

Insights into the rare Mediterranean endemic *Kallymenia spathulata*: DNA phylogenies resolve this species as Halymeniaceae (Halymeniales) rather than Kallymeniaceae (Gigartinales), with the proposal of *Felicinia spathulata* comb. nov.

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Abstract – The rare endemic Mediterranean alga *Kallymenia spathulata* was collected at Nice and Saint Raphael in June 2013 during a survey conducted along the French Mediterranean coast between Menton and Toulon (French Riviera). DNA barcode sequences (COI-5P) generated from the five collected specimens were identical and allied with *Felicinia marginata*, another Mediterranean endemic that is classified within the Halymeniaceae (Halymeniales) whereas the genus *Kallymenia* is representative of the Kallymeniaceae (Gigartinales). We further confirmed the alliance of *K. spathulata* with *Felicinia marginata* by conducting phylogenetic analyses inferred by combined genes including Cox1, *rbcL* and LSU. Unfortunately, none of the specimens were fertile, precluding emending the description of the reproductive anatomy of this species. In light of our phylogenies, we propose the novel combination *Felicinia spathulata*. The genus *Felicinia* now comprises two species, both endemic to the Mediterranean Sea.

COI-5P / DNA Barcode / endangered / endemic / *Felicinia* / Gigartinales / Halymeniaceae / Halymeniales / Mediterranean Sea / Kallymeniaceae / LSU / *rbcL* / Rhodophyta

INTRODUCTION

In recent years, efforts to generate molecular data from species of *Kallymenia* have significantly enhanced our understanding of the diversity of this genus (Vergés *et al.*, 2014; Robuchon *et al.*, 2014; Huisman *et al.*, 2016; Saunders *et al.*, 2017). Two new species have been described for Europe: *Kallymenia ercegovicii* Vergés & Le Gall (Vergés *et al.*, 2014) from the Mediterranean Sea and *Kallymenia crouaniorum*

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Vergés & Le Gall (Robuchon *et al.*, 2014) inhabiting the Atlantic. A comprehensive phylogeny of the family Kallymeniaceae Kylin (Saunders *et al.*, 2017) showed that the latter species did not join the type species of *Kallymenia*, *K. reniformis* (Turner) J.Agardh, and a new genus and new combination, *Nothokallymenia crouaniorum* (Vergés & Le Gall) A.Vergés & L.Le Gall were proposed. Similarly, the Indonesian and Australian taxon, *Kallymenia maculata* Weber-van Bosse, was not allied with *K. reniformis* and the new genus and combination, *Rhytymenia maculata* (Weber-van Bosse) Huisman & G.W.Saunders were erected (Huisman *et al.*, 2016). Among the European species of *Kallymenia* included in the comprehensive phylogeny, only *K. patens* (J. Agardh) Codomier, *K. feldmannii* Codomier, and *K. ercegovicii* joined *K. reniformis* (Saunders *et al.*, 2017). In the latter study, *Kallymenia lacerata* Feldmann formed a distinct lineage for which a new genus and a new combination were proposed, *Verlaquea lacerata* (Feldmann) L.Le Gall & A.Vergés. *Kallymenia requienii* (J.Agardh) J.Agardh joined *Cirrucarpus australis* Womersley & R.E.Norris as well as *K. tasmanica* Harvey and the genus *Euhymenia* was resurrected as well as the species *Euhymenia requienii* (J.Agardh) Kützing.

With the aim of including all species of *Kallymenia* known from the Mediterranean Sea, we sought to generate sequences for *Kallymenia spathulata* (J.Agardh) Codomier ex P.G.Parkinson, a Mediterranean endemic that is listed among the species “endangered or threatened species” which appears in annex II to the Protocol of the Barcelona Convention, concerning Specially Protected areas and biological diversity in the Mediterranean (UNEP, 2013). Records of this taxon from around the Mediterranean Sea have been restricted to a few localities from Spain, France, Italy and Croatia (Vergés, 2001). *Kallymenia spathulata* has been recorded from depths ranging from 50 to 90 m (lower infralittoral and the circalittoral zone), growing most often on maerl beds, and also on coralligenous outcrops (Vergés, 2001). In the middle of the 20th century the species was abundant in Marseille, forming part of rich, biodiverse assemblages on maerl bottoms (Costa, 1960). The species has also been reported to occur on soft sediments (Augier & Boudouresque, 1978) along with *Calliblepharis cilliata* (Hudson) Kützing, *Cryptonemia tunaeformis* (Bertoloni) Zanardini and *Lithothamnion corallioides* (P.Crouan & H.Crouan) P.Crouan & H.Crouan. *Kallymenia spathulata* was described as an emblematic species of the “Détritiques côtier” in the Habitat Repository (‘INPN-HABREF repository’ n.d.) concerning the “Typologie des biocénoses benthiques de Méditerranée “under the reference “IV.2.2.f. – Association à *Kallymenia spathulata* (Syn. *Halarachnion spatulatum*)” (Michez *et al.*, 2014).

In the course of a floristic survey between Menton and Toulon, we were fortunate to find five specimens of *Kallymenia spathulata*, from which we generated DNA sequences (CO1 for each and rbcL & LSU for one specimen). Unexpectedly, these sequences allied *K. spathulata* with the Halymeniaceae (Halymeniales) rather than with the Kallymeniaceae (Gigartinales). The aim of the present manuscript is therefore to assess the phylogenetic affinities of *K. spathulata* within the Halymeniaceae.

MATERIALS AND METHODS

Sample collection

Specimens observed in this study are listed in Table 1; they were collected during a cruise organized by Andromède Oceanology between Menton and Toulon in June 2013. The collected material was pressed as herbarium specimens and

Table 1. List of specimens of *Feliciinia spathulata* studied

ID	Herb. Num.	Collector	Date	Region	Locality
–	H3146	Huvé, P. & Huvé, H.	18/07/1953	Marseille Gulf	Marseille
–	H3147	Huvé, P. & Huvé, H.	26/05/1955	Marseille Gulf	Marseille, – 65 m
–	H3148	Huvé, P. & Huvé, H.	26/05/1955	Marseille Gulf	Marseille, – 65 m
–	HGI-A4307	Ballesteros, E.	22/06/1999	Columbretes Islands	I. Columbretes gran, – 44 m
LLG4860	PC0144609	Le Gall, L.	5/06/2013	Alpes maritimes, French Riviera	Le tombant des Americains, Nice, – 44 m
LLG4972	PC0144721	Le Gall, L.	7/06/2013	Var, French Riviera	Agay-Saint Raphael, – 40 m
LLG4972	PC0144721	Le Gall, L.	7/06/2013	Var, French Riviera	Agay-Saint Raphael, – 40 m
LLG4972	PC0144721	Le Gall, L.	7/06/2013	Var, French Riviera	Agay-Saint Raphael, – 40 m
LLG4972	PC0144721	Le Gall, L.	7/06/2013	Var, French Riviera	Agay-Saint Raphael, – 40 m
LLG4975	PC0144724	Le Gall, L.	7/06/2013	Var, French Riviera	Agay-Saint Raphael, – 40 m
LLG4976	PC0144725	Le Gall, L.	7/06/2013	Var, French Riviera	Agay-Saint Raphael, – 40 m
LLG4977	PC0144726	Le Gall, L.	7/06/2013	Var, French Riviera	Agay-Saint Raphael, – 40 m

fragments of plants were preserved in silica gel for DNA extraction. Voucher specimens (Table 1) are housed in the Herbarium of the Muséum National d'Histoire Naturelle of Paris, France (PC) [Herbarium abbreviation following Thiers (2014)]. In addition, specimens referred to as *Kallymenia spathulata* housed in the Herbarium from the University of Girona, Spain (HGI), the P. & H. Huvé from the Aix Marseille University, France and the lectotype located in the Botanical Museum, Sweden (LD 22382) were examined.

Anatomy and morphology

Anatomical features were observed in sections made by hand with a razor blade and subsequently stained in a 1% acidified aniline-blue/distilled water solution. Habit views were reproduced with a HP Officejet 6500A scanner (Hewlett-Packard, Palo Alto, CA, USA); photomicrographs were taken with an MRC5 (Zeiss, Berlin, Germany) attached to an Axio Imager A2 microscope (Zeiss, Berlin, Germany).

Molecular sequencing

DNA extraction, PCR and sequencing reactions were performed following the protocol as described in Vergés *et al.* (2014). Purification and sequencing reactions were performed by Eurofins Genomics (Paris, France). Forward and reverse electropherograms were edited and assembled with the software Codoncode (Dedham, Massachusetts, USA). Sequence data of the COI-5P region were generated for all newly collected specimens, while *rbcL* and *LSU* genes have been generated only for one specimen (LLG4860, Table 2), having all samples a full sequence identity for the COI-5P region. Obtained sequences were submitted to BOLD (<http://www.barcodinglife.org>) and to GenBank. Accession numbers are given in Table 2.

Table 2. GenBank accession numbers for the sequences generated in the present study

<i>ID</i>	<i>Cox1</i>	<i>rbcL</i>	<i>LSU</i>
LLG4860	MG648482	736bp	2610bp
LLG4972	MG648481	MG648477	MG648476
LLG4975	MG648480	–	–
LLG4976	MG648479	–	–
LLG4977	MG648478	–	–

Phylogenetic analysis

A blast search for the COI-5P, *rbcL* and LSU genes resulted in hits for species of Halymeniales rather than Kallymeniaceae. As a consequence of their alliance with species of Halymeniales rather than Kallymeniaceae, an alignment was built including the concatenated sequences of LSU and *rbcL* genes of the 21 Halymeniales species recently analysed by Manghisi *et al.* (2017).

Phylogenetic analyses of the combined *rbcL* and LSU alignments were conducted by Bayesian inference using MrBayes version 3.2.1 (Ronquist *et al.*, 2012). ML bootstrap values were calculated using RAXML version 8.0.0 (Stamatakis 2014). For both Bayesian and RAXML analyses, sequence data were partitioned by genes.

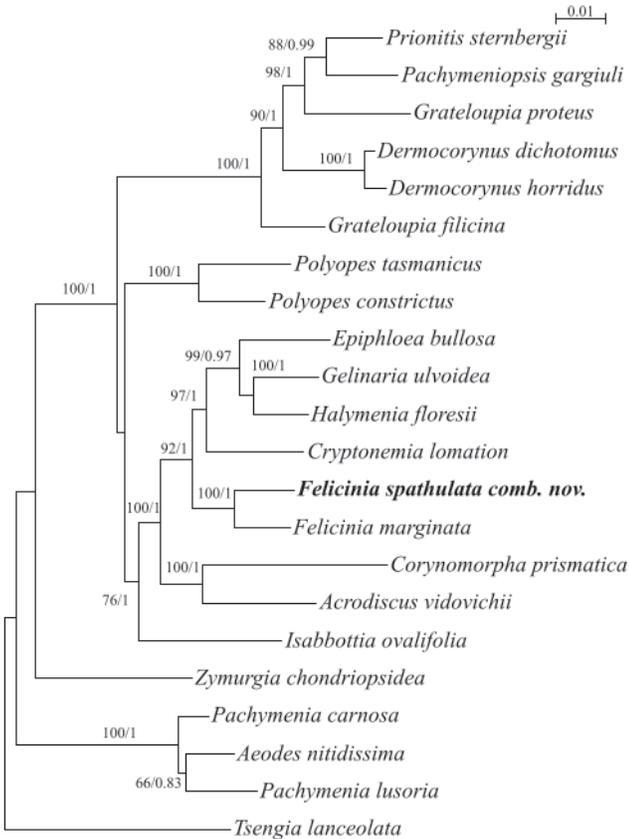


Fig. 1. RaxML phylogenies inferred from the combined alignment of LSU and *rbcL* genes. Support at nodes indicated RaxML bootstraps/Bayesian posterior probabilities. Scale bar: substitutions per site.

RESULTS

Molecular results

The COI-5P sequences obtained for the five specimens of *Kallymenia spathulata* included in this study (Table 2) were identical, indicating that all specimens are conspecific. A blast search of this sequence resulted in hits with the Halymeniales. To further confirm the ordinal placement of *K. spathulata*, we generated *rbcL* and LSU data for the specimen LLG4860 (Table 2) which a BLAST search also placed among the Halymeniales. Therefore, we included the *rbcL* and LSU data within the Halymeniales alignment analysed by Manghisi *et al.* (2017). Phylogenetic analyses of the *rbcL*-LSU concatenated alignment resolved *K. spathulata* as a sister species to *Felicinia marginata* (Roussel) Manghisi, L.Le Gall, Ribera, Gargiulo & M.Morabito with full support. Furthermore, the distance between the two species (4.33% for *rbcL* and 0.93% for LSU) is of the order of magnitude of interspecies variation observed within the family (Manghisi *et al.*, 2015). We therefore propose that *Kallymenia spathulata* should not be maintained in *Kallymenia* and should be transferred to the genus *Felicinia*.

DISCUSSION

Based on our DNA phylogenies we propose the transfer of *Kallymenia spathulata* (J. Agardh) Codomier to the recently described genus *Felicinia* Manghisi, L.Le Gall, Ribera, Gargiulo & M.Morabito (Manghisi *et al.*, 2014), which is a member of the Halymeniaceae (Halymeniales). We here propose the new taxonomic combination:

Felicinia spathulata (J. Agardh) L.Le Gall & A.Vergés *comb. nov.* **Figs 2-6**

Basionym: *Halymenia spathulata* J.Agardh 1842: 96. Type locality: French coast of the Mediterranean Sea (“a profundiori maris Galloprovinciae rejectam”). Lectotype: LD22382 (Fig. 2).

Homotypic synonym: *Halarachnion spathulatum* (J. Agardh) Kützing ex De Toni 1905: 1655 *nom. illeg.*; *Kallymenia spathulata* (J. Agardh) Codomier 1971: 32.

Heterotypic synonyms: *Halarachnion spathulatum* Kützing 1849: 722. Type locality: Mediterranean Sea. Type material: in Kützing Herbarium (L); *Halymenia spathulata* (Kützing) Kützing 1866: 31 *nom. illeg.*

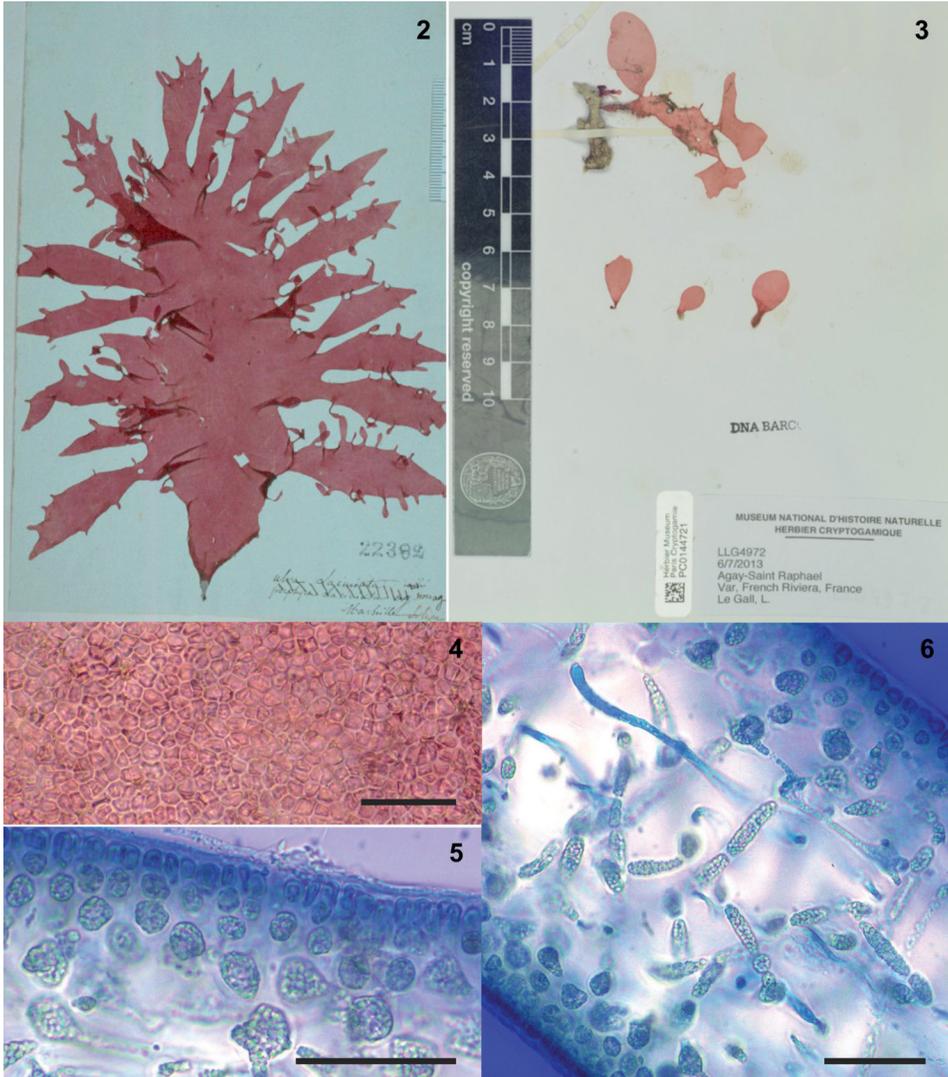
It is noteworthy to mention that two forms of this species have been previously proposed by Ercegovic (1949), and, more recently, combined under the genus *Kallymenia* (Antolic *et al.*, 2013), which can be distinguished by the shape of the frond and the distribution of proliferations, pinnate or irregular, respectively:

– *Halarachnion spathulatum* f. *luxurians* Ercegovic 1849: 35, fig. 16. Type locality: Adriatic sea **with the homotypic synonym:** *Kallymenia spathulata* f. *luxurians* (Ercegovic) Antolic & Span 2013: 57.

– *Halarachnion spathulatum* f. *pennatum* (‘pennata’) Ercegovic 1949: 32, fig. 15. Type locality: Adriatic sea **with the homotypic synonym:** *Kallymenia spathulata* f. *pennata* (Ercegovic) Antolic & Span 2013: 58.

In absence of anatomical and molecular data and observation of type material we refrain of proposing a new combination for these two forms before assessing that they are genuinely conspecific with *Felicinia spathulata*.

The novel placement of *Felicinia spathulata* is close to the original assignment of this species, as Agardh (1842, p. 96) first described it as *Halymenia spathulata* J.Agardh, on the basis of a specimen from Marseille collected by Solier (Agardh, 1842, p. 96) from Marseille (Agardh, 1851, p. 204; Agardh, 1876, p. 139).



Figs 2-6. *Felicinia spathulata* (J.Agardh) L.Le Gall & A.Vergés: habit, morphology and anatomical structure. 2. Lectotype of *Halymenia spathulata* J.Agardh (LD22382). 3. Sequenced specimens collected recently in the French Riviera (LLG4972). 4. Cortex in surface view (HGI-A4307). 5. Cross-section of thallus showing cortical filaments loosely arranged (HGI-A4307). 6. Cross section of the thallus (HGI-A4307). Scale bar = 50 μ m (Figs 3-5).

A few years later, Kützing (1849, p. 722), seemingly independently, also described this taxon based on a Lenormand specimen and placed it in the genus *Halarachnion* Kützing as *H. spathulatum* Kützing, but afterwards referred the species to *Halymenia* (Kützing, 1866, p. 31). Subsequent authors have reported this entity as *Halymenia spathulata* (Zanardini 1871) and also as *Halarachnion spathulatum* (De Toni, 1897; Ercegovic, 1949). It is only relatively recent that Louis Codomier transferred the species to the genus *Kallymenia* (Codomier, 1971).

Morphology and anatomy of *Felicinia spathulata* have been detailed by Codomier (1971) and Vergés (2001). Morphologically, *F. spathulata* and *F. marginata* share some characteristic anatomical features (Table 3), as both have a foliose frond of a relatively large size for the Mediterranean Sea, and a very similar composition and arrangement of cortex and medulla. However, several features serve to distinguish the two species. *Felicinia marginata* is a robust species with a cartilaginous texture, whereas *F. spathulata* is more delicate with a membranous texture (Fig. 3). Transverse sections of *F. spathulata* show a very compact cortex with many anticlinal filaments and a lax medulla with stellate cells intermixed with filaments (Figs 5-6). In transverse sections of *F. marginata* the cortex and medulla are both more loosely arranged than in *F. spathulata*, which contributes to its less rigid consistency.

Reproduction is known only for *Felicinia marginata* (Manghisi *et al.*, 2014), as reproductive structures of *F. spathulata* have not been observed (Vergés, 2001).

In the absence of female reproductive structures, it has not been possible until now to relate *F. spathulata* to existing members of the Halymeniaceae, owing to the importance of carpogonial and auxiliary-cell “ampullae” in the taxonomy of that family (Chiang, 1970; Gargiulo *et al.*, 2013; Saunders & Kraft, 1996).

Table 3. Comparison between morphological characters of *Felicinia marginata* and *F. spathulata*

	<i>F. marginata</i>	<i>F. spathulata</i>
Blade	Laminar, when adult sometimes perforated; cartilaginous texture.	Laminar, many times with spathulate proliferations around the blade; membranous texture.
Size and colour	Up to 30 cm long, purple red	Up to 20 cm long, pinkish
Stipe	Present (up to 5 mm)	Absent
Cortex	Formed by anticlinal filaments compactly arranged, of 5-7 ovoid cells. innermost up to 20 mm	Formed by anticlinal filaments loosely arranged, of 4-5 rounded to ovoid cells, innermost up to 30 mm
Medulla	Lax, with many filaments, interspersed with darkly staining stellate cells.	Lax, with few filaments, interspersed with lightly staining stellate cells
Gametangial structures	Female gametophytes non-procarpic, with carpogonial and auxiliary cell branch situated in <i>ampullae</i> ; male gametophytes unknown	Unknown
Cystocarps	Up to 280 mm wide, lacking an ostiole	Unknown
Tetrasporophyte	Isomorphic; tetrasporangia cruciate	Morphologically identical to sterile blades; tetrasporangia cruciate.
	Manghisi <i>et al.</i> , 2014	Ercegovic 1949; Codomier 1971; Vergés 2001

Halymeniacean vegetative structures are on the contrary quite similar to those of other families within the Gigartinales. As for other halymeniacean taxa where reproductive structure are unknown (Manghisi *et al.*, 2014; Manghisi *et al.*, 2017), even if the anatomy is typically halymeniaceous, only the molecular data are definitive for family placement. Moreover, molecular data contribute to the DNA library of life (Le Gall *et al.*, 2017) and will facilitate future identification of this plant on a molecular ground.

Even if an absence of proof is not a proof of absence, despite numerous collections along the coast of the Mediterranean Sea in Spain, France, Italy, Croatia and Greece, the only recent records of *F. spathulata* is from the Columbretes Islands, Spain (HGI-A4307, legit E. Ballesteros) and the two French sites reported in this study. Similarly, E. Ballesteros (personal communication) has not observed the species in the Mediterranean in the last 20 years. In both cases, the species was found on coralligenous outcrops around 40 m depth, and not on soft bottom as reported by Augier & Boudouresque (1978). This may be due to the fishing pressure on soft bottom which may have disturbed the habitat of *F. spathulata* and relegated it to the hard bottom. In light of our scarce collection, we recommend that *Felicinia spathulata* should be maintained on the list of endangered species.

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