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Lithophyllum artabricum V.Peña, sp. nov. (Corallinales, Rhodophyta): a cryptic species in the Atlantic Iberian Peninsula hitherto assigned to *Lithophyllum stictiforme* (Areschoug) Hauck

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ABSTRACT
Lithophyllum stictiforme (Areschoug) Hauck contributes to the formation of the Mediterranean coralligenous concretions. In the Atlantic Iberian Peninsula, *L. stictiforme* has also been reported based on subtidal collections showing the characteristic morphology described for this species. Recent studies uncovered a diverse complex of cryptic species from the Mediterranean Sea assigned to *L. stictiforme*. Thereafter, the Atlantic Iberian collections have been re-assessed with the aim of clarifying its taxonomic status. Based on molecular (COI, *psb*A) and morphological data, the new species *Lithophyllum artabricum* V.Peña, sp. nov. is described herein. Molecular phylogenetic analyses were congruent in delimiting the Atlantic Iberian collections as an independent lineage from the Mediterranean *L. stictiforme* complex. Morpho-anatomical characters of the new species showed an overlap with those provided for the Mediterranean clades of *L. stictiforme*. However, *L. artabricum* V.Peña, sp. nov. has a monomerous thallus construction whereas the Mediterranean taxa were mainly dimerous. Moreover, *L. artabricum* V.Peña, sp. nov. differs from other Atlantic European *Lithophyllum* species by a combination of characters related to the external morphology consisting of single or superimposed lamellae, the monomerous construction, the conical shape of the canal pore of sporangial conceptacles, and by occurring only in subtidal bedrocks. *Lithophyllum artabricum* V.Peña, sp. nov. is at present known from northern Spain to northern Portugal. One collection of *L. stictiforme* from southern Portugal showed similarities with *L. artabricum* V.Peña, sp. nov.; however, DNA sequence data are necessary to confirm this record. Based on the evidence presented herein, *L. stictiforme* is removed from the flora of northern and northwestern Spain, and northern Portugal. The finding of cryptic diversity in *L. stictiforme* suggested that further reports of this species in warm and temperate waters should be re-assessed.

KEY WORDS
Crustose coralline algae, DNA barcoding, *Lithophyllum frondosum*, *Lithophyllum grandiusculum*, Mediterranean, morpho-anatomy, NE Atlantic, new species.

RÉSUMÉ

Lithophyllum artabricum *V.Peña, sp. nov. (Corallinales, Rhodophyta): une espèce cryptique de la péninsule Ibérique atlantique jusqu'ici assignée à* Lithophyllum stictiforme *(Areschoug) Hauck.*

Lithophyllum stictiforme (Areschoug) Hauck contribue à la formation des concrétions coralligènes de la Méditerranée. Dans la péninsule Ibérique atlantique, *L. stictiforme* a également été signalé sur la base de collections subtidales présentant une morphologie caractéristique de cette espèce. Des études récentes ont mis en évidence un important complexe d'espèces cryptiques en Méditerranée parmi ce qui était jusqu'à présent considéré comme *L. stictiforme*. Ces découvertes ont suscité une réévaluation des collections ibériques atlantiques dans le but de clarifier le statut taxonomique des spécimens atlantique. Sur la base de données moléculaires (COI, *psb*A) et morphologiques, la nouvelle espèce est décrite ici. Les analyses moléculaires ont permis de délimiter les collections ibériques atlantiques comme une lignée indépendante du complexe méditerranéen *L. stictiforme*. Les caractères morpho-anatomiques de *L. artabricum* V.Peña, sp. nov. ont montré un chevauchement avec ceux fournis pour les lignées méditerranéennes de *L. stictiforme*. Cependant, *L. artabricum* V.Peña, sp. nov. présente une construction monomère alors que les taxons méditerranéens étaient principalement dimères. De plus, *L. artabricum* V.Peña, sp. nov. diffère des autres espèces de *Lithophyllum* de l'Europe atlantique par une combinaison de caractères liés à la morphologie externe consistant en des lamellae uniques ou superposées, la construction monomère, la forme conique du pore du canal des conceptacles sporangiaux, et par le fait qu'il ne se trouve que sur des roches subtidales. *Lithophyllum artabricum* V.Peña, sp. nov. est actuellement connu du nord de l'Espagne au nord du Portugal. Une collection de *L. stictiforme* du sud du Portugal présente des similitudes avec *L. artabricum* V.Peña, sp. nov. mais des données moléculaires sont nécessaires pour confirmer ce signalement. Sur la base des preuves présentées ici, *L. stictiforme* est retiré de la flore du nord et du nord-ouest de l'Espagne, et du nord du Portugal. La découverte d'une diversité cryptique chez *L. stictiforme* suggère que les autres signalements de cette espèce dans les eaux chaudes et tempérées devraient être réévalués.

MOTS CLÉS

Algues corallines crusteuses, DNA barcoding, *Lithophyllum frondosum*, *Lithophyllum grandiusculum*, Méditerranée, morpho-anatomie, NE Atlantique, espèce nouvelle.

INTRODUCTION

Lithophyllum Philippi (Corallinales, Rhodophyta) is considered one of the most diverse genera of coralline red algae with 129 species that are currently accepted taxonomically (Guiry & Guiry 2021). This genus contributes to the formation of characteristic bioconstructions in temperate waters, such as the coralligenous concretions that are developed in deep waters of the Mediterranean Sea (Garrabou & Ballesteros 2000; Ballesteros 2006; Rindi *et al.* 2019). This biogenic habitat of ecological relevance is mainly composed of two species of *Lithophyllum* – *L. stictiforme* (Areschoug) Hauck (type locality: Mediterranean Sea) and *L. cabiochiae* (Boudouresque & Verlaque) Athanasiadis (type locality: Pianottoli Caldarella, Corsica) – although, more recently several authors proposed that both species are considered conspecific with *L. stictiforme* having nomenclatural priority (Pezzolesi *et al.* 2019; Rindi *et al.* 2019). Compared to other species of *Lithophyllum* reported from the European coasts, *L. stictiforme* has a distinctive morphology consisting of foliose, superimposed lamellae with invertebrates growing beneath or in small cavities (Chamberlain & Irvine 1994; Garrabou & Ballesteros 2000; Hernández-Kantun *et al.* 2015a; Rindi *et al.* 2019). Nevertheless, recent DNA sequence studies using extensive collections from coralligenous habitats uncovered a complex of at least 11 cryptic species passing under the same entity – *L. stictiforme*- (De Jode *et al.* 2019; Pezzolesi *et al.* 2019). Moreover, the morpho-anatomical study of the so-called *L. stictiforme* complex, which also includes the Macaronesian *L. lobatum* Me.Lemoine (type locality: Puerto Orotava, Tenerife, Canary Islands) and the NW Atlantic *L. searlesii* P.W. Gabrielson, Freshwater, J.L.Richards & Hughey (type locality: Southwest Ledge, Onslow Bay, North Carolina), showed a substantial overlap for most of the characters examined (Pezzolesi *et al.* 2019).

Apart from the Mediterranean Sea, *L. stictiforme* has been widely reported from temperate and warm regions in both hemispheres (Guiry & Guiry 2021). However, in the NE Atlantic, literature records of *L. stictiforme* – or its currently regarded heterotypic synonyms *L. frondosum* (Dufour) G.Furnari, Cormaci & Alongi (type locality: San Nazzaro, Genoa, Italy) and *L. grandiusculum* (Montagne) Woelkerling, Penrose & Y.M.Chamberlain (type locality: Algeria) (Athanasiadis 1999; Pezzolesi *et al.* 2019; Guiry & Guiry 2021) – are almost restricted to the Atlantic Iberian Peninsula, where this species occurs subtidally on bedrock and shows the characteristic morphology described for this species consisting of foliose, superimposed lamellae (Cremades *et al.* 1996; Veiga *et al.* 1998; Bárbara *et al.* 2002, 2012; Lugilde Yáñez 2020). Molecular phylogenetic studies carried out on other species of *Lithophyllum* recorded from the European coasts (Hernández-Kantun *et al.* 2015a; Peña *et al.* 2018) confirmed a wide distribution of these species in both the NE Atlantic and Mediterranean Sea; thus, the occurrence of the generitype *Lithophyllum incrustans* (Philippi) and *L. nito-*

rum W.H.Adey & P.J.Adey were confirmed for both regions together with *L. hibernicum* Foslie. By contrast, the genetic differentiation found between Atlantic and Mediterranean populations of *L. byssoides* (Lamarck) Foslie suggested that different species might occur in each region (Pezzolesi *et al.* 2017). With regards to the Mediterranean clades recently discovered under *L. stictiforme,* some clades are widely distributed while others appear to have restricted geographic distributions (De Jode *et al.* 2019; Pezzolesi *et al.* 2019).

Based on the recent finding of multiple cryptic species passing under *Lithophyllum stictiforme* in the Mediterranean, we aimed to elucidate the phylogenetic relationships between the Atlantic Iberian records of *L. stictiforme* and this Mediterranean species complex.

MATERIAL AND METHODS

Collections studied

We studied 21 collections identified as *Lithophyllum stictiforme* – or under the heterotypic synonyms *L. frondosum* and *L. grandiusculum* – that are housed in the herbarium of Universidade de Santiago de Compostela (SANT, herbarium acronyms following Thiers 2021). These herbarium specimens were collected in different areas of the Atlantic Iberian Peninsula: Cantabria (1), Asturias (1), Galicia (18) and North Portugal (1) between 1994 and 2018 (Table 1). All specimens were collected from subtidal bedrocks, between 2-20 m depth (Fig. 1A-D), and they showed the gross morphology typical of *L. stictiforme* consisting of foliose lamellae, single or superimposed (Fig. 1E-G).

DNA sequencing and phylogenetic analyses

Genomic DNA was extracted using the NucleoSpinR 96 Tissue kit (Macherey-Nagel, GmbH and Co. KG, Germany) following the manufacture's recommendations. The mitochondrial COI-5P fragment was PCR-amplified using the primer pair Gaz-F1/Gaz-R1 (Saunders 2005). The chloroplast *psb*A gene was amplified using the primer pair *psb*A-F1/*psb*A-R2 (Yoon *et al.* 2002). Thermal profiles for PCR amplification for COI-5P and *psb*A followed Saunders & McDevit (2012) and Bittner (2009), respectively; PCR reactions for COI-5P and *psb*A followed Peña *et al.* (2015a). PCR products were purified and sequenced by Eurofins (Nantes, France). Sequences were assembled and aligned with the assistance of CodonCode AlignerR (CodonCode Corporation, USA) and adjusted by eye using SeaView version 4 (Gouy *et al.* 2010). Sequences were submitted to the Barcode of Life Data Systems (project 'NGCOR', BOLD, http://www.boldsystems.org; Ratnasingham & Hebert 2007) and GenBank (Appendix 1). The datasets used for the analyses comprised publicly available GenBank sequences pertaining to the Mediterranean clades of the *Lithophyllum stictiforme* complex (De Jode *et al.* 2019; Pezzolesi *et al.* 2019), other species of *Lithophyllum* reported from the Mediterranean and Atlantic regions and particularly in the Atlantic Iberian Peninsula (Hernández-Kantun *et al.* 2015a; Pardo *et al.* 2017; Pezzolesi *et al.* 2017; Peña *et al.* 2018; Caragnano *et al.* 2020), as well as the most relevant matches found in GenBank with our collections that also pertained to the genus *Lithophyllum*. Based on the phylogeny presented in Peña *et al.* (2020), *Porolithon onkodes* (Heydrich) Foslie was used as the outgroup (Appendix 1).

Phylogenetic relationships were inferred using Maximum Likelihood (ML) and Bayesian inference (BI) using Mega 6 and MrBayes 3.2.1, respectively (Ronquist & Huelsenbeck 2003; Tamura *et al.* 2013). Models of sequence evolution were estimated using the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) obtained in jModeltest 2.1.3 (Darriba *et al.* 2012). Maximum Likelihood and Bayesian analyses for the COI-5P and *psb*A alignments were performed under a generalized time-reversible with gamma + invariant sites heterogeneity model (GTR + G + I). The Bayesian analyses were performed under the same model with four Markov Chain Monte Carlo for 10 million generations, and tree sampling every 1000 generations.

Morphological studies

External morphological and anatomical characters of the Atlantic Iberian *Lithophyllum stictiforme* were examined and compared with those provided for the *L. stictiforme* complex that also includes two species described from the Atlantic, *L. lobatum* and *L. searlesii* (Pezzolesi *et al.* 2019), as well as with other *Lithophyllum* taxa reported in the Atlantic European coasts such as *L. hibernicum, L incrustans* or *L. nitorum* that have been recently re-assessed using DNA sequences (Hernández-Kantun *et al.* 2015a; Peña *et al.* 2018). Internal anatomical features were examined in 14 of the 16 Atlantic Iberian specimens studied using the scanning electron microscope (SEM, model JEOL JSM 6400, Universidade da Coruña, Spain). The anatomical terms medulla (equivalent to the terms hypothallium and core) and cortex (equivalent perithallium and peripheral region) follow Chamberlain & Irvine (1994). Cell length is the distance between primary pit-connections, and cell diameter is the measurement taken perpendicularly to this across the middle of the cell lumen. Other anatomical measurements assessed for the European *Lithophyllum* species were taken following Chamberlain & Irvine (1994), Hernández-Kantun *et al.* (2015a), Peña *et al.* (2018) and Pezzolesi *et al.* (2019).

RESULTS

Only four of the 21 herbarium specimens of Atlantic Iberian *L. stictiforme* were sequenced in this study: one specimen from Cantabria, two from Galicia and one from North Portugal. Unfortunately, the remaining specimens (17) were preserved in formalin after field collection (Table 1). Two COI-5P sequences were successfully amplified for specimens from Cantabria and Galicia, respectively. Three *psb*A sequences were obtained from Galicia (2) and North Portugal (1) collections. Both COI-5P and *psb*A sequences did not return any match with the GenBank database obtaining the highest similarity with sequences of the European species *L. incrustans* and *L. hibernicum* (*c.* 90% similarity in COI-5P; *c.* 96%

TABLE 1. — Collection details of the herbarium specimens examined and sequenced in the study.

Species	Collection data and herbarium information	COI-5P	*psb*A
Lithophyllum artabricum V.Peña, sp. nov.	SANT-Algae 33667, Praia das Fontes, Covas, Cabo Prior, Galicia, Spain, 19.V.2012, subtidal bedrock (10 m depth), coll. V. Peña & J. Souto. holotype.	MZ129194	MZ129197
	SANT-Algae 26900, Isla de Mouro, Bahía de Santander, Cantabria, Spain, subtidal bedrock (15 m depth), 16.VIII.2009, coll. C. Peteiro & N. Sánchez.	MZ129193	–
	SANT-Algae 33616, Punta Gallino, San Ciprián, Lugo, Galicia, Spain, subtidal sciophilous bedrock (6 m depth), 21.VII.2015, coll. I. Bárbara, A. García-Fernández & V. García-Redondo.	–	MZ129195
	SANT-Algae 33619, Apulia, Douro Litoral, Portugal, subtidal bedrock (9 m depth), 26.IX.2018, coll. J. Franco.	–	MZ129196
	SANT-Algae 14846, Playa de Cadavedo, Asturias, Spain, subtidal bedrock (2 m depth), 08.VIII.1998, coll. J. Cremades & J. Dosil. Identified as *L. frondosum*.	–	–
	SANT-Algae 11677, Pedra Sardiña, Ensenada de Sta. Marta, Ortigueira, Galicia, subtidal bedrock (4 m depth), 05.VIII.1999, coll. C. López-Varela. Identified as *L. grandiusculum*.	–	–
	SANT-Algae 30499, As Blancas, Ría de Cedeira, Galicia, Spain, subtidal bedrock (6 m depth), 20.IV.2016, coll. I. Bárbara & A. García-Fernández. Identified as *L. stictiforme*	–	–
	SANT-Algae 11684, Punta Prados, Valdoviño, Galicia, subtidal bedrock (12 m depth), 03.VIII.1999, coll. A. J. Veiga Villar. Identified as *L. grandiusculum*.	–	–
	SANT-Algae 13392, Punta Gaboteira, Sada, Galicia, subtidal bedrock (6 m depth), 26.VI.2001, coll. I. Bárbara. Identified as *L. frondosum.*	–	–
	SANT-Algae 15005, Islas San Pedro, A Coruña, Galicia, subtidal bedrock (5 m depth), 21.IX.2003, coll. I. Bárbara, P. Díaz & C. López-Varela. Identified as *L. grandiusculum*	–	–
	SANT-Algae 15006, Puerto de Sorrizo, Arteixo, Galicia, subtida bedrock (4 m depth), 18.X.2003, coll. I. Bárbara, P. Díaz & C. López-Varela. Identified as *L. grandiusculum*.	–	–
	SANT-Algae 11683, Xermania, Ensenada de Lourido, Caión, Galicia, subtidal bedrock (10 m depth), 31.VIII.1998, coll. C. López-Varela. Identified as *L. grandiusculum*.	–	–
	SANT-Algae 20954, Cambre, Malpica, Galicia, Spain, subtidal bedrock (2 m depth), 02.VI.2008, coll. I. Bárbara & P. Díaz. Identified as *L. stictiforme*.	–	–
	SANT-Algae 11670, Punto Morelo, Laxe, Galicia, subtidal bedrock (7 m depth), 17.VI.1999, coll. C. López-Varela. Identified as *L. grandiusculum*.	–	–
	SANT-Algae 11671, Arou, Camariñas, Galicia, Spain, subtidal bedrock (4 m depth), 17.VI.1999, coll. A. J. Veiga Villar. Identified as *L. grandiusculum*.	–	–
	SANT-Algae 11666, Cabo Cee, Corcubión, Galicia, Spain, subtidal bedrock (6 m depth), 25.VI.1999, coll. C. López-Varela. Identified as *L. grandiusculum*.	–	–
	SANT-Algae 7046, O Cabaliño, Sisarga Grande, Islas Sisargas, A Coruña, Spain, subtidal bedrock (5 m depth), 07.V.1995, coll. A. J. Veiga. Identified as *L. grandiusculum*.	–	–
	SANT-Algae 7490, A Sistela, Sisarga Grande, Islas Sisargas, A Coruña, Spain, subtidal bedrock (8 m depth), 27.III.1994, coll. I. Bárbara. Identified as *L. frondosum*.	–	–
	SANT-Algae 7491, Piedras Planas, Sisarga Grande, Islas Sisargas, A Coruña, Spain, subtidal bedrock (20 m depth), 03.XII.1995, coll. A. J. Veiga. Identified as *L. frondosum.*	–	–
	SANT-Algae 7492, O Cabaliño, Sisarga Grande, Islas Sisargas, A Coruña, Spain, subtidal bedrock (4-6 m depth), 18.I.1996, coll. A. J. Veiga & I. Bárbara. Identified as *L. frondosum*.	–	–
	SANT-Algae 7498, O Cabaliño, Sisarga Grande, Islas Sisargas, A Coruña, Spain, subtidal bedrock (3-6 m depth), 04.II.1996, coll. J. Cremades & A. J. Veiga. Identified as *L. frondosum.*	–	–

similarity in *psb*A). The comparison with Mediterranean *L. stictiforme* complex returned lower similarity (88-89% in COI-5P; 94-95% in *psb*A). The COI-5P alignment comprised 118 sequences resulting in 106 haplotypes, ranging from 553 to 664 bp, consisting of 298 variable sites. The ML analysis resolved the two Atlantic Iberian specimens (represented by a single haplotype, Fig. 2) in a lineage separated from remaining *Lithophyllum* taxa, including the Mediterranean *L. stictiforme* complex for which the divergence is estimated in 10.7-12.2% (uncorrected p-distance, 63-73 bp differences). The *psb*A alignment comprised 121 sequences resulting in 106 haplotypes, ranging from 543 to 851 bp, consisting of 289 variable sites. Both ML and Bayesian analyses (Fig. 3) resolved the Atlantic Iberian specimens into a fully supported lineage (96%/1 for ML and BI, respectively), as sister to *L. incrustans* with strong support (70%/0.98). The Atlantic Iberian specimens were resolved apart from the *L. stictiforme* complex with a divergence of 4.5-5.6 % (uncorrected p-distance, 34-41 bp differences). The lowest divergence was found compared with *L. incrustans* (2.1 % uncorrected p-distance, > 16 bp differences). The divergence estimated between the three Atlantic Iberian specimens sequenced was 0.6-0.9 % (uncorrected p-distance, 5-7 bp differences).

Given the molecular evidence shown above, we propose *Lithophyllum artabricum* V.Peña, sp. nov. to accommodate the Atlantic Iberian specimens previously assigned to *L. stictiforme* or under its heterotypic synonyms *L. frondosum* and *L. grandiusculum*.

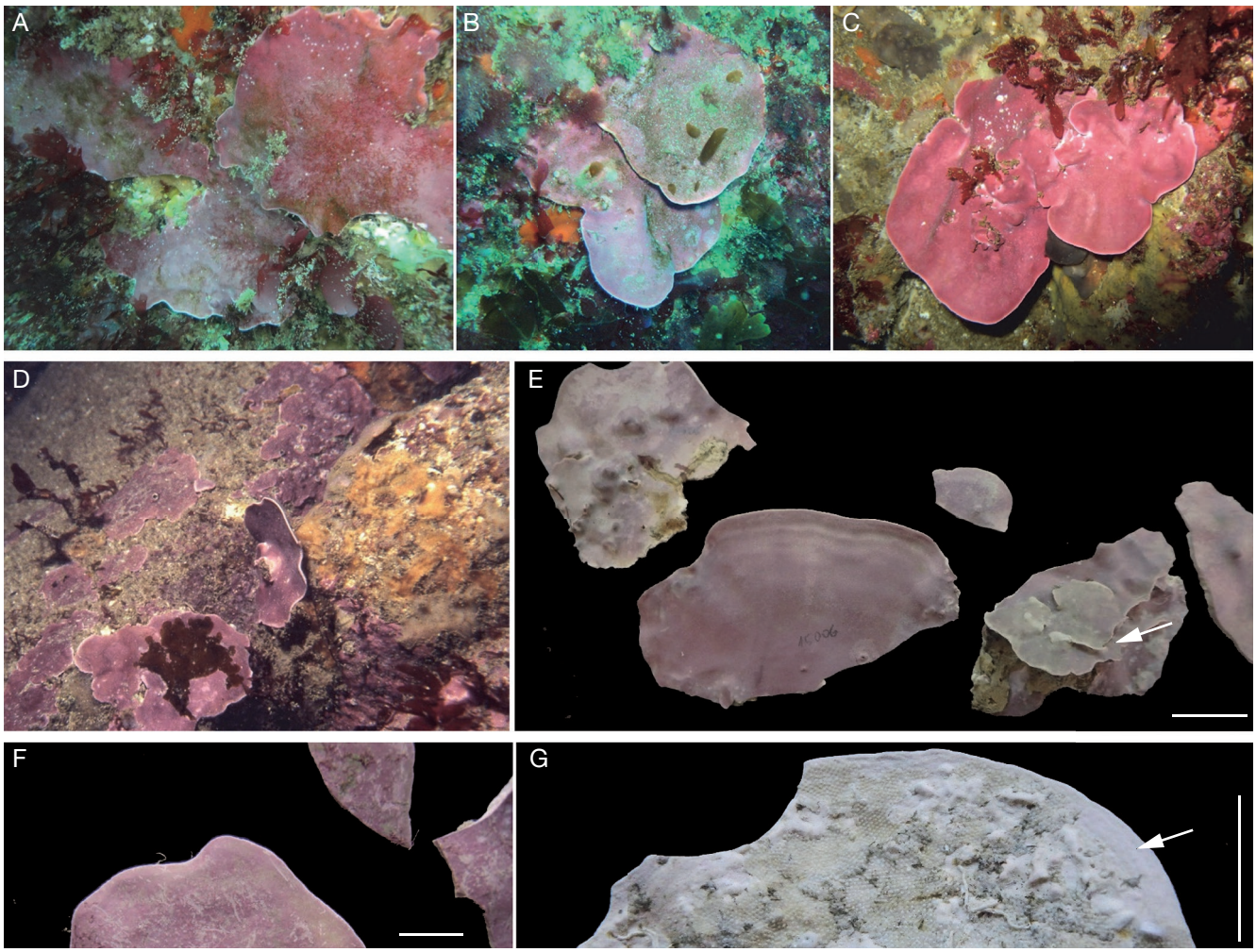

Fig. 1. — Habitat and habit of *Lithophyllum artabricum* V.Peña, sp. nov.: **A-D,** characteristic habitat of this species growing in subtidal bedrock, sometimes sciophilous, in the type locality (**A**), and other Galician localities (**B-D**, Cedeira, Cambre and Sisargas, respectively); **E**, **F,** gross morphology consisted on foliose lamellae or fan-like thallus, single or superimposed (arrow) observed in the specimen SANT-Algae 15006 (**E**) and in the holotype (**F**, SANT-33667); **G**, lower surface of the specimen showing concentric lines, particularly visible at the margins as the remaining surface is covered by sessile invertebrates (SANT-Algae 11666). Scale bars: E, 2 cm; F, G, 1 cm.

Family Lithophyllaceae Athanasiadis
Genus *Lithophyllum* Philippi

Lithophyllum artabricum V.Peña, sp. nov.
(Figs 1, 4, 5)

Holotype. — **Spain**. Galicia, Cabo Prior, Praia das Fontes, Covas; 43°33'29.56"N, 8°16'52.69"W; 10 m depth; SANT-Algae 33667, 19.V.2012, leg. V. Peña & J. Souto (Fig. 1A, F)

Holotype DNA sequences. — COI-5P and *psb*A, GenBank accession numbers MZ129194 and MZ129197.

Complementary collections. — **Spain**. Galicia, San Ciprián, Lugo, Punta Gallino; 21.VII.2015; 6 m depth, collectors I. Bárbara, A. García-Fernández & V. García-Redondo SANT-Algae 33616 (*psb*A: MZ129195), SANT-Algae 33619 (*psb*A: MZ129196). — **Portugal**. Douro Litoral, Apulia; 26.IX.2018; 9 m depth, collector J. Franco; SANT-Algae 26900 (COI-5P: MZ129193). — **Spain**. Cantabria, Bahía de Santander, Isla de Mouro ;16.VIII.2009; 15 m depth; collectors C. Peteiro & N. Sánchez. Additional collections in Table 1.

Etymology. — The specific epithet refers to the geographic location of the type locality, the Artabrian Gulf (historically known as *Portus Magnus Artabrorum*).

Description

Non-geniculate, foliose lamellae or fan-like thallus, single or superimposed, up to 10 cm diameter and 2 mm thick (Figs 1A-F, 4A). Colour pink to violet, texture smooth and matt when dried (Fig. 1E-F). Concentric lines along the lower surface, particularly visible at the margins as the remaining surface is covered by sessile invertebrates (Fig. 1G). Thallus pseudoparenchymatous, monomerous with medulla non-coaxial to occasionally coaxial, composed of cells 6-47 µm long by 4-27 µm diameter (Fig. 4A-B, D). Cortical cells (3) 4-19 µm × 3-21 µm, arranged in filaments laterally aligned (Fig. 4C) and

subepithallial cells 7-15 µm × 5-12 µm (Fig. 4E). Epithallial cells arranged in 1 (2) layers, flattened in transverse section, 1-3 µm long and 6-13 µm wide (Fig. 4E-F); in surface view, epithallial cells were polygonal (Fig. 4G). Secondary pit-connections present between cells of contiguous filaments (Fig. 4C, E). Trichocytes not observed. Gametangial plants were not observed. Tetra/bisporangial conceptacles were uniporate, flush with surface (Fig. 4H-I). Conceptacle chambers were dumbbell-shaped, 70-133 µm high and 236-448 µm wide, with canal pore conical tapering from bottom to top of the thallus surface (Fig. 5A-C). Conceptacle roofs were 8-14 cells thick, the depth of the floor between 14-25 cells. Central columella present (Fig. 5D). Tetra/bisporangia not observed. Buried conceptacles present, occasionally with inorganic infillings (Figs 4D, 5E, F).

HABITAT. — *Lithophyllum artabricum* V.Peña, sp. nov. is at presently known only from subtidal bedrock, sometimes in sciophilous habitats.

DISTRIBUTION. — Atlantic Iberian Peninsula, recorded from Cantabria to North Portugal (Douro Litoral province).

COMMENTS

The morpho-anatomical characters of *Lithophyllum artabricum* V.Peña, sp. nov. showed an overlap with vegetative and reproductive characters provided for many of the 13 clades recovered in the *L. stictiforme* complex, which also includes the Macaronesian *L. lobatum* and the NW Atlantic *L. searlesii* (Pezzolesi *et al.* 2019). However, the specimens of *L. artabricum* V.Peña, sp. nov. have a conspicuous monomerous thallus construction composed of a non-coaxial medulla to occasionally coaxial, whereas the clades comprising the *L. stictiforme* complex are described with mainly dimerous construction (Table 2). Moreover, the combination of characters such as concentric lines in the margins of the lower surface, the absence of trichocytes, the conical shape of the canal pore and the presence of buried conceptacles are considered useful to differentiate *L. artabricum* V.Peña, sp. nov. from some of the Mediterranean clades reported as well as *L. lobatum* (Table 2). In addition, *L. artabricum* V.Peña, sp. nov. differs from other species of *Lithophyllum* reported from the Atlantic European coasts by a combination of characters related to the external morphology consisting of single or superimposed lamellae or fan-like, the monomerous thallus construction with medulla non-coaxial to occasionally coaxial, the conical shape of the canal pore of sporangial conceptacles, and its occurrence seemingly limited to subtidal bedrocks (Table 3).

DISCUSSION

Lithophyllum artabricum V.Peña, sp. nov. is described as a new species for the Atlantic Iberian Peninsula based on phylogenetic analyses that encompassed the cryptic lineages recently uncovered under *Lithophyllum stictiforme* in the Mediterranean (De Jode *et al.* 2019; Pezzolesi *et al.* 2019). Until now, this new species collected from the subtidal bedrocks from North Spain to North Portugal was identified as *L. stictiforme* – or under their heterotypic synonyms *L. frondosum* or *L. grandiusculum* – because of the similar morphology consisting on foliose lamellae or fan-like plants with concentric bands along the lower surface (Cremades *et al.* 1996; Veiga *et al.* 1998; Bárbara *et al.* 2002, 2012; Lugilde Yáñez 2020). However, specimens of *L. artabricum* V.Peña, sp. nov. have a conspicuous monomerous thallus construction, while the taxa belonging to the *L. stictiforme* complex that also encompasses *L. lobatum* and *L. searlesii* are described with mainly dimerous thalli (Pezzolesi *et al.* 2019). Moreover, this characteristic external morphology and habitat restricted to subtidal bedrocks were considered the main differences between *L. artabricum* V.Peña, sp. nov. and ten species of *Lithophyllum* cited for the Atlantic European coasts, such as *L. bathyporum, L. hibernicum, L. incrustans, L. nitorum* and *L. subtenellum* that have been reassessed using molecular data obtained from type collections (Hernández-Kantún *et al.* 2015a; Peña *et al.* 2018; Richards *et al.* 2018).

Based on the specimens sequenced in the present study, the distribution range of *Lithophyllum artabricum* V.Peña, sp. nov. is restricted to the Atlantic Iberian Peninsula, from North Spain (Cantabria) to North Portugal (Douro Litoral province). A restricted geographic distribution has also been observed in some Mediterranean clades of the *L. stictiforme* complex (De Jode *et al.* 2019; Pezzolesi *et al.* 2019). However, the limited availability of coralline collections from subtidal bedrocks compared to other subtidal habitats such as maerl beds (Pardo *et al.* 2017; Peña *et al.* 2018) or from the intertidal (Hernandez-Kantun *et al.* 2015a) should be taken into account. Thus, further collections from this particular subtidal habitat should be addressed in order to confirm the restricted distribution of *L. artabricum* V.Peña, sp. nov. For instance, *L. stictiforme* was reported in South Portugal (Berecibar 2011). The morpho-anatomical examination of an available herbarium specimen collected in the locality of Armaçao de Pêra, Algarve, at 17 m depth (SANT-Algae 27308) also showed a conspicuous monomerous thallus construction (Appendix 2). However, this potential record of *L. artabricum* V.Peña, sp. nov. for the southern coasts of Atlantic Iberian Peninsula is hampered by the absence of DNA sequences from this collection because of formalin preservation. The region of South Portugal contains records of Mediterranean species (Berecibar *et al.* 2009; Peña & Bárbara 2013; Peña *et al.* 2014), therefore further collections from this region are needed to confirm with DNA sequences this potential southern range of distribution for *L. artabricum* V.Peña, sp. nov. With regards to the northern range of distribution, at present there are not records of *L. stictiforme* – or their heterotypic synonyms- any further North (Guiry & Guiry 2021). Lemoine (1965) examined collections from Guernesey, Channel Islands and showed that the record of *Pseudolithophyllum expansum* (Philippi) Mme. Lemoine (now considered *Mesophyllum expansum* (Philippi) M.L.Mendoza & Cabioch) were misidentifications of lamellate specimens of *L. incrustans.* In addition, inquiries to other herbaria that might contain collections potentially attributed to *L. artabricum* V.Peña, sp. nov. (e.g. BM and PC, with databases available online at Natural History Museum 2014 and Chagnoux 2021, respectively)

TABLE 2. — Comparative table of *Lithophyllum artabricum* V.Peña, sp. nov., the Mediterranean *L. stictiforme* and cryptic clades (2 to 10) uncovered under this species complex, and *L. lobatum*. Data from: **1**, Lemoine (1929); **2**, Hamel & Lemoine (1953); **3**, Bressan & Babbini (2003); **4**, Pezzolesi *et al.* (2019); **5**, present study.

	***Lithophyllum artabricum* sp. nov.[5]**	***Lithophyllum stictiforme*[4]**	**Clade 2[4]**	**Clade 3[4]**	**Clade 4[4]**	**Clade 5[4]**	**Clade 6[4]**	**Clade 7[4]**	**Clade 8[4]**	**Clade 9[4]**	**Clade 10[4]**	***Lithophyllum lobatum*[1-4]**
Habit	**Lamellae**	Lamellae	Lamellae	Thick crusts	Lamellae	Lamellae	Lamellae	Lamellae	Lamellae	Lamellae	Lamellae	Lobed crusts
Size	**Up to 10 cm**	Up to 25 cm	Up to 7 cm	Up to 10 cm	Up to 8 cm	Up to 8 cm	Up to 7 cm	Up to 8 cm	Up to 4 cm	Up to 15 cm	Up to 5 cm	Up to 3 cm
Color	**Light pink, dark pink, violet**	Violet, magenta, dark pink	Light to bright pink	Grayish violet to dark pink	Grayish violet to mauve	Dark to grayish pink	Grayish violet to mauve	Grayish pink	Pink	Dark to grayish pink	Pink, mauve	Red pink, greyish
Concentric lines (lower surface)	**+**	(usually)	(usually)	+/–	(usually)	+	+	+	–	–	+	Present
Maximum thickness (mm)	**< 2.5**	1.8	< 1	2.5	<1	1.7	< 0.5	< 1	< 0.5	–	< 1 mm	3-4
Thallus construction	**Monomerous**	Mainly dimerous	Mainly dimerous	Mainly dimerous	Mainly dimerous	Mainly dimerous	Mainly dimerous	Mainly dimerous	Mainly dimerous	Mainly dimerous	Mainly dimerous	Dimerous
Medullary cells (length, µm)	**6-47**	4.5-28	4-29	4-18	4-15	4-15	5-5	4-10	9-14	7-10	10-25	–
Medulllary cells (height / diameter, µm)	**4-27**	4-18	4-20	7-20	4-15	5-15	5-15	4-16	17-23	8-16	5-10	10-20
Cortical cells (length, µm)	**(3) 4-19**	5.5-42.5	8-38	9-50	7.5-25	5-20	4-18	5-22	9-18	13-25	7-24	(5) 10-20 (40)
Cortical cells (diameter, µm)	**3-21**	3-20	4.5-22	7-21	9-18	5-16	6-20	3-14	7-14	8-13	5-11	5-15
Number epithallial cells	**1(2)**	1-2	1-2	1(2)	1-2	1	1	1 -2	1	1	1-2	–
Shape epithallial cells	**Flattened**	Flattened	Flattened	Flattened	Flattened	Flattened	Flattened	Flattened	Flattened	Flattened	Flattened	Flattened
Epithallial cells (length, µm)	**1-3**	1-7.5	0.5-7.5	1.5-7.5	4-7.5	2.5-6	3 - 8	1-6	2 5	2.5-4	1-3	–
Epithallial cells (diameter, µm)	**6-13**	3-14	2.5-15	6-28	9-15	6-14	8 - 14	5-11	8-10.5	10-12.5	2-11	5-7.0
Trichocytes	–	(+)	+	–	–	(+)	–	(+)	–	–	–	–
Tetra/ bisporangial conceptacles (surface view)	**Flush with the surface**	Slightly protruding or flush with the surface	Flush to protruding	Slightly or not protruding	Slightly or not protruding	Flush with the surface	Flush with the surface	Slightly or not protruding	Slightly or not protruding	–	Slightly or not protruding	Not protruding
Shape of pore canal (from bottom to top)	**Tapering**	Cylindrical or tapering	Cylindrical or tapering	Tapering	Tapering	Tapering	Tapering	Tapering	–	Tapering	Tapering	–
Shape tetra / bisporangial conceptacle chamber	**Dumbbell**	Dumbbell	Dumbbell	Dumbbell / Elliptical	Dumbbell	Dumbbell	Dumbbell	Dumbbell	–	Dumbbell	Dumbbell	Dumbbell, round, reniform
Tetra / bisporangial conceptacle chamber (height, µm)	**96-127**	80-320	80-330	150-270	180	120-200	91-237	76-240	–	160-230	76-116	–
Tetra / bisporangial conceptacle chamber (diameter, µm)	**236-448**	328-440	350-460	320-430	320-330	300-340	93-335	244-300	–	290-320	260-290	180-250
Columella	**+**	+	+	+	+	+	+	+	–	+	+	–
Roof thickness (number of cells)	**8-14**	4-15	3-12	5-6	4-9	5-6	8-9	7-8	–	9-10	5-9	–
Depth of conceptacle floor (cells from bottom to thallus surface)	**14-25**	14-23	10-17	14-15	11-13	14-15	13-14	12-17	–	15-16	13-16	–
Buried conceptacles	**+**	+	+	+	–	+	–	+	–	–	–	+
Habitat	**Subtidal bedrock**	Coralligenous	Coralligenous	Coralligenous	Coralligenous	Coralligenous	Coralligenous	Coralligenous	Coralligenous	Coralligenous	Coralligenous	Subtidal
Distribution in the European coasts	**Atlantic Iberian Peninsula**	Mediterranean	Mediterranean	Mediterranea	Mediterranea	Mediterranea	Mediterranea	Mediterranea	Mediterranea	Mediterranea	Mediterranea	Macaronesia (Canary Islands), Mediterranean

TABLE 3. — Comparative table between *Lithophyllum artabricum* V.Peña, sp. nov. and the *Lithophyllum* species reported for the Atlantic European coast. Data from: **1**, Crouan & Crouan (1867); **2**, Foslie (1899); **3**, Lemoine (1929); **4**, Hamel & Lemoine (1953); **5**, Cabioch (1968); **6**, Ardré (1970); **7**, Adey & Adey (1973); **8**, Woelkerling (1983); **9**, Afonso-Carrillo (1983); **10**, Chamberlain & Irvine (1994); **11**, Chamberlain (1997); **12**, Bressan & Babbini (2003); **13**, Peña *et al.* (2013); **14**, Hernández-Kantun *et al.* (2015a); **15**, Cormaci *et al.* (2017); **16**, Pezzolesi *et al.* (2017); **17**, Peña *et al.* (2018); **18**, Richards *et al.* (2018); **19**, present study.

	***L. artabricum* sp. nov.**[19]	***L. bathyporum***[1, 10, 14]	***L. byssoides***[8, 11, 16]	***L. crouaniorum***[10]	***L. dentatum***[4, 12, 14, 15]	***L. hibernicum***[10, 14]	***L. incrustans***[5 ,8, 10, 13, 14]	***L. nitorum***[7, 10, 17]	***L. orbiculatum***[10]	***L subtenellum***[2, 18]	***L. vickersiae***[3,4, 6, 9]
Habit	**Lamellae**	Encrusting	lamellae, fan-shaped, finger-like branches	Encrusting	Lamellae	Encrusting smooth or with numerous excrecences; unattached (rhodolith)	Encrusting with or without protuberances; unattached (rhodolith)	Encrusting	Encrusting	Encrusting	Encrusting
Size	**Up to 10 cm**	2 cm	10 cm	Up to 15 cm	Up to 20 cm	Up to 10 cm	Up to 10 cm	Up to 2 cm	Up to 2.5 cm	–	Up to 3 cm
Color	**Light pink, dark pink, violet**	Pink	Pink, mauve	Ruddy purple	greenish white, pink, greyish mauve	Pink to dark pink and purple.	White to pink, violet to lilac-gray	Dark to pale pink, orange-pink	Dark grey-purple, greyish, yellowish to beige	Purplish	Pink to grey pink
Concentric lines (lower surface)	**Present**	–	–	–	–	–	–	–	–	–	
Maximum thickness (mm)	**< 2.5**	1.5	< 0.8	4	1.5	< 0.5	1	2	1	2.5	0.5
Thallus construction	**Monomerous**	Dimerous (mainly)	Monomerous, dimerous	Dimerous	Monomerous	Monomerous	Monomerous	Dimerous, monomerous	Dimerous	Dimerous	Dimerous
Medullary cells (length, µm)	**6-47**	–	11-31	(4) 8-13 (26)	10-42	7-20	6-38	10-20	8-20	3.5–8	7-10
Medulllary cells (height / diameter, µm)	**4-27**	–	2-9	7-33	6-11	4-7	4–14	9-27	11-21	5.4-7	7-10
Cortical cells (length, µm)	**(3) 4-19**	–	3-9	6-28	4-41	7-20	5-41	5-41	10-21	6-8.2 (15)	3-14
Cortical cells (diameter, µm)	**3-21**	–	4-18	(4) 7-16	6-11	4–7	5-11	7-20	7-14	3.5-6 (7)	3-10
Number epithallial cells	**1 (2)**	–	Up to 4	4 (6)	1	2-3	1-3	1-2	5-6	1 (2)	2-3
Shape epithallial cells	**Flattened**	–	Squarish, flat, domed	Flattened	rounded, elliptical	Flattened to triangular	Rectangular, rounded-elliptical to flattened	Flattened to triangular	Rectangular	–	Rectangular to ovoid, flattened
Epithallial cells (length, µm)	**1-3**	–	4-6	–	3-6	3-4	3-6	1-2	-	–	–
Epithallial cells (diameter, µm)	**6-13**	–	3-7	–	7-11	3-4	6-11	7-8	–	–	–
Trichocytes	**–**	swollen cells that may be trichocytes	–	(in European collections)	–	–	–	–	Large thick-walled cells that may be trichocytes	–	–
Tetra/bisporangial conceptacles (surface view)	**Flush with the surface**	Sunken	Slightly protruding	Flush with thallus surface	Not protruding	Flush with thallus surface or/and sunken	Not protruding, pore usually slightly lower than surface	Protruding surrounded by a white rim	Flat with central pore surrounded by a disc	–	Slightly protruding to sunken
Shape of pore canal (from bottom to top)	**Tapering**	–	–	Likely tapering (fig. 20)10	Cylindrical and narrower in the middle part (fig. 152D)12.	Cylindrical	Tapering	Tapering	Tapering	–	–

TABLE 3. — Continuation

	***L. artabricum* sp. nov.**[19]	***L. bathyporum***[1, 10, 14]	***L. byssoides***[8, 11, 16]	***L. crouaniorum***[10]	***L. dentatum***[4, 12, 14, 15]	***L. hibernicum***[10, 14]	***L. incrustans***[5 ,8, 10, 13, 14]	***L. nitorum***[7, 10, 17]	***L. orbiculatum***[10]	***L. subtenellum***[2, 18]	***L. vickersiae***[3,4, 6, 9]
Shape tetra /bisporangial conceptacle chamber	**Dumbbell**	–	Conical, elliptical	Globose	Dumbbell (figs 152B,D)	Dumbbell	Dumbbell	Elliptical	Dumbbell	Conical	–
Tetra /bisporangial conceptacle chamber (height, µm)	**96-127**	190	45-140	(55) 81-130	100-120	150-190	40-180	94-156.0	60-115	–	–
Tetra /bisporangial conceptacle chamber (diameter, µm)	**236-448**	390	71-200	(85) 120-160 (180)	130-230	264-380	260-352	245-385	180-260	300	175-200
		–		–	–	–	Tapering	Tapering	Tapering	–	–
Columella	**+**	+ (small)	absent (frequent) or small	–	+	+	+	+ (small)	+ (filamentous)	–	–
Roof thickness (number of cells)	**8-14**	–	2-4	2-3	–	8-23	7-10	5	Up to 9	–	–
Depth of conceptacle floor (cells from bottom to thallus surface)	**14-25**	–	5-8	–	–	11-31	14-22	–	–	–	–
Buried conceptacles	**+**	+	+ (only spermatangial)	+	+	+	+	+	–	–	–
Habitat	**Subtidal bedrock**	Intertidal, subtidal. Epilithic	Intertidal, shallow subtidal. Epilithic	Intertidal, subtidal. Encrusting on different substrates	Intertidal, subtidal. Epilithic	Intertidal, rarely subtidal. Encrusting on different substrates, free-living	Subtidal, rarely intertidal. Encrusting on different substrates, free-living	Subtidal. Encrusting on different substrates	Intertidal. Epilithic	Intertidal (likely). Epilithic	Intertidal, subtidal. Epilithic
Distribution in the European coasts	**Atlantic Iberian Peninsula**	Atlantic (Brittany, Asturias, Galicia)	Atlantic, Mediterranean	Atlantic	Atlantic, Mediterranean	Atlantic, Mediterranean	Atlantic, Mediterranean	Atlantic, Mediterranean	Atlantic, Mediterranean	Atlantic (France)	Atlantic (Macaronesia, Portugal and France)

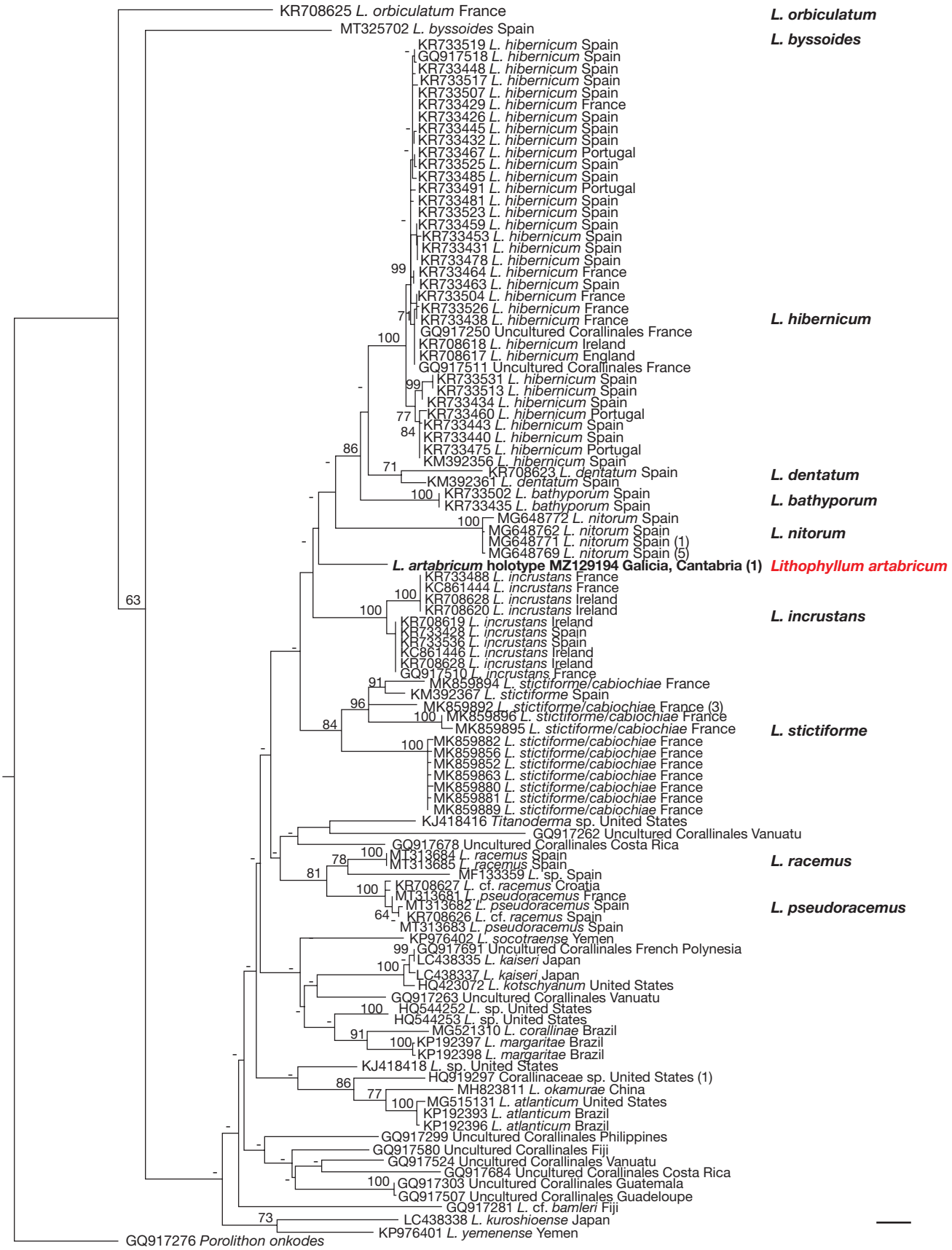

Fig. 2. — Maximum Likelihood (ML) tree of COI-5P sequences included in the present sudy. In **bold** *Lithophyllum* species reported for the European coasts. Bootstrap ML values >60% shown for each node. Scale bar: 0.03 substitutions per site.

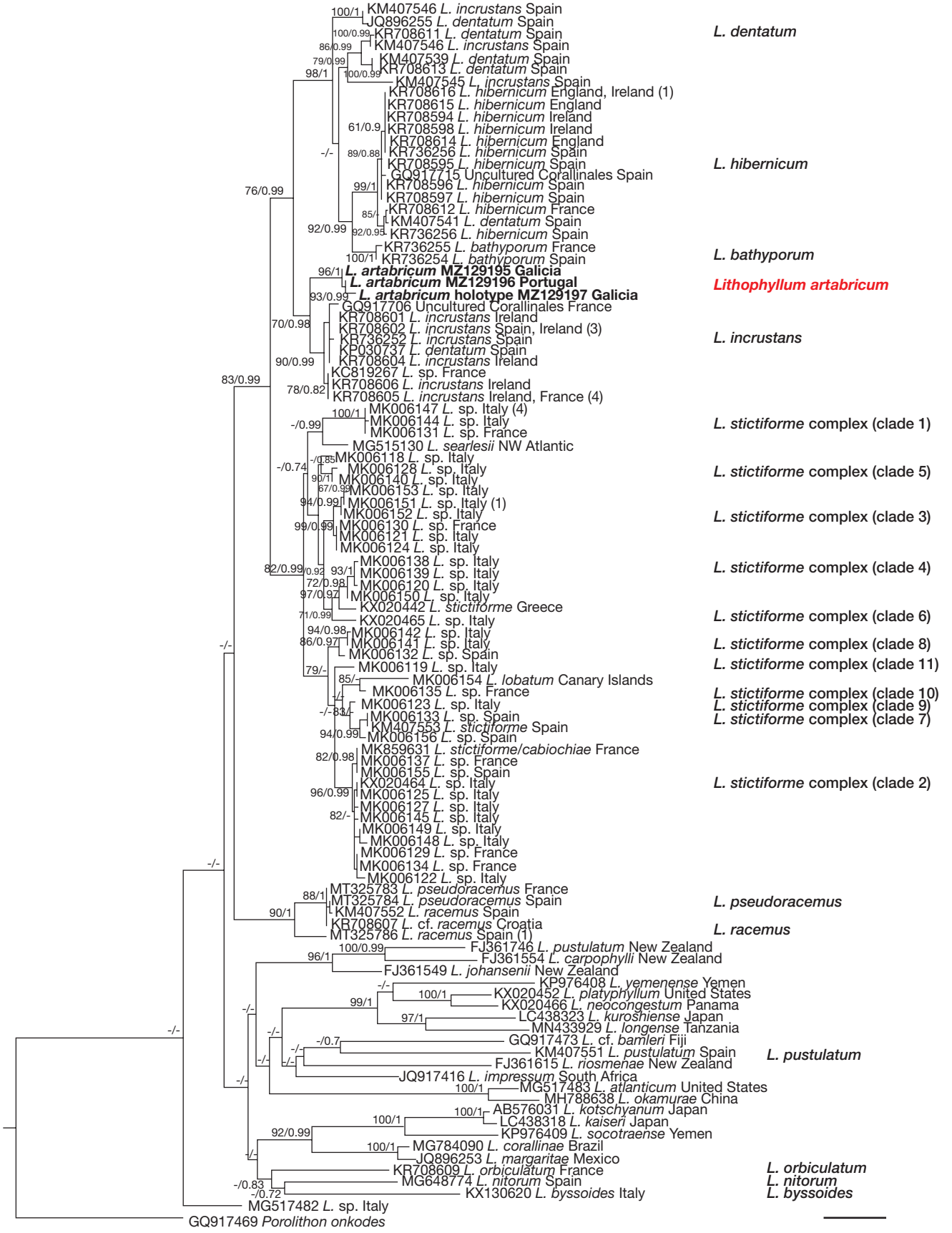

FIG. 3. — Phylogenetic tree inferred from maximum likelihood (ML) and Bayesian inference of *psb*A sequences included in the present study. In **bold** *Lithophyllum* species reported for the European coasts. Bootstrap ML values >60% and posterior probabilities >0.60 from Bayesian inference shown for each node. Scale bar: 0.03 substitutions per site.

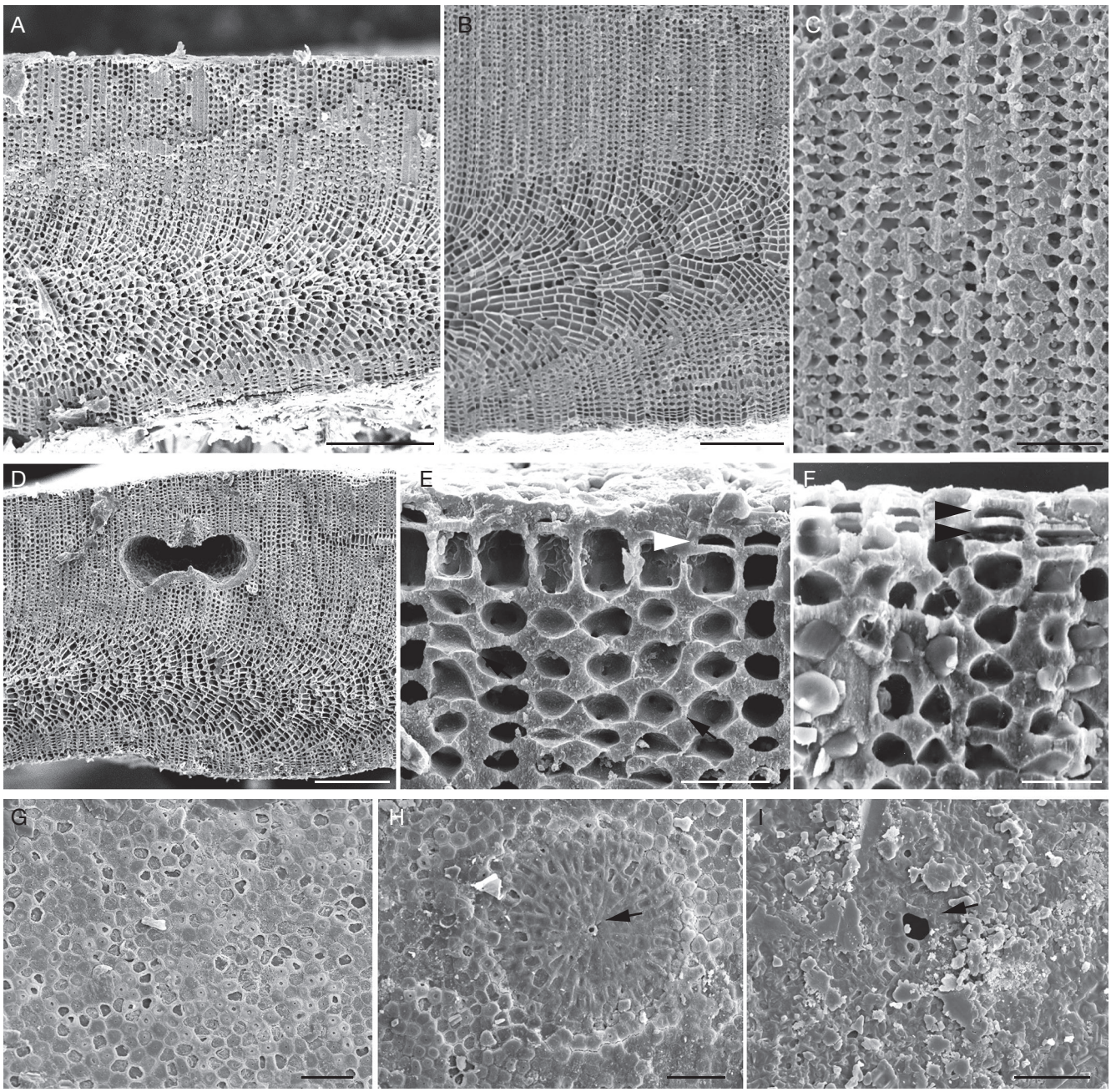

Fig. 4. — Morpho-anatomy of *Lithophyllum artabricum* V.Peña, sp. nov.: **A**, **B**, vertical section of the thallus showing a monomerous thallus construction with non-coaxial medulla; **C**, vertical section of the thallus showing cortical cells disposed in filaments laterally aligned; **D**, vertical section of the thallus showing a monomerous thallus construction with coaxial medulla, and a tetra/bisporangial uniporate conceptacle empty and buried; **E**, **F**, Vertical section of the thallus showing secondary pit-connections between contiguous filaments of cortical cells (**arrows**) and epithallial cells flattened disposed in 1-2 layers (**arrowheads**), **G**, surface view of the thallus showing polygonal epithallial cells; **H**, **I**, surface view of two different development stages of tetra/bisporangial uniporate conceptacles showing the pore flush with thallus surface (**arrows**). A, H, SANT-Algae 11671; B, C, holotype SANT-Algae 33667; D, E, SANT-Algae 26900; F, SANT-Algae 7046; G, SANT-Algae 11683; I, SANT-Algae 15006. Scale bars: A, B, D, 200 µm; C, G-I, 50 µm; E, F, 20 µm.

as well as to colleagues with expertise in diving surveys in algal communities did not result in any specimen resembling the characteristic morphology and habitat of *L. artabricum* V.Peña, sp. nov. It is worth mentioning that some previous records of *L. fasciculatum* (Lamarck) Foslie or *L. dentatum* (Kützing) Foslie from Ireland and Brittany (Cabioch 1968; Chamberlain & Irvine 1994; Peña *et al.* 2013) are described with lamellate branches, although they consisted of unattached specimens (maerl/rhodolith), and they are currently regarded as *L. incrustans* (Hernández-Kantun *et al.* 2015a).

Interestingly, the high cryptic diversity passing under the Mediterranean *Lithophyllum stictiforme* contrasts with the wide distribution and bathymetric range reported for *Mesophyllum expansum*. This latter species also contributes to the formation of coralligenous concretions in the Mediterranean (Ballesteros 2006), while in the Atlantic Iberian coasts it occurs

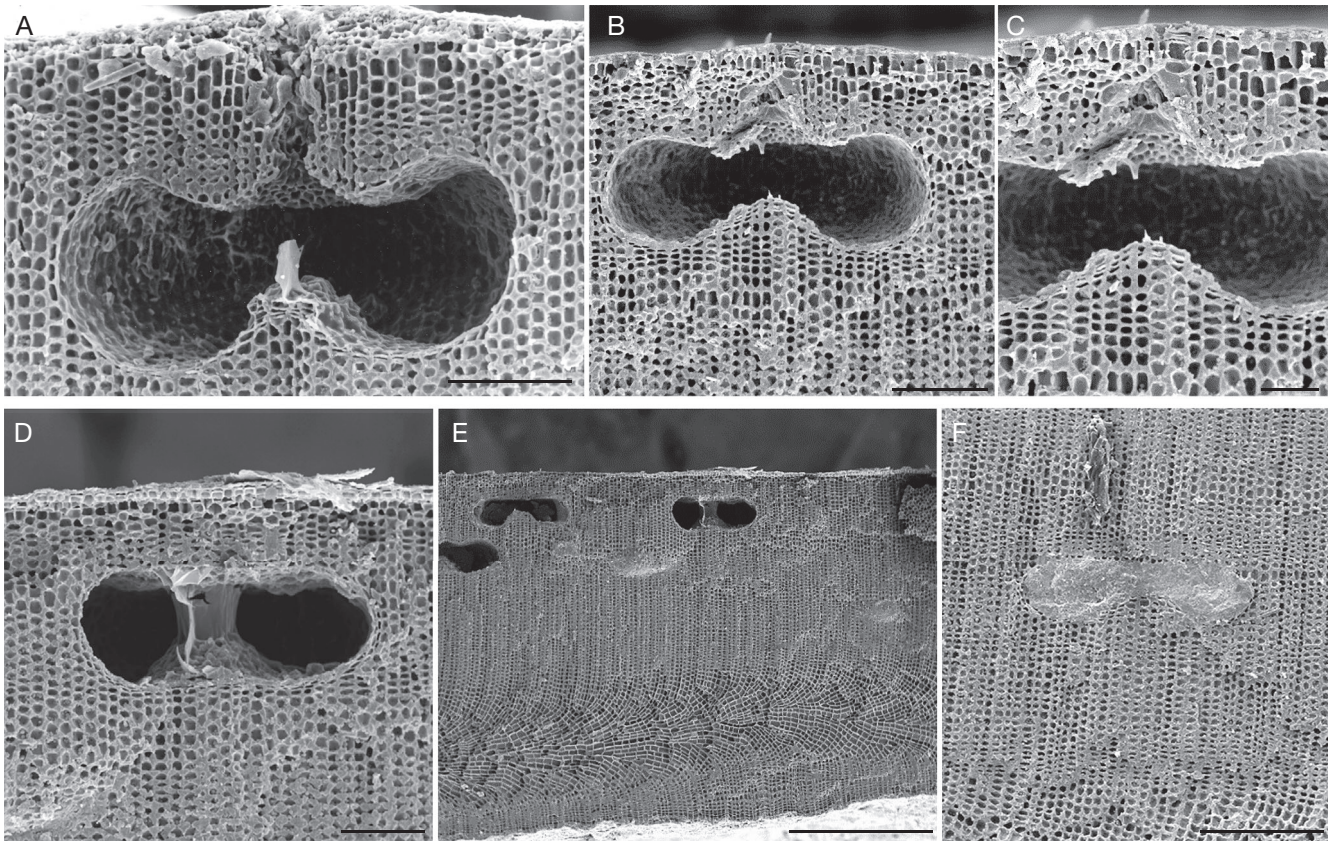

Fig. 5. — Tetra/bisporangial conceptacles of *Lithophyllum artabricum* V.Peña, sp. nov.: **A**, **B**, chambers dumbbell-shaped, empty; **C**, canal pore conical, tapering from the bottom to the roof surface; **D**, central calcified columella; **E**, buried conceptacles within the thallus; **F**, buried conceptacle with inorganic infilling. A, SANT-Algae 7046; B-D, E, holotype SANT-Algae 33667; F, SANT-Algae 15005. Scale bars: A, B, D, 100 µm; C, 50 µm; E, 500 µm; F, 200 µm.

in the shallow subtidal and even in the lower intertidal; this adaptation to a wide range of depths appeared to follow a positive correlation between depth and maximum sea surface temperature (Peña *et al.* 2015a).

The description of *Lithophyllum artabricum* V.Peña, sp. nov. constitutes another example of cryptic diversity in subtidal habitats of the Atlantic Iberian Peninsula. Recent studies on maerl beds uncovered two maerl-forming species in this region (Peña *et al.* 2011, 2015b), and a high diversity in encrusting species associated with this habitat, such as *L. nitorum* (Peña *et al.* 2018) and five cryptic species including an unidentified *Lithophyllum* species analysed herein and still pending to be formally described (Pardo *et al.* 2017: fig. 4i, m). Further explorations of subtidal bedrock along the Atlantic Iberian Peninsula might provide a better estimation of the diversity of coralline algal species of this region. Tittley (2002) suggested that the area comprising the Atlantic Iberian Peninsula, Atlantic France, southern England and Ireland maybe be considered a hotspot of macroalgal species richness. In particular, the species diversity and richness of Atlantic Iberian Peninsula also highlights the presence of rhodophyte species that are almost restricted to this part of the Lusitanian province, such as *Antithamnionella multiglandulosa* A.Secilla, A.Santolaria, I.Díez & J.M.Gorostiaga, *Calliblepharis hypneoides* P.Díaz-Tapia, I.Bárbara & M.H.Hommersand, *Lampisiphonia iberica* I.Bárbara, A. Secilla, P.Díaz-Tapia & H.-G.Choi, *Lophosiphonia simplicissima* P. Díaz-Tapia, *Phymatolithon lusitanicum* V.Peña or *Pseudopolyides furcellarioides* T.Gallardo, I.Bárbara & J.Cremades (Bárbara *et al.* 2005, 2013a, b; Secilla *et al.* 2006; Díaz-Tapia & Bárbara 2013; Díaz-Tapia *et al.* 2013; Peña *et al.* 2015b).

Here we describe the new species *Lithophyllum artabricum* V.Peña, sp. nov. based on collections identified as *L. stictiforme* or under the heterotypic synonyms *L. frondosum* and *L. grandiusculum.* Based on the evidence presented, *L. stictiforme* is removed from the flora of North and Northwest Spain, and North Portugal (Douro Litoral province). Apart from the European coasts, *L. stictiforme* is widely reported in warm and temperate waters (Guiry & Guiry 2021). According to the cryptic lineages of *L. stictiforme* uncovered in the Mediterranean Sea (De Jode *et al.* 2019; Pezzolesi *et al.* 2019) and the present description of *L. artabricum* V.Peña, sp. nov. for the Atlantic Iberian coasts, the status of *L. stictiforme* should be re-assessed globally.

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APPENDICES

Appendix 1. — List of GenBank accession numbers used in phylogenetic analyses.

Species	Collection details	COI-5P	psbA
L. atlanticum Vieira-Pinto, M.C.Oliveira & P.A.Horta	Brazil, Vieira-Pinto *et al.* (2014)	KP192393	
L. atlanticum	Brazil, Vieira-Pinto *et al.* (2014)	KP192396	
L. atlanticum	United States, Richards *et al.* (2018)		MG517483
L. atlanticum	United States, Richards *et al.* (2018)	MG515131	
L. bathyporum	France, Hernandez-Kantun *et al.* (2015a)		KR736255
L. bathyporum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733502	KR736254
L. bathyporum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733435	
L. byssoides	Italy, Pezzolesi *et al.* (2017)		KX130620
L. byssoides	Spain, Peña *et al.* (2020)	MT325702	
L. carpophylli (Heydrich) Heydrich	New Zealand, Farr *et al.* (2009)		FJ361554
L. cf. *bamleri*	Fiji, Bittner *et al.* (2010, as Uncultured Corallinales)	GQ917281	GQ917473
L. corallinae (P.Crouan & H.Crouan) Heydrich	Brazil, Torrano-Silva *et al.* (2018)	MG521310	MG784090
L. dentatum	Ireland, Hernandez-Kantun *et al.* (2015b)		JQ896255
L. dentatum	Spain, Hernandez-Kantun *et al.* (2015a)		KR708613
L. dentatum	Spain, Hernandez-Kantun *et al.* (2015a)	KR708623	KR708611
L. dentatum	Spain, Rösler *et al.* (2016)		KP030737
L. dentatum	Spain, Rösler *et al.* (2016)		KM407539
L. dentatum	Spain, Rösler *et al.* (2016)	KM392361	
L. hibernicum Foslie	England, Hernandez-Kantun *et al.* (2015a)		KR708616
L. hibernicum	England, Hernandez-Kantun *et al.* (2015a)		KR708615
L. hibernicum	England, Hernandez-Kantun *et al.* (2015a)		KR708614
L. hibernicum	England, Hernandez-Kantun *et al.* (2015a)	KR708617	
L. hibernicum	France, Hernandez-Kantun *et al.* (2015a)		KR708612
L. hibernicum	France, Hernandez-Kantun *et al.* (2015a)	KR733429	
L. hibernicum	France, Hernandez-Kantun *et al.* (2015a)	KR733438	
L. hibernicum	France, Hernandez-Kantun *et al.* (2015a)	KR733464	
L. hibernicum	France, Hernandez-Kantun *et al.* (2015a)	KR733504	
L. hibernicum	France, Hernandez-Kantun *et al.* (2015a)	KR733526	
L. hibernicum	Ireland, Hernandez-Kantun *et al.* (2015a)		KR708598
L. hibernicum	Ireland, Hernandez-Kantun *et al.* (2015a)		KR708594
L. hibernicum	Ireland, Hernandez-Kantun *et al.* (2015a)		KR708593
L. hibernicum	Ireland, Hernandez-Kantun *et al.* (2015a)	KR708618	
L. hibernicum	Ireland, Hernandez-Kantun *et al.* (2015b)		JQ896256
L. hibernicum	Portugal, Hernandez-Kantun *et al.* (2015a)	KR733460	
L. hibernicum	Portugal, Hernandez-Kantun *et al.* (2015a)	KR733467	
L. hibernicum	Portugal, Hernandez-Kantun *et al.* (2015a)	KR733475	
L. hibernicum	Portugal, Hernandez-Kantun *et al.* (2015a)	KR733491	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)		KR736256
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)		KR708597
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)		KR708596
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)		KR708595
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733426	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733431	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733432	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733434	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733440	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733443	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733445	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733448	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733453	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733459	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733463	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733478	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733481	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733485	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733507	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733513	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733517	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733519	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733523	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733525	
L. hibernicum	Spain, Hernandez-Kantun *et al.* (2015a)	KR733531	
L. hibernicum	Spain, Rösler *et al.* (2016)	KM392356	KM407541
L. hibernicum	France, Bittner *et al.* (2010, as uncultured Corallinales)		GQ918131
L. hibernicum	France, Bittner *et al.* 2010 (as uncultured Corallinales)	GQ917511	
L. hibernicum	Spain, Bittner *et al.* (2010, as uncultured Corallinales)	GQ917518	GQ917715
L. hibernicum	Spain, Bittner *et al.* (2010, as uncultured Corallinales)	GQ917250	

Appendix 1. — Continuation

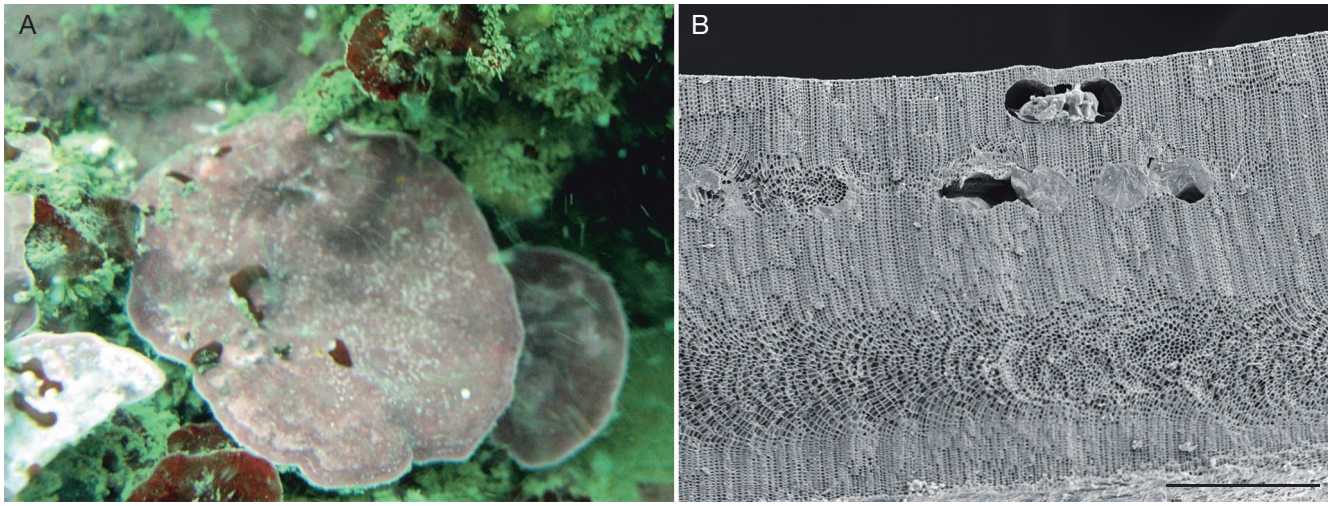
Species	Collection details	COI-5P	psbA
L. impressum Foslie	South Africa, van der Merwe *et al.* (2015)		JQ917416
L. incrustans (Philippi)	France, Bittner *et al.* 2010 (as uncultured Corallinales)	GQ917510	GQ917706
L. incrustans	France, Hernandez-Kantun *et al.* (2015a)		KR736253
L. incrustans	France, Hernandez-Kantun *et al.* (2015a)	KR733488	
L. incrustans	France, Pardo *et al.* (2014, as L. sp)	KC861444	KC819267
L. incrustans	France, Pardo *et al.* (2014, as L. sp)		KC819247
L. incrustans	France, Pardo *et al.* (2014, as L. sp)	KC861446	KC819246
L. incrustans	Ireland, Hernandez-Kantun *et al.* (2015a)	KR708628	KR708606
L. incrustans	Ireland, Hernandez-Kantun *et al.* (2015a)		KR708605
L. incrustans	Ireland, Hernandez-Kantun *et al.* (2015a)		KR708604
L. incrustans	Ireland, Hernandez-Kantun *et al.* (2015a)		KR708602
L. incrustans	Ireland, Hernandez-Kantun *et al.* (2015a)		KR708601
L. incrustans	Ireland, Hernandez-Kantun *et al.* (2015b)		JQ896239
L. incrustans	Ireland, Hernandez-Kantun *et al.* (2015b)	KR708620	JQ896238
L. incrustans	Ireland, Hernandez-Kantun *et al.* (2015b)	KR708619	JQ896237
L. incrustans	Ireland, Hernandez-Kantun *et al.* (2015b)		JQ896236
L. incrustans	Spain, Hernandez-Kantun *et al.* (2015a)		KR736252
L. incrustans	Spain, Hernandez-Kantun *et al.* (2015a)	KR733428	
L. incrustans	Spain, Hernandez-Kantun *et al.* (2015a)	KR733536	
L. incrustans	Spain, Rösler *et al.* (2016)		KM407546
L. incrustans	Spain, Rösler *et al.* (2016)		KM407545
L. incrustans	Spain, Rösler *et al.* (2016)		KM407543
L. johansenii Woelkerling & S.J.Campbell	New Zealand, Farr *et al.* (2009)		FJ361549
L. kaiseri (Heydrich) Heydrich	Japan, Kato & Baba (2019)	LC438335	LC438318
L. kaiseri	Japan, Kato & Baba (2019)	LC438337	
L. kotschyanum Foslie	Japan, Kato *et al.* (2011)		AB576031
L. kotschyanum	United States, Sherwood *et al.* (2010)	HQ423072	
L. kuroshioense A.Kato & M.Baba	Japan, Kato & Baba (2019)		LC438323
L. kuroshioense	Japan, Kato & Baba (2019)	LC438338	
L. lobatum Me.Lemoine (syntype)	Canary Islands, Pezzolesi *et al.* (2019)		MK006154
L. longense Hernández-Kantún, P.W.Gabrielson & R.A.Townsend	Tanzania, Townsend & Huisman (2018)		MN433929
L. margaritae (Hariot) Heydrich	Brazil, Vieira-Pinto *et al.* (2014)	KP192397	
L. margaritae	Brazil, Vieira-Pinto *et al.* (2014)	KP192398	
L. margaritae	Mexico, Hernandez-Kantun *et al.* (2015b)		JQ896253
L. neocongestum J.J.Hernandez-Kantun, W.H.Adey & P.W.Gabrielson	Panama, Hernandez-Kantun *et al.* (2016)		KX020466
L. nitorum W.H.Adey & P.J.Adey	Spain, Peña *et al.* (2018)	MG648766	MG648774
L. nitorum	Spain, Peña *et al.* (2018)	MG648762	
L. nitorum	Spain, Peña *et al.* (2018)	MG648763	
L. nitorum	Spain, Peña *et al.* (2018)	MG648764	
L. nitorum	Spain, Peña *et al.* (2018)	MG648765	
L. nitorum	Spain, Peña *et al.* (2018)	MG648767	
L. nitorum	Spain, Peña *et al.* (2018)	MG648768	
L. nitorum	Spain, Peña *et al.* (2018)	MG648769	
L. nitorum	Spain, Peña *et al.* (2018)	MG648770	
L. nitorum	Spain, Peña *et al.* (2018)	MG648771	
L. nitorum	Spain, Peña *et al.* (2018)	MG648772	
L. okamurae Foslie	China, Hu *et al.* (2020)	MH823811	MH788638
L. orbiculatum (Foslie) Foslie	France, Hernandez-Kantun *et al.* (2015a)	KR708625	KR708609
L. platyphyllum (Foslie) Foslie	United States, Hernandez-Kantun *et al.* (2016)		KX020452
L. pseudoracemus Caragnano, Rodondi & Rindi	Croatia, Hernandez-Kantun *et al.* (2015a, as *L.* cf. *racemus*)	KR708627	KR708607
L. pseudoracemus	France, Caragnano *et al.* (2020)		MT325783
L. pseudoracemus	France, Caragnano *et al.* (2020)	MT313681	
L. pseudoracemus	Spain, Caragnano *et al.* (2020)	MT313683	MT325784
L. pseudoracemus	Spain, Caragnano *et al.* (2020)	MT313682	
L. pseudoracemus	Spain, Hernandez-Kantun *et al.* (2015a, as *L.* cf. *racemus*)	KR708626	
L. pustulatum (J.V.Lamouroux) Foslie	New Zealand, Farr *et al.* (2009)		FJ361746
L. pustulatum	Spain, Rösler *et al.* (2016)		KM407551
L. racemus (Lamarck) Foslie	Spain, Caragnano *et al.* (2020)	MT313685	MT325785
L. racemus	Spain, Caragnano *et al.* (2020)	MT313684	MT325786
L. racemus	Spain, Rösler *et al.* (2016)		KM407552
L. riosmenae A.S.Harvey & Woelkerling	New Zealand, Farr *et al.* (2009)		FJ361615
L. searlesii P.W.Gabrielson, Freshwater, J.L.Richards & Hughey	United States, Richards *et al.* (2018)		MG515130
L. socotraense D.Basso, Caragnano, L.Le Gall & Rodondi	Yemen, Basso *et al.* (2015)	KP976402	KP976409
L. sp.	Costa Rica, Bittner *et al.* (2010, as uncultured Corallinales)	GQ917678	
L. sp.	Costa Rica, Bittner *et al.* (2010, as uncultured Corallinales)	GQ917684	
L. sp.	Fiji, Bittner *et al.* 2010 (as uncultured Corallinales)	GQ917580	

Appendix 1. — Continuation

Species	Collection details	COI-5P	psbA
L. sp.	French Polynesia, Bittner *et al.* (2010, as uncultured Corallinales)	GQ917691	
L. sp.	Guadeloupe, Bittner *et al.* (2010, as uncultured Corallinales)	GQ917507	
L. sp.	Guatemala, Bittner *et al.* (2010, as uncultured Corallinales)	GQ917303	
L. sp.	Italy, Richards *et al.* (2018)		MG517482
L. sp.	Philippines, Bittner *et al.* (2010, as uncultured Corallinales)	GQ917299	
L. sp.	Spain, Pardo *et al.* (2017)	MF133359	
L. sp.	United States, direct GenBank submission	HQ544252	
L. sp.	United States, direct GenBank submission	HQ544253	
L. sp.	United States, direct GenBank submission (as Corallinaceae sp.)	HQ919297	
L. sp.	United States, Richards *et al.* (2018)	KJ418418	
L. sp.	United States, Saunders (2014)	KM254978	
L. sp.	Vanuatu, Bittner *et al.* (2010, as uncultured Corallinales)	GQ917262	
L. sp.	Vanuatu, Bittner *et al.* (2010, as uncultured Corallinales)	GQ917263	
L. sp.	Vanuatu, Bittner *et al.* (2010, as uncultured Corallinales)	GQ917524	
L. stictiforme (Areschoug) Hauck	Italy, Pezzolesi *et al.* (2019)		KX020465
L. stictiforme	Italy, Pezzolesi *et al.* (2019)		KX020464
L. stictiforme	Italy, Pezzolesi *et al.* (2019)		KX020444
L. stictiforme	Italy, Pezzolesi *et al.* (2019)		KX020443
L. stictiforme	Italy, Pezzolesi *et al.* (2019)		KX020442
L. stictiforme	Spain, Rösler *et al.* (2016)	KM392367	KM407553
L. stictiforme (clade 1)	France, Pezzolesi *et al.* (2019)		MK006131
L. stictiforme (clade 1)	Italy, Pezzolesi *et al.* (2019)		MK006147
L. stictiforme (clade 1)	Italy, Pezzolesi *et al.* (2019)		MK006146
L. stictiforme (clade 1)	Italy, Pezzolesi *et al.* (2019)		MK006144
L. stictiforme (clade 1)	Italy, Pezzolesi *et al.* (2019)		MK006143
L. stictiforme (clade 1)	Italy, Pezzolesi *et al.* (2019)		MK006126
L. stictiforme complex (clade 10)	France, Pezzolesi *et al.* (2019)		MK006135
L. stictiforme complex (clade 11)	Italy, Pezzolesi *et al.* (2019)		MK006119
L. stictiforme complex (clade 2)	France, Pezzolesi *et al.* (2019)		MK006137
L. stictiforme complex (clade 2)	France, Pezzolesi *et al.* (2019)		MK006134
L. stictiforme complex (clade 2)	France, Pezzolesi *et al.* (2019)		MK006129
L. stictiforme complex (clade 2)	Italy, Pezzolesi *et al.* (2019)		MK006149
L. stictiforme complex (clade 2)	Italy, Pezzolesi *et al.* (2019)		MK006148
L. stictiforme complex (clade 2)	Italy, Pezzolesi *et al.* (2019)		MK006145
L. stictiforme complex (clade 2)	Italy, Pezzolesi *et al.* (2019)		MK006127
L. stictiforme complex (clade 2)	Italy, Pezzolesi *et al.* (2019)		MK006125
L. stictiforme complex (clade 2)	Italy, Pezzolesi *et al.* (2019)		MK006122
L. stictiforme complex (clade 2)	Spain, Pezzolesi *et al.* (2019)		MK006155
L. stictiforme complex (clade 3)	France, Pezzolesi *et al.* (2019)		MK006130
L. stictiforme complex (clade 3)	Italy, Pezzolesi *et al.* (2019)		MK006153
L. stictiforme complex (clade 3)	Italy, Pezzolesi *et al.* (2019)		MK006152
L. stictiforme complex (clade 3)	Italy, Pezzolesi *et al.* (2019)		MK006151
L. stictiforme complex (clade 3)	Italy, Pezzolesi *et al.* (2019)		MK006124
L. stictiforme complex (clade 3)	Italy, Pezzolesi *et al.* (2019)		MK006121
L. stictiforme complex (clade 4)	Italy, Pezzolesi *et al.* (2019)		MK006150
L. stictiforme complex (clade 4)	Italy, Pezzolesi *et al.* (2019)		MK006139
L. stictiforme complex (clade 4)	Italy, Pezzolesi *et al.* (2019)		MK006138
L. stictiforme complex (clade 4)	Italy, Pezzolesi *et al.* (2019)		MK006120
L. stictiforme complex (clade 5)	Italy, Pezzolesi *et al.* (2019)		MK006140
L. stictiforme complex (clade 5)	Italy, Pezzolesi *et al.* (2019)		MK006128
L. stictiforme complex (clade 5)	Italy, Pezzolesi *et al.* (2019)		MK006118
L. stictiforme complex (clade 7)	Spain, Pezzolesi *et al.* (2019)		MK006156
L. stictiforme complex (clade 7)	Spain, Pezzolesi *et al.* (2019)		MK006133
L. stictiforme complex (clade 8)	Italy, Pezzolesi *et al.* (2019)		MK006142
L. stictiforme complex (clade 8)	Italy, Pezzolesi *et al.* (2019)		MK006141
L. stictiforme complex (clade 8)	Spain, Pezzolesi *et al.* (2019)		MK006132
L. stictiforme complex (clade 9)	Italy, Pezzolesi *et al.* (2019)		MK006123
L. stictiforme/cabiochiae	France, De Jode *et al.* (2019)	MK859896	MK859631
L. stictiforme/cabiochiae	France, De Jode *et al.* (2019)	MK859852	
L. stictiforme/cabiochiae	France, De Jode *et al.* (2019)	MK859856	
L. stictiforme/cabiochiae	France, De Jode *et al.* (2019)	MK859863	
L. stictiforme/cabiochiae	France, De Jode *et al.* (2019)	MK859880	
L. stictiforme/cabiochiae	France, De Jode *et al.* (2019)	MK859881	
L. stictiforme/cabiochiae	France, De Jode *et al.* (2019)	MK859882	
L. stictiforme/cabiochiae	France, De Jode *et al.* (2019)	MK859889	
L. stictiforme/cabiochiae	France, De Jode *et al.* (2019)	MK859890	
L. stictiforme/cabiochiae	France, De Jode *et al.* (2019)	MK859891	

Appendix 1. — Continuation

Species	Collection details	COI-5P	psbA
L. stictiforme/cabiochiae	France, De Jode *et al.* (2019)	MK859892	
L. stictiforme/cabiochiae	France, De Jode *et al.* (2019)	MK859893	
L. stictiforme/cabiochiae	France, De Jode *et al.* (2019)	MK859894	
L. stictiforme/cabiochiae	France, De Jode *et al.* (2019)	MK859895	
L. yemenense D.Basso, Caragnano, L.Le Gall & Rodondi	Yemen, Basso *et al.* (2015)	KP976401	KP976408
Titanoderma sp.	United States, Richards *et al.* (2018)	KJ418416	
Porolithon onkodes (Heydrich) Foslie	Fiji, Bittner *et al.* (2010, as uncultured Corallinales)	GQ917276	GQ917469



Appendix 2. — *Lithophyllum stictiforme* (Areschoug) Hauck in Algarve, South Portugal (SANT-Algae 27308): **A**, habitat of the specimen collected on bedrock at 17 m depth; **B**, vertical section of the thallus showing a monomerous thallus construction. Scale bar: 500 µm.