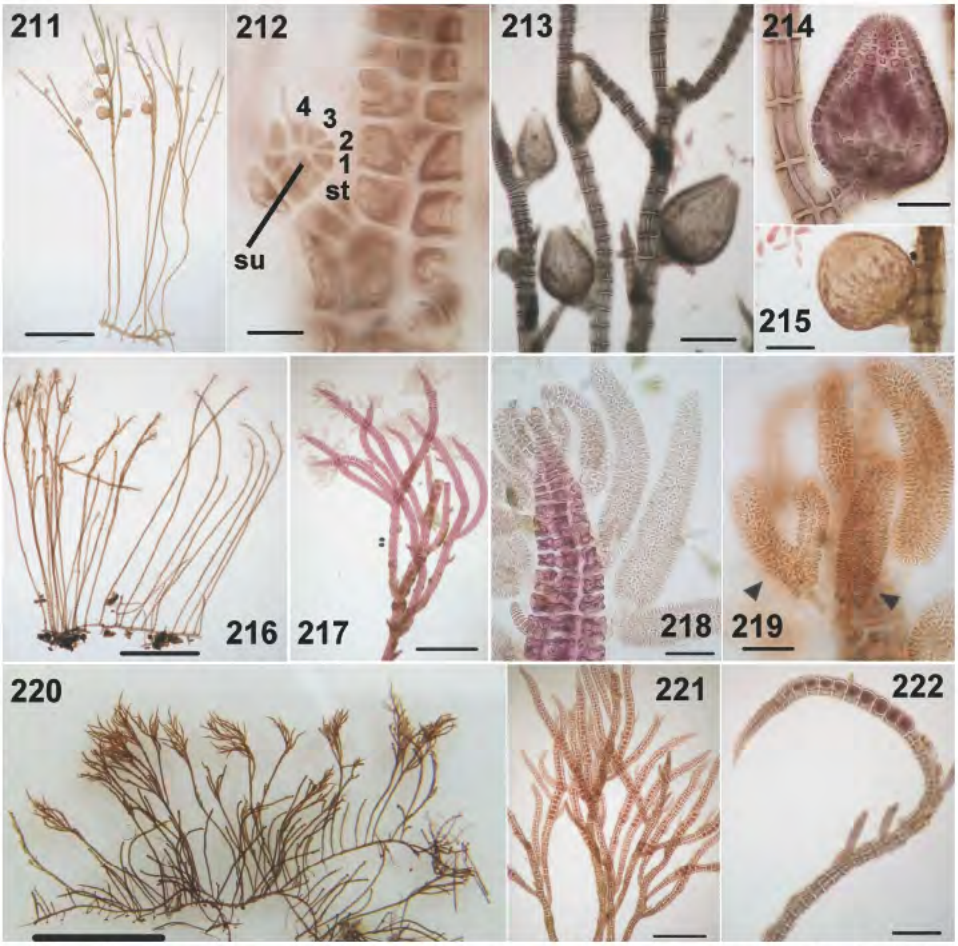
Axes fully ecorticate, consisting of an axial cell and 4 pericentral cells (Fig. 204). Prostrate axes indeterminate and dorsiventral, growing by transverse divisions of large and conspicuous apical cells, which are 20-25 µm in diameter; tips curved downwards, without trichoblasts neither scar cells (Figs 201, 202). They are (60-) 70-110 (-120) µm in diameter; composed of segments L/D (0.5-) 0.9-1.5 (-2.2). Prostrate axes dorsally branched endogenously, forming erect axes in an irregular pattern or at intervals of 2 segments (Figs 201-203). Prostrate axes



Figs 198-210. *Polysiphonia caespitosa*. Vegetative morphology. **198.** Turf in sand-covered rocks. **199.** Habit consisting of indeterminate prostrate axes with the tip downwards curved, and bearing dorsally erect axes, mostly unbranched. **200.** Habit of a sterile plant consisting of unbranched erect axes with trichoblasts at the apex. **201.** Tip of a prostrate axis bearing ventrally rhizoids and dorsally erect axes, which are slightly curved towards the tip. **202.** Apex of a prostrate axis with a prominent apical cell; producing dorsally erect axes and laterally further prostrate axes: arrowheads – lateral branches. **203.** Prostrate axis bearing erect axes every two segments. **204.** Cross section of an erect axis with four pericentral cells. **205.** Digitate rhizoid in open connection to the pericentral cell. **206.** Apex of an erect axis with a prominent apical cell. **207.** Surface view of erect axes with segments from long to short. **208.** Apex of an erect axis bearing immature tetrasporangia and endogenous young branches: arrowheads – endogenous branches. **209.** Apex of an erect axis bearing trichoblasts on every segment. **210.** Mature erect axes: arrowhead – scar cell of a trichoblast. Scale bars: 5 mm in Fig. 199; 2 mm in Fig. 200; 600 µm in Fig. 201; 200 µm in Figs 202, 203 and 205; 30 µm in Fig. 204; 50 µm in Figs 206 and 210; 100 µm in Figs 207-209.

often also produce abundant lateral endogenous branches at irregular intervals, forming further prostrate axes (Fig. 202). Sometimes, old parts of prostrate axes give rise to adventitious branches, both lateral and dorsal. Rhizoids scattered, formed in the ventral side of the prostrate axes, in open connection to pericentral cells, unicellular, one per segment, (20-) 30-60 (-80) µm in diameter and up to 500 (-1000) µm long, often terminated in digitate haptera (Figs 203, 205).

Erect axes growing from domed apical cells 20-25 µm in diameter (Fig. 206). Young erect axes formed by short segments and with the apices slightly



Figs 211-222. *Polysiphonia caespitosa*. Reproductive morphology. **211.** Habit of a female thallus. **212.** Procarp showing the supporting cell (su) bearing the 4-celled carpogonial branch (1-4) and the basal sterile cell (st). **213-215.** Cystocarps from ovoid (214) to globose (215). **216.** Habit of a male thallus. **217.** Spermatangial branches in the upper parts of erect axes. **218.** Cylindrical spermatangial branches replacing trichoblasts. **219.** Spermatangial branch twice branched: arrowheads – two forks, one of them in turn forked. **220.** Habit of a fertile tetrasporophytes bearing abundant short branches in upper parts. **221.** Tetrasporangia forming series in branches from upper parts of erect axes. **222.** Reflexed branch with tetrasporangia forming a straight serie. Scale bars: 2 mm in Figs 211 and 216; 20 µm in Fig. 212; 200 µm in Figs 213, 215 and 222; 100 µm in Fig. 214, 600 µm in Figs 217 and 221; 50 µm in Figs 218 and 219; 5 mm in Fig. 220.

curved in the direction of the apex of prostrate axes (Figs 199, 201, 202); while old axes have larger segments and straight apices (Fig. 200). Erect axes (50-) 60-90 (-110) µm in diameter, composed of segments L/D (0.4) 1-2.2 (-2.8) (Fig. 207). Sterile erect axes unbranched (Figs 199, 200); while erect axes bearing reproductive structures, particularly tetrasporophytes, often develop abundant endogenous lateral branches in upper parts, up to 3 orders; adventitious branches sometimes present. Trichoblasts usually absent in sterile plants (Figs 199, 201,

Figs 223-224. Distribution of *Polysiphonia caespitosa* and *P. scopulorum*. **223.** Collections of *P. caespitosa* along the Atlantic Iberian Peninsula. **224.** World distribution of *P. caespitosa* (blue) and *Polysiphonia scopulorum* (black), including records of *P. scopulorum* var. *villum*: arrowhead and arrow indicates the type locality of *P. caespitosa* and *P. scopulorum*, respectively.

202) but rarely well developed (Figs 200, 209); often present in fertile gametophytes from scarcely to well developed. When present, trichoblasts borne on every segment in a $^{1}/_{4}$ spiral; dichotomously branched up to 3 orders; deciduous and leaving conspicuous scar cells (Fig. 210).

Gametophytes dioecious (Figs 211, 216), with erect axes from barely to densely branched in upper parts; erect axes bearing trichoblasts which are from scarcely to well developed. Procarps are formed in the apices of erect axes, on suprabasal cells of modified trichoblasts; and they consist of a supporting cell bearing a four-celled carpogonial branch, a basal sterile cell (Fig. 212) and a lateral group of two sterile cells. Cystocarps globular to ovoid when mature (Figs 213-215), (250-) 300-400 (-480) µm high and (190-) 200-340 (-450) µm in diameter, with an ostiole (17-) 25-50 (-65) µm wide. Carposporangia clavate, (15-) 20-30 (-35) × (50-) 70-105 (-115) µm.

Spermatangial axes densely clustered at the apices of erect axes, borne on every segment in a $^{1}/_{4}$ spiral (Figs 216, 217). They arise on suprabasal cells of modified trichoblasts, sometimes on the third cell, and completely replacing them (Fig. 218). Spermatangial axes cylindrical, usually with curved tips and lacking sterile apical cells, (140-) 150-275 (-300) µm long and (30-) 35-55 (-65) µm in diameter (Fig. 218). Sometimes, spermatangial branches with one or two furcations (Fig. 129).

Tetrasporophytes usually densely branched in upper parts (Figs 220, 221). Tetrasporangia in upper branches, slightly thickened and often reflexed, forming straight or slightly spiral series with up to 9 mature tetrasporangia (Fig. 222). They are ovate, (35-) 40-65 (-70) µm in diameter, with 3 cover cells.

Phenology

Plants occur throughout the year, and they are probably perennial. All reproductive structures were frequently observed year-round; tetrasporangia were found in 35% of the collections, female structures in 19% and male ones in 14%.

The morphology of *Polysiphonia caespitosa* is rather variable, and mainly two types of plants can be differentiated. Some specimens are more robust (Fig. 199) and show a more regular branching pattern of prostrate axes, while others are more slender (Fig. 200) and have an irregular branching of prostrate axes. These differences seem to be related to the habitat because the first type is found from mid-upper intertidal in highly wave-exposed sites, while the second is more frequent in the mid-low intertidal, as well as in more sheltered sites. On the other hand, reproductive and sterile plants show great morphological differences in appearance, which are related to the development of branches and trichoblasts in upper parts of erect axes of fertile plants.

Habitat and distribution

Polysiphonia caespitosa grows forming turfs on sand-covered rocks from the mid to the low intertidal of sites from sheltered to extremely wave-exposed. Turfs of this species are usually small and appear as patches of *ca* 25-400 cm^2, between turfs dominated by other species. In some sites they were extensively developed and covered rocks surfaces up to 1 m^2. Turfs are monospecific or mixed with other species, particularly *Rhodothamniella floridula*. *Polysiphonia caespitosa* is one of the most frequent species in sand-covered rocks of the Atlantic Iberian Peninsula, and it was found along all the studied area (Fig. 223). *Polysiphonia caespitosa* was exclusively recorded in South Africa, its type locality, and along the Atlantic Iberian Peninsula. However, the closely similar species *P. scopulorum* (see remarks) was recorded in numerous locations from world temperate coasts (Fig. 224).

Remarks

Polysiphonia caespitosa was originally described from South Africa together with its parasite *Aiolocolax pulchellus* (Pocock, 1953, 1956, as *Falkenbergiella caespitosa*). The morphological delineation of this species with regard to *P. scopulorum* Harvey from Australia is doubtful. *Polysiphonia scopulorum* was described based on materials from Australia (Harvey, 1855) and subsequently it was widely reported in world temperate coasts (e.g., Hollenberg, 1968c; Ardré, 1970; Schneider & Searles, 1991; Stegenga *et al.*, 1997; Gómez-Garreta *et al.*, 2001; Guimarães *et al.*, 2004). These reports include the South African coasts and the Atlantic Iberian Peninsula. When Stegenga *et al.* (1997) reported *P. scopulorum* from South Africa, they mentioned that *P. caespitosa* (as *F. caespitosa*) might be a taxonomic synonym of the first species; and Rull Lluch (2002) accepted this proposed synonymy. By contrast, this synonymy has still not been properly studied neither by comparison of types materials of both species nor by molecular data. We have found some evidences that suggest that *P. caespitosa* and *P. scopulorum* are genuine different species and they are discussed below; however, further work is needed to solve definitively this issue.

In the Atlantic Iberian Peninsula, materials here assigned to *Polysiphonia caespitosa* were first reported by Ardré (1970) as *Lophosiphonia scopulorum*. Ardré based her identification of Portuguese materials in the comparison with specimens from Thuret´s herbarium, which were collected both in Biarritz (Atlantic South of France) as well as in Australia. Later, *P. caespitosa* (as *Falkenbergiella caespitosa*) was reported in Spain (Pérez-Cirera *et al.*, 1989) when the synonymy of this species and *P. scopulorum* was still not established. However, Pérez-Cirera *et al.* (1989) suggested that the Spanish material was conspecific with the Portuguese ones identified by Ardré. Pérez-Cirera *et al.* (1989) based their identification of the Galician (NW Spain) specimens on comparison with the original description of this species from South Africa and on the finding, for the first time in that area, of *Aiolocolax pulchellus*, a parasite described on *F. caespitosa*. This is the only available record for the species under the name *P. caespitosa* outside from its type locality. In the most recent floristic accounts from the Atlantic Iberian Peninsula the synonymy was followed and the species here treated was recorded as *P. scopulorum* (Bárbara *et al.*, 2005; Díaz *et al.*, 2008;

Araújo *et al.*, 2009; Bárbara *et al.*, 2013). In the course of the present study, we observed samples of the species from 21 sites distributed along all the Atlantic Iberian Peninsula, including several Portuguese locations reported by Ardré, as well as Biarritz (Atlantic France). We concluded that previous records from this area labelled as *P. caespitosa* and *P. scopulorum* belong to the same species, as previously suggested Pérez-Cirera *et al.* (1989). In addition, we obtained 11 COI-5P sequences of the species corresponding to different locations dispersed along all the Atlantic Iberian coast and they were identical, supporting our conclusion. We therefore now wonder what is the correct name for materials from the Atlantic Iberian Peninsula?

The most distinctive features found in *Polysiphonia caespitosa* from the Atlantic Iberian Peninsula are: 1) extensive system of prostrate axes with a dorsiventral structure, 2) all branches endogenous and independent of trichoblasts, 3) erect axes of sterile plants often unbranched, fertile ones from scarcely to densely branched in upper parts, 4) axes ecorticate with 4 pericentral cells, 5) rhizoids in open connection to pericentral cells, 6) trichoblasts often absent in sterile plants and present in reproductive ones, 7) 4-celled carpogonial branches, 8) spermatangial axes replacing trichoblasts, lacking sterile apical cells, sometimes branched, 9) one tetrasporangium per segment, formed in straight or slightly spiral rows. These features are in agreement with the original description of *Polysiphonia caespitosa* (Pocock, 1953), but also with descriptions of *P. scopulorum* from Australia (Womersley, 2003). The only detected differences regarding *P. scopulorum* are that erect axes of plants from the Iberian Peninsula are narrower than those from Australia (60-90 *vs.* 80-120 µm, respectively), and spermatangial branches are longer (200-340 *vs.* 120-200 µm). Perhaps the most relevant difference is that some exogenous branches are formed in the apices of erect axes of materials from Australia (Womersley, 2003), while exogenous branches were never observed in the Iberian Peninsula.

In addition to these morphological differences, the type locality of *Polysiphonia scolpulorum* is far from the Iberian Peninsula, although in general, *P. scopulorum* was reported in scattered and distant locations in worldwide temperate areas (Fig. 224). Within *Polysiphonia sensu lato*, there are numerous species with a similar worldwide distribution as for example *P. brodiei* (Dillwyn) Sprengel, *P. denudata* (Dillwyn) Greville *ex* Harvey or *P. sertularioides* (Grateloup) J. Agardh (Guiry & Guiry, 2013). By contrast, recent studies including molecular data show that some of these records correspond to distinct species. For example, *P. schneiderii* was recently described from Atlantic North America based on materials previously assigned to *P. denudata* (Stuercke & Freshwater, 2010). Thus, it would not be surprising that records of *P. scopulorum* from different areas would correspond to several distinct species.

Another distinctive feature in the materials from the Atlantic Iberian Peninsula is the presence of the parasite *Aiolocolax pulchellus*. It was originally described from South Africa on *Polysiphonia caespitosa* and up to date it was reported only on the eastern Atlantic coasts parasitic on materials labelled both as *P. scopulorum* and *P. caespitosa*. Parasites in red algae are usually highly specific regarding their hosts (Goff, 1982), and thus it seems plausible to think that the restricted distribution of *A. puchellus* to eastern Atlantic coasts might indicate that its host is also confined to the same geographical area and thus that *P. caespitosa* might be a genuine different species from *P. scopulorum*.

Other evidence that might indicate differences between materials from the Iberian Peninsula and *Polysiphonia scopulorum* from the Pacific relies in the molecular data. A comparison among *rbc*L sequences of materials labelled as

P. scopulorum from Pacific U.S.A. (GenBank AY396039, Kim *et al.*, 2004), as *P. scopulorum* var. *villum* from Atlantic USA (GenBank EU492915, Stuercke & Freshwater, 2008) and as *P. caespitosa* from the Iberian Peninsula (GenBank JX828149, Bárbara *et al.,* 2013, as *P. scopulorum*) indicates that they correspond to three different species. However, none of these materials came from any type locality of the species or varieties of *P. scopulorum* or *P. caespitosa*, and thus these data did not allow reaching a conclusion regarding the specific assignment of materials from different regions. In addition to the diversity detected through the few available molecular data, *Polysiphonia scopulorum* seems to present a high morphological variability and three varieties of the species are currently recognized (Hollenberg, 1968c): *P. scopulorum* var. *villum* (J. Agardh) Hollenberg, *P. scopulorum* var. *macrotrichia* Hollenberg and *P. scopulorum* var. *minima* Hollenberg (Hollenberg, 1968c); one of them, *P. villum* J. Agardh, originally described as a separate species. These varieties, first reported from Pacific coasts, share most of the main taxonomic characteristics, and they are separated by features as, for example, thallus size, length of trichoblasts, segments L/D, etc. (Hollenberg, 1968c).

All these lead us to believe that *Polysiphonia caespitosa* is most probably a different species than *P. scopulorum* from Australia, and accordingly we consider it more appropriate to reinstate *P. caespitosa* for materials from western Atlantic previously assigned to both *P. scopulorum* and *P. caespitosa*. Moreover, we have studied materials from South Africa (Tsitsikamma) labelled as *P. scopulorum* and we could not found morphological differences between these specimens and the Iberian ones. However, the relation between *P. caespitosa* and *P. scopulorum* is far to be solved, as this would require the study of materials from the type localities (i.e. Australia and South Africa). Considering the apparent absence of relevant morphological features to delineate the probable species, this study necessarily should involve molecular analyses. In addition to the doubts regarding the identity of this pair of species, whether the varieties described by Hollenberg (1968c) in the Pacific, as well as materials from Atlantic USA correspond to a single or to several species deserves further research.

Controversies on these species do not only involve their specific designation but also regards their generic assignment. *Polysiphonia scopulorum* and the species currently considered synonymous have been transferred between the genera *Polysiphonia*, *Falkenbergiella*, *Lophosiphonia* and *Vertebrata*. *Polysiphonia scopulorum* (as *P. caespitosa*) from eastern Atlantic was firstly included in the genus *Falkenbergiella*. Kylin (1938) proposed to group species related to *Lophosiphonia* which are characterized by the absence of trichoblasts in vegetative specimens. Subsequently, Hollenberg (1968c) studied materials of *F. prostrata* from Australia and the Pacific, and he questioned the validity of the features to distinguish the genus *Falkenbergiella*. As a result, the species of this genus were transferred to *Polysiphonia* or *Lophosiphonia* (Hollenberg, 1968c; Norris, 1992). On the other hand, *P. scopulorum* and *P. caespitosa* show the features used by Falkenberg (1901) to delinate the genus *Lophosiphoina* (Pocock, 1953; Womersley, 2003). However, the delineation of this genus needs a revision (see remarks on *Lophosiphonia reptabunda*), as previously noted Hollenberg (1968c) when he studied *P. scopulorum* var. *villum* (as *L. villum*).

The delineation of *Polysiphonia*, *Lophosiphonia* and *Falkenbergiella* has been largely discussed, and this controversy is still pending resolution. The concept of the genus *Polysiphonia sensu stricto* has been largely restricted in the last years. Recent studies based on molecular data have shown that there are 3 groups within *Polysiphonia sensu lato* (Choi *et al.*, 2001). *Polysiphonia sensu* *stricto* has been characterized by having 4 pericentral cells, rhizoids in open connection to pericentral cells, 4-celled carpogonial branches, spermatangial branches replacing trichoblasts and tetrasporangia in straight series (Choi *et al.*, 2001). *Polysiphonia scopulorum* shows these features and Choi *et al.* (2001) placed it in *Polysiphonia sensu stricto*. *Polysiphonia caespitosa* also present morphological features that fit the current concept of *Polysiphonia sensu stricto*.

Polysiphonia devoniensis Maggs *et* Hommersand **Figs 225-241**

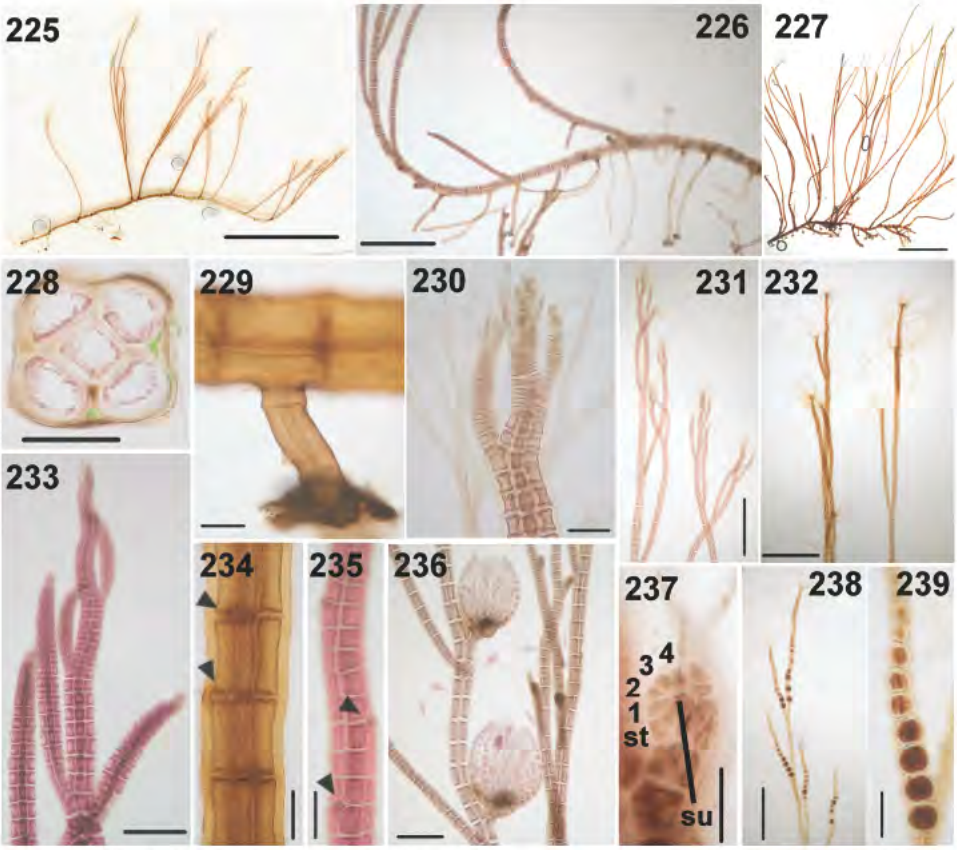
Holotype: BM.
Type locality: Sidmouth, Devon, England.
References: Maggs & Hommersand, 1993; Díez *et al.*, 1996; Bárbara *et al.*, 2012.
Molecular vouchers: GenBank accession numbers KF671149, KF671186.
Selected specimens: 1) Zumaia (43°17'59"N; 2°15'41"W), 9.ix.2006, SANT-Algae 20265, 21702 (tetrasporangial plants); 2) Ogeia (43°22'22"N; 2°32'35"W), 15.iii.2006, SANT-Algae 203320; 3) La Arena (43°21'16"N; 3°06'53"W), 22.iii.2011, SANT-Algae 25641, 25664; 4) Sonabia (43°24'51"N; 3°19'37"W), 27.iii.2006, SANT-Algae 20374; 5) Langre (43°28'37"N; 3°41'31"W), 10.ix.2006, SANT-Algae 20228 (tetrasporangial plants); 6.xi.2010, SANT-Algae 24621, 24630; 6) Virgen del Mar (43°28'40"N; 3°52'31"W), 28, iii. 2006, SANT-Algae 20397; 7.xi.2010, SANT-Algae 24647; 7) Somocueva (43°28'07"N; 3°56'43"W), 7.x.2006, SANT-Algae 19992 (female plants); Amio (43°23'42"N; 4°28'57"), 17.iii.2006, SANT-Algae 20422; 8) Llas (43°34'47"N; 7°15'27"W), 19.iv.2011, SANT-Algae 26229; 9) Cadín (43°44'33"N; 7°40'24"W), 1.x.2011, SANT-Algae 26654; 10) Olhos d'Agua (37°05'20"N; 8°11'27"W), 20.1ii.2011, SANT-Algae 26451 (tetrasporangial plants); 11) Cala Encendida (36°18'40"N; 6°09'12"W), 18.ii.2011, SANT-Algae 26634 (tetrasporangial plants); 12) Punta Plata (36°06'28"N; 5°49'41"W), 19.i.2011, SANT-Algae 26522.

Vegetative and reproductive morphology

Thalli forming dense tufts up to 2 cm high, covering rock surfaces of up to 900 cm^2 in extent. Thallus radially organized growing from indeterminate erect axes that become decumbent when developing rhizoids at their basal parts (Figs 225, 226), forming a system of prostrate interwoven axes bearing rhizoids. Erect axes irregularly branched, up to 5 orders (Fig. 227). Axes brownish red in colour; with a soft and flaccid texture.

Axes ecorticate, with 4 pericentral cells (Fig. 228). Prostrate axes 90-160 µm in diameter, growing when rhizoids developing at basal parts of erect axes as well as by the formation of cicatrigenous endogenous branches. Rhizoids in open connection to pericentral cells (Fig. 229). Erect axes 70-100 µm in diameter, branches mainly exogenous, replacing the trichoblasts, irregularly arranged (Figs 230, 231); adventitious branches frequently formed from scar cells of trichoblasts. Trichoblasts are usually present, from scarce to abundant, but sometimes they are almost absent (Figs 231-233), although the apical cell divides forming initials of trichoblasts and leaving scar cells throughout the axes. Trichoblasts irregularly arranged borne on every segment or 2-4 segments apart, in a ¼ spiral, deciduous and leaving conspicuous scar cells (Figs 234, 235).

Gametophytes dioecious. Procarps are formed in suprabasal cells of modified trichoblasts, and they consist of a four-celled carpogonial branch, a basal sterile cell (Fig. 237) and a group of two lateral sterile cells borne on the supporting cell. Cystocarps globular when mature, 350-420 µm high and 260-400 µm in diameter (Fig. 236). Male structures were not found on the Iberian Peninsula. Tetrasporangia in upper branches forming slightly spiral rows, with up to 8 mature tetrasporangia (Figs 238, 239); they are ovate, 50-80 µm in diameter, with 3 cover cells.



Figs 225-239. *Polysiphonia devoniensis*. Vegetative and reproductive morphology. **225.** Thallus consisting of a prostrate axes, becoming decumbent when erect axes develop rhizoids at their basal parts. **226.** Prostrate axes bearing rhizoids. **227.** Erect axes irregularly branched. **228.** Cross section of axes with an axial cell and four pericentral cells. **229.** Rhizoid in open connection to the pericentral cell. **230.** Apex of an erect axis forming exogenous branches replacing trichoblasts. **231-233.** Apex of erect axes with abundant trichoblasts (232) or without them (233, but the apical cells divide forming initials of trichoblasts and leaving scar cells). **234-235.** Scar cells of trichoblasts arranged on every segment (234) or every 3 segments (235): arrowheads – scar cells. **236.** Cystocarps. **237.** Procarp showing the supporting cell (su) bearing the 4-celled carpogonial branch (1-4) and the basal sterile cell (st). **238-239.** Tetrasporangia, forming slightly spiral rows. Scale bars: 5 mm in Fig. 225; 600 µm in Figs 226, 231, 232 and 238; 2 mm in Fig. 227; 50 µm in Figs 228-230, 234 and 235; 100 µm in Figs 233 and 239; 200 µm in Fig. 236; 25 µm in Fig. 237.

Phenology

Polysiphonia devoniensis was collected throughout the year, and it is probably perennial. Reproductive structures were rarely found. Female structures were only observed once (5% of the collections), in material collected at Somocueva (northern Spain) in October. Male structures were not found. Tetrasporangia were observed in 21% of the collections, in February-March and November.

Figs 240-241. Distribution of *Polysiphonia devoniensis*. **240.** Collections along the Atlantic Iberian Peninsula. **241.** World distribution: arrow – type locality.

Habitat and distribution

Polysiphonia devoniensis was found along the Atlantic Iberian Penisula (Fig. 240), especially in the warmer areas (Northeast and South), while in the colder ones it was rare and was found only in moderately wave-exposed sites. *Polysiphonia devoniensis* inhabits from the mid to the low intertidal of sand-covered rocks, forming almost monospecific turfs or, most commonly, growing entangled with other species typical from the habitat. The world distribution of *P. devoniensis* is restricted to the British Isles and the Atlantic Iberian Peninsula (Fig. 241).

Remarks

Polysiphonia devoniensis is similar in morphology to its Iberian congeners having 4 pericentral cells and rhizoids cut off from pericentral cells. The frequent presence of trichoblasts, decumbent habit with a well developed prostrate system, the irregular branching pattern and the brownish colour, differentiates *P. devoniensis* from *P. atlantica*, *P. stricta* and *P. caespitosa*. *Polysiphonia atlantica* and *P. stricta* have only rarely trichoblasts, have shorter prostrate systems, branches are regularly formed and are red in colour. Furthermore, *P. atlantica* has mostly endogenous branches, while in *P. devoniensis* branches are mostly exogenous. Finally, the habitat is also different in that *P. atlantica* typically grows in the upper intertidal of extremely exposed rocky shores. Furthermore, *P. stricta* is larger than *P. devoniensis. Polysiphonia caespitosa*, rarely has trichoblasts, is dorsiventral, has extensive prostrate axes growing from apical cells without trichoblasts and is black in colour. *Polysiphonia devoniensis* is also similar in habit to *P. foetidissima*, but they differ by the number of pericentral cells (4 *vs* 7-8).

Polysiphonia devoniensis was described from the British Isles (Maggs & Hommersand, 1993) and subsequently reported in the Basque Country (Díez *et al.*, 1996). The new records in Cantabria and in the southern Iberian Peninsula considerably extend the distribution of the species southward (Díaz *et al.*, 2008; Bárbara *et al.*, 2012). Maggs & Hommersand (1993) raised the question that *P. devoniensis* may be conspecific with *P. funebris* De Notaris *ex* Agardh, originally described from the Mediterranean Sea, or at least with records of this species from Portugal. Subsequently, Pizzuto *et al.* (1996) clarified the morphological differences between both species. Our findings confirm the presence of *P. devoniensis* along the Atlantic Iberian Peninsula, while material similar to *P. funebris* described in Pizzuto *et al.* (1996) was not found in the studied area. The morphological features of *P. devoniensis* fit the current delineation of *Polysiphonia sensu stricto* (Choi *et al.*, 2001).

Polysiphonia foetidissima Cocks *ex* Bornet **Figs 242-257**

Lectotype: PC (Maggs & Hommersand, 1993).
Type locality: Mount Edgcumbe, Plymouth, Cornwall, British Isles.
References: Maggs & Hommersand, 1993; Díaz-Tapia *et al.* 2013c.
Molecular vouchers: no available COI-5P data.

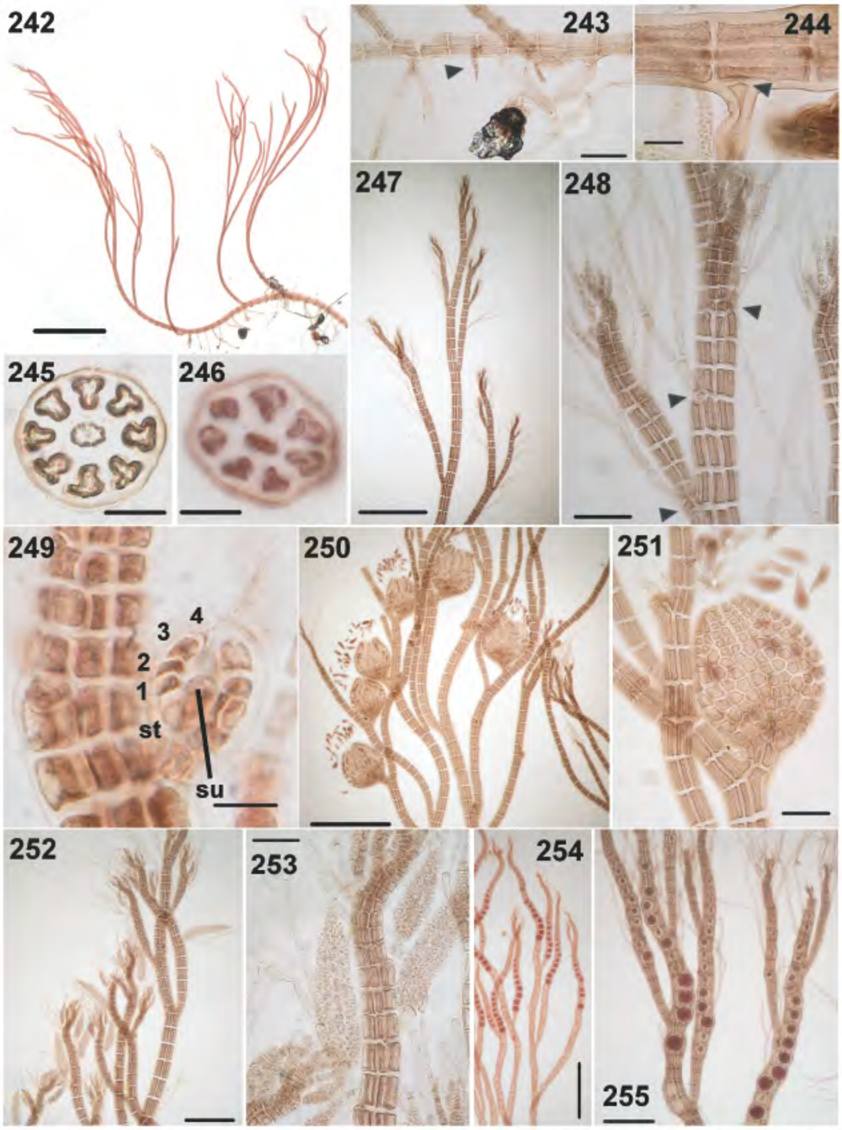
Selected specimens: 1) Biarritz (43°29'03''N; 1°33'46''W), 19.iii.2011, SANT-Algae 25433; 2) Laida (43°24'28''N; 2°40'54''W), 31.iii.2006, SANT-Algae 20286; 3) La Arena (43°21'16''N; 3°06'53''W), 07.ix.2006, SANT-Algae 20971 (tetrasporangial plants); 4) Langre (43°28'37''N; 3°41'31''W), 6.xi.2010, SANT-Algae 24620, 24628; 5) Virgen del Mar (43°28'40''N; 3°52'31''W), 7.xi.2010, SANT-Algae 24648; 6) Niembro (43°26'33''N, 4°50'20''W); 08.x.2006, SANT-Algae 21644; 28.v.2010, SANT-Algae 24162; 7) Serantes (43°33'27''N; 6°58'39''W), 28.vii.2010, SANT-Algae 25166; 8) Catedrales (43°33'16''N; 7°09'16''W), 04.xi.2002, SANT-Algae 16525 (tetrasporangial plants); 20-ix-2005, SANT-Algae 16577 (male, female and tetrasporangial plants); 01.iii.2006, SANT-Algae 21622, 21650; 15.vii.2010, SANT-Algae 24421 (tetrasporangial plants); 9) Punta do Castro (43°33'47''N; 7°10'35''W), 24.iv.2009, SANT-Algae 24656 (male and tetrasporangial plants); 10) Llas (43°34'47''N; 7°15'27''W), 19.iv.2011; SANT-Algae 24477; 11) Xilloe (43°44'41''N; 7°39'02''W), 10.ix.2002, SANT-Algae 24910 (tetrasporangial plants); 12) Barrañán (43°18'44''N; 8°33'22''W), 18.x.2002, SANT-Algae 21645 (tetrasporangial plants); 16.vi.2003, SANT-Algae 21646 (tetrasporangial plants); 13) Arnela (42°42'35''N; 9°00'47''W), 01.viii.2011, SANT-Algae 26444 (male and tetrasporangial plants); 14) Baleal (39°22'25''N, 9°19'56''W), 14.vi.2010, SANT-Algae 24255 (tetrasporangial plants); 15) Queimado (37°49'34''N; 8°47'34''W), 24.v.2005, SANT-Algae 24658; 16) Almograve (37°39'54''N; 8°48'04''W), 25.v.2005, SANT-Algae 24657 (male and tetrasporangial plants); 17) Ingrina (37°02'46''N; 8°52'43''W), 9.v.2005, SANT-Algae 24659; 18) Armaçao de Pêra (37°06'04''N; 8°22'17''W), 17.10.2005, SANT-Algae 24840; 19) Olhos d´Agua (37°05'20''N; 8°11'27''W), 20.ii.2011, SANT-Algae 26464; 20) Punta Plata (36°06'28''N; 5°49'41''W), 19.i.2011, SANT-Algae 26517.

Vegetative and reproductive morphology

Thalli forming turfs up to 2 cm high, covering substrate surfaces of up to 30 cm^2, developing an extensive horizontal system of interwoven decumbent axes growing from erect apices (Fig. 242). Erect axes became decumbent by the development of rhizoids from the basal segments. They are alternately branched up to five orders, bearing short branches (Fig. 242). Thalli brownish-red; erect axes with a soft and flaccid texture.

Axes ecorticate, with (6-) 7-8 (-9) pericentral cells (Figs 245, 246). Prostrate axes (60-) 90-150 (-180) µm in diameter, bearing conspicuous scar cells of trichoblasts, which often gave rise to adventitious branches (Fig. 243). Rhizoids cut off from pericentral cells (Fig. 244). Erect axes (50-) 60-110 (-130) µm in diameter. Exogenous branches formed in the axils of trichoblasts (Fig. 248), mostly at regular intervals of 6-8 (-9) segments; arranged alternately (Figs 247, 248). Trichoblasts usually numerous but sometimes scarcely developed, arising (2-) 3-4 (-5) segments apart; deciduous and leaving conspicuous scar cells (Fig. 248).

Gametophytes dioecious. Procarps are formed in suprabasal cells of modified trichoblasts, and they consist of a four-celled carpogonial branch, a basal sterile cell (Fig. 249) and a group of two lateral sterile cells borne on the supporting cell. Cystocarps globular to ovoid when mature (Figs 250, 251) and (220-) 300-350 µm high and (160-) 210-285 (-300) µm in diameter. Spermatangial axes formed in the apical parts of erect axes, 3-4 segments apart, on a branch of the first dichotomy of modified trichoblasts sometimes on the two basal branches, cylindrical (Figs. 252, 253) (100-) 110-170 (-188) µm long and (30-) 35-40 (-45) µm in diameter, with 1-3 sterile terminal cells when mature. Tetrasporangia forming



Figs 242-255. *Polysiphonia foetidissima*. Vegetative and reproductive morphology. **242.** Thallus consisting of a prostrate axes, becoming decumbent when erect axes develop rhizoids at their basal parts. **243.** Prostrate axes bearing rhizoids: arrowhead – adventitious branch. **244.** Rhizoid cut off from the pericentral cell: arrowhead – wall separating the pericentral cell and the rhizoid. **245-246.** Cross section of axes with an axial cell and 7 (246) or 8 (245) pericentral cells. **247.** Erect axes with alternate branches formed every 6-9 segments. **248.** Apex of erect axes with trichoblasts every 3 segments and branches formed in their axils: arrowheads – basal cells of trichoblasts. **249.** Procarp showing the supporting cell (su), the 4-celled carpogonial branch (1-4) and the basal sterile cell (st). **250-251.** Cystocarps. **252.** Spermatangial axes at the apices of erect axes. **253.** Spermatangial axes formed on one of the branches of the first dichotomy of a modified trichoblasts, persisting the other branch at maturity. **254-255.** Tetrasporangia, forming slightly spiral rows. Scale bars: 1.5 mm in Fig. 242; 200 µm in Figs 243, 252 and 255; 50 µm in Figs 244, 251 and 253; 30 µm in Figs 245 and 246; 600 µm in 247, 254 and 250; 100 µm in Fig. 248; 15 µm in Fig 249.

Figs 256-257. Distribution of *Polysiphonia foetidissima*. **256.** Collections along the Atlantic Iberian Peninsula. **257.** World distribution: arrow – type locality.

long series in a slight and irregular spiral; ovate, (35-) 40-60 (-65) µm in diameter (Figs 254, 255).

Phenology

Polysiphonia foetidissima was collected throughout the year. Thalli bearing tetrasporangia were frequently found year-round (50% of the collections). Gametophytes were more rarely observed: male and female structures were detected in less than 20% of the collections and only in April-June and September-October.

Habitat and distribution

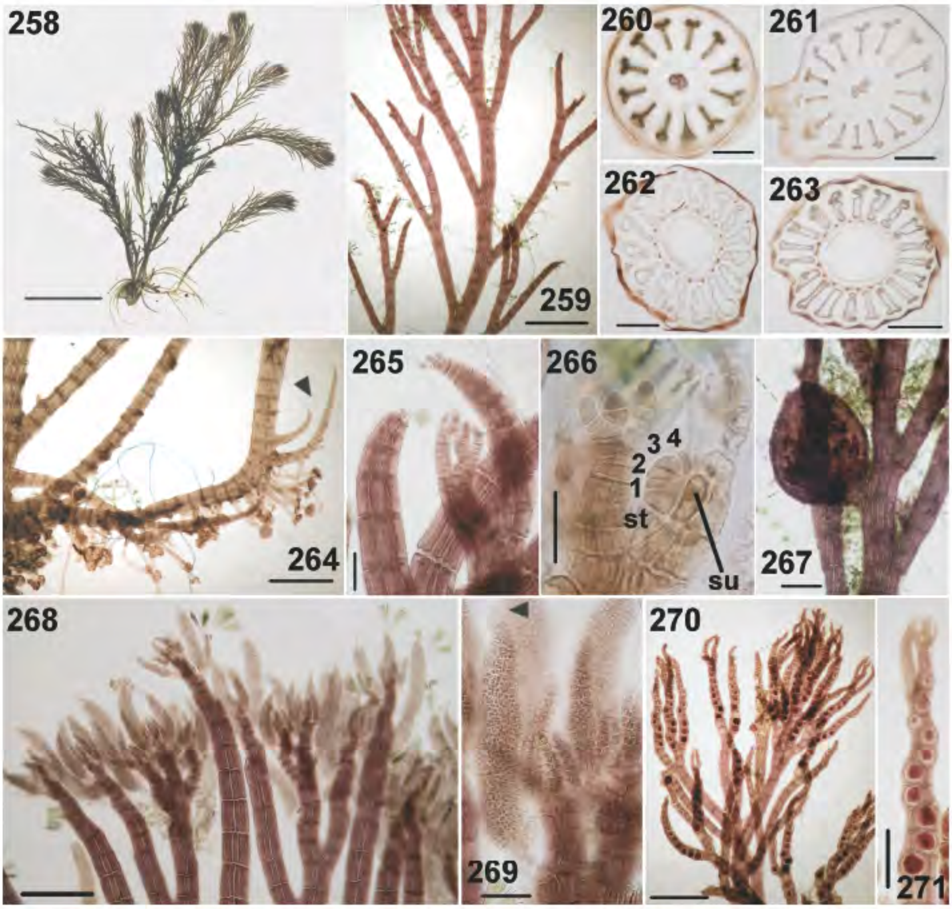
Polysiphonia foetidissima was found in throughout the Atlantic Iberian Peninsula (Fig. 256). It was collected at moderately to extremely wave-exposed sites, usually on sand-covered rocks from the middle to the lower intertidal. It develops dense turfs over bare rock but it also grows over other turf-forming seaweeds like *Rhodothamniella floridula*, *Polysiphonia nigra*, *Ophidocladus simpliciusculus* or *Pterosiphonia pennata*. The confirmed distribution of this species includes both European and American shores of the northern Atlantic, (Fig. 257, see Díaz-Tapia *et al.*, 2013c).

Polysiphonia fucoides (Hudson) Greville **Figs 258-273**

Basionym: *Conferva fucoides* Hudson.
Neotype: BM (Maggs & Hommersand 1993).
Type locality: York, England.
Synonym: *Polysiphonia nigrescens* (Hudson) Greville *ex* Harvey.
References: Rosenvinge, 1924; Veldkamp, 1950; Kapraun, 1977; Kapraun & Rueness, 1983; Schneider & Searles, 1991, as *P. nigrescens*; Maggs & Hommersand, 1993.
Molecular vouchers: no available COI-5P data.
Selected specimens: 1) Catedrales (43°33'16"N; 7°09'16"W), 20.ix.2005, SANT-Algae 16541 (tetrasporangial plants) 2) Peinzás (43°35'09"N; 7°16'13"W), 19.iv.2011, SANT-Algae 26231 (male, female and tetrasporangial plants); 3) Ber (43°23'51"N; 8°12'44"W), 2.iii.2006, SANT-Algae 22788 (male, female and tetrasporangial plants).

Vegetative and reproductive morphology

Thalli forming small turfs up to 7 cm high. Thallus radially organized and predominantly erect, attached to the substratum by rhizoids that grow in basal



Figs 258-271. *Polysiphonia fucoides*. Vegetative and reproductive morphology. **258.** Thallus consisting of a short prostrate system and erect axes. **259.** Main axes with branches every 2-4 segments. **260-263.** Cross section of axes showing 12 (260), 15 (261), 17 (262) and 19 (263) pericentral cells. **264.** Prostrate system with rhizoids: arrowhead – adventitious branches. **265.** Apex of an erect axes with scarcely developed trichoblasts or without them. **266.** Procarp showing the supporting cell (su), the 4-celled carpogonial branch (1-4) and the basal sterile cell (st). **267.** Cystocarp. **268.** Spermatangial axes densely clustered at the apices of erect axes. **269.** Spermatangial axes formed on the first dichotomy of a modified trichoblasts: arrowhead – sterile apical cell. **270-271.** Tetrasporangia arranged in spiral series. Scale bars: 1 cm in Fig. 258; 600 µm in Figs 259, 264, 268 and 270; 50 µm in Figs 260, 261, 265 and 269; 100 µm in Figs 262 and 263; 25 µm in Fig. 266; 200 µm in Figs 267 and 271.

parts of erect axes forming a short system of prostrate interwoven axes (Fig. 258). The main axes remain distinct, and are mostly branched every 2-4 segments, up to 4 orders (Figs 258, 259). Axes dark brown in colour; with a rigid texture.

Axes ecorticate, with 12-20 pericentral cells (Figs 260-263), although plants of this species can be corticated (Maggs & Hommersand, 1993). Prostrate axes 160-400 µm in diameter, growing as rhizoids develop at basal parts of erect axes as well as by the formation of adventitious branches (Fig. 264). Rhizoids cut off from pericentral cells. Erect axes 120-400 µm in diameter, branches exogenous,

Figs 272-273. Distribution of *Polysiphonia fucoides*. **272.** Collections along the Atlantic Iberian Peninsula. **273.** World distribution: arrow – type locality.

independent from trichoblasts (Fig. 265). Trichoblasts usually absent or scarcely developed.

Gametophytes dioecious. Procarps are formed in suprabasal cells of modified trichoblasts and they consist of a four-celled carpogonial branch, a basal sterile cell (Fig. 266) and a group of two lateral sterile cells borne on the supporting cell. Cystocarps globose when mature, 400-600 µm high and 320-500 µm in diameter (Fig. 267). Spermatangial axes cylindrical, occasionally bifurcated, 150-340 µm long and 35-63 µm in diameter, formed at the first dichotomy of modified trichoblasts, growing on every segment, with 2-4 sterile apical cells (Figs 268, 269). Tetrasporangia in upper branches forming spiral rows with up to 8 mature tetrasporangia (Figs 270, 271); tetrasporangia are ovate, 52-78 µm in diameter, with 2 cover cells.

Phenology

Polysiphonia fucoides was collected throughout the year, except in June and October-December; it is probably perennial. Reproductive structures were frequently observed when the species was collected. Female and male structures were observed in March-April (15% of the collections), and tetrasporangia in January-April and September (38%).

Habitat and distribution

Polysiphonia fucoides was found during this study only in some locations from Galicia (Fig. 272), where it was a rare species; although it has been also reported in the Cantabrian and Portugal (Gorostiaga *et al.*, 2004; Araújo *et al.*, 2009). It was collected from the mid to the low intertidal of sand-covered rocks from moderately to extremely wave-exposed sites, forming turfs entangled with other species typical from the habitat. *Polysiphonia fucoides* was reported in the North Atlantic and the Mediterranean Sea (Fig. 273).

Polysiphonia nigra (Hudson) Batters **Figs 274-294**

Basionym: *Conferva nigra* Hudson.
Neotype: BM (Maggs & Hommersand, 1993).
Type locality: Durham, Marsden, UK.
Synonym: *Polysiphonia atrorubescens* (Dillwyn) Greville.
References: Batten, 1923; Rosenvinge, 1924 (as *P. atrorubescens*); Veldkamp, 1950; Coppejans, 1981, 1995; Kapraun & Rueness, 1983; Maggs & Hommersand, 1993; Rull Lluch, 2002.

Molecular voucher: GenBank accession number KC130868 (Díaz-Tapia *et al.*, 2013a).

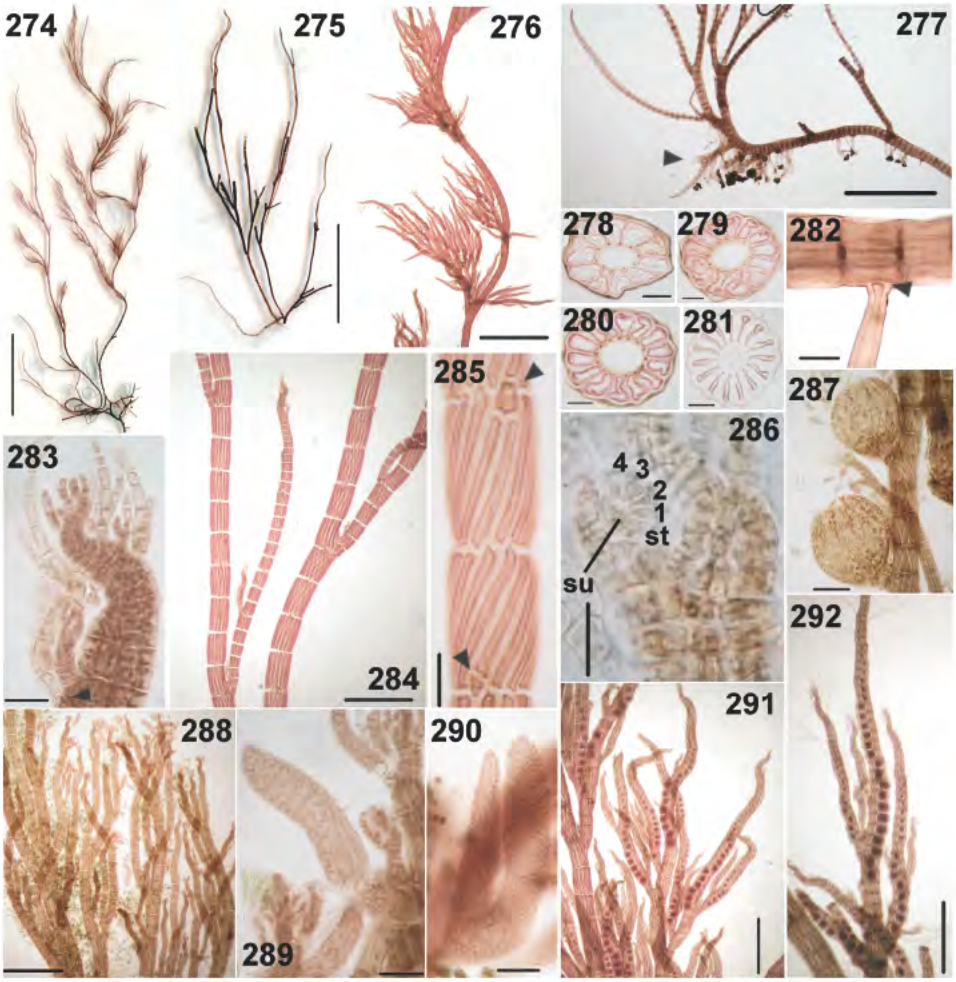
Selected specimens: 1) Kobarón (43°21'10"N; 3º07'54"W), 12.ix.2006, SANT-Algae 19881; 2) Amio (43°23'42"N; 4°28'57"), 17.iii.2006, SANT-Algae 20424; 3) Niembro (43°26'33"N, 4°50'20"W), 28.v.2010, SANT-Algae 24148; 4) Aguilar (43°33'28"N; 6°07'07"W), 17.iv.2007, SANT-Algae 19814 (tetrasporangial plants); 5) Catedrales (43°33'16"N; 7°09'16"W), 1-iii-2006, SANT-Algae 22629; 6) Linorsa (43°41'56"N; 7°27'14"W), 10.iii.2005, SANT-Algae 23122 (male, female and tetrasporangial plants); 25.iv.2005, SANT-Algae 22618 (tetrasporangial plants); 7) Doniños (43°30'08"N; 8°19'17"W), 12.iii.2005, SANT-Algae 24545; 8) Chanteiro (43°26'46"N; 8°18'15"W), 17.ix.2005, SANT-Algae 19597 (male, female and tetrasporangial plants); 9) Ber (43°23'51"N; 8°12'44"W), 2.iii.2006, SANT-Algae 22795 (female and tetrasporangial plants); 10) Perbes (43°22'34"N; 8°12'55"), 7.iii.2008, SANT-Algae 22569 (tetrasporangial plants); 11) Barrañán (43°18'44"N; 8°33'22"W), 19.iii.2003, SANT-Algae 15389, 15194 (male and tetrasporangial plants); 12) Seaia (43°19'41"N; 8°49'34"W), 26.x.2003, SANT-Algae 23041 (tetrasporangial plants), 25.iv.2006, SANT-Algae 24509; 13) Barizo (43°18'48"N; 8°52'27"W), 5.iv.2004, SANT-Algae 24492 (tetrasporangial plants), 15.v.2003, SANT-Algae 24556 (female and tetrasporangial plants); 14) Arou (43°11'03"N; 9°06'46"W); 6.iv.2004, SANT-Algae 26389 (tetrasporangial plants); 15) Lourido (43°05'28"N, 9°13'15"W), 1.ii.2006, SANT-Algae 22606. 16) Estorde (42°56'28"N; 9°13'04"), 11.iii.2005, SANT-Algae 15504 (tetrasporangial plants); 17) Arnela (42°42'35"N; 9°00'47"W), 30.i.2006, SANT-Algae 24351, 24353 (female and tetrasporangial plants); 18) Nerga (42°15'19"N; 8°50'07"W), 12-ii-2005, SANT-Algae 22823 (male and tetrasporangial plants).

Vegetative and reproductive morphology

Thalli forming dense turfs up to 7 cm high and covering rock surfaces of up to 1 m^2 in extent. Thallus radially organized and predominantly erect, with a short system of prostrate interwoven axes bearing rhizoids that attach to the substrate (Figs 274, 275). Erect axes showing an obvious main axis which is scarcely and irregularly branched up to 3 orders, also bearing short lateral branches or clusters of laterals which are especially abundant in tetrasporangial plants (Figs 274-276). Basal parts of axes black in colour and with a rigid texture, upper ones red in colour with a soft and flaccid texture.

Axes ecorticate with 9-15 pericentral cells (Figs 278-281) often forming a spirally-twisted (Fig. 285). Prostrate axes 150-240 µm in diameter, extending when rhizoids develop at basal parts of erect axes, as well as by the formation of endogenous branches that grow by divisions of an apical cell without trichoblasts, producing further prostrate axes (Fig. 277). Rhizoids cut off from pericentral cells (Fig. 282). Erect axes 200-310 µm in diameter, exogenous branches formed at apices in the axils of trichoblasts (Fig. 283), irregularly arranged (Fig. 284); endogenous branches are usually formed on scars cells of trichoblasts, as well as in axils of branches. Trichoblasts usually present but scarcely developed, formed every 2-6 segments, deciduous and leaving conspicuous scar cells (Figs 283, 285).

Gametophytes dioecious. Procarps are formed in suprabasal cells of modified trichoblasts and they consist of a four-celled carpogonial branch, a basal sterile cell (Fig. 286) and a group of two lateral sterile cells borne on the supporting cell. Cystocarps globose when mature, 350-650 µm high and 300-600 µm in diameter (Fig. 287). Spermatangial axes cylindrical and often slightly incurved, 190-350 µm long and 37-88 µm in diameter, formed on a branch of modified trichoblasts, sometimes bifurcated, without sterile apical cells (Figs 288-290). Tetrasporangia in upper branches forming slightly spiral rows with up to 20 mature tetrasporangia (Figs 291, 292); ovate, 60-100 µm in diameter, with 2 cover cells similar to pericentral cells.



Figs 274-292. *Polysiphonia nigra*. Vegetative and reproductive morphology. **274-275.** Habit of plants consisting of a short system of prostrate axes from which arise the irregularly branched erect axes. **276.** Erect axis of a tetrasporophyte bearing clusters of short lateral branches. **277.** Prostrate axes with rhizoids: arrowhead – adventitious branches producing further prostrate axes. **278-281.** Cross sections of axes showing 11 (278), 13 (279), 14 (280) and 15 (281) pericentral cells. **282.** Rhizoid cut off from pericentral cells: arrowhead – wall separating the pericentral cell and the rhizoid. **283.** Apex of an erect axis forming exogenous branches in the axils of trichoblasts: arrowhead – basal cell of a trichoblast. **284.** Erect axis with scattered branches. **285.** Erect axis with spirally-twisted pericentral cells and scars cells of trichoblasts every two segments: arrowheads – scar cells. **286.** Procarp showing the supporting cell (su), the four celled carpogonial branch (1-4) and the sterile basal cell (st). **287.** Cystocarps. **288.** Apex of an erect axis bearing spermatangial branches. **289.** Spermatangial branch formed on one of the branches of the first dichotomy of a modified trichoblast. **290.** Bifurcated spermatangial branch. **291-292.** Tetrasporangia forming long and slightly spiral series. Scale bars: 1 cm in Figs 274-275; 2 mm in Figs 276-277; 50 µm in Figs 278-281, 283, 289 and 290; 100 µm in Figs 282 and 285; 600 µm in Figs 284, 288, 291 and 292; 25 µm in Fig. 286; 200 µm in Fig. 287.

Figs 293-294. Distribution of *Polysiphonia nigra*. **293.** Collections along the Atlantic Iberian Peninsula. **294.** World distribution: arrow – type locality.

Phenology

Polysiphonia nigra was collected throughout the year and it is probably perennial. Reproductive structures were frequently found, especially tetrasporangia (40% of the collections), which were collected year-round, except in July and December. Female and male structures were more rarely observed (9%) and they were found in January-May and September.

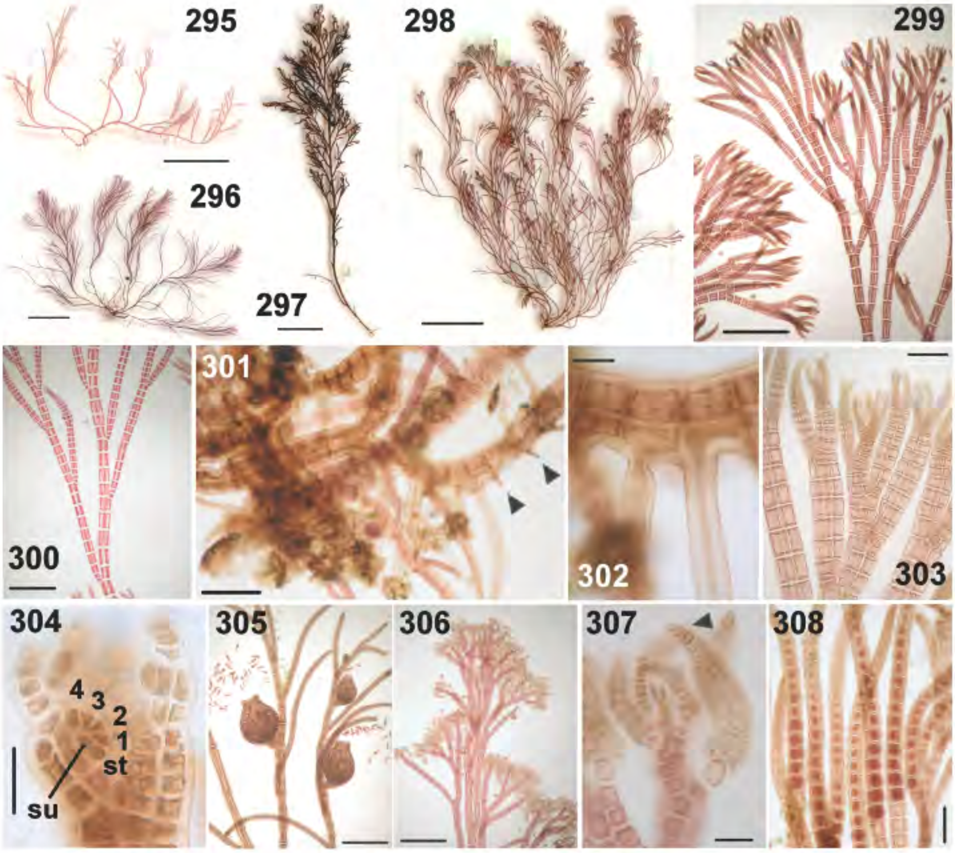
Habitat and distribution

Polysiphonia nigra was found along the Atlantic Iberian Penisula (Fig. 293), especially in northern locations, while in the southern ones it was only rarely collected. *Polysiphonia nigra* was collected from the mid to the low intertidal of sand-covered rocks, from moderately to extremely wave-exposed sites, forming almost monospecific turfs or most commonly growing entangled with other species typical from the habitat, especially *Ophidocladus simpliciusculus*. *Polysiphonia nigra* is usually dominant in locations where there is a sand layer of several centimetres, maintaining the basal parts of plants buried by sand of which only emerge the apical parts of the longest erect axes. Frequently, erect axes of *P. nigra* are broken and only the basal parts remain attached to the substrate (Fig. 275). These forms of *P. nigra* are very similar in the field to *O. simpliciusculus* and both species often form mixed turfs. Differences between this pair of species are commented in the remarks about *O. simpliciusculus*. *Polysiphonia nigra* has been reported from the northern Atlantic coasts, both in Europe and America, as well as in Namibia (Fig. 294).

Polysiphonia stricta (Dillwyn) Greville **Figs 295-310**

Basionym: *Conferva stricta* Dillwyn.
Lectotype: BM (Maggs & Hommersand, 1993).
Type locality: Glamorgan, Swansea, UK.
Synonym: *Polysiphonia urceolata* (Ligthfoot *ex* Dillwyn) Greville.
References: Veldkamp, 1950; Kapraun, 1977; Kapraun & Rueness, 1983; Maggs & Hommersand, 1993; Schneider & Searles, 1991; Kim *et al.*, 2000.
Molecular vouchers: GenBank accession numbers KF648514, KF648515, KF648521.

Selected specimens: 1) Tagle (43°25'59"N; 4°04'50"W), 1.iv.2006, SANT-Algae 20368; 2) Verdicio (43°37'30"N; 5°52'44"W), 19.iv.2007, SANT-Algae 19623; 3) Aguilar (43°33'28"N; 6°07'07"W), 17.iv.2007, SANT-Algae 19799 (tetrasporangial plants), 27.v.2010, SANT-Algae 24134 (tetrasporangial plants); 6) Linorsa (43°41'56"N;



Figs 295-308. *Polysiphonia stricta.* Vegetative and reproductive morphology. **295-298.** Habit, predominantly consisting of erect axes, with a short system of prostrate axes. **299-300.** Erect axes showing branches spirally arranged mostly every 3-6 segments. **301.** Prostrate system with rhizoids: arrowheads – adventitious branches. **302.** Rhizoids in open connection to pericentral cells. **303.** Apex of an erect axis developing exogenous branches. **304.** Procarp showing the supporting cell (su), the 4-celled carpogonial branch (1-4) and the basal sterile cell (st). **305.** Cystocarps, which are urceolate when mature. **306.** Spermatangial axes densely clustered in apical parts of the erect axis. **307.** Spermatangial axes replacing the trichoblasts: arrowhead – sterile apical cells. **308.** Tetrasporangia arranged in long straight rows. Scale bars: 5 mm in Figs 295-298; 600 μm in Figs 299, 300, 305 and 306; 200 μm in Figs 301 and 308; 50 μm in Figs 302 and 307; 100 μm in Fig. 303; 25 μm in Fig. 304.

7°27'14"W), 10.iii.2005, SANT-Algae 23124 (male and tetrasporangial plants); 7) Doniños (43°30'08"N; 8°19'17"W), 12.iii.2005, SANT-Algae 24533 (male, female and tetrasporangial plants); 8) Chanteiro (43°26'46"N; 8°18'15"W), 17.ix.2005, SANT-Algae 19601 (tetrasporangial plants); 9) Ber (43°23'51"N; 8°12'44"W), 23.i.2011, SANT-Algae 24696 (male, female and tetrasporangial plants). 10) Perbes (43°22'34"N; 8°12'55"), 7.iii.2008, SANT-Algae 22565 (tetrasporangial plants); 11) Seaia (43°19'41"N; 8°49'34"W), 26.x.2003, SANT-Algae 23036; 12) Hermida (43°15'47"N; 8°57'10"W), 26.iv.2006, SANT-Algae 24383 (male, female and tetrasporangial plants); 13) Estorde (42°56'28"N; 9°13'04"), 11.iii.2005, SANT-Algae 23060 (tetrasporangial plants); 15) Area da Cruz (42°27'40"N; 8°54'37"W), 22.viii.2005, SANT-Algae 25059.

Figs 309-310. Distribution of *Polysiphonia stricta*. **309.** Collections along the Atlantic Iberian Peninsula. **310.** World distribution: arrow – type locality.

Vegetative and reproductive morphology

Thalli forming dense tufts up to 7 cm high and covering rock surfaces of up to 100 cm^2 in extent. Thallus radially organized and predominantly erect, attached to the substratum by rhizoids formed in basal parts of erect axes, forming a short system of prostrate interwoven axes (Figs 295-298). Erect axes branched mostly every 3-6 segments, up to 3 orders (Figs 299, 300). Axes red in colour; with a flaccid texture.

Axes ecorticate, with 4 pericentral cells. Prostrate axes 90-190 µm in diameter, extending as rhizoids are developed at basal parts of erect axes, as well as by the formation of endogenous branches (Fig. 301) that produces further prostrate axes. Rhizoids in open connection to pericentral cells (Fig. 302). Erect axes 90-240 µm in diameter, branches mainly exogenous, arising independently from trichoblasts, spirally arranged (Fig. 303). Trichoblasts usually absent.

Gametophytes dioecious. Procarps are formed in suprabasal cells of modified trichoblasts and they consist of a four-celled carpogonial branch, a basal sterile cell (Fig. 304) and a group of two lateral sterile cells borne on the supporting cell. Cystocarps urceolate when mature, 400-700 µm high and 280-530 µm in diameter (Fig. 305). Spermatangial axes cylindrical and usually incurved, 175-350 µm long and 35-75 µm in diameter, formed on modified trichoblasts and replacing them, growing on every segment, with 2-4 sterile apical cells (Figs 306, 307). Tetrasporangia in upper branches forming long straight rows with up to 12 mature tetrasporangia (Fig. 308); they are ovate, 45-113 µm in diameter, with 2 cover cells similar to the pericentral cells.

Phenology

Polysiphonia stricta was collected throughout the year and it is probably perennial. Reproductive structures were frequently found, especially tetrasporangia (43% of the collections) that were collected all around the year. Sexual structures were found from January to April (11% and 8% of the collections with male and female structures, respectively).

Habitat and distribution

Polysiphonia stricta was found along the Atlantic Iberian Peninsula (Fig. 309), especially in northern locations, while it was rarely found in the South. It was collected from the mid to the low intertidal of sand-covered rocks from moderately to extremely wave-exposed sites, forming almost monospecific turfs or most commonly growing entangled with other species typical from the habitat.

Polysiphonia stricta was reported in the North Atlantic coasts and in Alaska (Fig. 310).

Remarks

Polysiphonia stricta is very similar to its Iberian congeners with 4 pericentral cells and rhizoids cut off from pericentral cells (*P. atlantica, P. caespitosa* and *P. devoniensis*). It can be easily separated from all them because *P. stricta* is the largest species, both in length and in diameter of axes.

The analysis of COI-5P sequences of materials labelled as *P. stricta* from 3 different locations showed that two groups of species can be molecularly differentiated, as they differ by 10.7% sequence divergence. Further studies are required to clarify the identity of these two entities, however our preliminary results suggest the presence of cryptic diversity within *P. stricta* over the Atlantic Iberian Peninsula. Interestingly, a remarkable cryptic diversity within materials morphologically assigned to *P. stricta* has been found also in Canada (Saunders & McDevit, 2013).

Polysiphonia tripinnata J.Agardh **Figs 311-327**

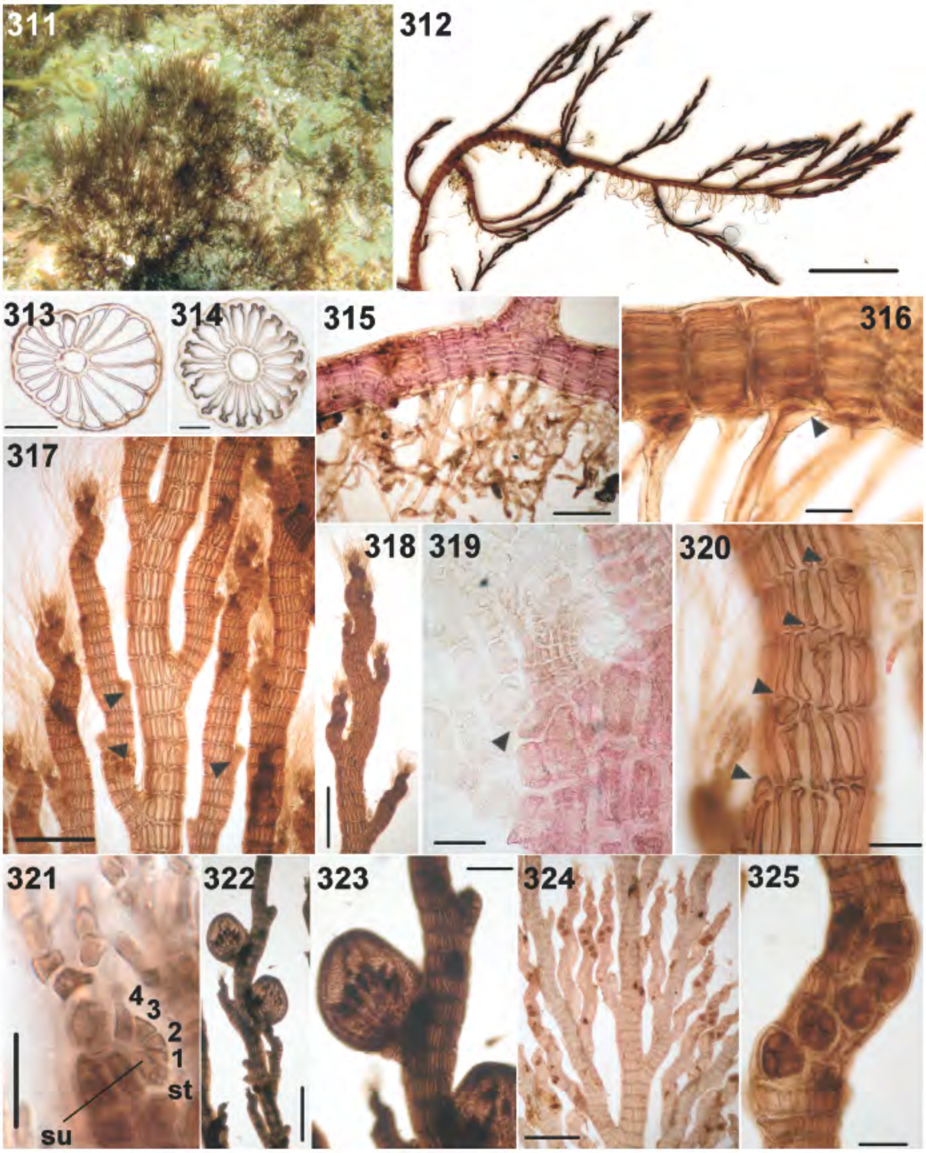
Lectotype: LD (Díaz-Tapia *et al.*, 2013a).
Type locality: Trieste, Italy.
References: Agardh, 1842; Kützing, 1849, 1863; Lauret, 1970; Rojas-González & Afonso-Carrillo, 2007; Díaz-Tapia *et al.*, 2013a.
Molecular vouchers: GenBank accession numbers KC130871, KC130870 (Díaz-Tapia *et al.*, 2013a).
Selected specimens: 1) Ogeia (43°22'22"N; 2°32'35"W), 9.x.2006, SANT-Algae 20965; 2) Punta do Castro (43°33'47"N; 7°10'35"W), 24.iv.2009, SANT-Algae 22807; 3) Peinzás (43°35'09"N; 7°16'13"W), 26.xi.2007, 20.ii.2008, 6.iv.2008, 6.vi.2008, 18.ix.2008, 10.i.2009, 25.i.2012, SANT-Algae 22244, 22245, 20470, 20396, 22246, 22247, 27307; 4) Baleal (39°22'25"N, 9°19'56"W), 14.vi.2010, SANT-Algae 24256, 27385 (female and tetrasporangial plants); 5) Queimado (37°49'34"N; 8°47'34"W), 24.v.2005, SANT-Algae 25264 (female plants); 6) Almograve (37°39'54"N; 8°48'04"W), 25.v.2005, 22.ii.2011, SANT-Algae 234763, 24675; 7) Olhos d'Agua (37°05'20"N; 8°11'27"W), 6.v.2005, SANT-Algae 25736; 8) Punta Plata (36°06'28"N; 5°49'41"W), 19.i.2011, SANT-Algae 26522.

Vegetative and reproductive morphology

Thalli forming dense tufts up to 5 cm high and covering rock surfaces of *ca* 200 cm^2 in extent (Fig. 311). Thallus radially organized, consisting of indeterminate erect axes that become decumbent when developing rhizoids at their basal parts, forming an extensive system of prostrate interwoven axes (Fig. 312). Erect axes alternately branched up to 3 orders. Axes are dark red to brown; with a rigid texture.

Axes ecorticate, with (14-) 17-19 (-20) pericentral cells (Figs 313, 314). Prostrate axes, often twisted, growing as the rhizoids are formed on the basal parts of erect axes, which become decument. Prostrate axes (300-) 350-650 (-800) µm in diameter. Rhizoids cut off from pericentral cells, abundantly developed, up to 4 per segment (Figs 315, 316).

Erect axes with tips markedly sinusoidal (Figs 317, 318), (250-) 300-450 (-600) µm in diameter. Branches exogenous, arising in the axils of trichoblasts, alternately arranged mostly every 5-6 segments (Figs 317-319), consist of short branchlets of determinate growth or branches of indeterminate growth (Fig. 317). Trichoblasts, from little to well developed, borne on every segment, deciduous and leaving conspicuous scars cells when shed (Fig. 320).



Figs 311-325. *Polysiphonia tripinnata*. Vegetative and reproductive morphology. **311.** Turf in sand-covered rocks. **312.** Thallus consisting of a an extensive prostrate axis and short erect axes, which becoming decumbent when rhizoids are developed at their basal parts. **313-314.** Cross section of axes showing 19 (313) and 17 (314) pericentral cells. **315.** Prostrate axis with abundant rhizoids. **316.** Rhizoids cut off from pericentral cells: arrowhead – wall separating the pericentral cell and the rhizoid. **317-318.** Erect axes with branches of determinate and indeterminate growth, branches alternately arranged every 5-6 segments: arrowheads – branches of determinate growht. **319.** Young branch formed in the axil of a trichoblast: arrowhead – basal cell of the trichoblast. **320.** Erect axes showing scar cells of trichoblasts on every segment: arrowheads – scar cells. **321.** Procarp showing the supporting cell (su), the 4-celled carpogonial branch (1-4) and the basal sterile cell (st). **322-323.** Cystocarps. **324-325.** Tetrasporangia arranged in spiral series. Scale bars: 5 mm in Fig. 312; 200 µm in Figs 313 and 323; 100 µm in Figs 314, 316, 320 and 325; 600 µm in Figs 315, 317, 318, 322 and 324; 50 µm in Fig 319; 25 µm in Fig. 321.

Figs 326-327. Distribution of *Polysiphonia tripinnata*. **326.** Collections along the Atlantic Iberian Peninsula. **327.** World distribution: arrow – type locality.

Procarps formed in suprabasal cells of modified trichoblasts in the upper parts of erect axes, consisting of a four-celled carpogonial branch, a basal sterile cell (Fig. 321) and a group of two lateral sterile cells borne on the supporting cell. Cystocarps are globular when mature, (550-) 600-750 (-800) µm high and (400-) 450-620 (-700) µm in diameter (Figs 322, 323).

Tetrasporangia formed on mid and basal branches of erect axes, forming spiral series with up to 5 mature tetrasporangia (Figs 324, 325). They are ovate, (35-) 40-50 (-55) µm in diameter, with 2 cover cells similar to pericentral cells.

Phenology

Plants of *Polysiphonia tripinnata* occur throughout the year, and are probably perennial. Reproductive structures were rare (6% of the collections) and found only at locations from central and southern Portugal. Tetrasporangia were collected in February and May, and female structures in May and June.

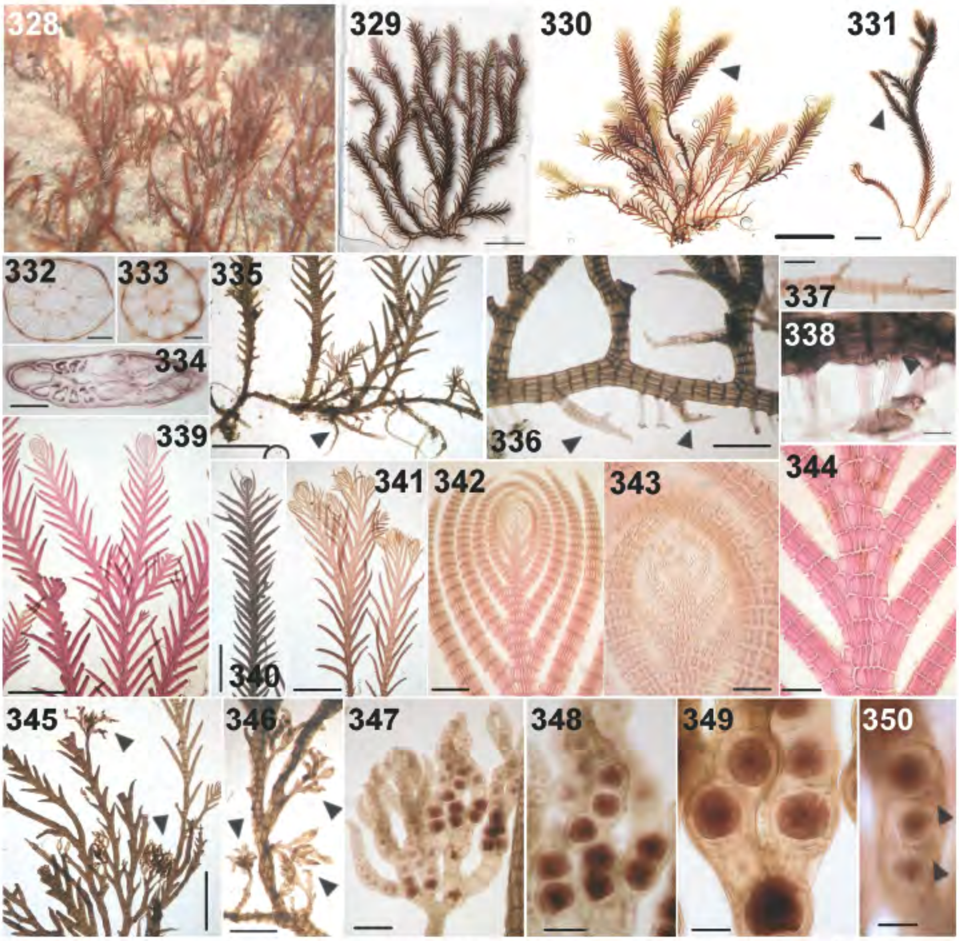
Habitat and distribution

Polysiphonia tripinnata forms dense turfs on sand-covered rocks from the low intertidal to the upper subtidal in moderately to wave exposed locations. Turfs are sometimes almost monospecific, but most commonly they are mixed with other species from sand-covered rocks, such as *Pterosiphonia ardreana*, *Ophidocladus simpliciusculus* or *Rhodothamiella floridula*.

Polysiphonina tripinnata is a frequent species along the southern coast of the Atlantic Iberian Peninsula (Fig. 326), where it forms extensive populations at most sites. Conversely, it is uncommon along the northern Iberian coast (Fig. 326), where it was abundantly collected in only two locations. The world distribution of *P. tripinnata* is restricted to the Mediterranean Sea, the Atlantic Iberian Peninsula and the Canary and Salvage Islands (Fig. 327).

Pterosiphonia ardreana Maggs *et* Hommersand **Figs 328-352**

Holotype: BM.
Type locality: Nerope Rocks, Padstow, Cornwall, England.
Synonym: *Pterosiphonia spinifera* var. *robusta* Ardré *nom. inval.*
References: Ardré, 1967 (as *P. spinifera* var. *robusta*); Maggs & Hommersand, 1993.
Molecular vouchers: GenBank accession numbers KF648517, KF648523, KF671167, KF671174.



Figs 328-350. *Pterosiphonia ardreana.* Vegetative and reproductive morphology. **328.** Turf of *P. ardreana* mixed with *Rhodothamniella floridula*. **329-331.** Habit consisting of a prostrate system of indeterminate branches bearing dorsally erect indeterminate branches, which mostly produce one order of alternate determinate branches, but occasionally producing two: arrowheads – branches of second order. **332-334.** Cross section of axes showing 9 (332), 10 (333) and 11 (334) pericentral cells surrounding the central axial cell. **335-336.** Prostrate axes: arrowheads – adventitious endogenous branches. **337.** Apex of a prostrate axis showing dorsal and lateral branches. **338.** Rhizoids cut off from pericentral cells: arrowhead – wall separating the pericentral cell and the rhizoid. **339-341.** Erect axes consisting of a main axes that mostly produces one order of determinate branches, but occasionally two. **342-343.** Apices of erect axes. **344.** Erect axes showing a coalescence of 2.5-3 segments between the main axes and lateral branches. **345-346.** Branchlets bearing tetrasporangia, formed on extensions of determinate laterals from mid and basal parts of erect axes: arrowheads – tetrasporangial branchlets. **347-348.** Branches with tetrasporangia forming spiral rows. **349.** Tetrasporangia. **350.** Branch with tetrasporangia: arrowheads – the third cover cell of tetrasporangia. Scale bars: 5 mm in Figs 329-331; 50 µm in Figs 332, 333, 343, 349 and 350; 100 µm in Figs 334, 338 and 348; 2 mm in Figs 335, 339-341 and 345; 600 µm in Figs 336 and 346; 200 µm in Figs 337, 342, 344 and 347.

Figs 351-352. Distribution of *Pterosiphonia ardreana*. **351.** Collections along the Atlantic Iberian Peninsula. **352.** World distribution: arrow – type locality.

Selected specimens: 1) Zumaia (43°17'59"N; 2°15'41"W), 30.iii.2006, SANT-Algae 20272; 18.iii.2011, SANT-Algae 25132; 2) San Juan de Gaztelougatxe (43°26'41"N; 2°46'41"W), 29.iii.2006, SANT-Algae 20294; 3) La Arena (43°21'16"N; 3°06'53"W), 22.iii.2011, SANT-Algae 25640 (tetrasporangial plants); 4) Kobarón (43°21'10"N; 3°07'54"W), 12.ix.2006, SANT-Algae 19878; 5) Langre (43°28'37"N; 3°41'31"W), 6.xi.2010, SANT-Algae 24617; 6) Tagle (43°25'59"N; 4°04'50"W), 1.iv.2006, SANT-Algae 20349 (tetrasporangial plants); 7) Amio (43°23'42"N; 4°28'57"), 17.iii.2006, SANT-Algae 20419; 8) Estaño (43°32'52"N; 5°35'50"W), 18.iv.2007, SANT-Algae 19843; 9) Verdicio (43°37'30"N; 5°52'44"W), 19.iv.2007, SANT-Algae 19626; 10) Aguilar (43°33'28"N; 6°07'07"W), 17.iv.2007, SANT-Algae 19821; 11) Punta do Castro (43°33'47"N; 7°10'35"W), 14.v.2003, SANT-Algae 14600; 12) San Román (43°43'17"N; 7°37'39"W), 16.vii.2008, SANT-Algae 21737; 13) Santa Comba (43°33'34"N; 8°15'30"W), 26.iv.2005, SANT-Algae 23096; 14) Seaia (43°19'41"N; 8°49'34"W), 26.x.2003, SANT-Algae 23037; 15) Lourido (43°05'28"N, 9°13'15"W), 1.ii.2006, SANT-Algae 22604 (tetrasporangial plants), 15.vii.2008, SANT-Algae 21372; 16) Area da Cruz (42°27'40"N; 8°54'37"W), 22.viii.2005, SANT-Algae 25057; 17) Almograve (37°39'54"N; 8°48'04"W), 25.v.2005, SANT-Algae 24767; 18) Ingrina (37°02'46"N; 8°52'43"W), 20.ii.2011, SANT-Algae 25474; 19) Armaçao de Pêra (37°06'04"N; 8°22'17"W), 17.10.2005, SANT-Algae 24825.

Vegetative and reproductive morphology

Thalli forming turfs up to 5 cm high, and covering rock surfaces of up to several meters in extent (Fig. 328). Thallus with a dorsiventral structure, consisting of an extensive system of indeterminate prostrate axes bearing ventrally rhizoids which attach to substrate, and arising dorsally erect axes of indeterminate growth that produce 1 order of alternate-distichous branches of determinate growth, some of which bear a second order of branches (Figs 329-331). Plants dark red to black in colour, with a rigid texture.

Axes ecorticate, consisting of a central axial cell and (8-) 9-11 (-12) pericentral cells (Figs 332-334). Prostrate axes and basal parts of the erect ones are cylindrical, while erect axes are complanate. Prostrate axes indeterminate and dorsiventral, growing by transverse divisions of apical cells; axes 170-280 µm in diameter, branched exogenously at irregular intervals forming dorsally erect axes, and laterally further prostrate axes, commonly also producing adventitious branches (Figs 335-337). Rhizoids cut off from pericentral cells, unicellular (Fig. 338). Erect axes of indeterminate growth with a prominent apical cell and without trichoblasts; axes 250-400 µm in diameter, producing alternate branches of determinate growth at regular intervals of 2-3 segments (Figs 339-343), coalesced with main axis over 2.5-3 axial segments (Fig. 344).

Sexual structures were not found. Tetrasporangia arranged in spiral rows, placed in incurved branches formed as extensions of determinate lateral branches from mid and basal parts of erect axes. Tetrasporangia are subspherical, 50-87.5 µm broad, with 3 cover cells (Figs 345-350).

Phenology

Pterosiphonia ardreana was found throughout the year and it is probably perennial. Most collections were sterile, and tetrasporangia were only rarely found (8% of the collections) in February-March, August and November. Sexual reproductive structures are unknown for the species.

Habitat and distribution

Pterosiphonia ardreana is a common species in sand-covered rocks along the Atlantic Iberian Peninsula (Fig. 351). It forms almost monospecific turfs from the low intertidal to the upper subtidal of sites from moderately to extremely wave-exposed, or it grows forming turfs mixed with other species typical from the habitat, such as *Rhodothamniella floridula* or *Pterosiphonia pennata*. *Pterosiphonia ardreana* was reported in Europe and northern Africa (Fig. 352).

Remarks

Pterosiphonia ardreana was described by Maggs and Hommersand (1993) based on materials from the British Isles and including specimens previously assigned by Ardré (1967) as *P. spinifera* var *robusta* nom. inval. *Pterosiphonia ardreana* is very similar in morphology to *P. pennata sensu lato*, but the former is more robust than the second species, which implies that the axes and the coalescence between branches and the main axis are wider in *P. ardreana*. In the Atlantic Iberian Peninsula, both species often share the same habitat and they grow together forming mixed turfs. Although some robust forms of *P. pennata* can be confused with *P. ardreana*, both species can be clearly separated in most of the cases. Nevertheless, we detected a gradient of plant sizes and robustness in this pair of species, in which the extreme forms correspond to very thin and slender specimens of *P. pennata* (perhaps *P. pinnulata*, see remarks on *P. pennata*), while *P. ardreana* represents the most robust plants in that gradient (Figs 353-358).

Pterosiphonia parasitica (Hudson) Falkenberg **Figs 359-378**

Basionym: *Conferva parasitica* Hudson.

Neotype: BM (Maggs & Hommersand, 1993).

Type locality: Yorkshire, Scarborough, England.

References: Suneson, 1940; Maggs & Hommersand, 1993.

Molecular voucher: GenBank accession number KF648524.

Selected specimens: 1) La Arena (43°21’16”N; 3°06’53”W), 22.iii.2011, SANT-Algae 25631, 25634; 2) Kobarón (43°21’10”N; 3°07’54”W), 12.ix.2006, SANT-Algae 19894; 3) Estaño (43°32’52”N; 5°35’50”W), 18.iv.2007, SANT-Algae 19842; 4) San Román (43°43’17”N; 7°37’39”W), 31.i.2006, SANT-Algae 17676, 16.xii.2008, SANT-Algae 21374; 5) Lago (San Ciprián, 43°42’28”N; 7°28’32”W), 10.ii.2005, SANT-Algae 17181 (tetrasporangial plants); 6) Lago (Camariñas) (43°07’49”N; 9°11’58”W), 16.v.2003, SANT-Algae 22858; 7) Area da Cruz (42°27’40”N; 8°54’37”W), 22.viii.2005, SANT-Algae 25056 (tetrasporangial plants); 8) Nerga (42°15’19”N; 8°50’07”W), 12-ii-2005, SANT-Algae 22824.

Figs 353-358. Gradient of size and robustness showed by different specimens *a priori* labelled as *Pterosiphonia ardreana* (353-354) and *P. pennata* (355-358). Scale bar: 1 cm.

Vegetative and reproductive morphology

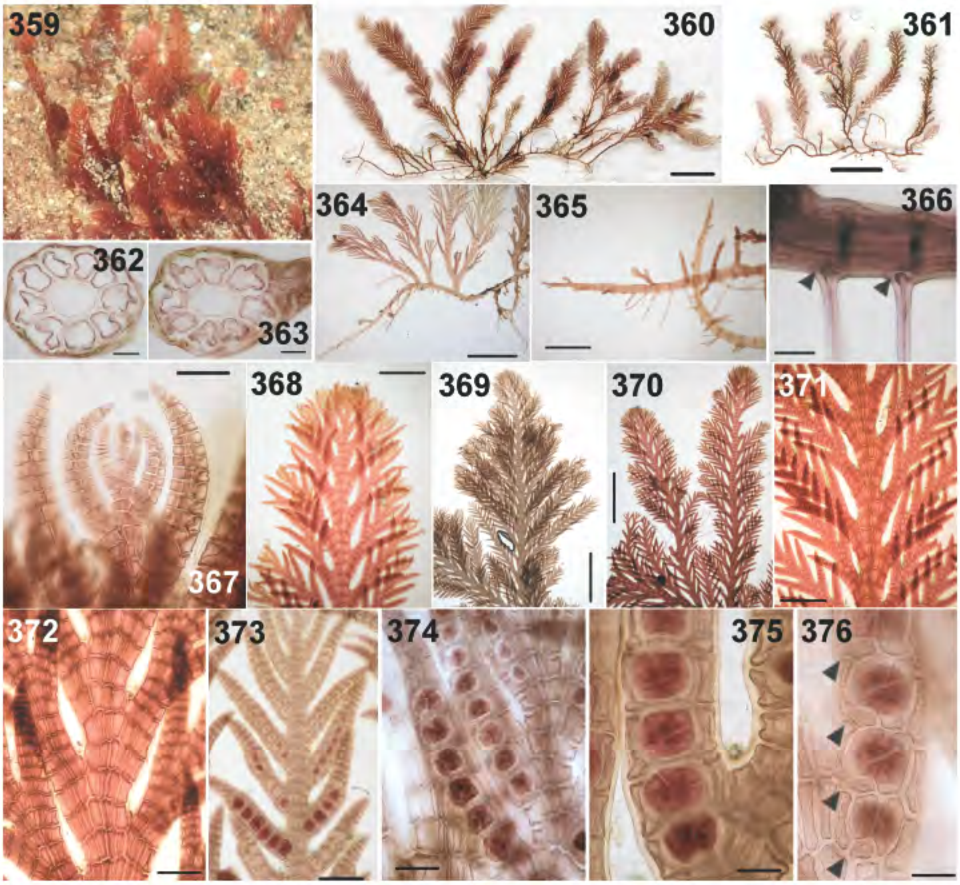
Thalli forming turfs up to 3 cm high, and covering rock surfaces of up to 400 cm^2 in extent (Fig. 359). Thallus dorsiventral, consisting of an extensive system of indeterminate prostrate axes bearing ventrally the rhizoids that attach to substrate, and from which arising dorsally the erect axes of indeterminate growth, which in turn produce 2 (-3) orders of alternate-distichous branches of determinate growth (Figs 360, 361). Plants are dark red or pink in colour, with a rigid texture.

Axes ecorticate, consisting of a central axial cell and (7-) 8-9 pericentral cells (Figs 362, 363). Prostrate axes indeterminate and dorsiventral, growing by transverse divisions of apical cells. They are cylindrical, 150-320 µm in diameter, laterally branched exogenously at irregular intervals forming erect axes and further prostrate axes, commonly producing also adventitious branches (Figs 364, 365). Rhizoids unicellular, cut off from pericentral cells (Fig. 366). Erect axes of indeterminate growth with a prominent apical cell, lacking trichoblasts (Figs 367, 368); cylindrical in the basal parts and complanate in upper ones, axes 250-400 µm in width, producing alternate branches of determinate growth at regular intervals of 2 segments (Figs 369, 370), coalesced with main axis over 1.5-2.5 axial segments (Figs 371, 372).

Gametophytes not found. Tetrasporangia arranged in straight series in the last order branches; subspherical, 55-87.5 µm broad, with 3 cover cells (Figs 373-376).

Phenology

Pterosiphonia parasitica was collected throughout the year, and it is probably perennial. Tetrasporangia were found in three sites (15% of the collections) in February and September. Sexual structures were not found.



Figs 359-376. *Pterosiphonia parasitica* Vegetative and reproductive morphology. **359.** Turf in sand-covered rocks. **360-361.** Habit consisting of an extensive prostrate system bearing erect axes of indeterminate growth, which in turn produce 2-orders of alternate branches of determinate growth. **362-363.** Cross section of axes showing an axial cell surrounded by 8 (363) and 9 (362) pericentral cells. **364.** Prostrate axis from which arises the erect axes and further prostrate axes. **365.** Apex of a prostrate axis which produces rhizoids and branches at irregular intervals. **366.** Rhizoids cut off from pericentral cells: arrowhead – wall separating the pericentral cell and the rhizoid. **367-368.** Apices of erect axes producing branches every two segments. **369-370.** Upper parts of erect axes. **371-372.** Erect axes showing a coalescence of 2.5 segments between main axis and lateral branches. **373-375.** Tetrasporangia forming straight series in the last-order branches. **376.** Branch with tetrasporangia: arrowheads – the third cover cell of tetrasporangia. Scale bars: 5 mm in Figs 360 and 361; 50 µm in Figs 362, 363, 367 and 373-376; 2 mm in Figs 364, 369 and 370; 600 µm in Figs 365, 368 and 371; 100 µm in Figs 366 and 374; 200 µm in Figs 372 and 373.

Habitat and distribution

Pterosiphonia parasitica was collected in sand-covered rocks from numerous locations of the northern Atlantic Iberian Peninsula, while it was absent in southern sampled sites (Fig. 377). However, it was reported in previous works

Figs 377-378. Distribution of *Pterosiphonia parasitica* **377.** Collections along the Atlantic Iberian Peninsula. **378.** World distribution: arrow – type locality.

from the southern areas of the Iberian Peninsula (Ardré, 1970; Seoane-Camba, 1965). Its frequency and abundance is moderate in sand-covered rocks, but sometimes it was found as the dominant species in turfs usually mixed with *Rhodothamiella floridula*. *Pterosiphonia parasitica* was reported in Atlantic and Mediterranean Europe, northern and southern Africa and Brazil (Fig. 378).

Remarks

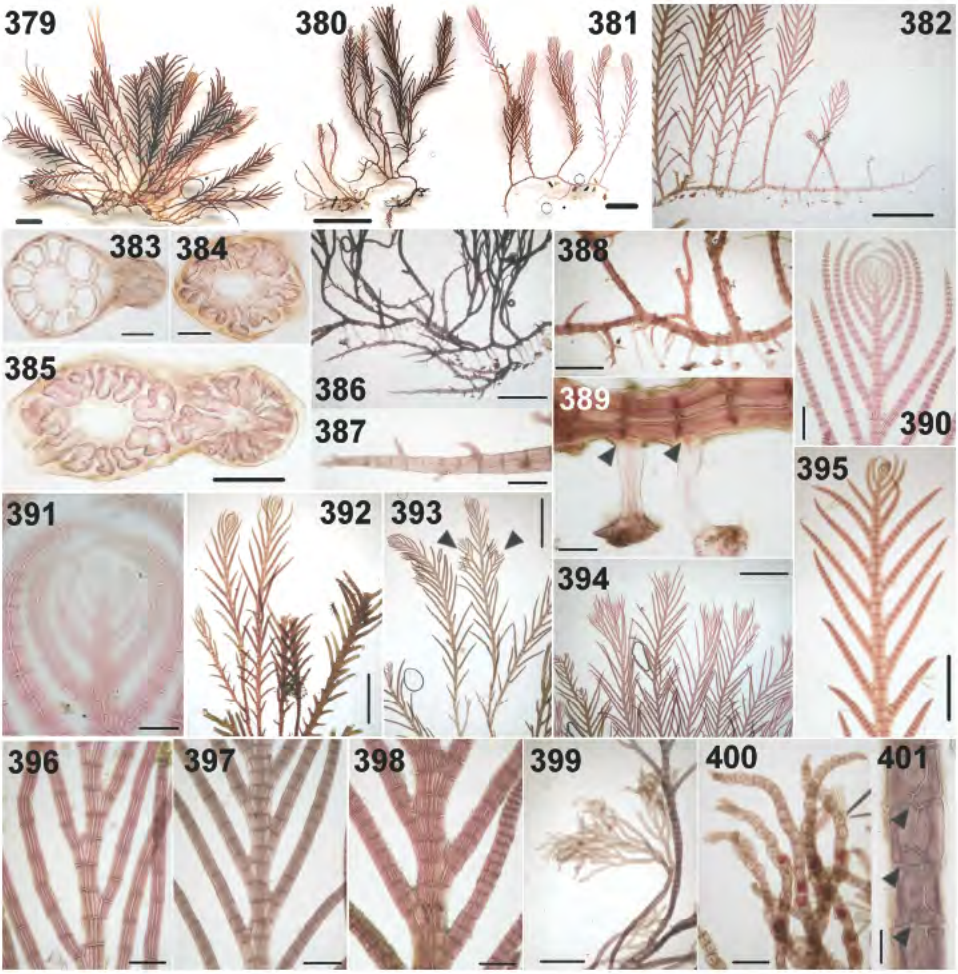
Pterosiphonia parasitica can be easily separated from its congeners from the Atlantic Iberian Peninsula; by its branching pattern consisting of one order of branches in the other species instead of the two orders characteristic of *P. parasitica*, and by its colour, which is dark-brown to black in the other species while it is pink to dark red in *P. parasitica.*

Specimens from sand-covered rocks of the Atlantic Iberian Peninsula show important differences from plants described from the British Isles by Maggs & Hommersand (1993), where is the type locality of the species. Main differences involve the number of pericentral cells (8-9 in the Iberian Peninsula *vs.* 7-8 in the British Isles), coalescence between lateral branches and main axes (1.5-2.5 in the Iberian Peninsula *vs* 0.7-1.3 in the British Isles), the branching pattern (main axes produce 2 (-3) branching orders in the Iberian Peninsula *vs* 3-4 in the British Isles), tetrasporangia (straight rows in the Iberian Peninsula *vs.* spiral in the British Isles). A comparative detailed study of plants from both provenances is required to clarify the significance of these morphological differences.

Pterosiphonia pennata (C. Agardh) Falkenberg **Figs 379-408**

Basionym: *Hutchinsia pennata* C. Agardh.
Lectotype: LD (Maggs & Hommersand, 1993).
Type locality: Mediterranean Sea (not specified).
References: Maggs & Hommersand, 1993; Díaz-Tapia & Bárbara, 2004.
Molecular vouchers: GenBank accession numbers KF671154, KF671155, KF671157, KF671164, KF671172.

Selected specimens: 1) Biarritz (43°29'03"N; 1°33'46"W), 19.iii.2011, SANT-Algae 25417-20, 25429-30; 2) Zumaia (43°17'59"N; 2°15'41"W), 30.iii.2006, SANT-Algae 20269, 18.iii.2011, SANT-Algae 25133, 25153-58; 3) Laida (43°24'28"N; 2°40'54"W), 31.iii.2006, SANT-Algae 20284 (tetrasporangial plants); 4) San Juan de Gaztelougatxe (43°26'41"N; 2°46'41"W), 8.ix.2010, SANT-Algae 20295; 5) La Arena (43°21'16"N; 3°06'53"W), 22.iii.2011, SANT-Algae 25636, 25647-50, 25652; 25654, 25656, 25658, 25661; 6) Langre (43°28'37"N; 3°41'31"W), 6.xi.2010, SANT-Algae 24315-16, 24618 (tetrasporangial plants); 7) Virgen del Mar (43°28'40"N; 3°52'31"W), 7.xi.2010, SANT-Algae 24640, 24643, 25650; 8) Valdearenas



Figs 379-401. *Pterosiphonia pennata.* Vegetative and reproductive morphology. **379-382.** Habit consisting of a prostrate system of indeterminate branches bearing ventrally rhizoids and dorsally erect indeterminate branches that mostly produce one order of alternate determinate branches (occasionally two). **383-385.** Cross section of axes showing 8 (383), 9 (384) and 10-11 (385) pericentral cells surrounding the central axial cell. **386-388.** Prostrate axes. **389.** Rhizoids cut off from pericentral cells: arrowhead – wall separating the pericentral cell and the rhizoid. **390-391.** Apices of erect axes. **392-395.** Erect axes consisting of a main axes that mostly produces one order of determinate branches, occasionally two (392-393): arrowheads – second order branches. **396-398.** Erect axes showing a coalescence of 1-1.25 (396), 1.25-1.75 (397), 1.5-2 (398) segments between the main axes and lateral branches. **399.** Erect axes with branchlets bearing tetrasporangia, formed on extensions of determinate laterals. **400.** Branches with tetrasporangia arranged in spiral rows. **401.** Branch with tetrasporangia: arrowheads – the third cover cell of tetrasporangia. Scale bars: 2 mm in Figs 379, 381, 382, 386 and 392-394; 5 mm in Fig. 380; 50 µm in Figs 383, 391 and 401; 100 µm in Figs 384, 385 and 389; 200 µm in Figs 387, 390, 396-398 and 400; 600 µm in Figs 388, 395 and 399.

Figs 402-403. Distribution of *Pterosiphonia pennata*. **402.** Collections along the Atlantic Iberian Peninsula. **403.** World distribution: arrow – type locality.

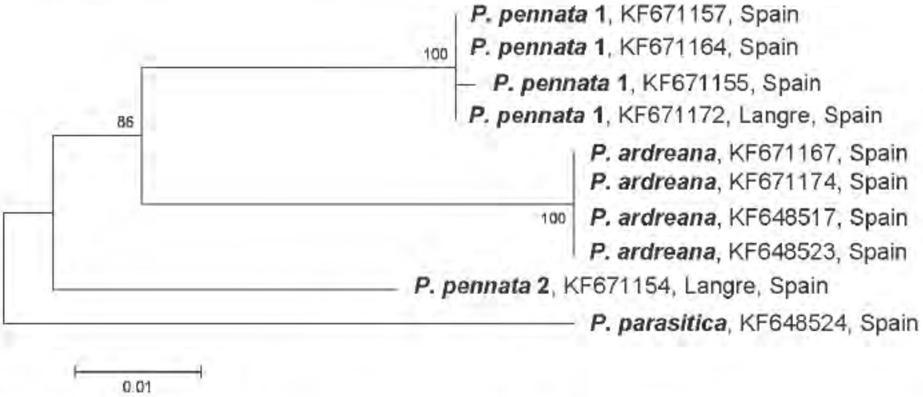
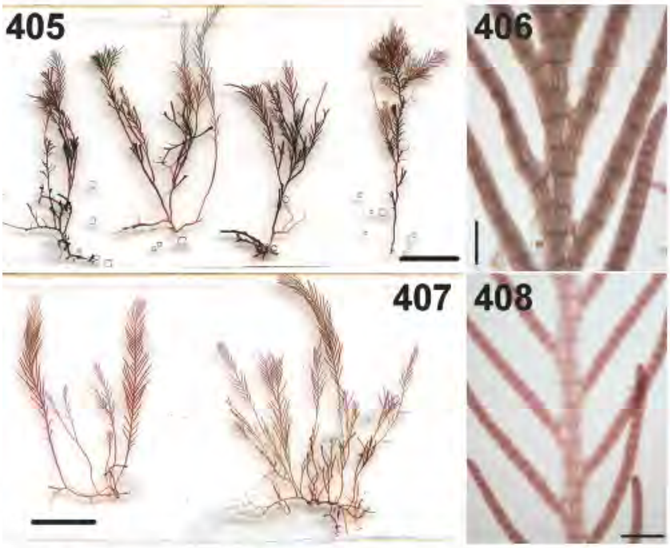


Fig. 404. Neighbour-joining tree inferred from the COI-5P sequences showing relationships among the 10 specimens of *Pterosiphonia* included in the present analysis.

(43°27’13”N; 3°57’37”W), 11.viii.2010, SANT-Algae 24444; 8) Tagle (43°25’59”N; 4°04’50”W), 1.iv.2006, SANT-Algae 20348; 9) Amio (43°23’42”N; 4°28’57”), 17.iii.2006, SANT-Algae 20418; 10) Verdicio (43°37’30”N; 5°52’44”W), 19.iv.2007, SANT-Algae 19622 (tetrasporangial plants); 11) Aguilar (43°33’28”N; 6°07’07”W), 17.iv.2007, SANT-Algae 19822; 12) Linorsa (43°41’56”N; 7°27’14”W), 10.iii.2005, SANT-Algae 23116; 13) San Román (43°43’17”N; 7°37’39”W), 31.i.2006, SANT-Algae 16872; 14) Xilloe (43°44’41”N; 7°39’02”W), 29.ix.2011, SANT-Algae 26649; 15) Picón (43°44’45”N; 7°44’30”W), 28.ix.2011, SANT-Algae 26660. 16) Ártabra (43°21’12”N; 8°28’38”), 6.vi.2008, SANT-Algae 20940; 17) Arou (43°11’03”N; 9°06’46”W); 6.iv.2004, SANT-Algae 26410; 18) Lariño (42°45’50”N; 9°07’04”W), 19.viii.2005, SANT-Algae 22777; 19) Area da Cruz (42°27’40”N; 8°54’37”W), 22.viii.2005, SANT-Algae 25055; 20) Barreiro (42°23’52”N; 8°47’37”W), 28.iv.2006, SANT-Algae 22650; 21) Nerga (42°15’19”N; 8°50’07”W), 12-ii-2005, SANT-Algae 15589, 22828; 22) Ingrina (37°02’46”N; 8°52’43”W), 21.ii.2011, SANT-Algae 25472-73; 23) Armaçao de Pêra (37°06’04”N; 8°22’17”W), 17.10.2005, SANT-Algae 24831, 24838, 24848; 24) Caneiros (37°06’14”N; 8°30’47”W), 18.x.2005, SANT-Algae 26205, 26208, 26209; Cádiz: 25) Caños de Meca (36°10’55”N; 6°00’06”W), 17.xi.2005, SANT-Algae 26148.

Vegetative and reproductive morphology

Thalli forming turfs up to 4 cm high, and covering rocky surfaces of several meters in extent. Thallus dorsiventral, consisting of an extensive system of indeter-



Figs 405-408. *Pterosiphonia pennata* collected at Langre (northern Spain). **405.** Habit of *P. pennata* 1. **406.** Erect axes of *P. pennata* 1 showing a coalescence of 1.25 segments between main axes and lateral branches. **407.** Habit of *P. pennata* 2. **408.** Erect axes of *P. pennata* 2 showing a coalescence of 1.25 segments between main axes and lateral branches. Scale bars: 5 mm in Figs 405 and 407; 200 µm in Figs 406 and 408.

minate prostrate axes bearing ventrally rhizoids, and dorsally producing erect axes of indeterminate growth, which in turn produce 1 order of alternate-distichous branches of determinate growth, some of which bear a second order of branches (Figs 379-382). Plants are dark red to black in colour, with a soft or rigid texture.

Axes ecorticate, consisting of a central axial cell and (7-) 8-11 pericentral cells (Figs 383-385). Prostrate axes indeterminate and dorsiventral, growing by transverse divisions of their apical cells; axes cylindrical, 130-250 µm in diameter, laterally branched exogenously at irregular intervals forming erect axes and further prostrate axes, commonly producing also adventitious branches (Figs 386-388). Rhizoids cut off from pericentral cells, unicellular (Fig. 389). Erect axes of indeterminate growth with a prominent apical cell and lacking trichoblasts; axes cylindrical to complanate, 110-270 µm in diameter, producing alternate branches of determinate growth at regular intervals of 2 segments, coalesced with main axis over (0.75-) 1-1.5 (-3) axial segments (Figs 390-398).

Sexual structures were not found. Tetrasporangia arranged in spiral rows on incurved branches formed as extensions of determinate lateral branches from the mid and basal parts of erect axes. Tetrasporangia are subspherical, 50-87.5 µm broad, with 3 cover cells (Figs 399-401).

Phenology

Pterosiphonia pennata was found throughout the year and it is probably perennial. Most collections were sterile and tetrasporangia were rare (7% of the collections) and found in February-April, June and November. Sexual structures are unknown for the species in Europe.

Habitat and distribution

Pterosiphonia pennata is one of the most common species in sand-covered rocks from the Atlantic Iberian Peninsula (Fig. 402). It forms almost monospecific turfs from the mid intertidal to upper subtidal of sites from moderately to extremely wave-exposed, or it grows forming turfs mixed with other species typical of the habitat, such as *Ophidocladus simpliciusculus* or *P. ardreana*. It is especially abundant in the eastern Cantabrian Sea and southern locations. *Pterosiphonia pennata* was widely reported in world temperate coasts (Fig. 403).

Remarks

Materials from the Atlantic Iberian Peninsula here labelled as *Pterosiphonia pennata* include at least two species that might match with those delineated by Maggs & Hommersand (1993): *P. pennata* and *P. pinnulata*. These sister species are distinguished by the fact that *P. pennata* has a higher number of pericentral cells and a wider coalescence between main axes and lateral branches (Maggs & Hommersand, 1993). In addition, Maggs & Hommersand (1993) noted that materials usually named *P. pennata* are more similar to *P. pinnulata*; and that *P. pinnulata* in the British Isles could be an introduced species. In the Atlantic Iberian Peninsula, a study on the morphology of *Pterosiphonia pennata sensu lato* from several sites of Galicia showed that most specimens have intermediate features between those proposed by Maggs & Hommersand (1993) to delineate the two species in the British Isles, and it was therefore suggested that both species could be conspecific (Díaz Tapia & Bárbara, 2004). However, we recently obtained COI-5P sequences of several specimens of *Pterosiphonia pennata sensu lato* from the Atlantic Iberian Peninsula and we found that two species can be clearly separated (Fig. 404), as "*P. pennata* 1" and "*P. pennata* 2" differ by 5.9-6.1% COI-5P sequence divergence. Although two molecular entities can be differentiated, we could not find diagnostic features to separate them, considering the characteristics previously used for species identification within the genus *Pterosiphonia*. *Pterosiphonia pennata* 1 and one of the samples of *P. pennata* 2 were collected in Langre (northern Spain) and the morphology of materials belonging to both entities was compared. Both specimens can be separated because *P. pennata* 1 (Figs 405, 406) is more slender while *P. pennata* 2 (Figs 407, 408) is more robust, but by contrast the number of pericentral cells, the coalescence between main axes and determinate branches and the diameter of axes were similar in both specimens (Figs 405-408). This scenario was not only found in Langre, since we identified specimens of *P. pennata* with different degrees of robustness in numerous locations along the Atlantic Iberian Peninsula. Indeed, we could identify still more robust materials (Fig. 379) and more slender ones (Fig. 382) than those observed from Langre.

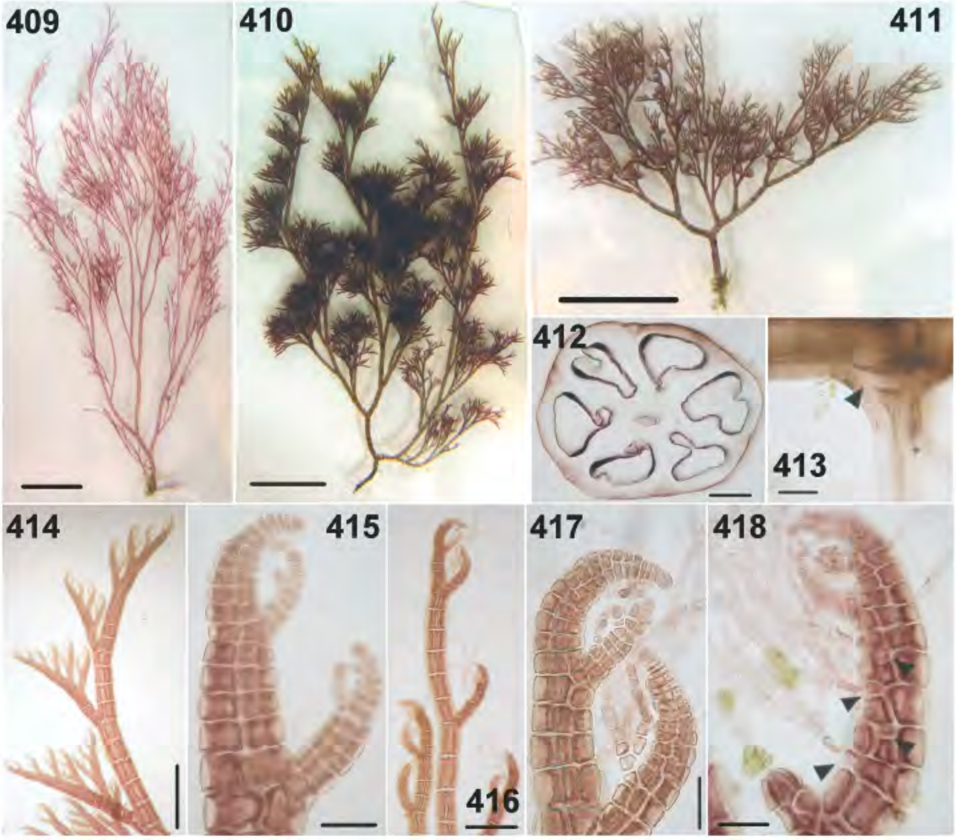
A priori, we might interpret that *P. pennata* 1 and 2, the most robust and slender species, respectively, may correspond to *P. pennata* and *P. pinnulata* described by Maggs & Hommersand (1993), but there are important differences between them. *Pterosiphonia pennata* 1 has a fewer number of pericentral cells and narrower axes and coalescence than the specimens from the British Isles assigned to *P. pennata*. Conversely, *P. pennata* 2 from the Atlantic Iberian Peninsula has a higher number of pericentral cells and wider axes and coalescence than the specimens from the British Isles assigned to *P. pinnulata*. In addition to these morphological differences, the habitat also varies between materials from the Atlantic Iberian Peninsula and those from the British Isles. Robust and slender specimens share the same habitat and localities along the Atlantic Iberian Peninsula, and even both morphologies can be found growing entangled in the same turfs. These turfs grow in sand-covered rocks from the mid intertidal to the upper subtidal of sites from moderately to extremely wave-exposed and most of our collections were carried out in pristine sites. By contrast, in the British Isles, the habitat of *P. pennata* was described as "muddy bedrock and pebbles and epiphytic on crustose corallines and maërl" and the habitat of *P. pinnulata* as "muddy pebbles, boulders and dead oyster shells"; and the second species was collected only in a harbour with an oyster farm, suggesting that the population was introduced (Maggs & Hommersand, 1993). Furthermore, collections of *P. pinnulata* from the British Isles were female thalli, while sexual structures were never observed in the Atlantic Iberian Peninsula for any materials assimilable to *P. pennata sensu lato*.

In summary and in agreement with findings of Maggs & Hommersand (1993) for the British Isles, *Pterosiphonia pennata* from the Atlantic Iberian Peninsula hosts more than one species. By contrast, specimens from the Atlantic Iberian Peninsula cannot be separated by the features proposed by Maggs & Hommersand (1993) to delineate *P. pennata* and *P. pinnulata*. Further researches including molecular analyses are necessary to clarify the identity of the materials here labelled as *P. pennata* and to identify the morphological features characterizing the different species. In our opinion, the study of materials of *P. pennata sensu lato* from the Mediterranean, which is the type locality of both *P. pennata* and *P. pinnulata*, is essential to clarify the specific assignment of the two molcular entities found in the Atlantic Iberian Peninsula.

Regarding other records of *Pterosiphonia pennata* along worldwide temperate coasts, it is difficult to assess its true distribution due to confusion between a group of morphologically similar species. Indeed, it has been recently demonstrated using molecular tools that the materials from Korea previously labelled as *P. pennata* are truly a different species from the one present along the Atlantic Iberian Peninsula (Kim *et al.*, 2012) and it has been described as a new species: *P. arenosa* M.S. Kim *et* B. Kim. Detailed descriptions of materials labelled as *P. pennata* were provided from the Atlantic North America (Schneider & Searles, 1991), the Canary Islands (Rojas-González & Afonso-Carrillo, 2001b), Brazil (Joly, 1965; Oliveira Filho, 1969; Cordeiro-Marino, 1978), Pacific North America (Dawson, 1944, 1963; Abbott & Hollenberg, 1976), Hawaii (Abbott, 1999), Japan and Korea (Masuda, 1973; Lee *et al.*, 1992), Australia (Womersley, 2003) and Atlantic Europe (Maggs & Hommersand, 1993; Díaz Tapia & Bárbara, 2004), and most of them match the features described. Interestingly, the scarce available data of reproductive structures might indicate that materials from certain areas are truly different species. For example, cystocarps of *P. pennata* from Australia are globose (Womersley, 2003), while these structures in *P. pennata* from Hawaii are urceolate (Abbott, 1999). Unfortunately, sexual structures are rarely found in *P. pennata sensu lato* and vegetative morphology is very similar between materials from different areas, which makes difficult the detection of possible cryptic diversity based on morphological features.

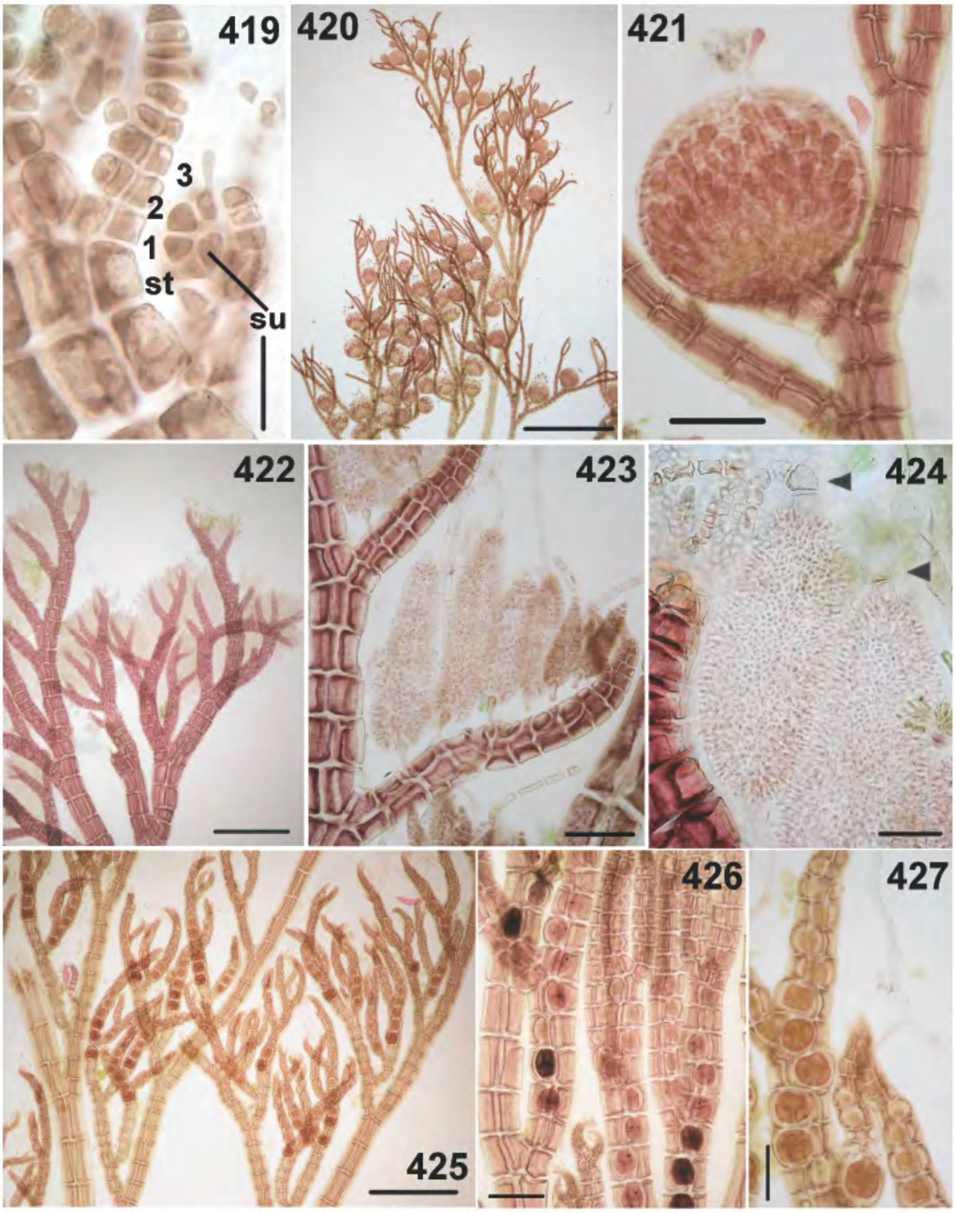
Streblocladia collabens (C. Agardh) Falkenberg **Figs 409-429**

Basionym: *Hutchinsia collabens* C. Agardh.
Syntypes: LD, Agardh herbarium numbers 40885-40887, 40890-40898.
Type locality: Cádiz, Spain.
Synonym: *Polysiphonia collabens* (C. Agardh) Kützing.
References: Falkenberg, 1901.
Molecular vouchers: GenBank accession numbers KF671151, KF671158.



Figs 409-418. *Streblocladia collabens*. Vegetative morphology. **409-411.** Habit consisting of erect axes pseudodichotomously branched and attached to the substratum by a small discoid holdfast (409, 411) or by a short prostrate axes (410). **412.** Cross section of an erect axis showing 6 pericentral cells. **413.** Rhizoid cut off from pericentral cells: arrowhead – wall separating the pericentral cell and the rhizoid. **414.** Upper part of dorsiventral erect axis, with unilaterally arranged branchlets. **415.** Apex of an axis with young exogenous branches. **416-417.** Upper parts of erect axes with scarcely developed trichoblasts. **418.** Apex of a female thallus with trichoblasts unilaterally formed on every segment showing a slight displacement between successive segments: arrowheads – basal cells of trichoblasts. Scale bars: 5 mm in Figs 409-411; 50 µm in Figs 412 and 413; 600 µm in Fig. 414; 50 µm in Figs 415, 417 and 418; 200 µm in Fig. 416.

Selected specimens: 1) Biarritz (43°29'03"N; 1°33'46"W), 19.iii.2011, SANT-Algae 25392 (female and tetrasporangial plants); 2) San Juan de Gaztelougatxe (43°26'41"N; 2°46'41"W), 8.ix.2010, SANT-Algae 19730 (male, female and tetrasporangial plants); 3) Tagle (43°25'59"N; 4°04'50"W), 1.iv.2006, SANT-Algae 20373 (male, female and tetrasporangial plants); 4) Virgen del Mar (43°28'40"N; 3°52'31"W), 28.iii.2006, SANT-Algae 20407 (male, female and tetrasporangial plants); 5) Aguilar (43°33'28"N; 6°07'07"W), 17.iv.2007, SANT-Algae 19824 (female plants); 6) Serantes (43°33'27"N; 6°58'39"W), 2.vi.2006, SANT-Algae 17829 (male, female and tetrasporangial plants); 7) Catedrales (43°33'16"N; 7°09'16"W), 20.ix.2005, SANT-Algae 16546 (male, female and tetrasporangial plants); 8) Ártabra (43°21'12"N; 8°28'38"), 14.v.2010, SANT-Algae 24127 (female and tetrasporangial plants); 9) Estorde (42°56'28"N; 9°13'04"), 11.iii.2005, SANT-Algae 23062 (male, female and tetrasporangial plants); 10) Lariño (42°45'50"N; 9º07'04"W), 19.viii.2005,



Figs 419-427. *Streblocladia collabens*. Reproductive morphology. **419.** Procarp formed in a modified trichoblast showing the supporting cell (su) bearing the 3-celled carpogonial branch (1-3) and a basal sterile cell (st). **420-421.** Cystocarps. **422.** Spermatangial branches arising in the upper parts of erect axes. **423-424.** Spermatangial branches unillaterally arranged: arrowheads- short apical filaments. **425-427.** Tetrasporangia forming straight to slightly spiral series in upper parts of erect axes. Scale bars: 25 µm in Fig. 419; 2 mm in Fig. 420; 200 µm in Figs 421 and 426; 600 µm in Figs 422 and 425; 100 µm in Figs 423 and 427; 50 µm in Fig. 424.

Figs 428-429. Distribution of *Streblocladia collabens*. **428.** Collections along the Atlantic Iberian Peninsula. **429.** World distribution: arrow – type locality.

SANT-Algae 22780, (male, female and tetrasporangial plants); 11) Nerga (42°15'19"N; 8°50'07"W), 12-ii-2005, SANT-Algae22830 (male and female plants); 12) Leça de Palmeira (41°12'22"N; 8°43'03"W), 11.vi.2010, SANT-Algae 24227 (male, female and tetrasporangial plants); 13) Baleal (39°22'25"N, 9°19'56"W), 14.vi.2010, SANT-Algae 24877 (male, female and tetrasporangial plants); 14) Guincho (38°43'29"N; 9°28'41"W), 13.vi.2010, SANT-Algae 24790 (female and tetrasporangial plants); 15) Olhos d´Agua (37°05'20"N; 8°11'27"W), 6.v.2005, SANT-Algae 25748 (female plants); 16) Encendida (36°18'40"N; 6°09'12"W), 18.ii.2011, SANT-Algae 26624.

Vegetative and reproductive morphology

Thalli epiphytic, growing isolated or forming tufts, up to 7 cm high. Thallus erect, radially organized, attaching to substrate by a solid mass of aggregated rhizoids or by short decumbent prostrate axes formed when rhizoids are developing at basal parts. Erect axes densely branched mostly every 4-8 segments, up to 8 orders (Figs 409-411). Branching pseudodichotomous, without a clear main axes (Figs 409, 410), sometimes in an open angle in basal parts (Fig. 411). Apices dorsiventral, with the upper branches unilaterally and adaxially arranged (Fig. 414). The oldest plants sometimes unilaterally bear tufts of short branches, profusely branched every 2-4 segments (Fig. 410). Axes from red to pale brown in colour, generally with a soft texture, but sometimes basal parts of thallus are rigid.

Axes completely ecorticate, formed by a small central axial cell and (5-) 6 pericentral cells (Fig. 412). Rhizoids cut off from pericentral cells (Fig. 413), unicellular, abundantly developed, often several per segment, up to 3; 40-80 (-120) µm in diameter and up to 1600 µm long, sometimes terminated in digitate haptera. Axes growing from domed apical cells *ca* 18 µm in diameter (Fig. 415), increasing to (140-) 200-450 (-600) µm in diameter in mid and basal parts, with segments L/D (0.4-) 0.6-1.5 (-2.2). Apices of axes curved, forming exogenous branches independently from trichoblasts (Fig. 415). Adventitious branches absent. Trichoblasts sometimes absent, although usually present but scarcely developed and scattered in some parts of the plants, arising at irregular intervals (Figs 416, 417); trichoblasts are only occasionally abundant, arising unilaterally on every segment and showing a slight displacement between successive segments (Fig. 418). Trichoblasts are usually short and dichotomously branched 1-2 (-3) orders, deciduous and leaving scar cells. Plastids lying only on radial walls of pericentral cells so the outer walls appear transparent (Figs 415-418).

Gametophytes dioecious. Procarps are formed in suprabasal cells of modified trichoblasts, in the upper parts of erect axes; and they consist of a three-celled carpogonial branch, a basal sterile cell (Fig. 419) and a group of two lateral sterile cells borning on the supporting cell. Cystocarps globular when mature, (350-) 400-6000 (-800) µm high, (260-) 350-550 (-700) µm in diameter (Figs 420, 421). Carposporangia clavate, (65-) 80-130 (-150) × (25-) 30-50 (-60) µm.

Spermatangial axes located at the apices of axes, densely clustered (Fig. 422), mostly formed on every segment, arising unilaterally and arranged in a straight row or showing a slight displacement between successive segments (Fig. 423). Spermatangial axes are formed on one of the two basal branches of modified trichoblasts, remaining the other branch of the trichoblast at maturity (Fig. 423). Spermatangial axes are cylindrical and straight, (210-) 250-400 (-500) µm long and (55-) 70-100 (-125) µm in diameter, with a sterile apical filament of up to 6 cells at maturity (Fig. 424), which usually broken remaining only one apical sterile cell (Fig. 423).

Tetrasporangia arising in the upper branches (Fig. 425), one per segment forming straight or slightly spiral series with up to 7 mature tetrasporangia (Figs 426, 427); spherical, (50-) 60-90 (-100) µm in diameter, with 2 cover cells.

Phenology

Plants occur throughout the year, and they are probably perennial. Reproductive structures were frequently and abundantly observed year-round: tetrasporangia in a 59% of the collections, male structures in a 48% and female ones in a 67% of the collections.

Streblocladia collabens is highly variable in size and colour between different collections, but without relation to season. In spite of the variability of its habit, it is clearly distinguishable from other species from the Atlantic Iberian Peninsula by its dorsiventral apices and the number of pericentral cells.

Habitat and distribution

Streblocladia collabens grows from the mid intertidal to the upper subtidal of moderately to extremely wave-exposed shores, typically epiphytic on almost all basal species present along the Atlantic Iberian Peninsula. It tolerates the presence of sand and is very common on rocks of beaches where it is sometimes abundant, but it also grows on rocky shores. *Streblocladia collabens* is very frequent along the Atlantic Iberian Peninsula (Fig. 428). Its distribution is restricted to the coasts between the Southwest of France and Cape Verde, including the northern coasts of the Mediterranean Sea (Fig. 429).

Remarks

Hutchinsia collabens was originally described by C. Agardh (1824) based on materials from Cádiz (Spain) and subsequently Kützing (1849) transferred it to the genus *Polysiphonia*. Later Schmitz created the genus *Streblocladia* to accommodate those erect species with primary dorsiventrality (Schmitz & Falkenberg, 1897) and accordingly *P. collabens* was transferred to *Streblocladia* (Falkenberg, 1901). *Streblocladia collabens* was widely reported along the Atlantic Iberian Peninsula and its distribution is restricted to this coast, the Mediterranean Sea, Morocco, Senegal and Cape Verde Islands (e.g. Ardré, 1970; Gómez-Garreta *et al.*, 2001; Benhissoune *et al.*, 2003; Bárbara *et al.*, 2005; Araújo *et al.*, 2009). In spite of being a very common species along the Atlantic Iberian Peninsula, there are no available updated descriptions of the species.

The most distinctive features found in *Streblocladia collabens* from the Atlantic Iberian Peninsula are: 1) thallus predominantly erect, 2) branches exogenous, growing independently of the trichoblasts, upper branches dorsiventral and unilaterally arranged, 3) axes ecorticate with 6 pericentral cells, 4) rhizoids cut off from pericentral cells, 5) trichoblasts unilaterally arranged, usually present in erect axes but scattered and scarcely developed, 6) 3-celled carpogonial branches, 7) spermatangial axes unilaterally arranged, growing on one of the basal branches of the fertile trichoblasts, with a short filament or one sterile apical cell, 8) one tetrasporangium per segment in straight or slightly spiral series.

These features fit those previously described for *Streblocladia collabens* (Falkenberg, 1901). The dorsiventrality of branches clearly separates this species from the other similar taxa from the Atlantic Iberian Peninsula. *Polysiphonia forfex* Harvey, whose type locality is in Australia, was reported from Biarritz (southwestern France) as a probably introduced species (McIvor *et al.*, 2001). However, this record is a misidentification, as demonstrate the *rbc*L sequences of *Streblocladia collabens* provided in Bárbara *et al.* (2013), which only differ by 0.1% sequence divergence (1 nucleotides) from the sequence of *P. forfex* from Biarritz (McIvor *et al.*, 2001). Both species are characterized by having 6 pericentral cells, but in contrast *P. forfex* has apices radially organized and it is corticated (Womersley, 2003).

The genus *Streblocladia*, was segregated from *Polysiphonia* based on *S. glomerulata* (Montagne) Papenfuss (Schmitz & Falkenberg, 1897, as *S. neglecta* F. Schmitz), and it is characterized by having primary dorsiventral apices (Schmitz & Falkenberg, 1897; Falkenberg, 1901; Hommersand, 1963). This genus was originally placed in the Herposiphonieae (Schmitz & Falkenberg, 1897; Falkenberg, 1901) and later was segregated together with *Microcolax* and *Fernandosiphonia* to the tribe Streblocladieae (Kylin, 1956). *Fernandosiphonia* and *Streblocladia* are superficially similar because both have unilaterally inserted branches, but by contrast, trichoblasts are spirally arranged in *Fernandosiphonia* while they are also unilaterally arranged in *Streblocladia*. This is the reason why Hommersand (1963) transferred the genus *Fernandosiphonia* to the tribe Polysiphonieae, where it is currently placed.

Apart from the dorsiventrality of apices, *Streblocladia* is similar to *Polysiphonia sensu lato*. *Streblocladia collabens* has 3-celled carpogonial branches, a feature that currently was reported only within *Polysiphonia sensu lato* in the species of the recently segregated genus *Neosiphonia* (Kim & Lee, 1999; Choi *et al.*, 2001). This morphological evidence of a relation between *Streblocladia collabens* and *Neosiphonia* is also supported in the analysis of *rbc*L sequences published in Bárbara *et al.* (2013). Accordingly, we propose the transfer of *Streblocladia collabens* to the genus *Neosiphonia*. Interestingly, this is the first time that 3-celled carpogonial branches are reported among the species whose type locality is in the western Atlantic. By contrast, most of the other species with this characteristic, which are currently included in the genus *Neosiphonia* are predominantly Pacific, as well as are distributed in the Caribbean and the tropical Atlantic but their origine has been interpreted as a spread via the Panama seaway (McIvor *et al.,* 2001, as *P. harveyii* clade). The distribution of *Neosiphonia,* together to the fact that *S. collabens* along the Atlantic Iberian Peninsula is a cosmopolitan epiphite with a wide diversity of basiphytes suggests that *S. collabens* might constitute an old introduced species in southern Europe and northern Afri*ca* However, our literature review looking for a similar species from other areas to establish a putative origin of this species was unsuccessful.

Among the morphological features proposed by Kim & Lee (1999) to delineate the genus *Neosiphonia, Streblocladia collabens* also shares the erect indeterminate branches formed from an erect main axes, rhizoids cut off from pericentral cells and spermatangial branches formed on a branch of trichoblasts.

By contrast, *S. collabens* disagrees with the concept of *Neosiphonia* proposed by these authors regarding the trichoblasts abundance, the branching pattern, and tetrasporangia arrangement. Kim & Lee (1999) included the abundance of trichoblasts as a feature of *Neosiphonia*, and this characteristic is variable in *S. collabens*, since trichoblasts are usually scarce and only rarely abundant. Furthermore, *S. collabens* also differs from *Neosiphonia* in the branching pattern, which consists of lateral branch initials or trichoblasts formed on successive segments in *Neosiphonia* (Kim & Lee, 1999). The arrangement of lateral branches and/or trichoblasts is variable in *S. collabens.* Branches are mostly formed at intervals of 4-8 segments, and trichoblasts are usually scarcely developed and then they appear scattered along apices of axes, while sometimes they are formed on every segment. Sometimes trichoblasts are absent in species in which they are typically abundant, but then they have their initials replacing the trichoblasts (e.g. *Polysiphonia devoniensis*). This is not the case of *S. collabens* in which usually no trichoblasts, branches or they initials were observed in successive segments. Finally, tetrasporangia were described forming spiral rows in *Neosiphonia* (Kim & Lee, 1999), while in *S. collabens* they sometimes form slightly spiral rows, while they are often straight. Although the evaluation of this feature in *S. collabens* might be unclear because series of mature tetrasporangia are usually short and this feature apparently can vary within species. *Streblocladia collabens* is not the only species molecularly placed in *Neosiphonia* that does not fit one or several of the morphological features proposed by Kim & Lee (1999). For example, *Polysiphonia pseudovillum* Hollenberg is placed in the *Neosiphonia* clade in the phylogenetic trees (see Mamoozadeh & Freshwater, 2011), but it has no initial branches on successive segments and it is chiefly prostrate (Hollenberg, 1968c; Mamoozadeh & Freshwater, 2012). In our opinion, the current morphological concept of *Neosiphonia* is untenable considering all the features proposed by Kim & Lee (1999) and it needs to be emended as previously suggested by Mamoozadeh & Freshwater (2012).

The 3-celled carpogonial branches are the only characteristic that is exclusive of *Neosiphonia* among those proposed by Kim & Lee (1999). Conversely, all the other features are variable within *Neosiphonia* species or they are also present in other members of *Polysiphonia sensu lato*. The number of cells in carpogonial branches has been considered virtually uniform in the Rhodomelaceae (Scagel, 1953), but Iyengar & Balakrishnan (1949) reported 3-celled carpogonial branches for the first time in *Polysiphonia platycarpa* Børgesen. Since then, studies of species of Rhodomelaceae show that there is a considerable number of taxa within *Polysiphonia sensu lato* with 3-celled carpogonial branches (e.g., Kim & Lee, 1999; Guimarães *et al.*, 2004; Bustamante *et al.*, 2012).

A morphological peculiarity found in *Streblocladia collabens* is that plastids are lying only on radial walls of pericentral cells, so the outer walls appear transparent. Interestingly, this feature has been stated as characteristic for the clade containing *N. harveyii* (McIvor *et al.*, 2001, as *Polysiphonia harveyi*) and it is shared with other species molecularly placed in *Neosiphonia*: *N. harveyii*, *N. sphaerocarpa*, *N. ferulacea*, *N. simplex*, *Polysiphonia pseudovillum* and *P. simplex* (Hollenberg, 1968a; Maggs & Hommersand, 1993; McIvor *et al.*, 2001; Mamoozadeh & Freshwater, 2011). Although the taxonomic value of plastid position has not been classically emphasized in *Polysiphonia sensu lato*, it could be another key feature to delineate the genus *Neosiphonia*. Again, this characteristic was detailed only in a few species, and further research is required to confirm its taxonomic significance.

Table 5. Comparison of selected morphological features in the species of the genus *Streblocladia*

Species	S. collabens *(C.Agardh) Falkenberg*	S. atrata *Baardseth*	S. camptoclada *(Montagne) Falkenberg*	S. corymbifera *(C.Agardh) Kylin*	S. glomerulata *(Montagne) Papenfuss*	S. spicata *M.A.Howe*	S. tenuissima *M.A.Pocock*
Cortication	–	–	–	+	+	–	–
Pericentrals	6	5	4	10-14	7-10	10-12	7-10
Rhizoids	Cut off	–	In open connection	Cut off	–	–	–
Trichoblasts	Present	Absent	Only in female gametophytes	Only related to reproduction	–	Absent	Absent (well developed)
Carpogonial branches	3-celled	–	–	–	–	–	–
Tetrasporangia	Straight to slight spiral	Straight	Straight	–	Spiral	–	Straight
Type locality	Cádiz, Spain	Tristan da Cunha	Callao, Perú	Cape Hood, South Africa	Auckland Islands	Pisco, Perú	Cove Rock, South Africa
Distribution	S. Europe to N. Africa	Tristan da Cunha	S. Africa, S. America	S. Africa, S. America	New Zealand	Perú	SE. Africa
References	Falkenberg, 1901; this work	Baardseth, 1941	Stegenga *et al.*, 1997; Rull Lluch, 2002	Stegenga *et al.*, 1997; Rull Lluch, 2002	Adams, 1994	Howe, 1914	Pocock, 1953

Unfortunately, there are no available data on the number of cells of the capogonial branches in the other 6 species currently assigned to *Streblocladia*, including the type of the genus, and their relationship to *Neosiphonia* cannot be evaluated. Some of the species of *Streblocladia* show differences in features that are currently considered relevant in the separation of groups within *Polysiphonia sensu lato* according to Choi *et al.* (2001). The rhizoids are cut off from pericentral cells in most species of the genus, except in *S. camptoclada* (Table 5) which has 4 pericentral cells. Furthermore, tetrasporangia are in straight series in most of species with the exception of *S. glomerulata* and sometimes in *S. collabens* (Table 5). Tetrasporangia in straight series and, especially, rhizoids in open connection to pericentral cells (in combination with having 4 pericentral cells) are currently related to *Polysiphonia sensu stricto*. Morphological variations observed in the genus *Streblocladia* seem to indicate that some species of this genus might be related to different groups of *Polysiphonia sensu lato,* despite the fact they are sharing dorsiventral apices.

Taxonomic proposal

Considering the morphological features of *Streblocladia collabens* we propose the following new combination:

***Neosiphonia collabens* (C.Agardh) Díaz-Tapia *et* Bárbara, comb. nov.**

Basionym: *Hutchinsia collabens* C. Agardh, 1824, *Systema algarum*: 153.

Synonyms: *Polysiphonia collabens* (C. Agardh) Kützing, 1849, *Species Algarum*: 822; *Streblocladia collabens* (C. Argardh) Falkenberg, 1901, *Die Rhodomelaceen des Golfes von Neapel und der angrenzenden Meeresabschnitte*: 348.

Type locality: Cádiz, Spain.

Aiolocolax pulchellus M.A. Pocock **Figs 430-445**

Type material: No published information.

Type locality: Miuzenberg, False Bay, Cape Province, South Africa.

References: Pocock, 1956; Pérez-Cirera *et al.*, 1989; Rojas-González & Afonso-Carrillo, 2000; Rull Luch, 2002.

Molecular voucher: GenBank accession number KF671160.

Selected specimens: 1) Zumaia (43°17'59"N; 2°15'41"W), 30.iii.2006, SANT-Algae 20268; 2) Somocueva (43°28'07"N; 3°56'43"W), 7.x.2006, SANT-Algae 19997; 3) Virgen del Mar (43°28'40"N; 3°52'31"W), 28.iii.2006, SANT-Algae 20403; 4) Tagle (43°25'59"N; 4°04'50"W), 1.iv.2006, SANT-Algae 20352; 5) Catedrales (43°33'16"N; 7°09'16"W), 1.iii.2003, SANT-Algae 22625; 6) Linorsa (43°41'56"N; 7°27'14"W), 10.iii.2005, SANT-Algae 23119; 7) San Román (43°43'17"N; 7°37'39"W), 16.vii.2008, SANT-Algae 17652; 8) Barrañán (43°18'44"N; 8°33'22"W), 5.xi.2002, SANT-Algae 15178; 9) Barizo (43°18'48"N; 8°52'27"W), 5.iv.2004, SANT-Algae 24956; 10) Coelho (37°4'22"N; 8°17'31"W), 7.v.2005, SANT-Algae 25286; 11) Caños de Meca (36°10'55"N; 6°00'06"W), 17.xi.2005, SANT-Algae 26143.

Vegetative and reproductive mohology

Thalli typically parasitic on *Polysiphonia caespitosa*; usually not causing any hypertrophy of the host (Figs 430, 431). Thallus consisting of a uniseriate filament running between the axial cell and the pericentral cells of the host (Fig. 432). Fertile parts of the thallus conspicuous, projecting pedicellate reproductive structures which are from globose to elongate (Figs 430, 431).

Female branches having several procarps with long trichogynes (Figs 433, 434), from which usually only one originates a globose cystocarp (Fig. 435), although sometimes female branches have two up to three cystocarps (Figs 436, 437). Male branches produce spermatangia from their surface, except from the apical cell (Figs 438-440). Asexual branches are usually elongate, producing numerous sporangia which divide forming 16-32 polyspores (Figs 441-443).

Phenology

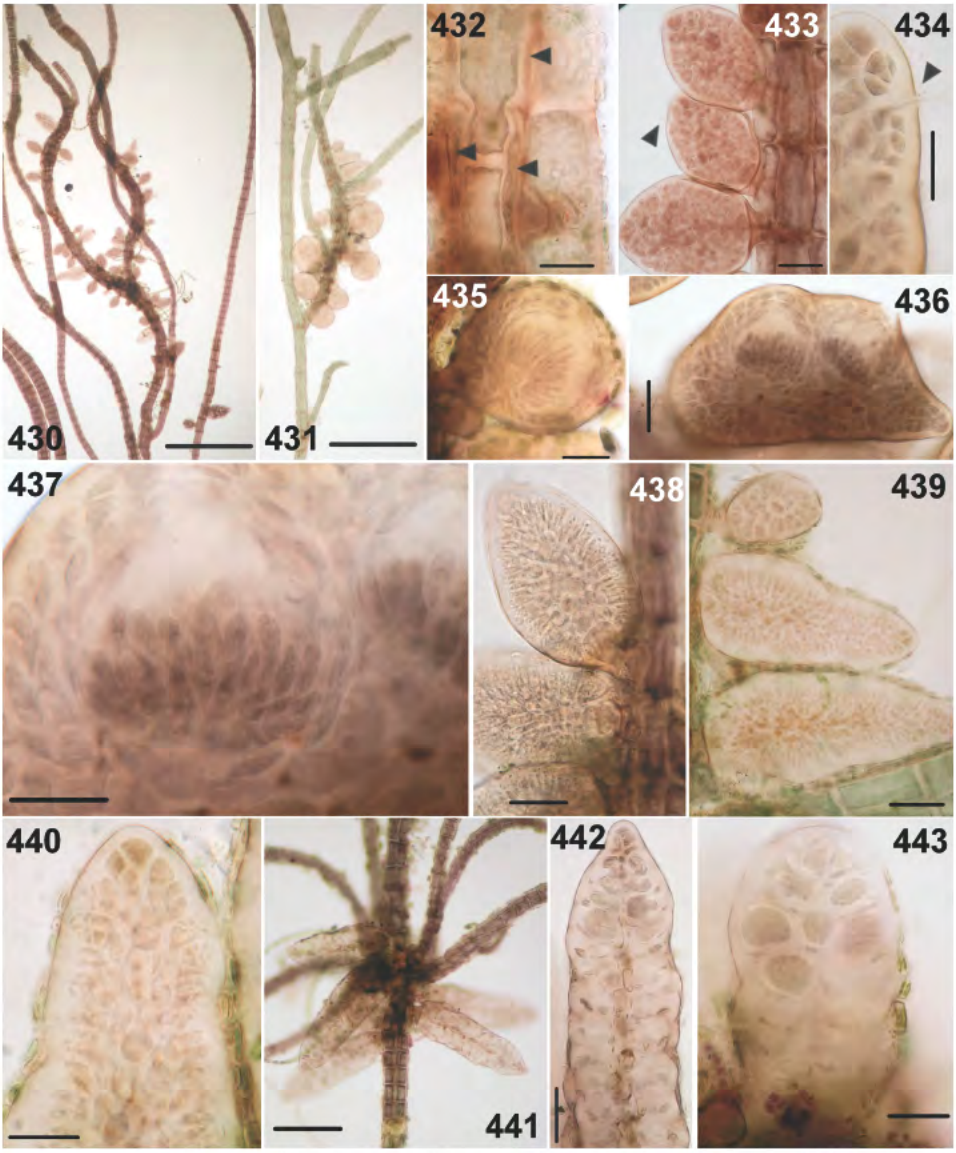
Aiolocolax pulchellus was recorded throughout the year, being identified by its reproductive structures.

Habitat and distribution

Aiolocolax pulchellus is very common along the Atlantic Iberian Peninsula (Fig. 444), and it was usually observed when its host (*Polysiphonia caespitosa*) was collected. Furthermore, the species was also found growing once on *P. atlantica* (Barrañán, Galicia) and twice on *P. devoniensis* (Virgen del Mar and Langre, Cantabrian). The known distribution of *A. pulchellus* is restricted to the eastern Atlantic (Fig. 445).

Remarks

Aiolocolax pulchellus was originally described from South Africa (Pocock, 1956) and subsequently reported in Atlantic Spain (Pérez-Cirera *et al.*, 1989). Most recently, it was also reported in Namibia and the Canary Islands (Rojas-González & Afonso-Carrillo, 2000; Rull Lluch, 2002). Specimens examined from the Atlantic Iberian Peninsula fit the original description of the species, as well as with the subsequent reports. *Aiolocolax pulchellus* is probably a common species within this distributional range, but the small size of the host and the parasite are probably causes of the scarce number of previous records. The taxonomic position of this species is still uncertain (Pocock, 1956, Rojas-González & Afonso-Carillo, 2000; Rull Lluch, 2002) and it was included in the Rhodomelaceae in this work because this is the family to which belongs its host species.



Figs 430-443. *Aiolocolax pulchellus*. Reproductive and vegetative morphology. **430-431.** Axes of *Polysiphonia caespitosa* with numerous projecting reproductive structures of *A. pulchellus*. **432.** Uniseriate filaments of *A. pulchellus* placed between axial and pericentral cells of the host: arrowheads – parasite filaments. **433-437.** Female branches bearing procarps (433-434 and cystocarps (435-437): arrowheads – trichogines. **438-440.** Male branches. **441-443.** Asexual branches bearing polyspores. Scale bars: 600 µm in Figs 430 and 431; 25 µm in Figs 432, 434, 437 and 440; 50 µm in Figs 433, 435, 436, 438, 439, 442 and 443; 200 µm in Fig. 441.

Figs 444-445. Distribution of *Aiolocolax pulchellus*. **444.** Collections along the Atlantic Iberian Peninsula. **445.** World distribution: arrow – type locality.

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