

*MESOPHYLLUM SPHAERICUM* SP. NOV. (CORALLINALES, RHODOPHYTA):  
A NEW MAËRL-FORMING SPECIES FROM THE NORTHEAST ATLANTIC<sup>1</sup>

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*Mesophyllum sphaericum* sp. nov. is described based on spherical maërl individuals (up to 10 cm) collected in a shallow subtidal maërl bed in Galicia (NW Spain). The thalli of these specimens are radially organized, composed of arching tiers of compact medullary filaments. Epithallial cells have flattened to rounded outermost walls, and they occur in a single layer. Subepithallial initials are as long as, or longer than the daughter cells that subtend them. Cell fusions are abundant. Multiporate asexual conceptacles are protruding, mound-like with a flattened pore plate, lacking a peripheral raised rim. Filaments lining the pore canal and the conceptacle roof are composed of five to six cells with straight elongate and narrow cells at their base. Carposporangial conceptacles are uniporate, protruding, and conical. Spermatangial conceptacles were not observed. Molecular results placed *M. sphaericum* near to *M. erubescens*, but *M. sphaericum* is anatomically close to *M. canariense*. The examination of the holotype and herbarium specimens of *M. canariense* indicated that both species have pore canal filaments with

elongate basal cells, but they differ in number of cells (five to six in *M. sphaericum* vs. four in *M. canariense*). Based on the character of pore canal filaments, *M. canariense* shows similarities with *M. erubescens* (three to five celled). The outermost walls of epithallial cells of *M. canariense* are flared compared to the round to flattened ones of *M. erubescens*, the latter being widely accepted for the genus *Mesophyllum*. The addition of *M. sphaericum* as new maërl-forming species suggests that European maërl beds are more biodiverse than previously understood.

**Key index words:** Corallinales; Galicia; Iberian Peninsula; maërl; *Mesophyllum canariense*; *Mesophyllum erubescens*; *Mesophyllum sphaericum*; NE Atlantic; nuclear SSU rDNA; rhodolith

**Abbreviations:** TBR branch, tree-bisection-reconnection branch; TrN model, Tamura-Nei model

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The genus *Mesophyllum* was described by Me. Lemoine (1928) based on the presence of a medulla (hypothallium) disposed in concentric rows (coaxial) separated by thicker walls and the presence of multiporate asexual conceptacles. This genus, originally described as intermediate between

*Lithophyllum* and *Lithothamnion*, included 10 nonfossil species and six fossil ones. Most of these species were reported from tropical regions except *Mesophyllum lichenoides*. Although this latter species was specified as the holotype (Hamel and Lemoine 1952), a recent assessment of the genus *Mesophyllum* designated an epitype because of the absence of the original Ellis specimens (Woelkerling and Irvine 1986, 2007).

Since the original description of *Mesophyllum*, further features were provided as diagnostic, such as the coaxial arrangement of the medulla, contiguous filaments connected by cell fusions rather than secondary pit connections, elongate subepithallial initial cells, outermost walls of epithallial cells rounded to flattened, and the occurrence of simple spermatangial mother cell systems on the floor walls and roof of conceptacle chambers (Adey and Johansen 1972, Cabioch 1972, Adey and Adey 1973, Johansen 1976, Lebednik 1977a, 1978, Woelkerling and Irvine 1986). These characters were not exclusive of this genus, including the coaxial medulla, which was also reported in *Clathromorphum* and *Synarthrophyton* (Woelkerling and Harvey 1992, Vidal et al. 2003). To delimitate *Mesophyllum* from other genera of Melobesioideae, Woelkerling and Harvey (1993) suggested a combination of features that were previously described by different authors for vegetative anatomy (internal construction monomerous, haustoria absent, terminal epithallial cells rounded or flattened but not flared, subepithallial initial cells as long as or longer than cells subtending them) and spermatangial initials forming simple spermatangial filaments directly from meristematic cells, which are overlain by a layer of protective cells, conceptacle roofs formed centripetally from groups of peripheral filaments.

A total of 26 characters related to substrate orientation, vegetative anatomy, and morphology and reproduction, which were previously proposed for the identification of *Mesophyllum* species, were reexamined in Woelkerling and Harvey (1992, 1993). They concluded that only features related with the sporangial conceptacle (roof morphology and pore canal structure) were consistent and consistently available for the delimitation of the southern Australian *Mesophyllum* species. These features were included and taken into account in later studies carried out in Europe (Irvine and Chamberlain 1994, Cabioch and Mendoza 1998, 2003, Athanasiadis 1999), South Africa (Keats and Chamberlain 1994, Chamberlain and Keats 1995, Chamberlain 2000, Maneveldt et al. 2008), Pacific coast of North America (Athanasiadis et al. 2004), Indonesia (Verheij 1993), Australia and New Zealand (Ringletaube and Harvey 2000, Harvey et al. 2005), and Brazil (De Castro et al. 2008). Nevertheless, the value of these features for species delimitation has been recently questioned. Broom et al. (2008) pointed out that *Mesophyllum erubescens* (Foslie) Me.

Lemoine cannot be separated as a distinct species from *M. printzianum* Woelk. et A. S. Harv., despite the fact that both differ in roof conceptacle morphology (flat-topped vs. sunken pore plate). According Vidal et al. (2003), the genus *Mesophyllum* is currently undergoing rapid evolution; thus diagnostic features are not well defined.

The genus *Mesophyllum* is widely distributed from the tropics to temperate regions, although it has not been found in the high Arctic. It occurs under different growth forms (from encrusting to fruticose or foliose), unbranched or with dorsiventral organized lamellate branches to radial organized protuberances (Adey et al. 1982, Woelkerling and Irvine 1986, Woelkerling 1988, Woelkerling and Harvey 1993, Irvine and Chamberlain 1994, Keats and Chamberlain 1994, Cabioch and Mendoza 1998, 2003, Athanasiadis et al. 2004). Although it is represented by >60 species (Athanasiadis et al. 2004), a world monograph for this genus has not been produced (Woelkerling and Harvey 1993). On the NE Atlantic and Mediterranean coasts, five *Mesophyllum* species are currently recognized: *M. alternans* (Foslie) Cabioch et M. L. Mend., *M. expansum* (Philippi) Cabioch et M. L. Mend., *M. lichenoides*, *M. macroblastum* (Foslie) W. H. Adey, and an endemic species from the Aegean Sea, *M. macedonis* Athanas. (Woelkerling and Irvine 1986, Basso 1994, Irvine and Chamberlain 1994, Cabioch and Mendoza 1998, 2003, Athanasiadis 1999). In the Macaronesian region, *M. canariense* (Foslie) Me. Lemoine is also reported (Lemoine 1929, Reyes and Afonso-Carrillo 1993, John et al. 2003). All these species have been described as encrusting foliaceous thalli, although with lamellae or protuberances more or less adherent to the substratum. However, unattached maërl specimens of *M. alternans* were recorded in the Mediterranean (Basso 1994, Cabioch and Mendoza 1998), and unattached sterile specimens assigned to *M. lichenoides* occur in the British Isles (Woelkerling and Irvine 1986, Irvine and Chamberlain 1994). The unattached growth produced branches rather than the foliose and lamellate thalli of Mediterranean encrusting species (Basso 1996).

In the northwestern Iberian Peninsula, the genus *Mesophyllum* has only been represented by encrusting thalli of *M. lichenoides*. The sole record of *M. expansum* was made by Donze (1968), as *Pseudolithophyllum expansum* (Philippi) Me. Lemoine. The rest of the Galician records correspond to *Lithophyllum stictaeforme* (Aresch.) Hauck [as *L. frondosum* (Dufour) G. Furnari, Cormaci et Alongi by Veiga et al. 1998 and Bárbara et al. 2002]. Those records were incorrectly transferred to *M. expansum* in the taxonomic updating of the Galician checklist (Bárbara et al. 2005).

During recent extensive surveys of the Galician maërl beds, several unattached fruticose and spherical specimens of greater size were found in a shallow subtidal maërl bed (Fig. 1a) and also as drift on

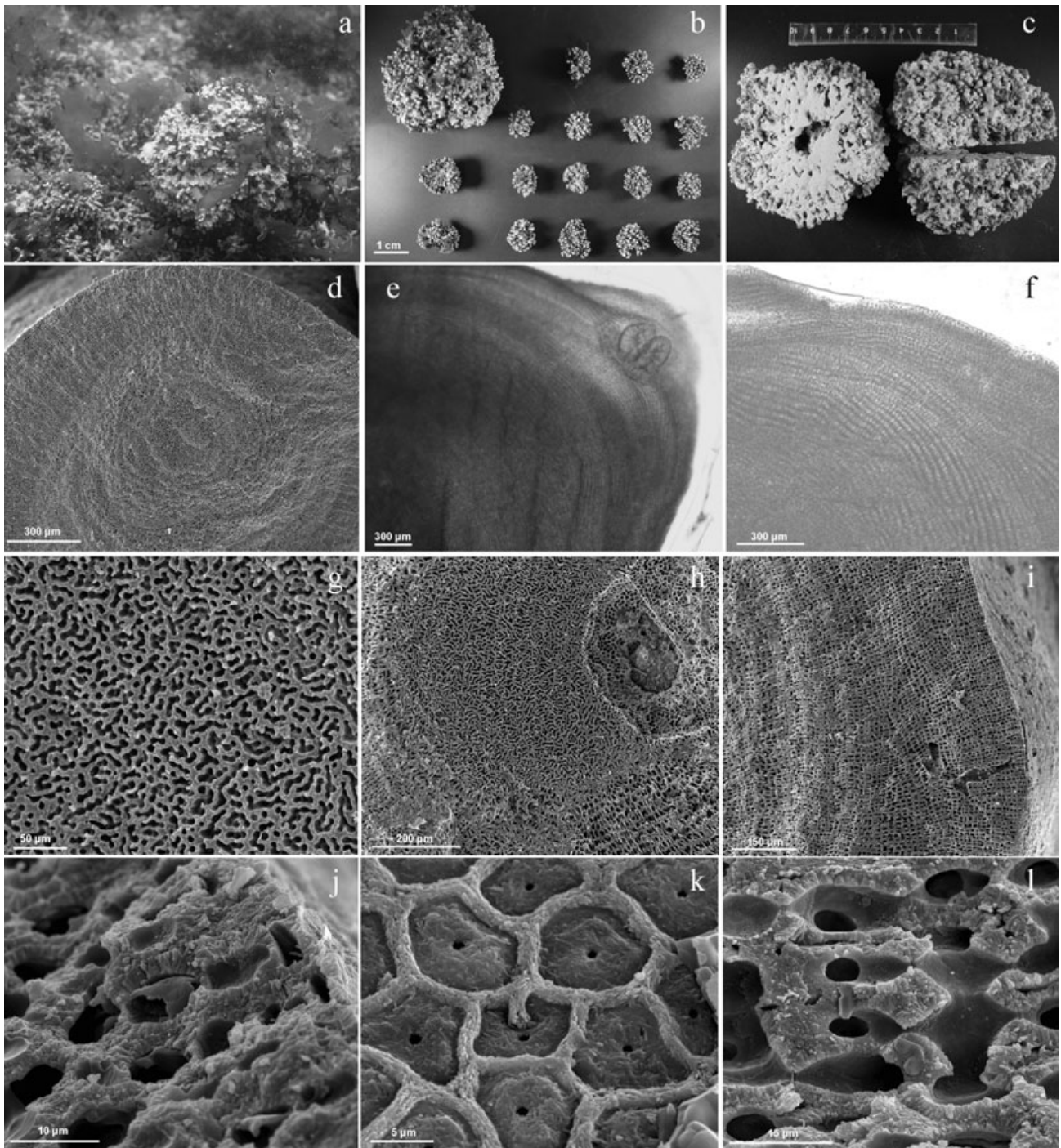


FIG. 1. *Mesophyllum sphaericum* sp. nov. (a) Unattached specimens in the maërl bed off Benencia Island at 3 m depth. (b) Range of size of the specimens. (c) Specimen (9 cm in diameter) densely branched and showing radial organization. (d) Branch radially organized (VS, SEM). (e, f) Branch showing the medulla disposed in arching tiers (LS). (g, h) Arrangement of the medullary filaments in the central portion of the branch (VS, SEM). (i) Cortex disposed in the peripheral region of the branch (VS, SEM). (j) Branch showing a single layer of flattened epithallial cells derived from long subepithallial initials, arrow (VS, SEM). (k) Surface view of polygonal epithallial cells (SEM). (l) Branch showing cell fusions among cortical cell (VS, SEM). LS, longitudinal section; VS, vertical section.

a maërl beach (Peña and Bárbara 2008a). These specimens are typically larger than the dominant species *Phymatolithon calcareum* (Pallas) W. H. Adey et D. L. McKibbin. Anatomical features observed in

the new material do not match with previous maërl-forming species reported from the Galician region, such as *P. calcareum* and *Lithothamnion corallioides* (P. L. Crouan et H. M. Crouan) P. L. Crouan et

H. M. Crouan (Hamel 1928, Miranda 1934, Donze 1968, Adey and McKibbin 1970, Bárbara et al. 2004, Peña and Bárbara 2004). Diagnostic features and molecular investigations revealed that this is a new fruticose *Mesophyllum* species not related to other species. Based on recent evaluations of characters used in delimiting genera of nongeniculate Corallinaceae and our molecular data, we propose *M. sphaericum* as a new species and a new maërl-forming species for the European coast. Despite the sampling effort carried out in the Galician maërl beds during the last several years (Bárbara et al. 2004, Peña and Bárbara 2004, 2008a,b, 2009), the occurrence of *M. sphaericum* is currently restricted to this unique Galician maërl bed.

#### MATERIALS AND METHODS

Unattached plants of *M. sphaericum* were collected by dredging and SCUBA diving at 3 m depth off Benencia Island as well as in drift on the maërl beach (Ría de Arousa, Galicia, Spain). Collections were carried out at different months (February, April, May, July, August, October, and November) during 2004–2008. For anatomical study, specimens were fixed in 4% formalin in seawater in the field and transported to the laboratory where they were preserved in total darkness at 4°C. The growth form of specimens was characterized according to Woelkerling et al. (1993). For the molecular study, fresh specimens of *M. sphaericum* collected in April 2008 and October 2008 were oven-dried (50°C) and preserved in double zipper bags with silica gel. Fresh specimens of *M. canariense* were not available for molecular investigations, even though sampling surveys were carried out in the Canary Islands.

**Molecular analyses.** Collection information for taxa investigated is provided in Table S1 (see the supplementary material). To determine nuclear SSU rDNA sequences, samples were processed, and genomic DNA from samples was extracted using a DNeasy® Plant Mini Kit (Qiagen, Hilden, Germany). The SSU rDNA was PCR-amplified from total genomic DNA using the primer combinations of Saunders and Kraft (1994, 1996). Agarose gel purification or direct purification with High Pure™ PCR Product Purification Kit (Roche Diagnostics, Indianapolis, IN, USA) or LaboPass PCR Purification Kit (COSMO Genetech, Seoul, Korea) was used to clean PCR products. DNA purified using this method was sequenced using the BigDye™ terminator cycle sequencing ready reaction kit (PE Applied Biosystems [ABI], Foster City, CA, USA). Sequence data were collected using an ABI PRISM 3730 DNA Analyzer. Sequence data were edited using the SeqEd DNA sequence editor (ABI) software package. The edited sequences were aligned relative to one another using the SeqPup multiple alignment program (Gilbert 1995) and MacClade 4 program (Maddison and Maddison 2003). The final alignment for SSU consisted of 25 taxa, including 22 previously published red algal SSU sequences (Table S1). The 1,820 aligned nucleotide positions of SSU data were edited to remove the 5' and 3' PCR primer regions (G01 and G07, Saunders and Kraft 1994) as well as ambiguously aligned regions, to yield 1,774 sites for phylogenetic inference.

Distance and parsimony analyses were completed in PAUP\* 4.0b10 (Swofford 2002). For distance analysis, we used Modeltest 3.7 (Posada and Crandall 1998, Posada and Buckley 2004) to determine the best model for our data. The best model was Tamura-Nei (TrN) model with a gamma correction for among-site variation ( $\Gamma$ ) and invariant sites (I). Distance analysis was completed with neighbor joining (Saitou and Nei 1987) and was subjected to 2,000 rounds of bootstrap resampling

(Felsenstein 1985). Parsimony analysis (unweighted, gaps treated as missing data) was completed under a heuristic search (100 random additions) with tree-bisection-reconnection (TBR) branch swapping in effect. To estimate the robustness of internal nodes, bootstrap resampling was completed for the parsimony analysis (1,000 replicates; random additions set to 10). The SSU data were also used to generate trees using MrBayes 3.0b4 (Huelsenbeck and Ronquist 2001). Five million generations were run with four chains and sampling every 100 generations (burn-in subsequently identified at 30,000 generations). In all analyses, unrooted trees were calculated and the ingroup taxa subsequently rooted with *Heydrichia woelkerlingii* and *Sporolithon durum* as designated outgroups (Bailey and Chapman 1998, Bailey et al. 2004, Broom et al. 2008).

**Morphological studies.** Specimens of *M. sphaericum* were examined by LM and SEM (models JEOL JSM 6400 and Leica Stereoscan 440). For LM, fragments of selected specimens were previously decalcified and embedded in gelatine according to Cremades et al. (1997). Longitudinal and transverse sections were obtained by hand with a stainless steel razor blade. All the sections were made from branches since the specimens lacked basal crusts. Resulting sections were stained with Harris's hematoxylin (Fragoso-Tejas et al. 1994). Permanent slides were mounted in Karo® syrup (50%–80%). Representative material of *M. sphaericum* has been incorporated to the SANT-Algae (University of Santiago de Compostela, acronym follow Holmgren et al. 1990). In addition, *M. sphaericum* was compared with the following *Mesophyllum* species morphologically or geographically related: *M. canariense* (TRH C15-3210 and permanent slide nos. 1012, 1056, 1057 housed in Trondheim Herbarium, Norway; permanent slides Julio Afonso-Carrillo (JAC) 58-511, 58-512, and 59-523; PC 0118265 deposited at Museum National d'Histoire Naturelle, Paris; TFC Phyc 13118, 13206 deposited at Herbario de la Universidad de La Laguna, Canary Islands; FT-139 deposited at U.S. National Herbarium), *M. lichenoides* (SANT-Algae 21829, 21830), *M. erubescens* (isotype FT-148, deposited at U.S. National Herbarium), *M. expansum* (TFC Phyc 2546, 2548, 2549, 2585, and 5253).

**Anatomical terminology.** Woelkerling (1988) suggested that some terms employed in classical literature, such as hypothallium, perithallium, and epithallium, should not be employed as thalli of nongeniculate Corallinaceae are pseudoparenchymatous and composed of filaments rather than tissues. While that conclusion is debatable, the present study follows the anatomical terminology proposed in Woelkerling (1988) for thallus organization (dorsiventral, radial, and isobilateral) and anatomical construction (monomerous and dimerous). The anatomical terms medulla (equivalent to the terms hypothallium and core) and cortex (equivalent to the terms perithallium and peripheral region) are employed since monomerous thalli are considered analogous to the pseudoparenchymatous thalli of other red algae, except for the presence of epithallial cells (Irvine and Chamberlain 1994) and an intercalary meristem (initials). 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. Conceptacle measurements were taken according to Adey and Adey (1973) and Irvine and Chamberlain (1994).

#### RESULTS

*Mesophyllum sphaericum* V. Peña, Bárbara, W. H. Adey, Riosmena-Rodríguez et H. G. Choi **sp. nov.** (Figs. 1 and 2).

**Diagnosis:** Thallus liber, monomerous, rami abundantes, clavati. Epithallium ex unico strato

cellularum, cellulis rotundatis ad applanatas 1–2  $\mu\text{m}$  longis et 3–10  $\mu\text{m}$  latis in transversale sectione, 6–11  $\mu\text{m}$  diametro aspectu superficiali. Cellulae subepithalliales elongatae, 6–10  $\mu\text{m}$  longae et 2–7  $\mu\text{m}$  latae. Cortex tenuis, cellulis 5–8  $\mu\text{m}$  longis at 3–4  $\mu\text{m}$  latis. Medulla pluristratosa coaxialis, cellulis 10–15  $\mu\text{m}$  longis atque 5–7  $\mu\text{m}$  latis. Conjunctionibus frequentibus. Trichocyti ignoti. Conceptacula tetrasporangialia multiporata, elevata, 143–300  $\mu\text{m}$  alta, 225–540  $\mu\text{m}$  diametro; tecto 40–80  $\mu\text{m}$  crasso, sine margine, pori usque ad 50; fila prope porum instructa ex 5–6 cellulis, cellulae basales sunt elongatiores. Aspectu superficiali, pori circumdati 7–8 cellulis maioribus atque depressioribus quam ceteris tecti. Tetra-(bi-) sporangia zonatim divisa, 130–190  $\mu\text{m}$  alta at 50–95  $\mu\text{m}$  diametro. Conceptacula carposporangialia uniporata, elevate, 121–300  $\mu\text{m}$  alta at 395–516  $\mu\text{m}$  lata; carposporangia 40–140  $\mu\text{m}$  longa  $\times$  27–85 lata. Conceptacula mascula ignota.

Thalli unattached, monomerous, densely branched with claviform branches. Single epithallial layer, cells flattened to rounded, 1–2  $\times$  3–10  $\mu\text{m}$  in vertical section, 6–11  $\mu\text{m}$  in diameter in surface view. Subepithallial initials elongate, 6–10  $\mu\text{m}$   $\times$  2–7  $\mu\text{m}$ . Cortex less developed, composed of cells 5–8  $\times$  3–4  $\mu\text{m}$ . Medulla coaxial composed of cells 10–15  $\mu\text{m}$  long  $\times$  5–7  $\mu\text{m}$  diameter. Cell fusions frequent. Trichocytes absent. Asexual conceptacles multiporate, protruding, 143–300  $\mu\text{m}$  high  $\times$  225–540  $\mu\text{m}$  in diameter; roof, without a peripheral rim 40–80  $\mu\text{m}$  thick, up to 50 pores. Filaments lining the pore canal 5–6 celled, with elongate cells at their base. In surface view, pores are surrounded by a rosette of 7–8 cells wider and sunken than the rest of roof cells. Tetrasporangia and bisporangia zonate, 130–190  $\times$  50–95  $\mu\text{m}$ . Carposporangial conceptacles uniporate, protruding, 121–300  $\times$  395–516  $\mu\text{m}$ ; carposporangia 40–140  $\times$  27–85  $\mu\text{m}$ . Spermatangial conceptacles unknown.

*Morphology:* Specimens are nongeniculate, unattached, fruticose, densely branched up to seventh-order branching, and radially organized forming mainly spheroidal rhodoliths, (2) 3–9 (10) cm in diameter (Fig. 1, a–c). Terminal branches are claviform, ending in rounded to flattened apices, usually 3–5 mm long and 1–2 mm wide, but thicker in eroded and dead specimens, 2–4 mm wide (Fig. 1c). Color is pink to purplish pink, and the texture smooth and glossy.

*Anatomy:* Plant structure is pseudoparenchymatous, monomerous, and radially organized (Fig. 1d). In longitudinal sections of branches, the medulla occupied a large area up to 1,300  $\mu\text{m}$  in thickness (65% of the branch) and consisted of arching tiers of compact longitudinal filaments composed of cylindrical cells 10–15  $\times$  5–7  $\mu\text{m}$  (Fig. 1, e and f). In transverse sections of branches, the cell fusions are very evident, and coenocytes are (5) 8–10 (15)  $\mu\text{m}$  in diameter (Fig. 1g). The cortex can be up to 700  $\mu\text{m}$  in thickness, composed of cells 5–18  $\times$

3–10  $\mu\text{m}$  (Fig. 1, h and i). The subepithallial initials are as long as or longer than cells subtending them, ranging from 6 to 10  $\mu\text{m}$  long by 2 to 7  $\mu\text{m}$  in diameter (Fig. 1j). Each cortical filament produces one epithallial cell with rounded to flattened outermost walls in transverse section; they are 1–2  $\mu\text{m}$  long by 3–10  $\mu\text{m}$  wide and are disposed in a single layer; in surface view, epithallial cells are very thick walled and polygonal, 6–11  $\mu\text{m}$  in diameter (Fig. 1k). Fusions between cells of neighboring filaments are very abundant, but secondary pit connections are absent (Fig. 1l). Trichocytes are absent.

*Reproductive structures:* Uniporate and multiporate conceptacles occur separately, but they were occasionally observed in the same rhodolith (Fig. 2a). Multiporate and, more scarcely, uniporate conceptacles were recorded in February, May, July, October, and November. Spermatangial conceptacles were not seen. Carpogonial conceptacles are uniporate and conical (Fig. 2b), 75  $\mu\text{m}$  high by 225  $\mu\text{m}$  in diameter, with a chamber of 110  $\mu\text{m}$  high by 125  $\mu\text{m}$  in diameter. Pore canals are  $\sim$  25  $\mu\text{m}$  in diameter. Carpogonial filaments extend across conceptacle floor and consist of a terminal carpogonium composed of an elongate trichogyne up to 55  $\mu\text{m}$  long ending in a button-like apex, and 1–2 basal cells 25–40  $\mu\text{m}$  long by 8  $\mu\text{m}$  wide (Fig. 2b). Carposporangial conceptacles are uniporate, protruding and conical to rounded (Fig. 2, a and c), with a chamber (121) 187–294 (300)  $\mu\text{m}$  high by (395) 400–470 (516)  $\mu\text{m}$  in diameter. Cells projecting into the single conceptacle pore of 200  $\mu\text{m}$  long by 100  $\mu\text{m}$  wide (Fig. 2c). Carposporangia are rounded to elongate, each (40) 54–100 (140)  $\mu\text{m}$  long by (27) 36–75 (85)  $\mu\text{m}$  wide. Tetrasporangial and bisporangial conceptacles (Fig. 2d) are multiporate, protruding, and occasionally fused (Fig. 2e); these flattened mound-like structures have a pore plate lacking differentiation into a peripheral raised rim. Chambers are elliptical, 143–300  $\mu\text{m}$  high by (225) 267–467 (540)  $\mu\text{m}$  wide (Fig. 2, f and g). Tetrasporangia and bisporangia are 130–150 (190)  $\mu\text{m}$  long  $\times$  (50) 65–75 (95)  $\mu\text{m}$  wide (Fig. 2h). Conceptacle roofs are flat topped, (40) 45–53 (80)  $\mu\text{m}$  thick, perforated by 30–50 pores (Fig. 2i). Filaments lining the pore canal are composed of 5–6 cells, with straight, elongate, and narrow cells at their base 5–7 (10)  $\mu\text{m}$  long by 2–4  $\mu\text{m}$  wide (Fig. 2, j and k). The upper cells lining the pore are from 5–6  $\mu\text{m}$  long by 4–5  $\mu\text{m}$  wide to 2–4  $\mu\text{m}$  long by 4–6  $\mu\text{m}$  wide in the apical cells. The remainder of the roof filaments are 5–6 celled, 3–5  $\mu\text{m}$  long by 4–6  $\mu\text{m}$  in diameter. The pore canals are 22–30  $\mu\text{m}$  in length, with the basal parts being 11–14  $\mu\text{m}$  in diameter, narrowing in the distal portion to 4–8  $\mu\text{m}$  in diameter. In surface view (Fig. 2l), the pores are surrounded by a rosette of 7–8 cells (3–5  $\times$  5  $\mu\text{m}$ ) sunken and wider than surrounding roof cells. Apical plugs (sporangial plugs) are present. Both uniporate and multiporate senescent conceptacles

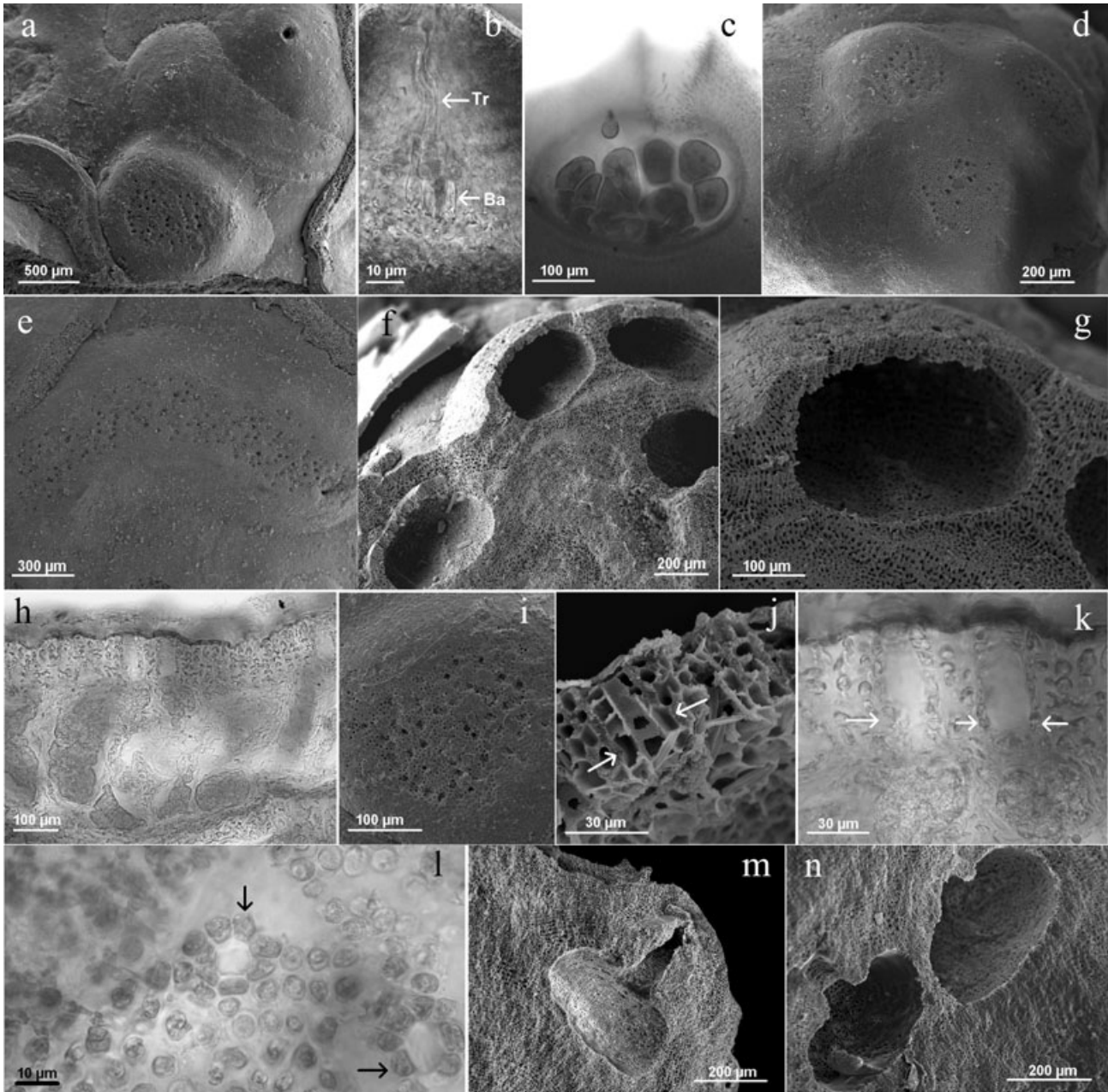


FIG. 2. *Mesophyllum sphaericum* sp. nov. (a) Surface view of uniporate (sexual) and multiporate (asexual) conceptacles on the same specimen (SEM). (b) Carpogonial conceptacle showing carpogonium composed of an elongate trichogyne (Tr) and basal cells (Ba) (LS). (c) Carposporangial conceptacle uniporate protruding with cells projected into the canal pore (LS). (d) Surface view of multiporate asexual conceptacles protruding without differentiation into a peripheral raised rim and a central pore plate (SEM). (e) Surface view showing multiporate asexual conceptacles fused (SEM). (f, g) Multiporate asexual conceptacles protruding with flattened pore plate (VS, SEM). (h) Multiporate asexual conceptacle containing tetrasporangia (VS). (i) Surface view of the pore plate of a multiporate asexual conceptacle showing pores surrounded by rosette cells sunken (SEM). (j, k) Roof of multiporate asexual conceptacles showing pore canal filaments 5–6 celled with elongate and straight basal cell, arrows (VS, j; SEM). (l) Surface view a multiporate asexual conceptacle showing pores surrounded by seven rosette cells wider than the rest of roof cells, arrows. (m, n) Branch empty uniporate conceptacles buried within the thallus (VS, SEM). LS, longitudinal section; VS, vertical section.

tend to be buried within the thallus but are not refilled with new tissue (Fig. 2, m and n).

**Etymology:** The specific epithet refers to the spherical morphology observed on this maërl-forming species.

**Habitat:** *M. sphaericum* occurs as maërl (rhodoliths) in a unique shallow subtidal maërl bed area (1–5 m depth) mixed with *P. calcareum* located in the eastern side of the Benencia Island (Ría de Arousa, Galicia, Spain). Dead and eroded individuals

were also collected from drift on a maërl beach. The maërl bed, which occupies an area of  $\sim 0.4 \text{ km}^2$ , is composed of large areas of dense maërl cover that support a high species diversity of attached fleshy, filamentous, and crustose algae (137 species, Peña & Bárbara 2008a).

*Distribution:* Galicia, NW Spain.

*Holotype:* Benencia Island, Ría de Arousa, Galicia, Spain;  $42^\circ 36.036' \text{ N}$ ,  $08^\circ 52.459' \text{ W}$ ;  $-3 \text{ m}$  depth; V. Peña & I. Bárbara; 14-x-2008, SANT-Algae 21804.

*Isotypes:* SANT-Algae 21805-21828.

*Complementary collection:* Benencia Island, Ría de Arousa, Galicia, Spain;  $42^\circ 36.036' \text{ N}$ ,  $08^\circ 52.459' \text{ W}$ ;  $-3 \text{ m}$  depth; V. Peña & I. Bárbara; 13-VII-2004, SANT-Algae 21843; 04-II-2005, SANT-Algae 21831-21841; 25-V-2005, SANT-Algae 21844-21854; 11-XI-2005, SANT-Algae 21842.

*Molecular data:* The SSU sequences of CH1814, CH1816, CH1818, CH1825, CH1884, CH1888, and CH1891 were identical to each other. The sequence data of CH1814 and CH1891 were deposited in GenBank (Table S1).

*Phylogenetic relationships of Mesophyllum species based on nuclear SSU rDNA sequence data.* Eight SSU sequences were newly determined for this study. No ambiguities were observed in the SSU data. Three sequences (CH1392, CH1814, and CH1891) have been deposited in GenBank (Table S1). A tree was generated by Bayesian inference with posterior probabilities and bootstrap results from the distance and maximum-parsimony analyses appended for the SSU data (Fig. 3). The family Hapalidiaceae was monophyletic with strong support (100% in posterior probabilities and bootstrap support in all analyses). Monophyly of the genus *Mesophyllum*, however, was not supported. Our analyses resolved five paraphyletic clades among the included *Mesophyllum* spp.: (i) a single species clade, *M. lichenoides*; (ii) a strongly supported clade containing *Mesophyllum* sp. from New Zealand and *M. engelhartii* from South Africa weakly to strongly allied to *Synarthrophyton schielianum* from New Zealand and *S. patena* from South Australia in turn; (iii) a distinct clade consisting of *M. printzianum* from New Zealand and two separate clades of *M. erubescens*? from New Zealand; (iv) a clade of *M. erubescens* from New Zealand; and (v) the strongly supported clade including *M. sphaericum* from Spain and *M. erubescens* from Brazil and Hawaii. *M. sphaericum* was strongly (99%–100%) allied to the distinct clade *M. erubescens* from Brazil and *M. erubescens*? from Hawaii, and it was remotely related with *M. erubescens*? from New Zealand in all analyses. Maximum parsimony generated six trees (length = 491, consistency index = 0.692, retention index = 0.729). A strict consensus of six equally parsimonious solutions differed from the distance tree in the relative positioning of *Clathromorphum* spp., *Leptophyllum* spp., and *Mastophoropsis* among the Melobesioidean members. There was no support for any of these relationships (tree not shown).

## DISCUSSION

*M. sphaericum* demonstrates all of the primary features established for the genus *Mesophyllum*: a monomerous thallus with coaxial medulla, long sub-epithallial initials, cell fusions, absence of secondary pit connections, epithallial cells flattened with rounded outermost walls and multiporate asexual conceptacles (Adey 1970, Adey and Johansen 1972, Cabioch 1972, Adey and Adey 1973, Johansen 1976, Adey et al. 1982, Woelkerling and Irvine 1986, Woelkerling 1988, Irvine and Chamberlain 1994, Athanasiadis et al. 2004, Harvey and Woelkerling 2007, Maneveldt et al. 2008). Despite the fact that spermatangial conceptacles were not observed, and their ontogeny and morphology are considered critical features to distinguish *Mesophyllum* from the genera *Clathromorphum* and *Synarthrophyton* (Lebednik 1978, Woelkerling 1988, Woelkerling and Harvey 1993, Harvey et al. 2003), the Galician specimens differ from these genera in having: (i) a strongly coaxial medulla composed of arching tiers (coaxial areas are usually more localized in *Synarthrophyton*) and (ii) cortex filaments terminating in one epithallial cell at the thallus surface—more than two cells in *Clathromorphum*—(Adey 1970, Adey and Johansen 1972, Lebednik 1977b, Cardinal et al. 1978, Woelkerling 1988, Harvey et al. 1994).

In recent studies of *Mesophyllum* multiporate conceptacles, the morphology and anatomy of their pore canal filaments compared with the remainder of the roof filaments have been considered to be diagnostic (Verheij 1993, Woelkerling and Harvey 1993, Keats and Chamberlain 1994, Cabioch and Mendoza 1998, 2003, Athanasiadis 1999, Chamberlain 2000, Harvey et al. 2003, 2005). *M. sphaericum* has multiporate conceptacles with a protruding, but flat-topped roof without a peripheral raised rim. These features were also described for the species *M. lichenoides*, *M. expansum*, and *M. canariense* recorded in the NE Atlantic (Table 1), as well as for *M. engelhartii* (Foslie) W. H. Adey; *M. erubescens* (Foslie) Me. Lemoine; *M. syrphetodes* W. H. Adey, R. A. Towns. et Boykins; *M. crassiusculum* (Foslie) Lebednik; and *M. aleuticum* Lebednik, in which unattached thalli were also reported (Table 2), although their occurrence was occasional and even rare in the two latter species (Athanasiadis et al. 2004). Cabioch and Mendoza (2003) pointed out that *M. expansum* showed multiporate conceptacles slightly protruding that, according to their figures, had pore canal filaments 6–7 celled. It was also indicated that pore canal filaments were composed of cells longer than the remainder of the roof cells (or similar according to the table enclosed by the authors). A recent study of *M. expansum* (Athanasiadis and Neto 2010) pointed out pore canal filaments 6–10 celled with cells increasing in size toward the base and occasionally “thinner-wider.” The examined specimens of *M. expansum* from the

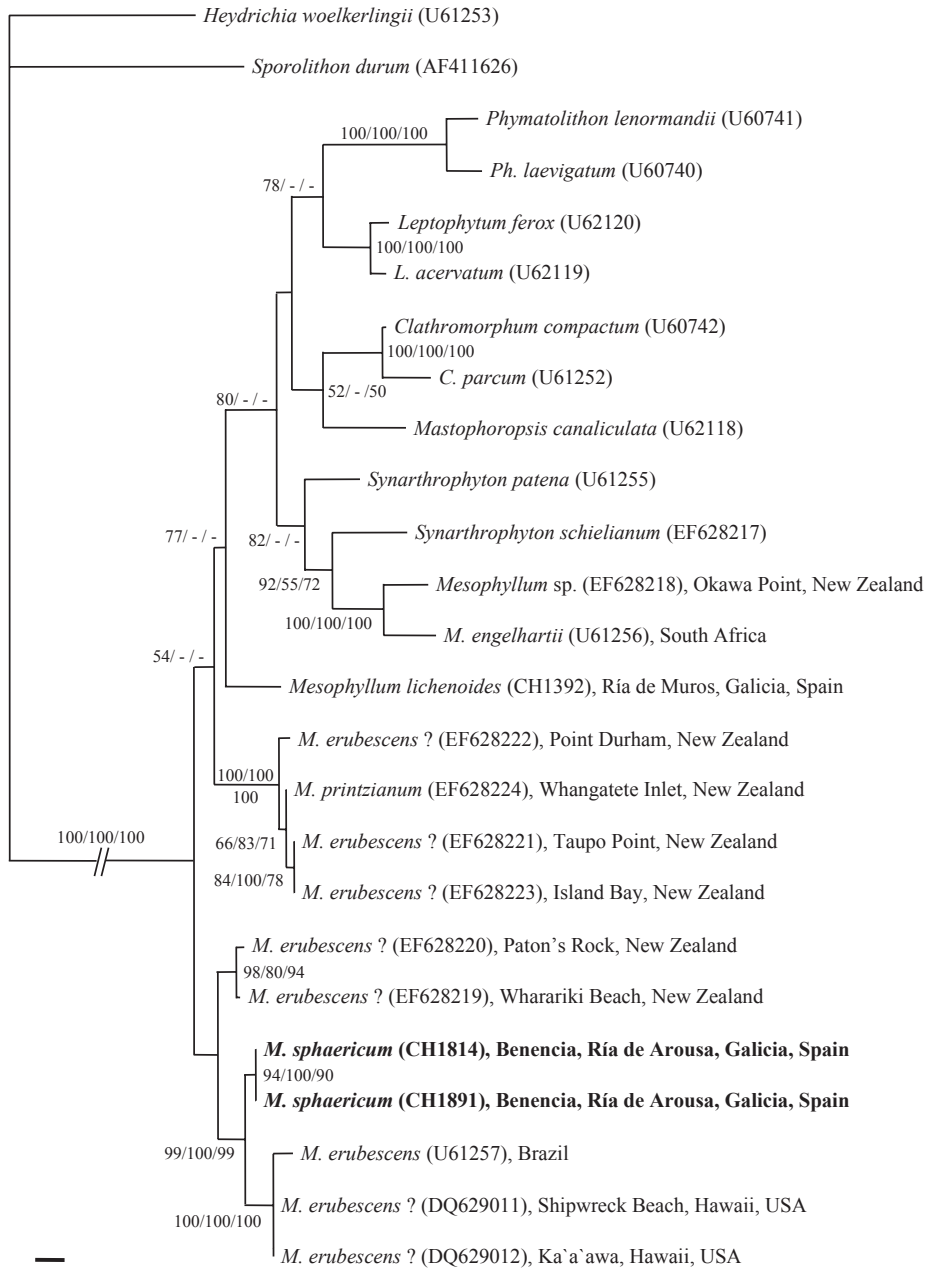


FIG. 3. Tree constructed with Bayesian inference for the SSU alignment. Values at branches represent Bayesian posterior probabilities (left value) and percentage of 2,000 and 1,000 bootstrap replicates for distance and parsimony analyses (middle and right values, respectively). Branches lacking values received <50% support. Scale bar = 0.005 substitutions per site.

Canary Islands exhibit pore canal filaments that were 6–7 celled and were wider than the remainder of the roof cells; all roof filaments including the pore canal filament had elongate basal cells (Table 1). On the other hand, surface views of *M. expansum* showed pore canals surrounded by 8–12 rosette cells that were sunken and smaller than the rest of roof cells (Cabiocch and Mendoza 2003) or similar to the rest of roof cells or “thinner-wider” (Athanasiadis and Neto 2010). In addition, this species was characterized by having lamellate thalli and a surface with concentric undulations.

In *M. lichenooides*, pore canal filaments are composed of 7–10 cells smaller than the remainder of the roof filaments, and either “thinner-wider” or

squarish; in surface view, pores are surrounded by 6–10 rosette cells similar to the rest of roof cells or “thinner-wider” (Athanasiadis and Neto 2010, Table 1). The examination of the Galician *M. lichenooides* showed that pore canal filaments were 7–9 celled (basal cells 7–9  $\mu\text{m} \times 5\text{--}7\ \mu\text{m}$ , upper cells 5  $\times$  5), whereas the remainder of the roof filaments were 5 celled (9–10  $\mu\text{m} \times 5\ \mu\text{m}$ ); each pore is surrounded in surface view by 7–12 rosette cells that are slightly protruding and similar to the rest of roof cells (Table 1).

The general morphology of multiporate conceptacles of *M. sphaericum* is generally similar to that described for *M. canariense* (Foslie 1929, Lemoine 1929, Masaki 1968, Reyes and Afonso-Carrillo 1993,



TABLE 1. Comparative table between *Mesophyllum sphaericum* and the *Mesophyllum* species reported for the NE Atlantic and Mediterranean regions.

	<i>M. sphaericum</i> <sup>17</sup>	<i>M. alternans</i> <sup>5,8,10,11,12,13</sup>	<i>M. canariense</i> <sup>1,2,3,6,17</sup>	<i>M. expansum</i> <sup>1,4,13,16,17</sup>	<i>M. lichenooides</i> <sup>1,5,7,9,12,13,16,17</sup>	<i>M. macedonis</i> <sup>10,11,13</sup>	<i>M. macroblastum</i> <sup>1,7,13,14,15</sup>
Thallus form and anatomical organization	Unattached, fruticose, densely branched. Radial.	Encrusting or nonadherent lamellae; surface smooth or with short protuberances.	Encrusting base adherent to substratum, with numerous erect protuberances. Dorsiventral (base) to radial (protuberances). Polygonal, thick walled.	Encrusting thallus nonadherent to substratum, irregularly lobate lamellae; surface with concentric undulations. Dorsiventral. Rounded, thick walled.	Encrusting nonadherent, foliose lamellae; surface smooth or warty, with concentric markings. Dorsiventral. Rounded.	Encrusting lamellae, partly growing free with superimposed lamellae. Dorsiventral.	Encrusting or nonadherent lamellae; surface smooth or warty with protuberances. Dorsiventral (base) to radial (protuberances). Rounded.
Epithallial cells (surface view)	Polygonal, thick walled.	Polygonal, walls weakly mineralized.					
Epithallial cells (in section, $\mu\text{m}$ )	Single layer, rounded to flattened, 1-2 $\times$ 3-10.	Single layer, rounded to flattened, 3-4 $\times$ 10-13.	Single layer, flared, 3-4 $\times$ 5-7.	Single layer, rounded to flattened, 1-8 $\times$ 7-11.	Single layer, rectangular-rounded to flattened, 2-10 $\times$ 5-15.	Single layer, rectangular, 3-4 $\times$ 7-8.	Single layer, rounded to flattened, 2-6 $\times$ 3-7.
Subepithallial initials ( $\mu\text{m}$ )	As long as or longer than cells subtending them, 6-10 $\times$ 2-7.	As long as cells subtending them.	As long as or longer than subtending them, 7-25 (30) $\times$ 3-7 (11).	As long as cells subtending them.	Longer than cells subtending them, 10-17 $\times$ 5-10.	Longer than cells subtending them.	As long as or longer than cells subtending.
Medulla (radial longitudinal section, $\mu\text{m}$ )	Arching tiers (coaxial), up to 1,300 $\mu\text{m}$ thick, cells cylindrical, 10-15 $\times$ 5-7.	Coaxial to noncoaxial, 150 $\mu\text{m}$ thick, cells 8-30 $\times$ 5-15.	Coaxial, up to 150 $\mu\text{m}$ thick, cells 6-30 $\times$ 5-25.	Coaxial, up to 500 $\mu\text{m}$ thick, cells 20-60 $\times$ 5-20.	Coaxial, rarely noncoaxial, up to 220 $\mu\text{m}$ thick, cells 15-50 $\times$ 10-18.	Noncoaxial, cells 16-40 $\times$ 3-10.	Coaxial to noncoaxial, up to 150 $\mu\text{m}$ thick, cells 3-42 $\times$ 3-16.
Cortex (radial longitudinal section, $\mu\text{m}$ )	Up to 700 $\mu\text{m}$ thick, cells 5-18 $\times$ 3-10.	Up to 700 $\mu\text{m}$ thick, stratification of small ovoid cells (8-15 $\times$ 3-7) and large rectangular cells (15-20 $\times$ 6-10).	Up to 150 $\mu\text{m}$ thick, cells 4-15 $\times$ 3-10.	Up to 150 $\mu\text{m}$ thick, cells 8-30 $\times$ 4-10.	Up to 45 $\mu\text{m}$ thick (5 cell layers), cells 6-14 $\times$ 4-14.	3-4 layers, cells 5-10 $\times$ 4-12.	Up to 500 $\mu\text{m}$ thick, cells 9-18 $\times$ 3-9.
Trichocytes	-	-	Very few.	-	-	+	-
Spermatangial uniporate conceptacles (chamber measures, height $\times$ diameter, $\mu\text{m}$ )	ND	Conical, slightly protruding, 150 $\times$ 500-600.	ND	Conical, protruding, 60-120 $\times$ 410-625.	Conical, 90-120 $\times$ 370-700.	ND	Protruding, 67-81 $\times$ 243-310.
Carposporangial uniporate conceptacles (chamber measures, height $\times$ diameter, $\mu\text{m}$ )	Protruding, conical, 121-300 $\times$ 395-516.	Protruding, conical, 350-400 $\times$ 600-700.	Conical, 160-200 $\times$ 240-500.	Conical, 170-210 $\times$ 390-600.	Protruding, 220-320 $\times$ 430-1,000.	ND	Conical, 54-270 $\times$ 175-540.

TABLE 1. Continued.

	<i>M. sphaericum</i> <sup>17</sup>	<i>M. alternans</i> <sup>5,8,10,11,12,13</sup>	<i>M. canariense</i> <sup>1,2,3,6,17</sup>	<i>M. expansum</i> <sup>1,4,13,16,17</sup>	<i>M. lichenoides</i> <sup>1,5,7,9,12,13,16,17</sup>	<i>M. macdonis</i> <sup>10,11,13</sup>	<i>M. macroblastum</i> <sup>1,7,13,14,15</sup>	
Multiporate asexual conceptacles (chamber measures, height × diameter, µm)	Protruding, mound-like, flat topped without peripheral raised rim, 143–300 × 225–540.	Protruding, hemispherical, flattened to slightly concave, with peripheral raised rim, 150–300 × 350–600.	Protruding, hemispherical, mound-like, flat topped without peripheral raised rim, 90–150 × 175–455.	Slightly protruding, mound-like, flattened to convex, without peripheral raised rim, 310–400 × 610–800.	Protruding, hemispherical, mound-like, somewhat flat topped, without peripheral raised rim, 150–380 × 323–800.	Protruding, convex roof, without peripheral raised rim, 110–125 × 320–500.	Protruding, sunken pore plate with peripheral raised rim, 90–155 × 145–355.	
Roof thickness of multiporate conceptacles (µm)	40–80	ND	20–30	50–115	52–130	30–55	27–35	
Number of pores of multiporate conceptacles	30–50	12–24	30–50	30–67	29–118	63–108	35	
Pore canal filament (in section, µm)	5–6 celled; basal cell elongate 5–10 × 2–4, upper cells 2–6 × 4–6.	6–8 celled; cells smaller, rounded, each 3–4 × 4–5.	4 celled; basal cell elongate, banana shaped, 11–15 × 3–4, upper cells 4–6 × 3–4.	6–10 celled; cells longer, similar or wider than the remainder of the roof filaments, 5–10 × 5–6; 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; basal cells 7–9 × 5–7, upper cells 5 × 5.	4–6 celled; cells slender and narrower than the remainder of the roof filaments; basal cell elongate.	6–7 celled; cells similar in shape and size than the remainder of the roof filaments, 3–10 × 3–6.	
Rest of the roof filaments (in section, µm)	5–6 celled, each 3–5 × 4–6.	4–5 celled, each 5–10 × 4–5.	6 celled, each 2–6 × 4.	6–7 celled.	5–7 celled, 9–10 × 5.	4–7 celled.	4–7 celled.	
Pore (in surface view)	7–8 rosette cells sunken, wider than the surrounding roof cells.	11–12 rosette cells sunken, similar to the surrounding roof cells.	8 rosette cells sunken, smaller than the surrounding roof cells.	8–12 rosette cells sunken, smaller, similar or “thinner-wider” than the surrounding roof cells.	6–12 rosette cells somewhat raised, similar or “thinner-wider” than the surrounding roof cells.	4–6 rosette cells wider than the surrounding roof cells.	8–9 rosette cells not sunken, similar to the surrounding roof cells.	
Tetrasporangia/bisporangia (length × diameter, µm)	130–190 × 50–95	75–130 × 200–240	60–140 × 25–100	180–300 × 50–150	180–500 × 90–250	60–100 × 20–40	70–145 × 29–70	
Buried conceptacles	Unattached as maërl (rhodolith). Subtidal.	Epilithic, epiphytic, unattached as maërl (rhodolith). Subtidal.	Epilithic. Subtidal.	Epilithic. Subtidal.	Epiphytic, epilithic, epizoic, unattached as maërl (rhodolith). Lower intertidal to subtidal.	Epilithic, Upper subtidal.	Epiphytic, epilithic, epizoic. Intertidal to subtidal.	
Habitat	Galicia, NW Spain.	Atlantic and Mediterranean.	Atlantic (Macaronesian region).	Atlantic and Mediterranean.	Atlantic and Mediterranean.	Mediterranean (Aegean Sea).	Mediterranean.	
Distribution in Europe								

Data from: 1, Foslie (1929); 2, Lemoine (1929); 3, Masaki (1968); 4, Woelkerling (1983); 5, Woelkerling and Irvine (1986); 6, Reyes and Afonso-Carrillo (1993); 7, Woelkerling and Harvey (1993); 8, Basso (1994); 9, Irvine and Chamberlain (1994); 10, Cabioch and Mendoza (1998); 11, Athanasiadis (1999); 12, Bressan and Babbini (2003); 13, Cabioch and Mendoza (2003); 14, Harvey et al. (2003); 15, Harvey et al. (2005); 16, Athanasiadis and Neto (2010); and 17, present study. ND, no data available.

TABLE 2. Comparative table between *Mesophyllum sphaericum* and other *Mesophyllum* species reported in the literature as unattached specimens (maërl/rhodolith).

	<i>M. sphaericum</i> <sup>18</sup>	<i>M. aleuticum</i> <sup>12</sup>	<i>M. crassiusculum</i> <sup>12,17</sup>	<i>M. engelhartii</i> <sup>6, 8,9,15,17</sup>	<i>M. erubescens</i> <sup>1-7,9-11,13-18</sup>	<i>M. sphaeroides</i> <sup>3,5,15,16</sup>
Thallus form and anatomical organization	Fruticose, densely branched. Radial.	Foliose, surface smooth, without protuberances.	Lumpy with irregular terete, unbranched protuberances.	Encrusting, warty with short unbranched protuberances, or foliose, partly or entirely attached.	Fruticose, warty, lumpy, discoid, layered to foliose.	Encrusting, sometimes with overgrowing margins.
Epithallial cells (surface view)	Polygonal, thick walled.	ND	ND	ND	Thin walled.	ND
Outermost walls of epithallial cells (in section, $\mu\text{m}$ )	Single layer, rounded to flattened, 1-2 $\times$ 3-10.	Up to 2 layers, flattened, 2-5 $\times$ 5-9.	Up to 3 layers, flattened to flared-like, 2-5 $\times$ 3-9.	Single layer, flattened to domed, 3-9 $\times$ 3-5.	Single layer, flattened, rounded, domed, 2-10 $\times$ 4-12.	1-2 layers, rounded, 2-4 $\times$ 4-8.
Subepithallial initials ( $\mu\text{m}$ )	As long as or longer than cells subtending them, 6-10 $\times$ 2-7.	As long as cells subtending them, 4-8 $\times$ 4-7.	As long as or longer than cells subtending them.	As long as or longer than cells subtending them.	As long as or longer than cells subtending them, 6-21 $\times$ 4-10.	Not markedly elongate, 3-7 $\times$ 3-5.
Medulla (radial longitudinal section, $\mu\text{m}$ )	Arching tiers (coaxial), up to 1,300 $\mu\text{m}$ thick, cells cylindrical 10-15 $\times$ 5-7.	Coaxial, up to 155 $\mu\text{m}$ thick, cells 9-42 $\times$ 4-11.	Coaxial, up to 300 $\mu\text{m}$ thick, cells 10-31 $\times$ 5-13.	Coaxial to noncoaxial, cells 11-50 $\times$ 4-19.	Coaxial to noncoaxial, up to 170 $\mu\text{m}$ thick, cells 5-49 $\times$ 3-15.	Parallel to coaxial, 20-75 $\mu\text{m}$ thick, cells 10-20 $\times$ 5-9.
Cortex (radial longitudinal section, $\mu\text{m}$ )	Up to 700 $\mu\text{m}$ thick, cells 5-18 $\times$ 3-10.	Up to 1,200 $\mu\text{m}$ thick, cells 5-14 $\times$ 4-8.	Up to 800 $\mu\text{m}$ thick, cells 4-23 $\times$ 4-9.	Cells 5-20 $\times$ 2-11.	Up to 500 $\mu\text{m}$ thick, cells 6-35 $\times$ 4-15.	Multilayered, cells rounded 5-15 $\times$ 3-9.
Trichocytes	-	+	-	Sometimes present, isolated or in small fields.	Rare to abundant, isolated or in groups, 7-19 $\times$ 7-18.	Occasional.
Spermatangial uniporate conceptacles (chamber diameter, $\mu\text{m}$ )	ND	40-175 $\times$ 235-785.	ND	Protruding, 21-108 $\times$ 54-442.	Slightly raised, 31-120 $\times$ 80-420.	ND
Carpoporangial uniporate conceptacles (chamber diameter, $\mu\text{m}$ )	Protruding, conical, 121-300 $\times$ 395-516.	Protruding, conical, 205-290 $\times$ 435-720.	ND	Slightly to markedly prominent, 48-230 $\times$ 189-520.	Protruding, conical, 75-350 $\times$ 213-550.	ND

TABLE 2. Continued.

	<i>M. sphaericum</i> <sup>18</sup>	<i>M. alenticum</i> <sup>12</sup>	<i>M. crassiusculum</i> <sup>12,17</sup>	<i>M. engelhardtii</i> <sup>6, 8,9,15,17</sup>	<i>M. erubescens</i> <sup>1-7,9-11,13-18</sup>	<i>M. siphonoides</i> <sup>3,5,15,16</sup>
Multiporate asexual conceptacles (chamber measures, height × diameter, µm)	Protruding, mound-like, flat topped without peripheral raised rim, 143–300 × 225–540.	Protruding, mound-like to flattened roof, without peripheral raised rim, 165–320 × 420–720.	Protruding, mound-like to flattened roof, without peripheral raised rim, 130–190 × 250–410.	Protruding, mound-like to flattened roof without peripheral raised rim, 65–260 × 160–500.	Protruding, mound-like to flattened roof, without peripheral raised rim, 60–300 × 140–655.	Protruding, raised, domed without peripheral raised rim, 70–120 × 150–350.
Roof thickness of multiporate conceptacles (µm)	40–80	50–95	40–70	24–104	25–38	ND
Number of pores of multiporate conceptacles	30–50	Up to 130	36–50	60–70	14–75	20–40
Pore canal filament (in section, µm)	5–6 celled; basal cell elongate 5–10 × 2–4, upper cells 2–6 × 4–6.	6–9 celled; basal cell elongate and thinner.	6–8 celled, similar to the remainder of the roof filaments.	4–6 celled, similar to the remainder of the roof filaments, each 3–10 × 3–6	3–5 celled; basal cells elongate, banana shaped 5–25 × 2–6.	4–6 celled, similar to the remainder of the roof filaments
Rest of the roof filaments (in section, µm)	5–6 celled, each 3–5 × 4–6.	5–9 celled.	7–8 celled.	4–6 celled squarish to elongate	4–7 celled.	ND
Pore (in surface view)	7–8 rosette cells sunken, wider than surrounding roof cells.	6–9 rosette cells sunken, similar to surrounding roof cells.	6–10 rosette cells not sunken, similar to surrounding roof cells.	5–9 rosette cells not sunken, similar surrounding roof cells.	7–13 rosette cells sunken, smaller than surrounding roof cells.	ND
Tetrasporangia/bisporangia (length × diameter, µm)	130–190 × 50–95	90–290 × 20–125	110–200 × 25–70	65–120 × 22–104	55–230 × 30–140	80–90 × 25–45
Buried conceptacles	Unattached as maërl (rhodolith).	Epilithic, rarely unattached fragments.	Epilithic, occasionally unattached.	Epilithic, epizoic and epiphytic, unattached as maërl (rhodolith).	Epilithic, epizoic and epiphytic, unattached as maërl (rhodolith).	Epilithic, unattached as maërl (rhodolith).
Habitat	Subtidal.	Intertidal to subtidal.	Intertidal.	Intertidal to subtidal.	Intertidal to subtidal.	Subtidal
Distribution	Galicia, NW Spain.	NE Pacific (Alaska).	Pacific (California, Japan).	Atlantic (Namibia, South Africa), Pacific (Australia, New Zealand).	Atlantic (Brazil, South Africa), Indian Ocean (Tanzania, Indonesia), and Pacific (Australia, New Zealand, Japan).	Pacific (Hawaii) and Indian Ocean (Indonesia).

Data from: 1, Foslie (1929); 2, Masaki (1968); 3, Adey et al. 1982; 4, Woelkerling and Harvey (1992); 5, Verheij (1993); 6, Woelkerling and Harvey (1993); 7, Keats and Chamberlain (1994); 8, Chamberlain and Keats (1995); 9, Keats and Maneveldt (1997); 10, Ringeltaube and Harvey (2000); 11, Harvey et al. (2003); 12, Athanasiadis et al. (2004); 13, Harvey et al. (2005); 14, Oliveira et al. (2005); 15, Harvey and Woelkerling (2007); 16, De Castro et al. (2008); 17, Guiry and Guiry (2009); and 18, present study. ND, no data available.

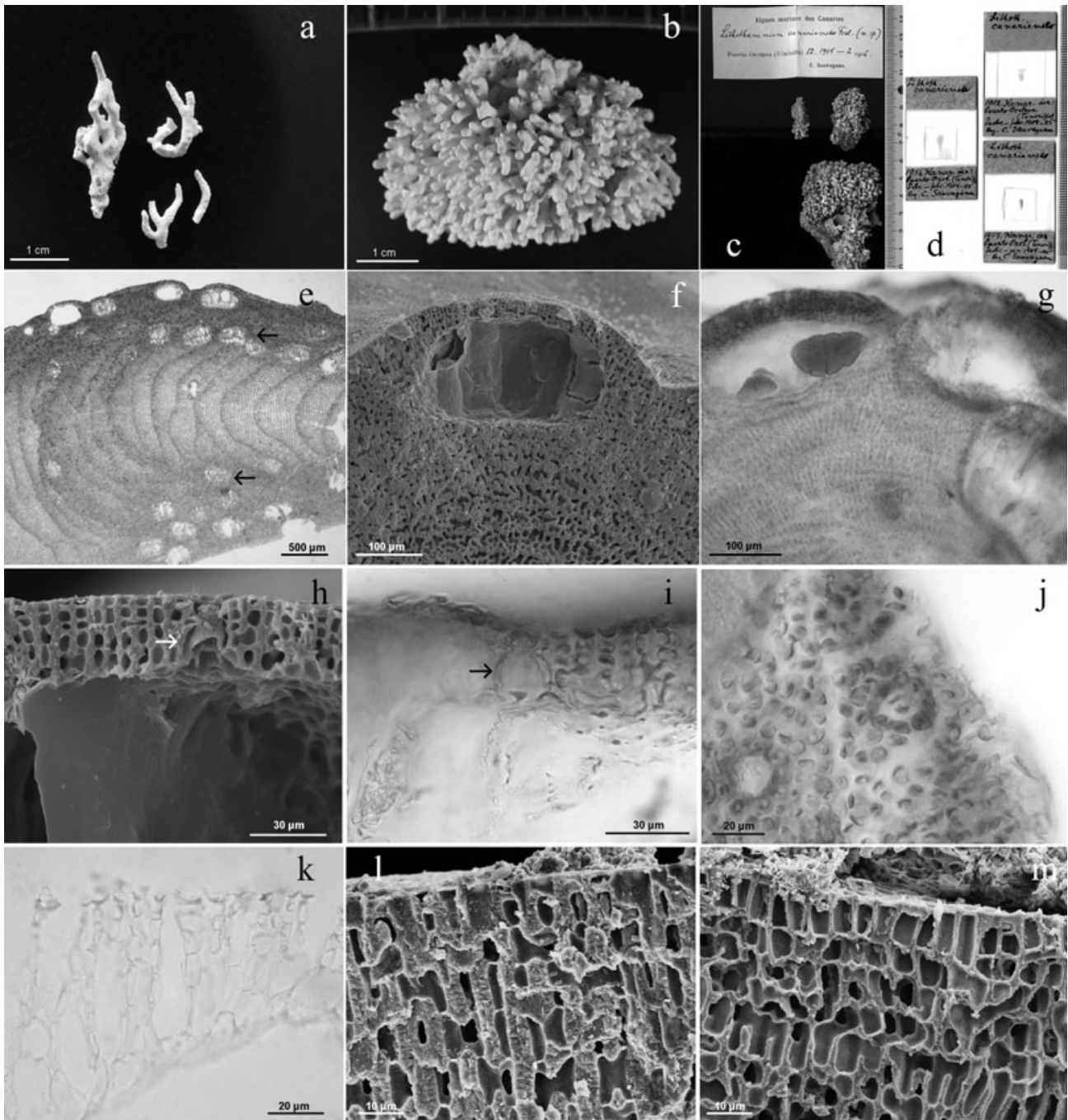


FIG. 4. *Mesophyllum canariense* (a–l) and *M. erubescens* (m). (a, b) Herbarium specimens (TFC Phyc 13118 and 13206) without basal crust region showing abundant protuberances, in some parts anastomosed. (c, d) Holotype of *M. canariense* (TRH C15-3210 and permanent slides 1012, 1056, 1057). (e) Holotype of *M. canariense* (TRH, permanent slide 1012) showing the coaxial arrangement of the medulla and infilled multiporate conceptacles, arrows (LS). (f, g) Branches showing multiporate asexual conceptacles mound-like, containing tetrasporangia (VS, f: SEM). (h, i) Multiporate asexual conceptacle showing pore canal filaments 4 celled with basal cell elongate, banana shaped, arrows (VS, h: SEM). (j) Surface view of the pore plate of multiporate asexual conceptacles showing a pore surrounded by 8 rosette cells sunken and smaller than the rest of roof cells. (k) Holotype of *M. canariense* (JAC slide 59-523) showing outermost walls of epithallial cells flared (LS). (l) Isotype of *M. canariense* (FT-139) showing a thick-walled cortex (LS, SEM). (m) Isotype of *M. erubescens* (FT-148) showing a thin-walled cortex (LS, SEM). LS, longitudinal section; VS, vertical section.

John et al. 2003), but information is lacking on the pore canal filaments in the latter species. The examination of herbarium material of *M. canariense*

(Fig. 4, a–l) showed that the pore filaments are 4 celled (Fig. 4, h and i), composed of narrow and elongate banana-shaped basal cells (basal cells

11–15  $\mu\text{m} \times 3\text{--}4 \mu\text{m}$ , upper cells 4–6  $\mu\text{m} \times 3\text{--}4 \mu\text{m}$ ), whereas the remainder of the roof filaments are 6 celled, 2–6  $\mu\text{m} \times 4 \mu\text{m}$ . In surface view, each pore is surrounded by 8 rosette cells that are sunken and smaller than the remainder of the roof cells (Fig. 4j). In addition, the outermost walls of epithallial cells of the specimens of *M. canariense* studied, including the holotype (basal crust region and protuberances), were flared (Fig. 4k), agreeing with the subtriangular shape described by Masaki (1968) for specimens recorded from the Japanese coast. Spermatangial conceptacles have not been observed. Although the occurrence of flared-like epithallial cells was occasionally reported in herbarium specimens of *M. crassiusculum*, *M. lamellatum* (Setch. et Foslie) W. H. Adey, and *M. vancouveriense* (Foslie) Steneck et R. T. Paine from the northern Pacific (Athanasiadis et al. 2004), in *M. canariense* this was a constant feature, over all the specimens studied including the holotype. However, in the absence of gametangial and molecular information on *M. canariense*, which could confirm a new generic position, we retain this species in *Mesophyllum*. Taking into account these observations, *M. sphaericum* showed marked differences with *M. canariense* (Table 1). Likewise, thermogeographic models based on the biogeography of crustose coralline algae (Adey and Steneck 2001) distinctly separates the Iberian Peninsula from the tropical west Atlantic, the latter including the Canary Islands with warmer temperatures (differences of 7°C in winter and 5°C in summer).

Concerning other *Mesophyllum* species in which maërl forms were also reported (Table 2), *M. sphaericum* as well as *M. aleuticum*, *M. crassiusculum*, *M. engelhartii*, *M. syrphetodes*, and *M. erubescens* have in common the presence of protruding multiporate conceptacles with mound-like to flattened roofs without peripheral raised rims. However, *M. sphaericum* differs from the remainder of the maërl species in: (i) the number and shape of cells of the pore canal filaments of multiporate conceptacles (5–6 celled with elongate basal cells in *M. sphaericum* vs. 6–9 celled with elongate basal cells in *M. aleuticum*; 6–8 celled similar to the remainder of the roof filaments in *M. crassiusculum*; 4–6 celled similar to the remainder of the roof filaments in *M. engelhartii* and in *M. syrphetodes*; and 3–5 celled with elongate, banana-shaped basal cells in *M. erubescens*; Table 2), (ii) the number of cells in the remainder of the roof filaments (5–6 celled in *M. sphaericum* vs. 5–9 celled in *M. aleuticum*, 7–8 celled in *M. crassiusculum*, 4–6 celled in *M. engelhartii*, and 4–7 celled in *M. erubescens*; Table 2) and (iii) the number and shape of rosette cells surrounding the pores (7–8 cells sunken and wide in *M. sphaericum* vs. 6–9 cells similar to the rest of roof cells in *M. aleuticum*, 6–10 cells similar to the rest of roof cells in *M. crassiusculum*, 5–9 cells not sunken and similar to the rest of roof cells in *M. engelhartii*, and 7–13 cells sunken

and small in *M. erubescens*). In addition, *M. sphaericum* differs from *M. aleuticum*, *M. crassiusculum*, and *M. syrphetodes* in the number of epithallial layers (single layer vs. 2–3). Moreover, trichocytes were absent in *M. sphaericum*.

Nonetheless, our observations indicated that *M. canariense* is closely related to *M. erubescens*. In fact, Reyes and Afonso-Carrillo (1993) already pointed out the similarity between this species with the vegetative anatomy of the protuberances reported in *M. erubescens* by Foslie (1904). This species was reported from the Canary Islands as subfossil species (Lemoine 1964), although this record requires reconfirmation (John et al. 2004). On the other hand, *M. erubescens* is a widely distributed species and highly variable in growth form and anatomical features (Table 2). According to the literature, *M. canariense* and *M. erubescens* have in common pore canal filaments with elongate basal cells (4 celled in *M. canariense* vs. 3–5 celled in *M. erubescens*). However, observations also indicated that *M. canariense* differs from *M. erubescens* in the shape of the outermost walls of epithallial cells (flared vs. flattened-domed-rounded; Tables 1 and 2). In addition, the cortex of *M. canariense* is thick walled (Fig. 4l) compared to the thin-walled cortex of the isotype of *M. erubescens* (Fig. 4m).

On the basis of the presence of elongate basal cells bordering the canal pore, *Mesophyllum incisum* (Foslie) W. H. Adey was recently considered a heterotypic synonym of *M. erubescens* (Harvey et al. 2003), despite the fact that both entities differ in the number of sunken rosette cells surrounding the canal pore (6–7 in *M. incisum* vs. 7–9 in the holotype of *M. erubescens*, Keats and Chamberlain 1994). Harvey et al. (2005) also proposed to bring together the complex *M. erubescens*–*M. printzianum*, although both species differ in the shape of multiporate conceptacles (flat topped vs. volcano-like). This complex, which was placed as a separate clade in a phylogenetic study, confirmed the genetic diversity of the current entity *M. erubescens* (Broom et al. 2008). In fact, our SSU data indicated that *M. sphaericum* was closely related with *M. erubescens* from Brazil and *M. erubescens*? from Hawaii, and it was remotely related with *M. erubescens*? from New Zealand.

The taxonomical criteria recently introduced for the genus *Mesophyllum* suggest that the genus and its representative species are taxonomically unstable. Our results agree with recent molecular studies that indicate that further studies are needed to clarify the taxonomic position of *Mesophyllum* species (Broom et al. 2008). Given the apparent instability of many diagnostic features used for species delimitation in this genus, we propose the following combination of characters as reliable diagnostic characters for *M. sphaericum*: (i) growth form (fruticose, spherical, unattached forming maërl/rhodolith); (ii) thalli radially organized; (iii) a single layer

of epithelial cells rounded to flattened in section with polygonal, thick-walled cells in surface view; (iv) medulla strongly coaxial (arching tiers) composed of cells 10–15 × 5–7; (v) cortical cells 7–18 × 3–10; (vi) trichocytes absent; (vii) multiporate conceptacles protruding, flat topped without a peripheral raised rim; (viii) multiporate conceptacles perforated by 30–50 pores; (ix) pore canal liner filaments 5–6 celled and composed of elongate and straight basal cells; (x) the remainder of the roof filaments 5–6 celled; (xi) 7–8 surface rosette cells sunken and wider than rest of roof cells; and (xii) buried conceptacles not infilled with new tissue.

The occurrence of *M. sphaericum*, which is presently restricted to a unique Galician maërl bed, should be taken into account in further conservation plans for the European maërl beds. Conservation measures for the maërl bed off Benencia Island (Ría de Arousa, Galicia, Spain) are required to protect this species and type locality; conservation for this species and the study area have already been proposed by Peña and Bárbara (2008a, 2009).

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**Supplementary Material**

The following supplementary material is available for this article:

**Table S1.** Sample information for species included in the molecular analyses.

This material is available as part of the online article.

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