Eur. J. Phycol. (2015), **50**: 20–36

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An integrative systematic approach to species diversity and distribution in the genus *Mesophyllum* (Corallinales, Rhodophyta) in Atlantic and Mediterranean Europe

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(Received 16 December 2013; revised 25 July 2014; accepted 3 August 2014)

For the first time, a comprehensive assessment of *Mesophyllum* species diversity and their distribution in Atlantic Europe and the Mediterranean Sea is presented based on molecular (COI-5P, *psb*A) and morphological data. The distribution ranges were redefined for the four species collected in this study: *M. alternans, M. expansum, M. macroblastum* and *M. sphaericum. Mesophyllum sphaericum,* which was previously known only from a single maerl bed in Galicia (NW Spain), is reported from the Mediterranean Sea. The known range of *M. expansum* (Mediterranean and Macaronesia) was extended to the Atlantic Iberian Peninsula. The occurrence of *M. alternans* was confirmed along the Atlantic French coast south to Algarve (southern Portugal). *Mesophyllum lichenoides* was only recorded from the Atlantic, whereas *M. macroblastum* appears to be restricted to the Mediterranean Sea. A positive correlation was observed between maximum Sea Surface Temperature (SSTmax) and the depth at which *M. expansum* was collected, suggesting that this species may compensate for higher SST by growing in deeper habitats where the temperature is lower. The latter indicates that geographic shifts in the distribution of coastal species as a result of global warming can possibly be mitigated by changes in the depth profile at which these species occur. *Mesophyllum expansum*, an important builder of Mediterranean coralligenous habitats, may be a good target species to assess its response to climate change.

Key words: biodiversity, climate change, coralligenous, crustose coralline algae, distribution, DNA barcoding, maerl, Mediterranean, NE Atlantic, systematics

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Introduction

Coralline algae (Corallinales) constitute a highly diverse order within the Rhodophyta, with *c*. 600 currently recognized species (Guiry & Guiry, 2013). Apart from being considered ecosystem engineers of high diversity habitats such as maerl/rhodolith beds or the Mediterranean coralligenous assemblages (Foster, 2001; Barberá *et al*., 2003; Ballesteros, 2006; Peña *et al.,* 2014*a*), they also fulfil an important structural role in tropical reef ecosystems and in the settlement of coral larvae (Littler & Littler, 1984; Adey, 1998; Díaz-Pulido *et al.,* 2010). Nevertheless, the geographic ranges of coralline species are poorly known. Only a few studies by Adey (1966*a*, *b*, *c*, 1970, 1971) and Adey & Adey (1973) have provided detailed data on the distribution and abundance of dominant crustose coralline species in the North Atlantic, showing that temperature is the main factor controlling their bathymetric distribution. Last but not least, thermo-geographic models for benthic species have been validated using coralline algae (Adey & Steneck, 2001).

The current global average ocean warming exceeds 0.1ºC per decade in the upper 75 m (IPCC, 2013), and models that take into account the increase of anthropogenic carbon input to the atmosphere and ocean forecast further significant increases of sea surface temperatures (SST) during the next century (IPCC, 2013). Recent studies have reported profound changes in the algal flora during the last two decades (Díez *et al.*, 2012), and species distribution models suggest that the seaweed flora is likely to continue to change

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ISSN 0967-0262 (print)/ISSN 1469-4433 (online)/14/010020-36 © 2014 British Phycological Society
http://dx.doi.org/10.1080/09670262.2014.981294

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(Harley *et al.*, 2012). In particular, European coasts have been identified as one of the areas that will be more impacted by future warming (Bartsch *et al.*, 2012), and algal species are expected to track shifting thermoclines (Jueterbock *et al.*, 2013).

Coralline algae are particularly vulnerable to global change because the negative effects of a lower pH (ocean acidification), causing dissolution of the high-Mg calcite skeleton, are exacerbated by rising temperatures (Hall-Spencer *et al.*, 2008; Nelson, 2009; Büdenbender *et al.*, 2011; Porzio *et al.*, 2011; Díaz-Pulido *et al.*, 2012; Kamenos *et al.*, 2013; Noisette *et al.*, 2013; Brodie *et al.,* 2014). Our limited knowledge on the actual distribution of most coralline algal species (Pardo *et al.*, 2014) hampers the monitoring of this important component of coastal ecosystems. Considerable efforts are therefore needed to assess the current distribution and diversity of coralline algae to create the baseline for further monitoring studies. This task requires comprehensive sampling schemes as well as efficient identification tools. Molecular systematics have fostered the study of coralline diversity (e.g. Bailey & Chapman, 1998; Broom *et al.*, 2008; Le Gall *et al.*, 2010; Bittner *et al.*, 2011; Kato *et al.*, 2011; Hind & Saunders, 2013) and rendered the mitochondrial gene coding the cytochrome c oxidase subunit 1 (COI-5P fragment) a common tool for species identification and alpha diversity assessment (e.g. Walker *et al.*, 2009; Sherwood *et al.*, 2010; Kato *et al.*, 2013; Carro *et al.*, 2014; Pardo *et al.*, 2014; Peña *et al.,* 2014*b*, *c*). The plastid-encoded *psb*A and *rbc*L genes (coding for the D1 protein of photosystem II and the large subunit of RUBISCO, respectively) have been employed previously for species identification and for phylogenetic reconstructions in combination with nuclear markers (Broom *et al*., 2008; Bittner *et al.*, 2011; Gabrielson *et al.*, 2011; Martone *et al*., 2012).

Apart from molecular data, the approach referred to as integrative systematics also includes the use of morphological, ecological and geographic data to reliably identify species (Puillandre *et al*., 2012). This approach has been successfully employed to delimit maerl species in Atlantic Europe and the Caribbean Sea (Pardo *et al.*, 2014; Peña *et al.*, 2014*b*). The genus *Mesophyllum* Me.Lemoine (1928) currently comprises 59 accepted extant and fossil taxa (Guiry & Guiry, 2013), six of which have been recorded in Europe: *M. lichenoides* (Ellis) Me.Lemoine, the type species of the genus, *M. alternans* (Foslie) Cabioch & M.L. Mendoza, *M. expansum* (Philippi) Cabioch & M.L. Mendoza, *M. macroblastum* (Foslie) W.H. Adey, *M. macedonis* Athanasiadis, and *M. sphaericum* V. Peña, Bárbara, W.H. Adey, Riosmena-Rodríguez & H.G. Choi. Typically, these species are found as encrusting plants attached to the substratum except for *M. sphaericum,* which is a maerl-forming species (Peña *et al.*, 2011). Occasionally, unattached specimens of *M. alternans* and *M. lichenoides* have also been reported (Basso, 1994; Irvine & Chamberlain, 1994). In this study, morphological and molecular data were used in an integrative systematic approach to assess the diversity and distribution ranges of Atlantic and Mediterranean *Mesophyllum* species. Moreover, the correlation between the levels of major environmental drivers of coralline distribution (temperature and water transmittance) and the collection depth of *M. expansum* across the study area was also investigated.

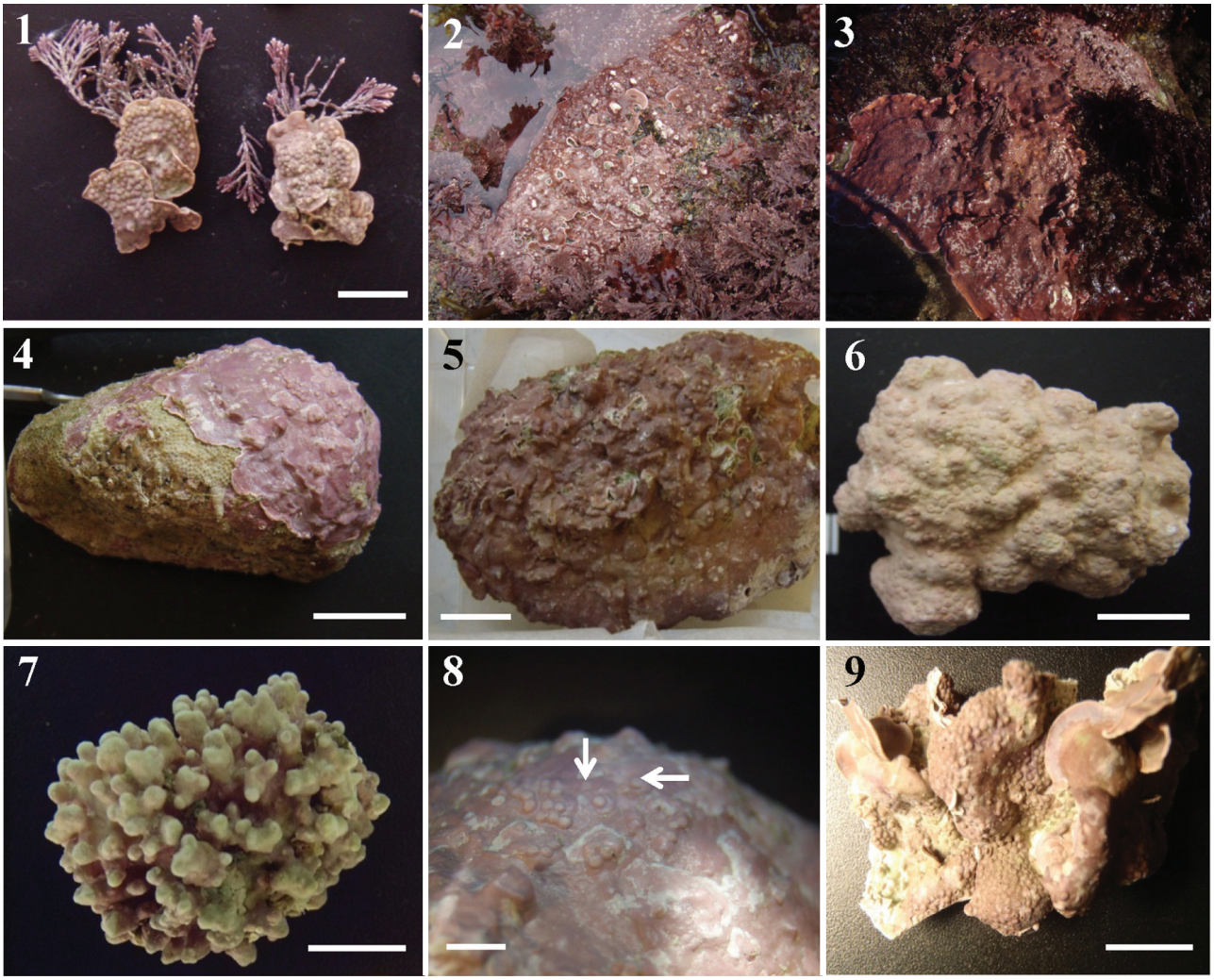
Materials and methods

Sample collection

The study area comprised 36 localities: 19 along the coasts of Atlantic Europe, 16 in the Mediterranean Sea, and one in the Macaronesian region (Canary Islands) (Table S1). Intertidal samples were collected on rocky shores using a hammer and chisel. Subtidal specimens were collected by scuba diving and dredging in different habitats: rocky substrata, maerl beds and the Mediterranean coralligenous outcrops (that consist of calcareous formations of encrusting algae growing in dim light conditions, at 0.05–3% of the surface irradiance; Ballesteros, 2006) to 50 m deep. The Atlantic collections contain epiphytic intertidal specimens (Fig. 1) as well as large encrusting individuals up to 15 cm in diameter growing epilithically in the intertidal and subtidal of the Iberian Atlantic coasts (Figs 2–3). In the Mediterranean Sea, collections were made of encrusting as well as unattached specimens assigned to *Mesophyllum* forming maerl and rhodoliths (unattached individuals with or without a coralline algal nucleus, respectively; Irvine & Chamberlain, 1994; Figs 4–8). The sampling scheme included taxonomically and biogeographically significant localities for the European Atlantic and Mediterranean *Mesophyllum* species (Table 1): *M. lichenoides* was collected near its epitype locality (Cornwall), *M. expansum* was collected at its type locality (Sicily) and also in the Macaronesian biogeographic region where it has been reported (Canary Islands, Table 1, Fig. 9), while *M. alternans* (type locality: Tangier, Morocco, Table 1) was collected in one of the European Atlantic localities where it had been previously reported (Biarritz, France). Specimens were deposited in the herbaria PC, NCU and SANT (Muséum National d´Histoire Naturelle, University of North Carolina and Universidade de Santiago de Compostela, respectively; acronyms follow Thiers (2014).

Molecular studies

A total of 81 specimens were air or oven-dried (50ºC) and preserved in zipper bags with silica gel. The surface of the specimens was cleaned of epiphytes using a toothbrush, and surfaces selected under a stereomicroscope were ground with a drill bit of 2 mm in diameter for DNA extraction. Genomic DNA was extracted using a NucleoSpin® 96 Tissue kit (Macherey-Nagel, GmbH and Co. KG, Germany). The mitochondrial COI-5P fragment was PCR-amplified using the primer pair GazF1 and GazR1 (Saunders, 2005); in addition, other primers were used for specimens that failed to amplify with this first



Figs 1–9. Specimens of *Mesophyllum* collected in the present study. **Fig. 1**. *M. lichenoides* epiphytic on geniculate coralline algae (VPF00357A, Oia, Galicia). **Fig. 2**. Intertidal epilithic specimen of *M. expansum* (VPF00211, San Juan de Gaztelugatxe, Basque Country). **Fig. 3**. Intertidal epilithic specimen of *M. alternans* (VPF00104, Itziar, Basque Country). **Fig. 4**. Encrusting specimen of *M. sphaericum* (LLG3755, Reggio Calabria). **Fig. 5**. *M. expansum* from the type locality (LLG4061, Sicily). **Fig. 6**. *M. macroblastum* from the Mediterranean Sea (VPF00506, Alborán Sea). **Fig. 7**. Maerl specimen of *M. sphaericum* (VPF00136, Columbretes Islands). **Fig. 8**. Mound-like to flattened multiporate sporangial conceptacles (arrows) in the encrusting specimen of *M. sphaericum* (LLG3755, Reggio Calabria). **Fig. 9**. *M. expansum* from the Canary Islands (VPF00218, Tenerife). Scale bars = 1 cm (Figs 1, 4, 5–7, 9) and 0.5 cm (Fig. 8).

primer pair: GWSFn (forward; Le Gall & Saunders, 2010), GWSRx (reverse, Saunders & McDevit, 2012), GCorR3 (reverse, 5′ TGATTYTTYGGACATCCTGA 3′), DumR1 (reverse, Saunders, 2005), and COX1R1 (reverse, Saunders, 2008). The *psb*A locus was amplified using *psb*A-F1 and *psb*A-R2 (Yoon *et al*., 2002). The thermal profile for PCR amplification for COI-5P included an initial denaturation at 95°C for 2 min followed by 40 cycles of 30 s denaturation at 94°C, 40 s annealing at 50°C and 40 s of extension at 72°C followed by an additional 5 min at 72°C and storage at 12°C. For the combination of forward primer GazF1 with reverse primers COX1R1, DumR1, GCorR3, PCR amplification followed Saunders & McDevit (2012). The thermal profile for PCR amplification for *psb*A followed Bittner (2009). PCR reactions used the Taq PCR core kit ® (Qiagen SAS France) and were performed in 25 µl containing 2 µl of DNA template (diluted 1/25), 2.5 µl of 10× CoralLoad PCR buffer, 2.5 mM $MgCl_2$, 0.192 mM dNTPs, 0.8 µg BSA (Bovine Serum Albumin), 1% PVP (polyvinylpyrrolidone), 0.1 µM of each primer and 0.6 U of Taq DNA Polymerase. PCR products were purified and sequenced by Genoscope (Bibliothèque du Vivant program, Centre National de Séquençage, France). Sequences were assembled and aligned with the assistance of CodonCode Aligner® (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 (accession numbers listed in Table S1). For the molecular study, the COI-5P and *psb*A sequences of the holotype of the maerl-forming species *Mesophyllum sphaericum* were obtained from BOLD (project 'maerl-NE Atlantic') and GenBank (Pardo *et al*., 2014). The holotype fragment of *M. macroblastum* deposited in PC (Table 1) was also processed for the present study but, unfortunately, all attempts at COI-5P and *psb*A amplifications were

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Table 1. Comparative table of the diagnostic anatomical features, habitat, distribution and type information for *Mesophyllum* species reported from European coasts.

Species name and references	***M. alternans*** 5,7,9,10-12,19	***M. expansum*** 2,4,12,16,18,19	***M. lichenoides*** 1-3,5,6,8,11,12,15,16,18	***M. macedonis*** 10,12	***M. macroblastum*** 2,6,12-14,17,19	***M. sphaericum*** 18,19
Thallus form	Encrusting or non-adherent, occasionally unattached; surface smooth or with short protuberances	Encrusting, non-adherent, irregularly lobate lamellae; surface with concentric undulations	Encrusting non-adherent, foliose lamellae, occasionally unattached; surface smooth or warty, with concentric markings	Encrusting, partly growing free with superimposed lamellae	Encrusting or non-adherent lamellae, occasionally unattached; surface smooth or warty with protuberances	Unattached thalli with protuberances, occasionally encrusting
Multiporate sporangial conceptacles (chamber measures, height x diameter, µm)	Protruding, hemispherical, flattened to slightly concave roof, with peripheral raised rim, 150–300 × 350–600	Slightly protruding, mound-like, flattened to convex roof, without peripheral raised rim, 260–400 × 450–900	Protruding, hemispherical, mound-like, somewhat flat topped roof, without peripheral raised rim, 150–380 × 323–800	Protruding, convex roof, without peripheral raised rim, 110–125 × 320–500	Protruding, sunken roof with peripheral raised rim, 90–200 × 145–355	Protruding, mound-like, flat topped roof without peripheral raised rim, 143–300 × 225–540
Pore canal filaments (in section, µm)	6–8 celled; cells smaller, rounded	6–10 celled; cells longer, similar or wider than the remainder of the roof filaments, basal cell elongate, and occasionally 'thinner-wider'	7–10 celled; cells short and compact, squarish to 'thinner-wider' than the remainder of the roof filaments	4–6 celled; cells slender and narrower than the remainder of the roof filaments; basal cell elongate	6–7 celled; cells similar in shape or slightly larger than the remainder of the roof filaments	5–6 celled; basal cell elongate
Pore (in surface view)	(9–) 11–12 rosette cells, similar to the surrounding roof cells	8–12 rosette cells, smaller, similar or 'thinner-wider'than the surrounding roof cells	6–12 rosette cells, similar or 'thinner-wider' than the surrounding roof cells	4–6 rosette cells wider than the surrounding roof cells	8–10 rosette cells, similar or slightly smaller in size to the surrounding roof cells	7–8 rosette cells, wider than the surrounding roof cells
Buried conceptacles	+	–	–	+	+	+
Habitat	Epilithic, epiphytic, unattached. Low intertidal to subtidal	Epilithic. Low intertidal to subtidal	Mostly epiphytic but also epilithic, epizoic, unattached. Lower intertidal to subtidal	Epilithic. Upper subtidal	Epilithic, epiphytic, epizoic, also unattached as rhodolith. Intertidal to subtidal	Mostly unattached as maerl/rhodolith, but also epilithic. Subtidal
Distribution on European coasts	Atlantic and Mediterranean	Atlantic and Mediterranean	Atlantic and Mediterranean	Mediterranean (Aegean Sea)	Mediterranean	Atlantic (NW Spain) and Mediterranean
Type information (locality, type)	Tangier, Morocco. Holotype: TRH B16-2493	Sicily, Italy. Lectotype: L 9395 no. 2	Hannafore Point, Cornwall, UK Epitype: BM, Algal Box Collection 1658	Pigeon Cave, Sithonia Peninsula, Greece Holotype: GB SC010784	Gulf of Naples, Italy Holotype: TRH B16-2435 and PC (fragment)	Ría de Arousa, Galicia, Spain Holotype: SANT-Algae 21804

Data from: 1: Lemoine (1913), 2: Foslie & Printz (1929), 3: Adey & Adey (1973), 4: Woelkerling (1983), 5: Woelkerling & Irvine (1986*b*), 6: Woelkerling & Harvey (1993), 7: Basso (1994), 8: Irvine & Chamberlain (1994), 9: Cabioch & Mendoza (1998), 10: Athanasiadis (1999), 11: Bressan & Babbini (2003), 12: Cabioch & Mendoza (2003), 13: Harvey *et al.* (2003), 14: Harvey *et al.* (2005), 15: Woelkerling & Irvine (2007), 16: Athanasiadis & Neto (2010), 17: Kaleb *et al.* (2011), 18: Peña *et al.* (2011), and 19: Present study.

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unsuccessful. In addition, BOLD and GenBank databases were searched for publicly available sequences of *Mesophyllum*. Four COI-5P sequences identified as *Mesophyllum erubescens* (Foslie) Me.Lemoine from Hawaii (HQ422717-HQ422718) and Japan (AB713929 and AB713930) were found and included in the alignments. In the case of *psb*A, sequences of *M. erubescens* from Japan and New Zealand, *M. printzianum* Woelkerling & A.S. Harvey, *M. engelhartii* (Foslie) W.H. Adey and *M. macroblastum* from New Zealand were also available (Broom *et al.*, 2008; Farr *et al.*, 2009; Sherwood *et al.*, 2010; Kato *et al.*, 2013, Table S1). Searches for sequences of *Mesophyllum* from Europe were unsuccessful except for two specimens from Atlantic and Mediterranean France labelled as 'Uncultured Corallinales' (Bittner *et al.*, 2010, Table S1).

A general mixed Yule–coalescent (GMYC) model, where species boundaries are based on an ultrametric tree, was applied to delimit *Mesophyllum* species (Pons *et al.*, 2006; Fujisawa & Barraclough, 2013). The ultrametric tree resulted from Bayesian phylogenetic analyses of the COI-5P alignment run in BEAST v1.7.4 (Drummond *et al.*, 2012) under a generalized time-reversible model with gamma+invariant sites to accommodate rate heterogeneity (GTR+G+I), an uncorrelated log normal (UCLN) relaxed molecular clock, and using a coalescence tree prior. Two Markov Chain Monte Carlo (MCMC) analyses were run for 10 million generations, sampling every 1000th generation. The information from a sample of trees was summarized onto a single 'target' tree (10% burn-in discarded at the start of the run, 0.5 of posterior probability limit of the nodes in target tree) using Tree Annotator v 1.7.4 (http://beast.bio.ed.ac.uk). GMYC analyses were performed using the SPLITS package for R (http://r-forge.r-project.org/project/splits). Phylogenetic relationships were inferred using Maximum likelihood (ML) and Bayesian inference (BI) using Mega 5.02 and MrBayes 3.2.1, respectively (Ronquist & Huelsenbeck, 2003; Tamura *et al.*, 2011). 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 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), and a generalized time-reversible gamma distributed (GTR+G) alignments, respectively, and the bootstrap consisted of 1000 replicates. The Bayesian analysis was conducted for the *psb*A alignment under a transition model gamma distributed (TIM2+G) with four Markov Chain Monte Carlo for 10 million generations, and tree sampling every 1000 generations. The Melobesioideae *Phymatolithon calcareum* (Pallas) W.H. Adey & McKibbin and *Lithothamnion corallioides* (P.L. Crouan & H.M. Crouan) P.L. Crouan & H.M. Crouan were included as outgroups; their COI-5P and *psb*A sequences were available in BOLD systems and GenBank (Table S1). *Phymatolithon calcareum* was collected at the type locality and its COI-5P sequence matched the one obtained from the neotype deposited in the BM Herbarium (BM Box 1626, Falmouth; Woelkerling & Irvine, 1986*a*; Peña *et al.*, 2014*c*). *Lithothamnion corallioides* was collected at the type locality (Rade de Brest; Crouan & Crouan, 1867), and was identified based on morpho-anatomical features available in the literature (Adey & McKibbin, 1970; Irvine & Chamberlain, 1994).

Morphological studies

Representative specimens of each species were selected for anatomical examination, except for *M. lichenoides* and *M. sphaericum* for which detailed descriptions were already provided in the literature (Woelkerling & Irvine, 1986*b*; Peña *et al.*, 2011). Characters related to multiporate sporangial conceptacles are considered diagnostic for species identification (Woelkerling & Harvey, 1993; Cabioch & Mendoza, 1998, 2003; Athanasiadis, 1999; Athanasiadis & Neto, 2010; Peña *et al.*, 2011). Fragments of selected specimens with multiporate conceptacles were decalcified according to Cremades *et al.* (1997), and sectioned at 15–20 µm thickness in a cryostat Jung Frigocut 2800E (Leica, Heidelberg, Germany). Sections were stained with 1% aniline blue in distilled water and examined under light microscopy. The surface view of multiporate conceptacle roofs were decalcified and examined without sectioning. Permanent slides were mounted in Karo® syrup (25–30%).

Relationship between the depth of M. expansum *and environmental variables*

The correlation between the depth at which *M. expansum* was collected and two abiotic variables (sea surface temperature and water transmittance) that have been identified as main environmental drivers of the abundance and distribution of coralline algae (Adey, 1966*a–c*, 1970, 1971; Littler & Littler, 1984) was investigated. Environmental data for sampling localities were extracted from Bio-Oracle (http://www.bio-oracle.ugent.be; Tyberghein *et al.*, 2012). 'Maximum Sea Surface Temperature' (SSTmax) and 'Mean Diffuse Attenuation' (DAmean) as a function of light availability in the water column were compared with collection depth using the Pearson correlation coefficient (r).

Results

The 81 sequences generated in this study for the COI-5P DNA barcode region ranged from 571 to 664 base pairs (bp) and comprised 38 haplotypes with 170 variable sites. The COI-5P alignment, including publicly available sequences from GenBank and BOLD, consisted of 48 haplotype sequences. The phylogenetic tree obtained from the ML analysis of the COI-5P alignment resolved the collections of *Mesophyllum* into six fully supported lineages (Fig. 10). Infralineage variation (uncorrected p-distance) ranged from 0.19% to 3.24%. The GMYC model estimated eight putative species with a confidence interval ranging from 8 to 18. The fit of the likelihood of the GMYC model was significantly higher ($P = 0.020$) than that of a null model of uniform coalescent branching rates. The threshold time (the estimated depth from the branch tips at which the transition

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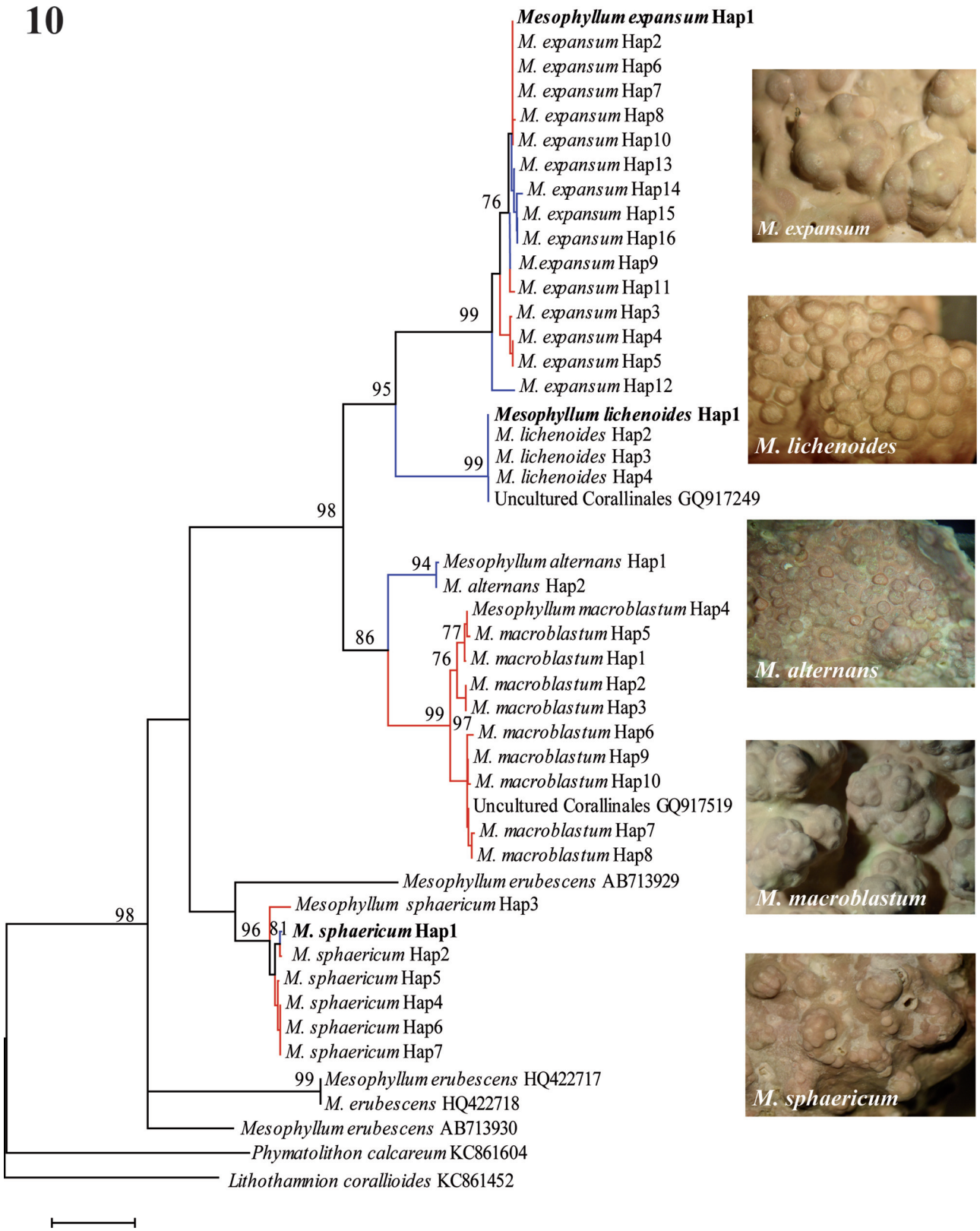

Fig. 10. Maximum likelihood tree inferred from the DNA barcode sequences (COI-5P) of haplotypes observed in each species delimited according to the GMYC model. In bold, haplotypes of type specimens (*Mesophyllum sphaericum*) or specimens collected from type localities or nearby (*M. expansum* and *M. lichenoides,* respectively). Bootstrap values > 70% between the species of *Mesophyllum* are shown for each node. Members of the subfamily Melobesioideae were used as outgroup. Blue colour indicates those haplotypes collected in Atlantic Europe, red indicates haplotypes collected in the Mediterranean and the Canary Islands. The pore plate morphology of sporangial multiporate conceptacles for each European *Mesophyllum* species studied is shown. Scale bar: 0.05 substitutions per site.

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from population to species level branching patterns occur) was determined at −0.0159 substitutions per site.

Both GYMC and ML analyses of the COI-5P alignment were congruent in delimiting five species for European *Mesophyllum*, in addition to the Hawaiian and Japanese *M. erubescens* which were resolved as three different species (Fig. 10). The five European taxa were assigned to *M. alternans, M. expansum, M. lichenoides, M. macroblastum* and *M. sphaericum* based on comparisons with holotype (*M. sphaericum*) or topotype material (*M. expansum, M. lichenoides*), as well as the occurrence of morphological diagnostic features detailed below. The phylogenetic analysis resolved two pairs of sister lineages with strong (*M. alternans* and *M. macroblastum*) and full support (*M. expansum* and *M. lichenoides*, Fig. 10). The Hawaiian specimens and one of the Japanese samples of *M. erubescens* (AB713930) were resolved as different species separated from the rest of the *Mesophyllum* taxa analysed. The GenBank sequences obtained from European vouchers of uncultured Corallinales (Bittner *et al.*, 2010) were resolved within the lineage of *M. lichenoides* (GQ917249, collected in Atlantic France) and *M. macroblastum* (GQ917519, from Mediterranean France).

The *psb*A alignment including publicly accessible sequences comprised 23 sequences ranging from 589 to 851 bp, with 222 variable sites. The phylogenetic analyses of the *psb*A gene resolved the same pairs of European sister lineages as with COI-5P (*Mesophyllum lichenoides/M. expansum* and *M. alternans/M. macroblastum*) with strong support (> 90% and > 0.99 in ML and BI, respectively, Fig. 11). These four European *Mesophyllum* species were resolved separately with high Bayesian support (0.99) from *M. sphaericum* as well as the *Mesophyllum* taxa from Japan and New Zealand, including *M. macroblastum* from this latter region. *Mesophyllum sphaericum* was resolved as sister taxon of the Japanese *M. erubescens* with strong support (82%/1 for ML and BI, respectively), and a grouping with the New Zealand group of *M. erubescens* and *M. printzianum* was only supported by BI (0.90). The New Zealand group of *M. macroblastum* and *M. engelhartii* was also resolved as sister lineage of the rest of *Mesophyllum* taxa studied supported only by BI (0.99).

Mesophyllum alternans (Tables 1, S1, Figs 3, 10, 12, 16–19)

Six specimens were collected from intertidal Atlantic localities. Two COI-5P haplotypes with 1 bp difference were detected, each haplotype occurring in a different area: French coast; Northern Spain and Portugal (Table S1, Fig. 12). *Mesophyllum alternans* was described from Tangier (Morocco), and has been reported from the same Atlantic French locality studied here (Biarritz; Cabioch & Mendoza, 1998). All the specimens collected were epilithic in the low intertidal (Table S1). They were large encrusting individuals up to 15 cm in diameter with smooth surfaces or with short protuberances (Table 1). Specimens had multiporate sporangial conceptacles with sunken pore plates and a peripheral raised rim (Table 1, Figs 10, 16). Chambers were 200–230 µm high by 400 µm wide (Fig. 17). In section, the pore canal filaments were 7–8 celled, shorter than the other roof filaments (Fig. 18). Pores were surrounded in surface view by 9 rosette cells similar to surrounding roof cells (Fig. 19).

Mesophyllum expansum (Tables 1, S1, Figs 2, 5, 9, 10, 13, 20–23)

Thirty-seven specimens were collected in the study area. They corresponded to 16 COI-5P haplotypes with 1–26 bp differences that were distributed as follows (Table S1, Fig. 13): 10 from the Mediterranean Sea, five from the Atlantic Iberian Peninsula and one from the Canary Islands. None of the haplotypes was shared among the three areas. Although one haplotype was widespread in intertidal and subtidal Atlantic Iberian localities (haplotype '15'), the local diversity was notable and up to four haplotypes were detected at a single Atlantic locality (Camelle, Galicia, haplotypes '12–15'). In the Mediterranean Sea, haplotype '6' was common in three localities (Catalonia, Columbretes Islands and the Alborán Sea). All individuals were epilithic, from the low intertidal to 11 m depth in the Atlantic European coast while Mediterranean specimens were restricted to the subtidal (10–50 m depth, Table S1). Specimens of *M. expansum* were encrusting, non-adherent to the substratum with irregularly lobate lamellae and concentric undulations on the surface (Table 1). The morphological characters of the specimens collected in the Mediterranean Sea and the Canary Islands matched those observed in specimens from the intertidal and subtidal of the Atlantic Iberian Peninsula: large encrusting specimens up to 15 cm in diameter with mound-like to flattened multiporate sporangial conceptacles without peripheral raised rim (Table 1, Figs 2, 5, 9, 10, 20–23). In section, pore canal filaments were 7–8 celled, wider than the other roof filaments and with elongate basal cells (Fig. 22). In surface view, pores were surrounded by 8–12 rosette cells similar in size to the surrounding roof cells (Fig. 23).

There was a significant positive correlation between the depth at which *M. expansum* was collected and SSTmax ($r(16) = 0.85$, $P < 0.005$,

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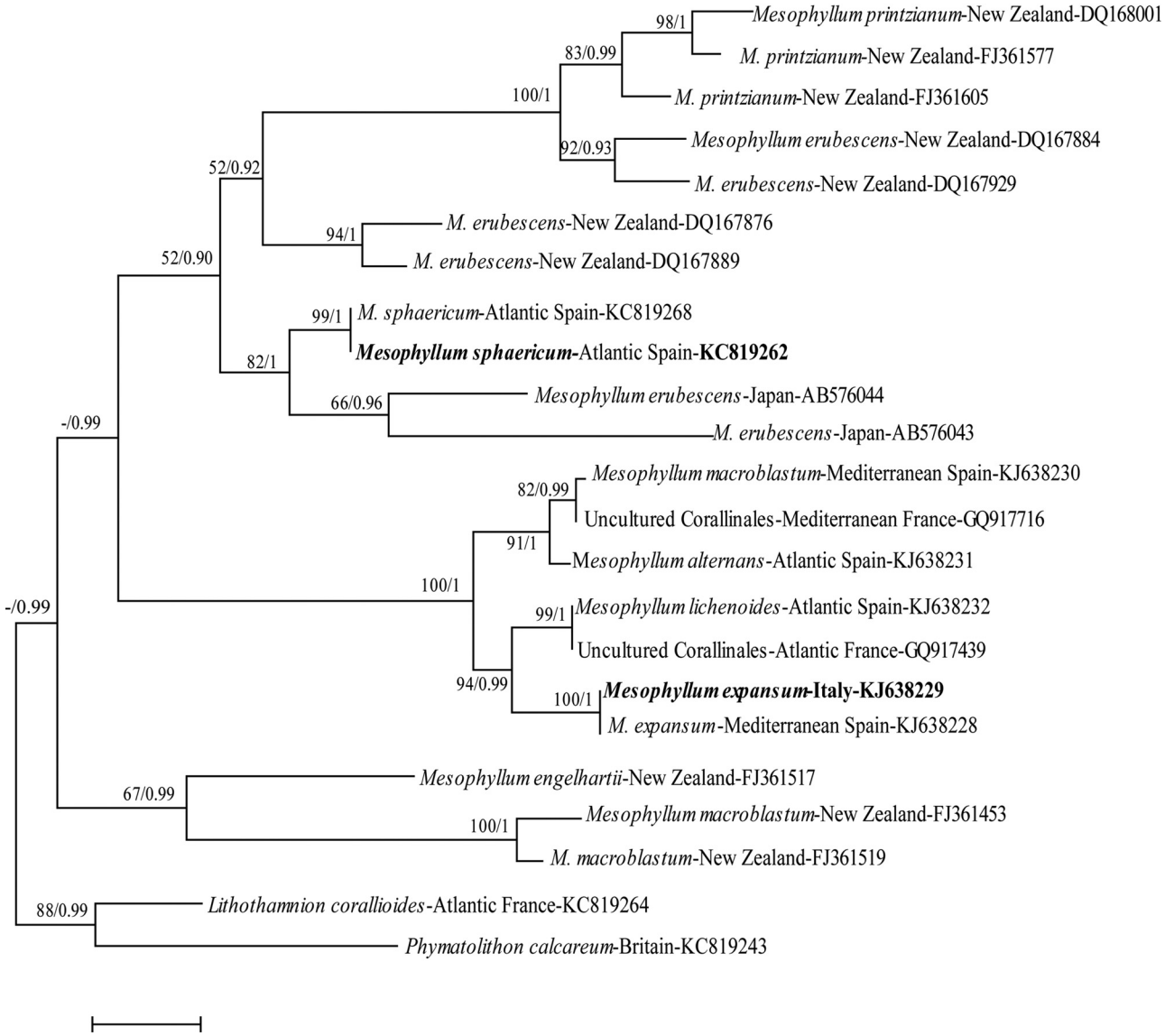

Fig. 11. Phylogenetic tree inferred from ML and BI analyses of the *psb*A sequences of European *Mesophyllum* and publicly available sequences for this genus. In bold, holotype of *M. sphaericum*, and the topotype material of *M. expansum*. Bootstrap ML values > 50% and posterior probabilities > 0.50 from Bayesian inference are shown for each node. Members of the subfamily Melobesioideae were used as outgroup. Scale bar: 0.02 substitutions per site.

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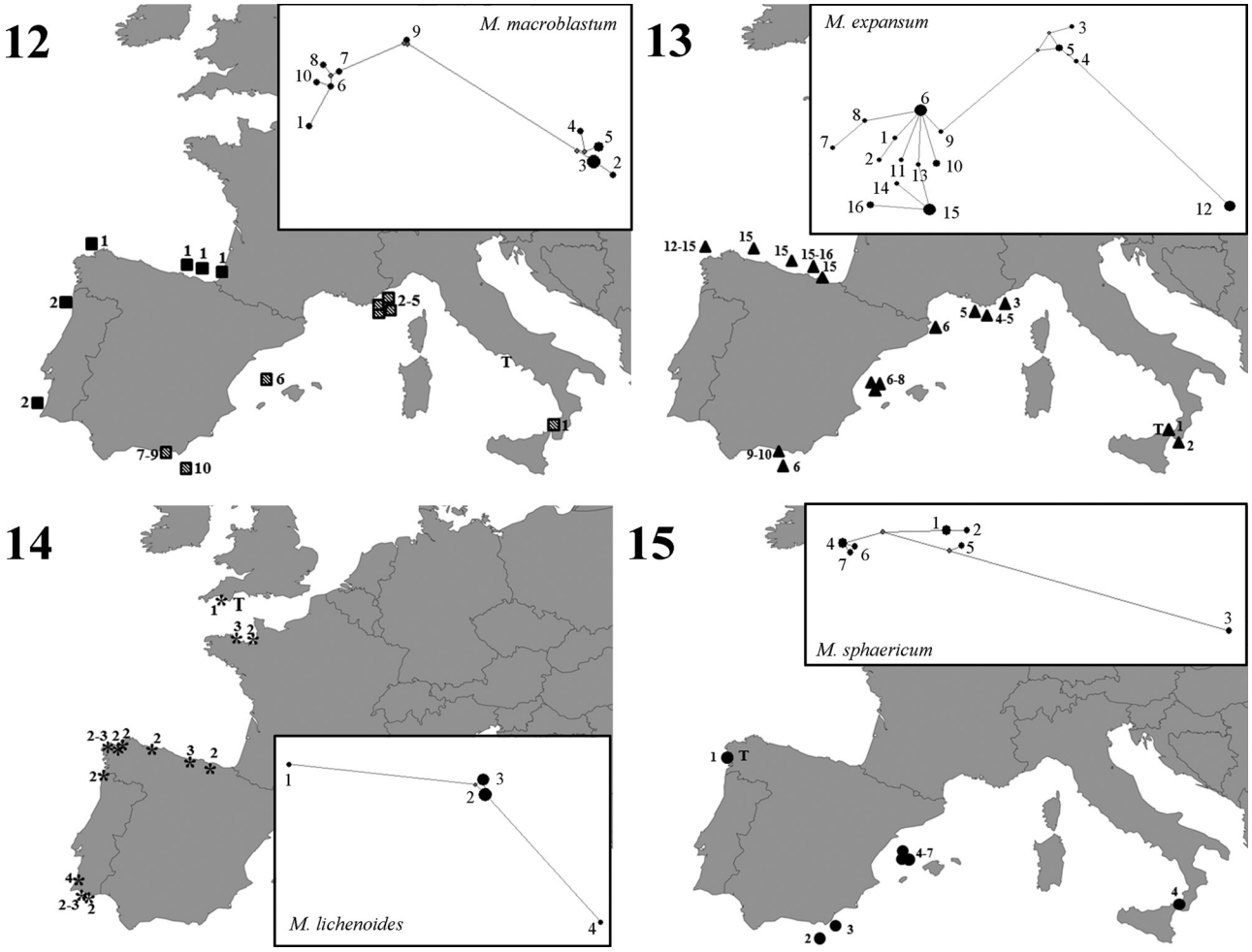
Fig. 24), and a significant negative one with DAmean (r(16) = −0.8, $P < 0.005$, Fig. 25).

Mesophyllum lichenoides (Tables 1, S1, Figs 1, 10, 14)

Seventeen specimens were collected along the Atlantic coast. Four COI-5P haplotypes with 1 bp difference were detected with haplotypes '2' and '3' common in Brittany and the Iberian Peninsula (Table S1, Fig. 14). Specimens of *M. lichenoides* were recorded as non-adherent crusts, with foliose lamellae and smooth or warty surfaces with concentric markings (Table 1). All specimens, including the collection from near the type locality (Cornwall), were intertidal, most of them epiphytic on geniculate coralline algae such as *Ellisolandia elongata* (Ellis & Solander) Hind & Saunders and *Corallina* spp., and occasionally epilithic (Tables 1, S1, Fig. 1). The multiporate sporangial conceptacles were protruding, mound-like, with a hemispherical to somewhat flat-topped roof, and without a peripheral raised rim (Table 1, Fig. 10).



Figs 12–15. Geographic distribution of European *Mesophyllum* species and their COI-5P haplotypes (haplotype network is not shown for *M. alternans*). Type localities (T) are shown except for *M. alternans* (Tangier, Morocco). **Fig. 12**. Haplotype distribution in *M. alternans* (black squares) and in *M. macroblastum* (striped squares). **Fig. 13**. Haplotype distribution in *M. expansum*, except haplotype '11′ recorded in the Canary Islands. **Fig. 14**. Haplotype distribution in *M. lichenoides*. **Fig. 15**. Haplotype distribution in *M. sphaericum*.

Mesophyllum macroblastum (Tables 1, S1, Figs 6, 10, 12, 26–29)

Fourteen specimens were collected along the Mediterranean coast. Ten COI-5P haplotypes with 2–23 bp difference were found, and up to three haplotypes were observed at a single site (La Herradura, Granada, Table S1, Fig. 12). They were found only in the Mediterranean Sea as epilithic crusts or rhodoliths in subtidal localities from 15 to 50 m depth (Table 1). Sequenced specimens of *M. macroblastum* had smooth surfaces (Table 1). The multiporate sporangial conceptacles had sunken pore plates and a peripheral raised rim (Table 1, Figs 6, 10, 26), and the pore canal filaments were composed of 7 cells with thinner cell walls and were wider than the other roof filaments (Fig. 27). In surface view, pores were surrounded by 8–9 rosette cells similar to or smaller than the surrounding roof cells (Figs 28–29).

Mesophyllum sphaericum (Tables 1, S1, Figs 4, 7, 8, 10, 15)

The name *M. sphaericum* was assigned to specimens resolved in the same lineage as the holotype, for which a COI-5P sequence was available. Our study revealed the presence of *M. sphaericum* in the Mediterranean Sea, at the Columbretes Islands, Alborán Sea (westernmost area to the Strait of Gibraltar) and Sicily. The nine specimens studied corresponded to seven COI-5P haplotypes with16–20 bp differences: one haplotype was detected at the type locality in the Atlantic, the only known location for this taxon until this study, and six in the Mediterranean Sea. Four haplotypes were detected in the Columbretes Islands, one shared with a sample from Italy (Table S1, Fig. 15). The Mediterranean specimens consisted of unattached plants forming maerl and rhodoliths and also grew as epilithic crusts at 20–50 m depth (Tables 1, S1, Figs 4, 7). The multiporate sporangial conceptacles of the Mediterranean

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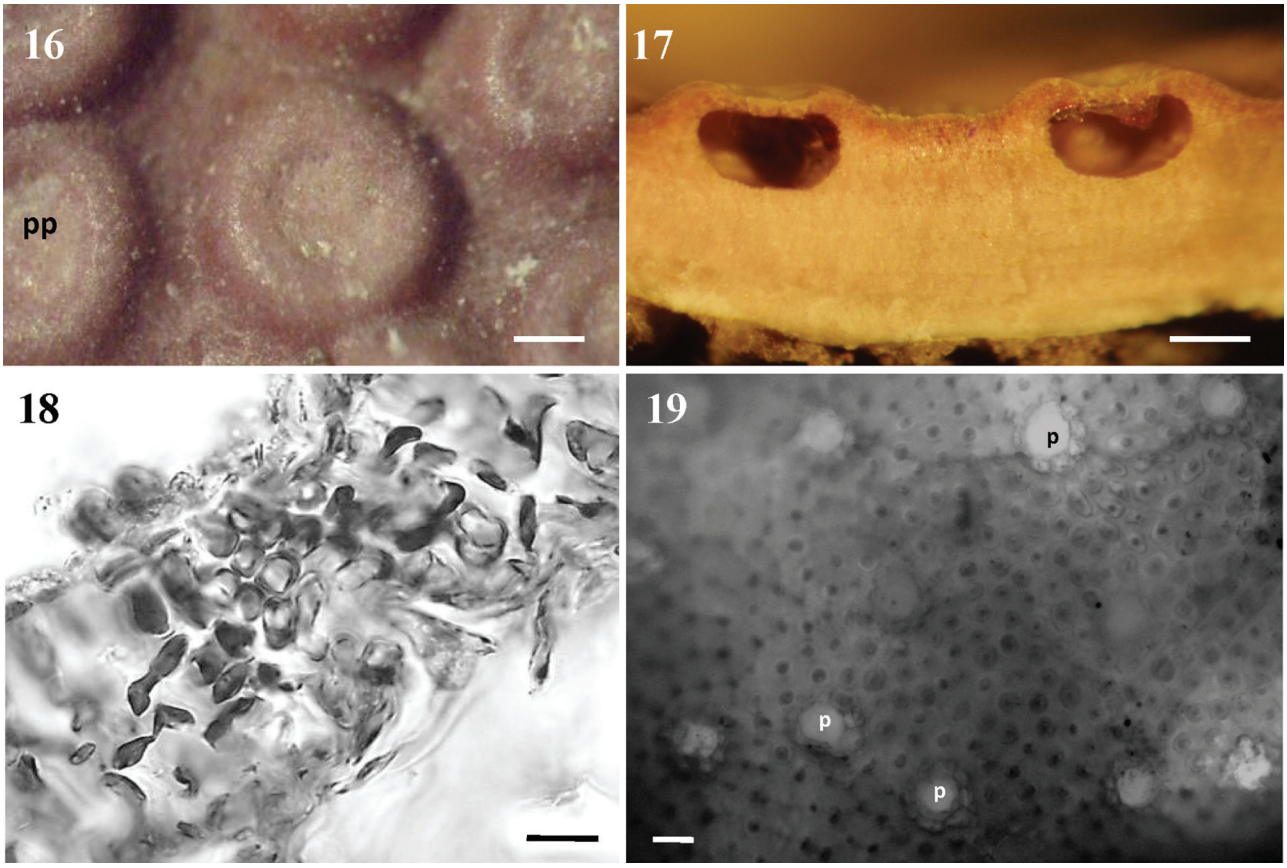

Figs 16–19. *Mesophyllum alternans* (VPF00104, Itziar, Basque Country). **Fig. 16**. Surface view of multiporate sporangial conceptacles with sunken pore plates (pp) with peripheral rim. **Fig. 17**. Transverse section showing multiporate sporangial conceptacles immersed in cortex. **Fig. 18**. Longitudinal section showing pore canal filament composed of cells shorter than other roof filaments. **Fig. 19**. Surface view of multiporate sporangial conceptacle showing pores (p) surrounded by 9 rosette cells. Scale bars = 200 µm (Figs 16–17) and 10 µm (Figs 18–19).

specimens were protruding, mound-like, with a flat-topped roof without a peripheral raised rim (Table 1, Figs 8, 10).

Discussion and conclusions

This study illustrates how broad geographic sampling combined with an integrative systematic approach can significantly improve the assessment of the alpha diversity and distribution of non-geniculate coralline algae. DNA barcodes proved to be particularly useful for delimiting species within this challenging group of non-geniculate corallines where phenotypic plasticity greatly complicates the use of conventional, morphology-based approaches (Steneck, 1986). Moreover, phylogenies defined by the plastid marker (*psb*A) corroborated the species delimitation inferred from DNA barcodes. Among the European species of *Mesophyllum*, only *M. sphaericum* was sister to specimens from New Zealand, Japan and Hawaii according to the COI-5P analysis. *Mesophyllum macroblastum* (type locality: Gulf of Naples, Italy) from Europe and New Zealand were resolved as different species so the New Zealand taxon should not be assigned to *M. macroblastum*. Our results also showed the cryptic diversity found under the name *M. erubescens*. In New Zealand, Broom *et al.* (2008) pointed out the existence of cryptic species under this taxon. According to the SSU rDNA analyses of Peña *et al.* (2011), the clade composed of *M. sphaericum* and *M. erubescens* from Brazil and Hawaii is distant from New Zealand taxa. However, the published SSU rDNA sequence of Brazilian *M. erubescens* corresponded to a specimen collected in Sao Sebastiao (Bailey & Chapman, 1998) which is > 2500 km from the type locality (Fernando de Noronha; Woelkerling, 1993). Furthermore, another species resembling *M. engelhartii* (type locality: Cape Jaffa, South Australia; Silva *et al.*, 1996) is also reported along the Brazilian coast (Amado-Filho *et al.*, 2010; Villas-Boas *et al.*, 2014). In consequence, we consider that further studies involving the type specimen, or fresh material collected at the Brazilian type locality, are required to circumscribe this species.

DNA-assisted taxonomy has enabled us to get a better understanding of species distributions. For example, the results revealed that two European *Mesophyllum* species (*M. sphaericum* and *M. expansum*) had larger ranges than previously indicated. Based on our identification of *M. alternans*, which

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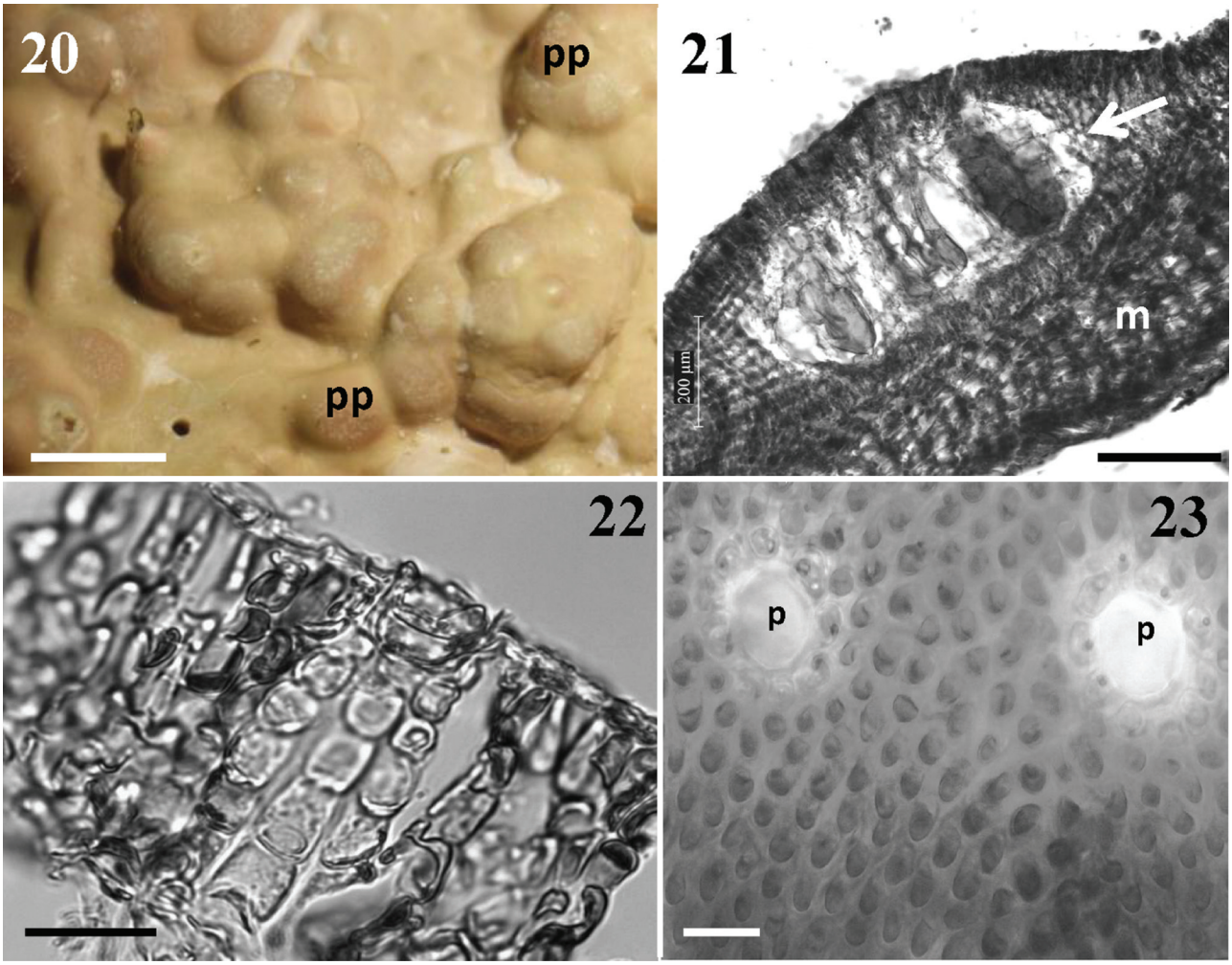
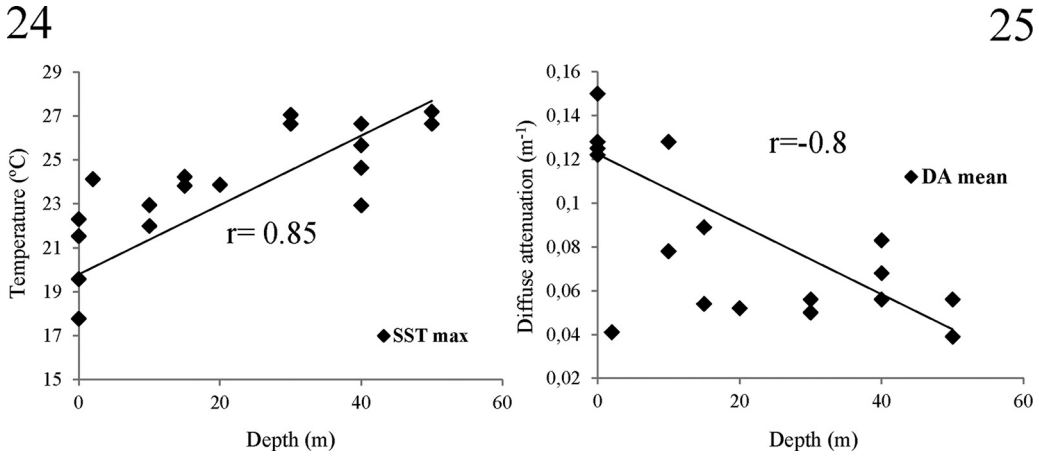
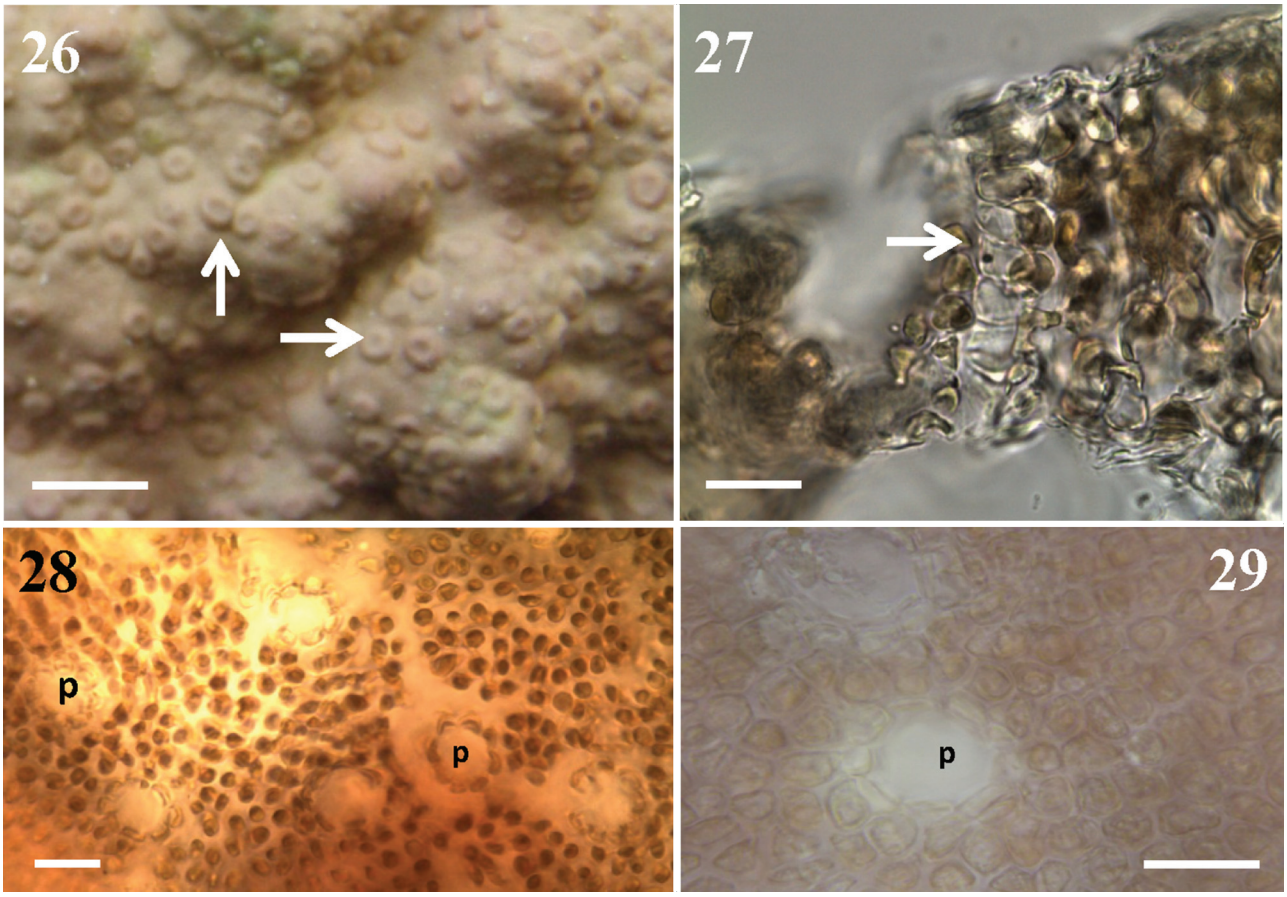


Figs 20–23. *Mesophyllum expansum* (VPF00019, VPF00216, Ziérbena and San Juan de Gaztelugatxe, Basque Country). **Fig. 20**. Multiporate sporangial conceptacles with mound-like to flattened pore plates (pp**)** without peripheral rim. **Fig. 21**. Longitudinal section showing coaxial medulla (m) and multiporate sporangial conceptacle with tetrasporangia immersed in cortex (arrow). **Fig. 22**. Longitudinal section showing pore canal filaments composed of cells wider than other roof filaments. **Fig. 23**. Surface view of multiporate sporangial conceptacle showing pores (p) surrounded by 9–10 rosette cells. Scale bars = 1 cm (Fig. 20), 200 µm (Fig. 21) and 20 µm (Figs 22–23).



Figs 24–25. Correlation between depth collection of *Mesophyllum expansum* and abiotic variables involved in coralline algal distribution. **Fig. 24**. Positive correlation between collection depth of *Mesophyllum expansum* and maximum Sea Surface Temperature (SSTmax) recorded at each sampling site. **Fig. 25**. Correlation between collection depth of *M. expansum* and Mean Diffuse Attenuation (DAmean) recorded at each sampling site. r = Pearson correlation coefficient.



Figs 26–29. *Mesophyllum macroblastum* (LLG3804 –Reggio Calabria; VPF00506 –Alborán Sea). **Fig. 26**. Multiporate sporangial conceptacles with sunken pore plates with peripheral rim (arrows). **Fig. 27**. Longitudinal section showing pore canal filaments composed of cells with thinner cell walls and wider than other roof filaments (arrow**). Figs 28–29**. Surface view of multiporate sporangial conceptacles showing pores (p) surrounded by 8–9 rosette cells. Scale bars = 1 cm (Fig. 26) and 20 µm (Figs 27–29).

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was supported by morpho-anatomical similarities, including one collection from a locality previously known for this species (Biarritz; Cabioch & Mendoza, 1998), *Mesophyllum alternans* occurs more frequently in Atlantic Europe than previously recorded. The detection of Mediterranean populations of *M. sphaericum*, both as unattached and as encrusting plants, represents another significant contribution to our knowledge of the range and habit of this recently discovered species. Prior to this study, and despite a considerable sampling effort carried out in the framework of former studies addressing the diversity of European non-geniculate coralline algae (Carro *et al.*, 2014; Pardo *et al.*, 2014), *M. sphaericum* was only known growing as maerl in a single locality on the Atlantic Iberian Peninsula (Peña *et al.*, 2011). Its occurrence at several sites along the Mediterranean Sea suggests that this species may have gone unnoticed, possibly misidentified as *M. expansum* (both species have flattened to mound-like multiporate sporangial conceptacles without a peripheral rim). In addition, the bathymetric range of the Mediterranean populations (23–50 m depth) limits their accessibility to collection by scuba divers.

The anatomical features of the specimens delineated within the lineage of *M. expansum, M. alternans* and *M. macroblastum* were largely consistent with the previous descriptions of these species. However, the range of diameters of the multiporate sporangial chambers observed in Atlantic specimens of *M. expansum* was greater than values reported in the literature (450–900 µm vs 610–800 µm, Table 1). Also, the pores observed in the specimens of *M. alternans* were surrounded in surface view by 9 rosette cells, whereas the literature indicates 11–12 cells (Table 1). The diagnostic value of the pore plate morphology of the multiporate sporangial conceptacles has been questioned previously in a study of *Mesophyllum* from New Zealand (Broom *et al.*, 2008). In addition, two pore plate morphologies were reported in the same Mediterranean specimen of *M. macroblastum* (Kaleb *et al.*, 2011). The authors, however, concluded that mound-like conceptacles represented either aberrant morphologies or immature conceptacles. Athanasiadis & Neto (2010) proposed the number of rosette cells as the most reliable character following observations of shape variation of the pore canal structure in *M. lichenoides* and *M.*

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expansum. Our results indicate that a combination of features of multiporate sporangial conceptacles that are currently considered diagnostic for the genus *Mesophyllum* can be useful for delimiting the European species.

We confirm the presence of *M. alternans* in southern Atlantic France, and show that this species also occurs in other Atlantic Iberian localities including southern Portugal. Our observations fill the gap in its distribution between the type locality, Tangier, Morocco, and previous records in the low intertidal and subtidal of Atlantic France (Guéthary and Biarritz; Cabioch & Mendoza, 1998). We did not find *M. alternans* in the Mediterranean Sea, even though there are literature records of this species from sites ecologically similar to ours (coralligenous habitat, 20–40 m depth; Cabioch & Mendoza, 1998, 2003; Bressan & Babbini, 2003). However, further studies will be required to determine whether *M. alternans* is present in the Mediterranean Sea.

Our results extend the northern range of *M. expansum* to northern Spain. Previously, this species was thought to be restricted to the Mediterranean Sea, the Canary Islands and Morocco (Woelkerling, 1983; Cabioch & Mendoza, 2003; Athanasiadis & Neto, 2010). A single record of *M. expansum* was reported in Galicia by Donze (1968, as *Pseudolithophyllum expansum* (Philippi) Lemoine). However, review of the voucher material (Nationaal Herbarium Nederland L0789614) revealed that it consisted of a maerl specimen of *Phymatolithon calcareum* with a crustose *Lithophyllum* sp. overgrowing it. *Mesophyllum expansum* is common on the lower intertidal and subtidal rocky shores of the northern Iberian Peninsula, whereas it appears to be confined to the subtidal in the Mediterranean Sea. Recently, it was reported from intertidal and subtidal localities in the Canary Islands and Azores (Athanasiadis & Neto, 2010). Although an extensive cover of subtidal epilithic plants of *M. lichenoides* (3–9 m) was recorded by Adey & Adey (1973) in northern Spain, our results suggest that their records might correspond to misidentifications of *M. expansum* given the widespread occurrence of the latter as epilithic plants in the low intertidal and subtidal zones of the Atlantic Iberian Peninsula.

In the NE Atlantic, *M. lichenoides* has been reported from Scotland to Mauritania, the Azores and the Canary Islands (Adey & Adey, 1973; Irvine & Chamberlain, 1994; John *et al.*, 2004). However, the southern distribution records in the Azores, Canary Islands and Morocco are questionable given the re-identification of Macaronesian records as *M. expansum* (Athanasiadis & Neto, 2010). According to Athanasiadis & Neto (2010), the southernmost confirmed record for *M. lichenoides* is Cabo Higuer, on the Atlantic French–Spanish border, although Peña *et al.* (2011) provided anatomical and molecular data (nuclear SSU rDNA) of *M. lichenoides* from further west on the Galician coast. The present study confirms the widespread occurrence of *M. lichenoides* along the Atlantic coast of the Iberian Peninsula from the Basque Country to southern Portugal, in agreement with the literature (Ardré, 1970; Gorostiaga *et al.*, 2004; Bárbara *et al.*, 2005; Araújo *et al.,* 2009). In contrast, we did not find *M. lichenoides* in the Mediterranean Sea. Along Atlantic European coasts, *M. lichenoides* is commonly found epiphytic on geniculate coralline algae in the intertidal and shallow subtidal zones (Woelkerling & Irvine 1986*b*, 2007; Irvine & Chamberlain, 1994), whereas in the Mediterranean Sea, this species is frequently reported from subtidal shady localities, both epilithic and epiphytic (Bressan & Babbini, 2003). Further studies with larger sample sizes, particularly in the habitats described in the Mediterranean literature, are needed to assess its occurrence in the Mediterranean Sea.

The lack of shared haplotypes between Atlantic and Mediterranean populations of both *M. sphaericum* and *M. expansum* suggests that these taxa might be good candidates for intraspecific phylogeographic studies. Further research on this subject using a population genetic sampling design with highly variable markers would enable the study of contemporary and past gene flow between these two regions.

The observation that collection depth of *M. expansum* was significantly correlated with SSTmax and DAmean is in agreement with the widespread belief that these two variables are the main drivers of coralline algal distribution (Adey, 1966*a–c*, 1970, 1971; Littler & Littler, 1984). The depth range observed for *M. expansum* (from the lower intertidal down to 50 m) indicates that the species can adapt to a wide range of depths. Unlike other European species of algae for which a northward shift has been predicted as the likely response to global climate change (Jueterbock *et al.,* 2013), *M. expansum* may respond to global warming by changing its bathymetric profile. Further research focusing on the bathymetric distribution of *M. expansum* along a latitudinal gradient, with *in situ* measurements of ecologically relevant environmental parameters (e.g. temperature and photosynthetically active radiation) could shed light on the potential mechanisms of the species to mitigate the effects of global warming.

In contrast, *M. lichenoides* is commonly found in the intertidal zone. In the case of other European Atlantic intertidal species such as *Fucus serratus* Linnaeus, *Ascophyllum nodosum* (Linnaeus) Le Jolis or *Himanthalia elongata* (Linnaeus) S.F. Gray, a northwards shift with isolated populations in upwelling areas is predicted under future climate scenarios (Martínez *et al.*, 2012; Jueterbock *et al.*, 2013). *Mesophyllum lichenoides* is less likely to follow this strategy since predictions about the combined effect of global warming and ocean acidification in the Northeast Atlantic expect a loss of calcified algae at

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high latitudes derived from reduction in aragonite saturation (Brodie *et al.,* 2014). By contrast, the Lusitanian region which today encompasses the southern part of the distribution range of *M. lichenoides* would still be suitable for the persistence of coralline algae. The resilience of European intertidal coralline algae to ocean acidification has been studied on the geniculate species *Ellisolandia elongata* and *Corallina officinalis* Linnaeus (Hofmann *et al*., 2012; Egilsdottir *et al*., 2013), which are frequently overgrown by *M. lichenoides.* While *C. officinalis* may show a lower ability to compete with other non-coralline algae, which could result in structural changes in intertidal communities (Hofmann *et al.,* 2012), *E. elongata* from intertidal rock pools was relatively robust because of its acclimation to the natural daily fluctuations of pCO_2 (Egilsdottir *et al.*, 2013). Studies on the sensitivity of *M. lichenoides* to ocean warming and acidification which include both growth and reproduction are required to evaluate accurately future potential changes in its distribution range.

The present study provides a comprehensive dataset that will serve as a baseline reference for future studies of members of the genus *Mesophyllum* that inhabit European coasts. On Atlantic and Mediterranean coasts, *Mesophyllum expansum* occurs commonly in both intertidal and subtidal communities. Given the ecological role of *M. expansum* as an important contributor to the coralligenous habitat, we propose that it should be included in monitoring studies of ocean warming on the Mediterranean Sea.

Acknowledgements

Financial support came from the following institutions and projects: Action Transversale du Muséum National d'Histoire Naturelle ('Taxonomie moléculaire: DNA Barcode et gestion durable des collections' and 'Biodiversité actuelle et fossile. Crises, stress, restaurations et panchronisme: le message systématique'), British Phycological Society (Small Grant Scheme-Project Award 2011-2012), Spain's Ministerio de Economía y Competitividad (CTM2010-18787), CGL2009-09495/BOS (partially founded by ERDF) and Xunta de Galicia (10MMA103003PR). Acquisition of molecular data was carried out at the CNRS-UMS 2700 in Service de Systématique Moléculaire, MNHN, Paris. This project was supported by the network 'Bibliothèque du Vivant' funded by CNRS, Muséum National d'Histoire Naturelle, INRA and CEA (Centre National de Séquençage). VPF acknowledges support by the postdoctoral programmes Axudas de apoio á etapa inicial de formación posdoutoral do Plan I2C (Xunta de Galicia), Programa Nacional de Movilidad de Recursos Humanos (Spain´s Ministerio de Economía y Competitividad), and University of A Coruña (Estadías posdoutorais de investigación, 2014). IB acknowledges financial support by the University of A Coruña (2011) for collections in Mediterranean France. We sincerely thank Paul Gabrielson, Antonio Secilla, Jazmin J. Hernández-Kantún, Pilar Díaz, Cristina Pardo, Diego Kurt-Kersting, Luisa Mangialajo and Alberto Santolaria for field collaboration and/or for providing samples. LLG acknowledges Andromede oceanology for inviting her to participate to the RECOR expedition in June 2013. We also thank the project INDEMARES for providing samples from the Alborán Sea and the Marine Reserve of Columbretes Islands for providing permits and for field support. We are also grateful to the anonymous reviewer as well as Paul Gabrielson and Juliet Brodie for their helpful comments on the manuscript.

Supplementary information

The following supplementary material is accessible via the Supplementary Content tab on the article's online page at http://dx.doi.org/10.1080/09670262.2014.981294

Table S1. Sample information for species included in the molecular analyses. In bold letters, holotype specimens (*Mesophyllum sphaericum*), or specimens collected at the type locality (*M. expansum*) or nearby (*M. lichenoides*). Haplotypes observed for each species are provided. Additional COI-5P and *psb*A sequences available from GenBank are detailed.

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