PHYLOGENETIC RELATIONSHIPS OF CORALLINACEAE (CORALLINALES, RHODOPHYTA): TAXONOMIC IMPLICATIONS FOR REEF-BUILDING CORALLINES[1]

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A new, more complete, five-marker (SSU, LSU, *psb*A, COI, 23S) molecular phylogeny of the family Corallinaceae, order Corallinales, shows a paraphyletic grouping of seven well-supported monophyletic clades. The taxonomic implications included the amendment of two subfamilies, Neogoniolithoideae and Metagoniolithoideae, and the rejection of Porolithoideae as an independent subfamily. Metagoniolithoideae contained *Harveylithon* gen. nov., with *H. rupestre* comb. nov. as the generitype, and *H. canariense* stat. nov., *H. munitum* comb. nov., and *H. samoënse* comb. nov. *Spongites* and *Pneophyllum* belonged to separate clades. The subfamily Neogoniolithoideae included the generitype of *Spongites, S. fruticulosus,* for which an epitype was designated. *Pneophyllum* requires reassesment. The generitype of *Hydrolithon, H. reinboldii,* was a younger heterotypic synonym of *H. boergesenii.* The evolutionary novelty of the subfamilies Hydrolithoideae, Metagoniolithoideae, and Lithophylloideae was the development of tetra/bisporangial conceptacle roofs by filaments surrounding and interspersed among the sporangial initials.

Key index words: coral reef; Corallinales; coralline algae; Hydrolithoideae; Mastophoroideae; Metagoniolithoideae; molecular phylogeny; Neogoniolithoideae

The ongoing scientific interest in coralline algae is based on many factors, from their ecological importance in various shallow marine habitats (Nelson 2009) through their sensitivity to climate change and ocean acidification (Hall-Spencer et al. 2008, Burdett et al. 2012, Diaz-Pulido et al. 2012, Kato et al. 2014, McCoy and Kamenos 2015), to their use as paleoenvironmental indicators (Braga et al. 2010, Abbey et al. 2011, Aguirre et al. 2012, Novak et al. 2013). Coralline red algae are important components in many shallow-water marine ecosystems (Adey and Mcintyre 1973, Adey 1986). They are major builders in coral reefs (Littler and Littler 1984, Mallela 2013) and contribute significantly to the preservation of reef health and biodiversity (Morse et al. 1996, reviewed in Nelson 2009, Vermeij et al. 2011). The main coralline reef builders are members of the order Corallinales, family Corallinaceae, that are predominant in the fossil record (since the Miocene) and on recent coral reefs to a depth of ~50 m (Adey et al. 1982, Braga et al. 2010).

Despite their significance, the taxonomy of coralline algae is not resolved at any rank, although it has been subject to continuous debate since the 19th century (Johansen 1981, Woelkerling 1988, Le Gall et al. 2010, Bittner et al. 2011, Kato et al. 2011, Woelkerling et al. 2012). Recent systematic work based on multigene analyses resulted in the separation of the new order Hapalidiales from Corallinales sensu Silva and Johansen (1986), characterized by multiporate and uniporate tetrasporangial conceptacles, respectively (Nelson et al. 2015). Coralline algae show extreme phenotypic plasticity dependent on external factors (Steneck 1986, Woelkerling 1988, Braga et al. 1993, Woelkerling et al. 1993a, Farr et al. 2009) and, on the other hand, they possess a relatively simple thallus with limited morphoanatomical character variation. Several

diagnostic features (e.g., gametangial conceptacle primordia or developing gametangial conceptacles) are rarely observed in samples with the added difficulty that sample preparation to detect those features is arduous (Woelkerling 1988, Farr et al. 2009). Woelkerling (1988) (pp. 62–73 and table 5.2) listed the characters historically considered delimiting for subfamilies and genera and proposed a classification scheme for both taxonomic ranks. Since this seminal publication, the diagnostic features and circumscription of a number of genera and subfamilies have changed (Harvey et al. 2003, Le Gall and Saunders 2007, Le Gall et al. 2010, Kato et al. 2011, Adey et al. 2015), demonstrating that even at the subfamily rank the taxonomy of coralline algae is still unresolved (Bittner et al. 2011, Woelkerling et al. 2012).

As stated by Harvey et al. (2003), one of the main impediments to classifying coralline taxa is to determine which morphological characters result from homoplasy and which from common ancestry. The uncertainties in the answers to this question led to the proposal of very different classification schemes during the last decades (e.g., Adey 1965, Cabioch 1971, Bailey 1999, Le Gall et al. 2010, Nelson et al. 2015). However, molecular phylogenetics is now providing new insights into biological systematics. In fact, in the last 10 years the use of molecular tools in phylogeny and species identification has seen a sharp increase in genetic sequences of coralline algae available in GenBank. In 2003, for example, the orders Corallinales and Hapalidiales (sensu Nelson et al. 2015) had 38 entries of only the nuclear marker SSU (18S rDNA) (Bailey et al. 2004), which had risen to 5,845 total sequences by 2015, including 463 SSU sequences (http://www.ncbi.nlm.nih.gov/nuccore/, verified 21 October 2015).

Bailey et al. (2004) recognized that the subfamily Mastophoroideae sensu Harvey et al. (2003) was polyphyletic. Later, Bittner et al. (2011) and Kato et al. (2011) analyzed with multigen approaches the new placement of the genera once grouped in this obsolete subfamily within Corallinaceae. Based on two genetic markers, Kato et al. (2011) established the subfamily Porolithoideae, including *Porolithon onkodes* (Heydrich) Foslie, the generitype species, *P. pachydermum* (Foslie) Foslie, and *P. gardineri* (Foslie) Foslie, characterized by horizontal fields of trichocytes without interspersed vegetative cells. The subfamily Hydrolithoideae, whose members lack those "tightly packed" trichocyte fields, was restricted to *Hydrolithon reinboldii* (Weber-van Bosse & Foslie) Foslie. No subfamily, therefore, was assigned to another subclade comprising three other species of *Hydrolithon* (Foslie) Foslie sensu Penrose (1996a): *H. improcerum* (Foslie & M.Howe) Foslie, *H. murakoshii* Iryu & S.Matsuda, and *H. samoënse* (Foslie) Keats & Y.M.Chamberlain that appeared as sister to a clade comprising Metagoniolithoideae, Porolithoideae, and *Pneophyllum*

conicum (E.Y.Dawson) Keats, Y.M.Chamberlain & M.Baba. On the other hand, *H. munitum* (Foslie & M.Howe) Penrose, *H. cymodoceae* (Foslie) Penrose, and *H. rupestre* (Foslie) Penrose were not included in the analyses of Kato et al. (2011).

Using four genetic markers (SSU, LSU, *psbA* and COI), Bittner et al. (2011) also separated *Porolithon* Foslie from *Hydrolithon*. In this work, *Porolithon* comprised those coralline taxa possessing primarily monomerous thalli and trichocytes in large horizontal pustulose fields without interspersed filaments. Woelkerling et al. (2012), however, pointed out that the separation based on horizontal trichocyte fields would be untenable because this character is not present in every specimen, as already stated by Mendoza and Cabioch (1986). In Bittner et al. (2011) and Kato et al. (2011), Metagoniolithoideae was sister to *Porolithon*.

In this study, the phylogeny of Corallinaceae was analyzed with a set of five DNA markers (SSU, LSU, *psbA*, COI, and 23S). SSU was the first marker used in coralline algal phylogeny (Bailey and Chapman 1996) and has been confirmed to be a highly informative marker in phylogenetic studies for a very broad group of organisms (White et al. 1990, Armando Sánchez et al. 2003, Meyer et al. 2010). However, SSU is a conservative marker for coralline algae, showing little variation in shallow phylogenies (Bailey and Freshwater 1997). Later, Broom et al. (2008) also used *psbA*, a plastid gene with substantial variation between genera and between taxa to improve phylogenetic resolution within the order Corallinales. The combination of the first four already showed good resolution of the phylogeny of coralline algae in Bittner et al. (2011). UPA (universal plastid amplicon, 23S) has been used as a fifth marker due to its utility in evolutionary studies and high amplification success (Sherwood and Presting 2007, Clarkston and Saunders 2010). It is able to distinguish species but is also applicable over a broad phylogenetic distance. Herein, we provided new insights in the evolutionary history of Corallinaceae, and clarified some taxonomic uncertainties still remaining in this family.

MATERIALS AND METHODS

Fifty-seven intertidal and subtidal samples were collected, snorkeling and scuba diving in different localities in the Pacific, Indian, and Atlantic Oceans and the Caribbean and Mediterranean Seas (see Table 1 for details). Samples collected by AR and JCB were air-dried for at least one hour and then stored in silica gel that was changed several times until the sample was completely dried. Voucher specimens are stored in the herbarium of the University of Granada (GDA). The rest of the samples were air-dried or oven-dried (50°C), preserved in zipper bags with silica gel, and later deposited in the Muséum National d'Histoire Naturelle (PC), Universidade de Santiago de Compostela (SANT), and Ghent University (GENT) (acronyms follow Thiers 2015). In addition, VP examined the morphoanatomy and sequenced the type material of *Goniolithon accretum* f. *canariensis* Foslie and

TABLE 1. Own specimens used for the study.

Genus	Species	Herbarium voucher	GB access numbers					Collection data
			18S	28S	psbA	COI	23S	Collection date/Region/Country/Locality/Depth/Collector
Amphiroa	sp.	GDA61370	KM073302	KM073344	–	–	–	22/11/2011/Almeria, Spain/Cala de Plomo/5–10 m/A. Rösler
Corallines	sp.	GENT_ODC2235b	–	–	–	KM392375	–	20/09/2012/Madeira/Portugal/Cais de Carvão, Funchal/subtidal/O. De Clerck, M. Kaufman & C. Delgado
Harveylithon	canariensis	PC0533586[1]	–	–	KM407560	–	–	1904–1905/Canary Islands/Spain/Puerto Orotava, Tenerife//C. Sauvageau
Harveylithon	munitum	GDA61348	–	KM073336	KM407531	–	KM073307	18/05/2011/GBR, Australia/One Tree Island/0.2–1 m/A. Rösler
Harveylithon	rupestre	GDA61360	KM073303	–	KM407535	–	KM073335	27/10/2009/Victoria, Australia/Westernport Bay/2 m/A. Harvey
Harveylithon	sp.	GDA61365	KM073273	KM073345	–	–	KM073310	15/01/2005/La Desirade/16° 18' 22" N, 61° 05' 36" W/0–0.5 m/J.C. Braga
Hydrolithon	boergesenii	GDA61364	KP030741	–	KM407537	–	–	15/01/2005/La Desirade/French West Indies/16° 18' 22" N, 61° 05' 36" W/0–0.5 m/J.C. Braga
Hydrolithon	boergesenii	GDA61363	KM073301	–	KM407536	–	–	15/01/2005/La Desirade, French West Indies/16° 18' 22" N, 61° 05' 36" W/0–0.5 m/J. C. Braga
Lithophyllum	acrocamptum	GDA61344	KM073277	KM073338	KM407538	KM392360	KM073311	17/05/2011/GBR, Australia/One Tree Island/0.2–1 m/A.Rösler
Lithophyllum	dentatum	GDA61339	KM073278	–	KP030737	KM392364	KM073311	19/10/2010/Almeria, Spain/Cala Chumba /5–10 m/A. Rösler
Lithophyllum	dentatum	GDA61377	KM073286	KM073353	KM407546	KM392364	KM073320	22/11/2011/Almería, Spain/Cala de Plomo/5–10 m/A. Rösler
Lithophyllum	dentatum	GDA61377	KM073286	KM073353	KM407546	KM392364	KM073320	22/11/2011/Almería, Spain/Cala de Plomo/5–10 m/A. Rösler
Lithophyllum	dentatum	GDA61356	KM073281	KM073339	KM407542	KM392361	KM073315	16/12/2011/Cádiz, Spain/La Gallega/0.5 m/J.C. Braga
Lithophyllum	dentatum	GDA61355	KM073280	KM073349	KM407541	KM392356	KM073314	16/12/2011/Cádiz, Spain/La Gallega/0.5 m/J.C. Braga
Lithophyllum	dentatum	GDA61349	KM073279	KM073348	KM407539	–	KM073312	26/11/2006/Almeria, Spain/Cala del arco/1 m/D. Moreno
Lithophyllum	incrustans	GDA61354	KM073283	KM073351	KM407543	KM392363	KM073317	16/12/2011/Cádiz, Spain/La Gallega/0.5 m/J.C. Braga
Lithophyllum	incrustans	GDA61376	KM073285	–	KM407544	KM392365	KM073319	22/11/2011/Almería, Spain/Cala de Plomo/5–10 m/A. Rösler
Lithophyllum	incrustans	GDA61375	KM073284	KM073352	–	KM392357	KM073318	22/11/2011/Almería, Spain/Cala de Plomo/5–10 m/A. Rösler
Lithophyllum	incrustans	GDA61353	KM073282	KM073350	KM407545	KM392362	KM073316	16/12/2011/Cádiz, Spain/La Gallega/0.5 m/J.C. Braga
Lithophyllum	insipidum	GDA61341		KM977985	–	–	–	15/11/2006/Kenya/Diani/0–2 m/Jennifer O'Leary
Lithophyllum	kotschyanum	GDA61367		KM977984	–	–	KM073323	18/05/2011/GBR, Australia/One Tree Island/0.2–1 m/A. Rösler

(continued)

TABLE 1. (continued)

| Genus | Species | Herbarium voucher | GB access numbers | | | | | Collection data |
			18S	28S	psbA	COI	23S	Collection date/Region/Country/ Locality/Depth/Collector
Lithophyllum	kotschyanum	GDA61351	KM073296	KM977983	KM407548	–	–	18/05/2011/GBR, Australia/One Tree Island/0.2–1 m/A. Rösler
Lithophyllum	kotschyanum	GDA61350	KM073287	KM073354	KM407547	KP030740	KM073321	17/05/2011/GBR, Australia/One Tree Island/0.2–1 m/A. Rösler
Lithophyllum	kotschyanum	GDA61362	KM073288	–	KM407549	–	KM073322	15/11/2006/Kenia/Mombasa/0–2 m/J. O'Leary
Lithophyllum	kotschyanum	GDA61368	KM073289	–	KM407550	–	KM073324	18/05/2011/GBR, Australia/One Tree Island/0.2–1 m/A. Rösler
Lithophyllum	pustulatum	GDA61379	KM073290	KM073340	KM407551	–	KM073327	15/08/2000/Canary Islands/Spain/Punta de Hidalgo Tenerife/0.5 m/J.C. Braga
Lithophyllum	racemus	GDA61340	KM073291	–	KM407552	KM392366	KM073325	19/10/2010/Almería, Spain/Cala Chumba /5–10 m/A. Rösler
Lithophyllum	racemus	GDA61357	KM073292	KM073343	–	–	KM073326	22/11/2011/Almería, Spain/Cala de Plomo/5–10 m/A. Rösler
Lithophyllum	racemus	GDA61358	–	KM073341	KP030736	–	–	22/11/2011/Almería, Spain/Cala de Plomo/5–10 m/A. Rösler
Lithophyllum	stictaeforme	GDA61337	KM073293	KM073357	KM407553	KM392367	–	19/10/2010/Almería, Spain/Cala Chumba/5–10 m/A. Rösler
Lithophyllum	stictaeforme	GDA61372	KM073304	KM073362	KM407554	–	–	22/11/2011/Almería, Spain/Cala de Plomo/5–10 m/A. Rösler
Neogoniolithon	brassica-florida	SANT-Algae 29040	–	–	–	KM392368	–	08/05/2011/Archipel de Frioul/France/ Sur Île Ratonneau/1 m/I. Bárbara & M. Verlaque
Neogoniolithon	fosliei	GDA61361	KM073295	–	KM407556	KM392358	KM073328	15/11/2006/Kenia/Vipingo/0–2 m/ J. O'Leary
Neogoniolithon	fosliei	GDA61345	KM073294	KM073358	KM407555	–	–	17/05/2011/GBR, Australia/One Tree Island/0.2–1 m/A. Rösler
Neogoniolithon	frutescens	GDA61369	KM073297	KM073359	–	KM392371	KM073329	15/10/2007/Moorea/17° 29′ 20″ S, 149° 54′ 47″ W/0–10 m/J.C. Braga
Neogoniolithon	sp.2	PC0144045				KM392372		03/05/2012/Guadeloupe, French West Indies/Île de Gosier, Petit Cul-de-Sac marin /6 m/F. Rousseau, Y. Buske, J. Espinosa & D. Guillaume (Expedition Karubenthos)
Neogoniolithon	sp.	PC0533585			KP682501	KP689495		10/05/2012/Guadeloupe, French West Indies/Petit-Havre, Le Gosier/1 m/C. Laurent, P. Rémy, J. Poupin, F. Rousseau, G. Dirberg & S. Soubzmaigne (Expedition Karubenthos)
Neogoniolithon	sp.	GDA61374	KM073299	KM977987	KM407558	–	KM073330	22/11/2011/Almería, Spain/Cala de Plomo/5–10 m/A. Rösler
Neogoniolithon	sp.	SANT-Algae 29041				KM392370		18/04/2011/Panama/Cayos Holandeses/ subtidal/J.Cremades
Neogoniolithon	sp.	GDA61346	KM073298	KM073337	KM407557	–	–	17/05/2011/GBR, Australia/One Tree Island/0.2–1 m/A. Rösler

TABLE 1. (continued)

Genus	Species	Herbarium voucher	GB access numbers					Collection data Collection date/Region/Country/ Locality/Depth/Collector
			18S	28S	psbA	COI	23S	
Neogoniolithon	sp.	GDA61378	KM073300	KM073360	KM407559	–	KM073331	22/11/2011/Almería, Spain/Cala de Plomo/5–10 m/A. Rösler
Neogoniolithon	strictum	GDA61366	–	–	–	–	KM073332	15/01/2005/La Desirade/16° 18' 22" N, 61° 05' 36" W/0–0.5 m/J.C. Braga
Pneophyllum	confervicola	GDA61373	KM073305	KM977988	KP030738	KM392373	KM073334	22/11/2011/Almería, Spain/Cala de Plomo/5–10 m/A. Rösler
"*Pneophyllum*"	conicum	GDA61343	–	–	KM407561	–	KM073333	17/05/2011/GBR, Australia/One Tree Island/0.2–1 m/A. Rösler
"*Pneophyllum*"	sp.	PC0166760	–	–	KP682500	KP682497	–	14/05/2010/Madagascar/Andavak/0–1 m/F. Rousseau, R. Anderson & J.T. Tsarahevitra (Expedition Atimo Vatae)
Porolithon	onkodes	GDA61352	KM073275	KM073347	KM407534	–	KM073309	25/06/2011/Borneo, Indonesia/Mangkalihat peninsula/intertidal A. Rösler
Porolithon	onkodes	GDA61347	–	KM977989	KM407533	–	–	17/05/2011/GBR, Australia/One Tree Island/0.2–1 m/A. Rösler
Porolithon	onkodes	GDA61359	KM073276	KM073342	–	–	–	18/05/2011/GBR, Australia/One Tree Island/0.2–1 m/A. Rösler
Porolithon	onkodes	GDA61342	KM073274	KM073346	KM407532	KM392359	KM073308	17/05/2011/GBR, Australia/One Tree Island/0.2–1 m/A. Rösler
Porolithon	sp.	GENT_NTV1053e	–	–	KP682499	KP682498	–	01/05/2012/Vietnam/Nha Trang, Yen island/1.5 m/VT. Nguyen, O. De Clerck, NH. Le
Spongites	fruticulosus	PC0533587	–	–	–	KM392374	–	23/10/2008/France/Le sec des Langoustiers, Porquerolles/35 m/L. Le Gall
Spongites	fruticulosus	PC0142664	–	–	–	KJ710340	–	07/09/2011/Greece/Kalithea, Rhodos Island/5 m/L. Le Gall
Spongites	fruticulosus	GDA61338	KM073306	KM073361	–	KP030739	KM073335	19/10/2010/Almería, Spain/Cala Chumba/5–10 m/A. Rösler
Spongites	sp.	PC0533588	–	–	–	KP682496	–	07/06/2009/France/Montremian, Port-Cros/30 m/L. Le Gall
Spongites	sp.	PC0144239	–	–	–	KJ710339	–	23/05/2012/Guadeloupe, French West Indies/Passe à Caret, Grand Cul-de-Sac Marin/32 m/Karubenthos Expedition
Spongites	sp.	PC0144244	–	–	–	KJ710347	–	23/05/2012/Guadeloupe, French West Indies/Passe à Caret, Grand Cul-de-Sac Marin/32 m/Karubenthos Expedition

[1] As *Goniolithon accretum* f. *canariensis*, 1904–1905.

the isotype of *H. munitum* preserved in the PC Herbarium of the Museum National d'Histoire Naturelle, France (Woelkerling and Lamy 1998), as well as the isotype material of *P. conicum* preserved in the US Herbarium of the Smithsonian Institution, Washington D.C., USA (US Dawson 12148, Keats et al. 1997, Yoshida 1998).

Morphological examination was performed at the CIC (Centro de Instrumentación Científica) of the University of Granada. Specimens were fractured, mounted on aluminum stubs with Leit-C conductive carbon after Glöcke (Plano GmbH, Germany), and examined with a Quanta 400 environmental scanning electronic microscope (ESEM) FEI at 15 or 20 kV. Other specimens were cut in ultrathin sections (48 × 28 mm, 10–15 µm thick) and subsequently studied and photographed (software AxioVision, version 4.6; Carl Zeiss Microscopy GmbH, Jena, Germany) with a light microscope. Thallus and algal growth-form terminology follow Woelkerling (1988) and Woelkerling et al. (1993a).

The DNA was extracted using the GenElute Plant Genomic DNA Miniprep Kit (Sigma-Aldrich, Munich, Germany), NucleoSpin® 96 Tissue kit (Macherey-Nagel, GmbH and Co. KG, Berlin, Germany), and also QIAamp DNA Micro Kit (Qiagen, Les Ulis, France) for the type collections, following the manufacturer's instructions. Five markers were amplified: two ribosomal rDNAs, SSU of ~1,700 base pairs (bp) raw data length, and LSU (1,100 bp unedited length); one chloroplastidial gene (*psb*A, unedited length 800 bp); one region of the chloroplastidial 23S rDNA (DomainV), also called UPA (universal plastid amplicon, unedited length ~400 bp); and one mitochondrial gene, COI (or cox1) (unedited length 600 bp). Internal transcribed spacers (ITS) were also amplified as a sixth marker but turned out to be mutational saturated and were not incorporated in the final alignment. Tests for saturation for each marker were performed using the DAMBE software package (Xia 2013b). Primers for SSU rDNA amplifications were the same as in Saunders and Kraft (1994), but the thermocycling program was modified to: (i) 94°C, 4 min, (ii) 30 times (94°C, 25 s; 52°C, 25 s; 72°C, 40 s), (iii) 72°C, 6 min, and (iv) 4°C infinitely. For LSU rDNA amplification, the primers and protocols published by Freshwater and Bailey (1998) were used. The *psb*A locus was amplified using the primers and protocols as in Yoon et al. (2002). ITS was amplified following White et al. (1990), Tai et al. (2001), and Hu et al. (2007). COI was amplified with the primers and methods published by Saunders (2005) and Clarkston and Saunders (2010). UPA amplification followed Sherwood and Presting (2007) and Clarkston and Saunders (2010). Amplified DNAs were sequenced by the company "Macrogen Europe" (Amsterdam, The Netherlands). The PCR reactions and thermal profile for the COI-5P and *psb*A markers produced by VP follows Peña et al. (2015), except for the PCR reactions of the type material in which the DNA template was not diluted. PCR products by VP were purified and sequenced by Genoscope (Bibliothèque du Vivant program, Centre National de Séquençage, France) and Eurofins MWG Operon (France).

Sequences of 55 samples of six genera were obtained and deposited in GenBank. From the type collections, only sequences from *Goniolithon accretum* f. *canariensis* were obtained; unfortunately, no sequences could be obtained from the isotype material of *P. conicum* and *H. munitum*. All samples provided by the authors are listed with their collection information and GenBank accession numbers in Table 1. In addition, publicly available sequences for 143 taxa were downloaded from GenBank (Table S1 in the Supporting Information). Two species were chosen for the OTUs of the outgroup: *Mesophyllum lichenoides* (J.Ellis) Me.Lemoine and *Sporolithon ptychoides* Heydrich.

Data storage, sequence processing, and first alignments were conducted in Geneious versions 5 and R6 (Drummond et al. 2009). For the calculation of sequence divergence, the number of base substitutions per site from between sequences of the COI marker were analyzed using the Maximum Composite Likelihood model (Tamura et al. 2004) with MEGA6 (Tamura et al. 2013). Sequence alignments were later optimized by hand and with G-Blocks Version 0.91b (Talavera and Castresana 2007) on Phylogeny.fr (Dereeper et al. 2008) and afterwards realigned with MAFFT version 7 (Katoh and Standley 2013). Alignments were concatenated in Geneious 5. The global alignment constitutes a supermatrix, with five markers and 198 OTUs containing 50% missing data (N), which has been shown to be unproblematic (Thomson and Shaffer 2010). The partition of the sequence alignment was done by genetic marker, statistically justified by Partitionfinder v.1.1.1 (Lanfear et al. 2012). The evolution model was found with MrModeltest (Nylander 2004) using Modeltest algorithms (Posada and Crandall 1998). All partitions indicated a GTR+I+G evolutionary model under Akaike information criteria. The first global alignment contained 259 OTUs. To improve phylogenetic accuracy, rogue taxa selected by RogueNaRok (Aberer et al. 2013) were eliminated and sequences with low-quality or doubtful taxonomic attribution were excluded. Bootstrap analyses necessary for RogueNaRok analysis were performed with RAxML (Stamatakis 2006, Ott et al. 2007). MrBayes 3.2 (Huelsenbeck et al. 2001, Ronquist and Huelsenbeck 2003) was used to obtain a Bayesian consensus tree. Four chains of eight million generations with Temp = 0.01 were launched and sampled every 1,000 generations. Chain convergence was achieved at around 7.9 million generations with an average standard deviation of split frequencies of 0.010. The software Tracer (version 1.6, Rambaut and Drummond 2007) was used to determine whether the stationary phase was reached. The first two million generations of trees were excluded (="burnin") for the final calculation of the consensus tree.

RESULTS

The phylogenetic tree obtained for the family Corallinaceae (Fig. 1) shows a paraphyletic grouping of well-supported monophyletic clades, which are the following:

1 A clade formed by members of the subfamily Corallinoideae (Areschoug) Foslie.
2 A clade formed by representatives of *Mastophora* Decaisne and *Metamastophora* Setchell of the subfamily Mastophoroideae (Setchell) A.Kato & M.Baba.
3 A group of two clades: (3.1) contains *Spongites fruticulosus* Kützing and *Spongites* sp. from the Mediterranean Sea, Caribbean Sea, and Hawai'i, *Pneophyllum confervicola* (Kützing) Y.M.Chamberlain from SE Spain, and a thin encrusting coralline alga collected in Madeira, Macaronesia. Clade (3.2) contains all species of *Neogoniolithon* Setchell & L.R.Mason employed in this study, from the Indian, Pacific and Atlantic oceans, and the Mediterranean Sea.
4 A clade comprising *Hydrolithon reinboldii* and *H. boergesenii* Foslie (Foslie), collected in the Pacific Ocean and the Caribbean Sea, which is coincident with the subfamily Hydrolithoideae.

5 A group with two clades: One (5.1) comprises *Porolithon onkodes* (Heydrich) Foslie, *P. gardineri* (Foslie) Foslie, and *P. pachydermum* (Foslie) Foslie, and several specimens attributed to *Porolithon* by Bittner et al. (2011) but not further identified. The second clade (5.2) includes three further subclades. The first (5.2a) is a branch comprising *Metagoniolithon* Weber-van Bosse species, the second (5.2b) is formed by several species belonging to *Hydrolithon* sensu Penrose (1996a) and the type of *Goniolithon accretum* f. *canariensis*, and the third (5.2c, a sister group of 5.2b) comprises specimens attributed to *P. conicum*. Clade 5.2b is here assigned to a new genus, *Harveylithon* gen. nov. (see formal description below). It includes *H. rupestre* (Foslie) comb. nov., *H. canariense* (Foslie) comb. nov., *H. munitum* (Foslie & M.Howe) comb. nov., and *H. samoënse* (Foslie) comb. nov.

6 A clade comprising coralline algae attributed to *Pneophyllum* Kützing and *Spongites* Kützing from the Southern Hemisphere, especially from New Zealand, hereafter called the Southern Hemisphere group. It forms a sister group to clade 7 within a weakly supported clade.

7 A monophyletic clade of Lithophylloideae sensu Bailey (1999) containing several species of *Lithophyllum* Philippi from Atlantic and Pacific oceans, and Mediterranean Sea localities,

and *Amphiroa* J.V. Lamouroux from Caribbean Sea, Pacific Ocean, and Mediterranean Sea localities. This clade is a sister to the Southern Hemisphere clade.

DISCUSSION

The results of this work shown in the cladogram (Fig. 1) require changes in the infrafamilial systematics of Corallinaceae. The inferred phylogenetic relationships validate the monophyly of subfamilies Corallinoideae, Mastophoroideae, Hydrolithoideae, and Lithophylloideae. The concept and circumscription of Neogoniolithoideae and Metagoniolithoideae must be amended, and Porolithoideae cannot be held as an independent subfamily.

The clades grouping members of the subfamily Lithophylloideae and Mastophoroideae, respectively, are maintained as subfamilies, and, as a consequence, a subfamily rank is also assigned to the other monophyletic groups observed in the cladogram (Fig. 1, see below). All taxa of the ingroup possess uniporate tetra/bisporangial conceptacles and tetrasporangia without apical plugs. Corallinoideae, Mastophoroideae, and Neogoniolithoideae share the development of tetra/bisporangial conceptacles from filaments surrounding the fertile area (Harvey et al. 2006). By contrast, Hydrolithoideae, Metagoniolithoideae, and Lithophylloideae
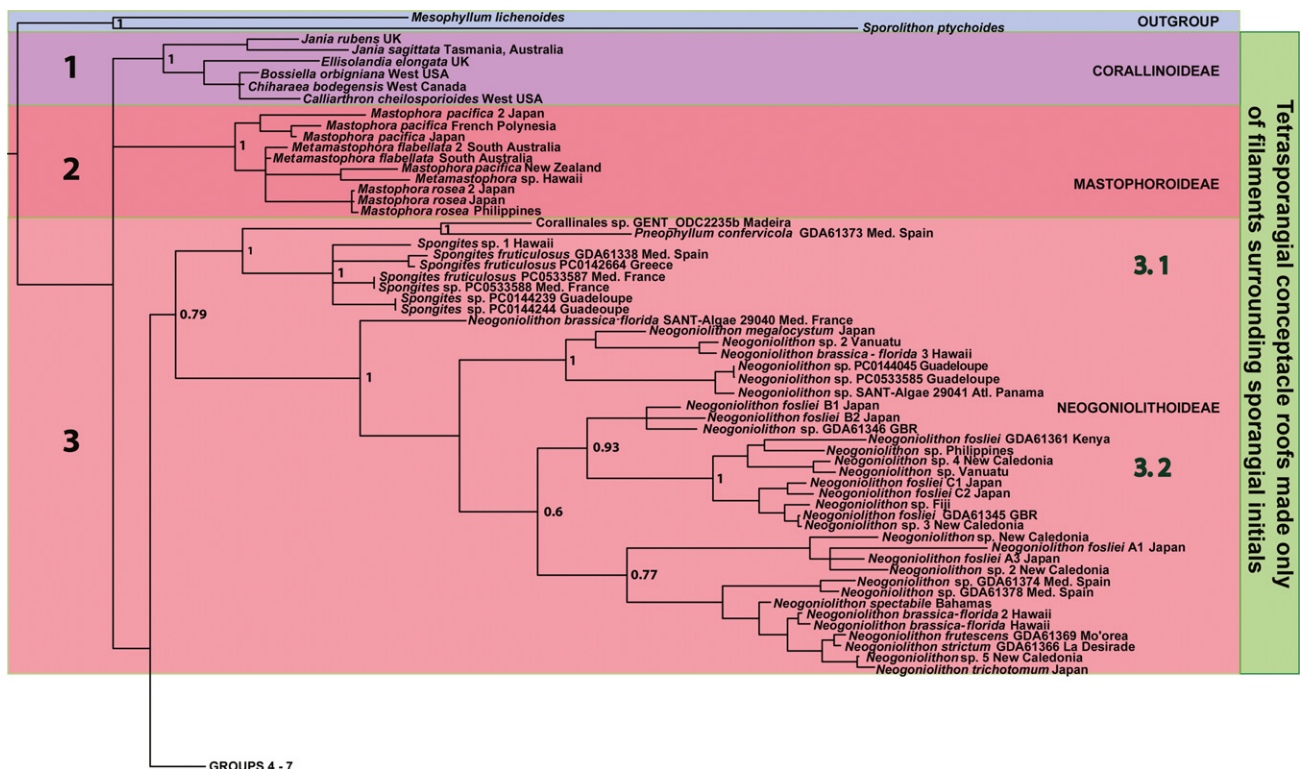

FIG. 1. Bayesian phylogenetic tree inferred by five marker dataset, including 198 OTUs. Numbers at nodes represent posterior probabilities; nodes below 0.5 are shown as polytomies; Monophyletic lineages within Lithophylloideae represented by triangles.
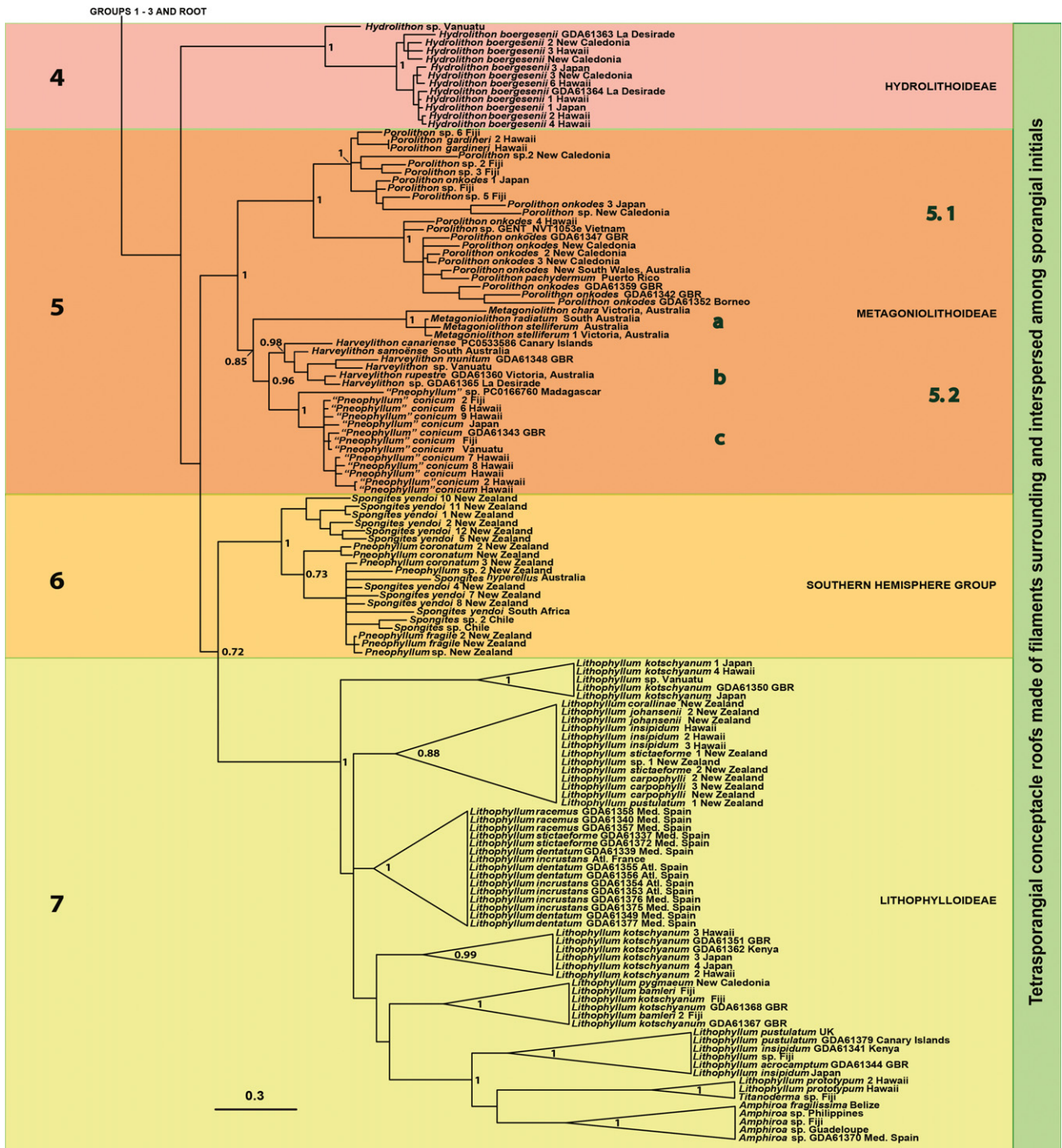
Fig. 1. Continued

show development of the sporangial conceptacle chamber from filaments surrounding and interspersed within the fertile area as a derived character (Mendoza and Cabioch 1986, Harvey et al. 2006).

Based on the results obtained, the following taxonomic account of the order Corallinales, family Corallinaceae, is presented.

(1) Subfamily Corallinoideae (Areschoug) Foslie 1908: 19

Description: Most members of the subfamily possess a geniculate thallus, with an encrusting holdfast. Multigene phylogenetic analyses, however, have shown that non-geniculate corallines attributed to *Pseudolithophyllum muricatum* (Foslie) Steneck & R.T.Paine also belong to this clade (Hind and Saun-

ders 2013). Cells of adjacent filaments connected by cell fusions, secondary pit connections absent. The tetra/bisporangial conceptacle roof is composed of filaments that arise peripherally and surround and enclose a fertile region. In geniculate forms, branches are multiaxial, genicula with a single tier of non-calcified cells, intergenicula with 1–40 tiers of cells. Spermatangia develop on the floor and side walls of male conceptacles (Womersley and Johansen 1996a).

Type genus: *Corallina* Linnaeus 1758: 646, 805

Remarks: The subfamily Corallinoideae was positioned differently in the phylogenies of Bailey et al. (2004), Bittner et al. (2011), Kato et al. (2011), and Nelson et al. (2015). Bailey et al. (2004) and Bittner et al. (2011) resolved Corallinoideae as a sister clade of *Neogoniolithon*. The spermatangia in Corallinoideae are borne on the floor and side walls of the male conceptacle (Womersley and Johansen 1996a), sharing this feature with *Neogoniolithon*. In Kato et al. (2011), Corallinoideae appeared as a sister clade to the complex formed by subfamilies Hydrolithoideae, Porolithoideae, Lithophylloideae, and clades grouping taxa here included in clades 5.2b, 5.2c, and 6, but support for this relationship was weak. The subfamily had a similar position in the phylogram of Nelson et al. (2015), forming a sister clade to the rest of Corallinaceae. The exact position of Corallinoideae within Corallinaceae still lacks high certainty, although a basal one and a strong relation with *Neogoniolithon* seems likely. As the non-geniculate species *P. muricatum* belongs to this subfamily, there are currently no diagnostic morphoanatomical characters separating Corallinoideae from Neogoniolithoideae (Hind and Saunders 2013).

(2) Subfamily Mastophoroideae (Setchell) A.Kato & M.Baba in Kato et al. 2011: 8

Description: Thallus nongeniculate, dimerous, primigenous filaments are composed of palisade cells throughout the thallus. Secondary pit connections absent or rare, cell fusions between adjacent filaments are common. Tetrasporangial conceptacle roof composed of filaments that arise peripherally and surround and enclose a fertile region. Spermatangia develop on the floor of male conceptacles.

Type genus: *Mastophora* Decaisne 1842: 365

Remarks: Subfamily members analyzed in this study are attributed to *Mastophora*, the type genus, and *Metamastophora*. The latter is distinguished from *Mastophora* by generating a distinct holdfast and stipe and producing, in older parts, postigenous filaments dorsally and ventrally from primigenous cells. Our results suggest a weak separation of *Mastophora* and *Metamastophora* or cryptic speciation within *Mastophora*, which was also found by Kato et al. (2011) and Bittner et al. (2011). This subfamily is a monophyletic group and forms one of the basal branches in the phylogeny of Corallinaceae.

One of the genera of Corallinaceae not treated in this analysis is *Lithoporella* (Foslie) Foslie, comprising tiny thalli difficult to collect for genetic analyses. In obvious morphological characters such as the possession of palisade cells in primigenous filaments, it is very similar to Mastophoroideae. Mastophoroideae and *Lithoporella*, however, show a different mode of tetrasporangial conceptacle roof development (Woelkerling 1988), a key character separating clades. The affinities of *Lithoporella* therefore remain uncertain and should be tested with molecular phylogeny.

(3) Subfamily Neogoniolithoideae (A.Kato & M.Baba) emendavit A.Rösler, Perfectti, V.Peña & J.C.Braga

Neogoniolithoideae consists of two main clades, one containing the type species of *Spongites*, *S. fruticulosus*, for which we propose an epitype (below), as well as a group of very thin encrusting corallines with trichocytes on their dorsal surface from Madeira and Mediterranean Spain and the other including all treated species of *Neogoniolithon*. In our phylogenetic analyses, both clades have strong support (posterior probability (pp) = 1), and therefore we include *Spongites* in Neogoniolithoideae, although this does not include all species currently placed in *Spongites* (Fig. 1).

Description: In accordance with the proposed amendment, Neogoniolithoideae encompasses corallines with nongeniculate, monomerous, or thin dimerous thalli, with primigenous filaments not composed of palisade cells, trichocytes present. Uniporate tetra/bisporangial conceptacle roofs are formed by filaments peripheral to the fertile area. In mature sporangial conceptacles, the filaments lining the pore canal are oriented parallel to oblique to the thallus surface and may protrude laterally into the pore.

Type genus: *Neogoniolithon* Setchell & L.R.Mason 1943: 89

Remarks: Currently, no morphoanatomical characters are useful to separate this subfamily from Corallinoideae (Hind and Saunders 2013). Neogoniolithoideae shows the ancestral corallinacean tetrasporangial conceptacle development. *Neogoniolithon* shares with Corallinoideae the distribution of spermatangia in the male conceptacle on floor and roof. Species relationships within this genus do not resolve clearly. The species name *N. brassica-florida* (Harvey) Setchell & L.R.Mason (type locality: Algoa Bay, Cape Province, South Africa, Silva et al. 1996: 261) has apparently been too widely applied (for example, Woelkerling et al. 1993b). *Neogoniolithon fosliei* (Heydrich) Setchell & L.R.Mason (type locality: El Tor, Sinai Peninsula, Egypt, Silva et al. 1996: 262) is split into three polyphyletic clades, reconfirming the results of Kato et al. (2013). Algae assigned to this species are interspersed in the cladogram with several specimens attributed to other species from the Indo-Pacific,
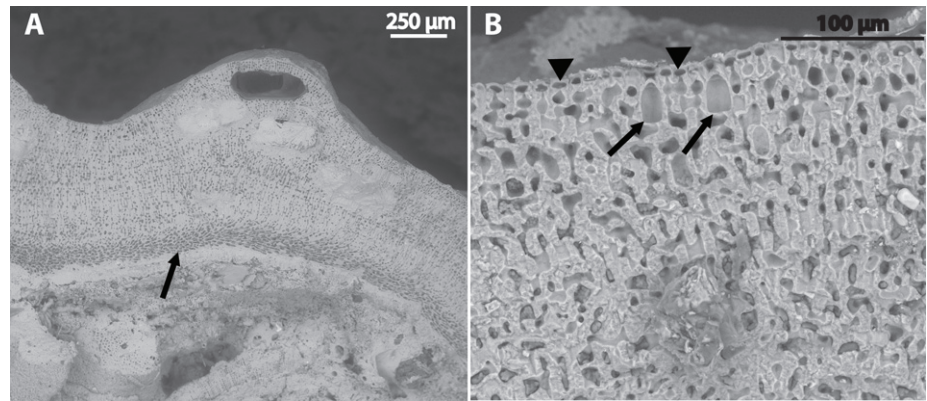
FIG. 2. SEM images of epitype of *Spongites fruticulosus* GDA 61338. Cala Chumba, Almería, SE Spain. (A) Section showing non-coaxial ventral core (arrow) and uniporate tetrasporangial conceptacle. (B) Detail of thallus showing transversely compressed epithallial cells (arrowheads) and solitary trichocytes (arrows).

including *N. frutescens* (Foslie) Setchell & L.R.Mason, *N. trichotomum* (Heydrich) Setchell & L.R.Mason, *N. strictum* (Foslie) Setchell & L.R.Mason, and *N. spectabile* (Foslie) Setchell & L.R.Mason. Resolving the taxonomy at the species level is beyond of the scope of this work.

The cladogram shows at least two morphoanatomically identical or highly similar species within the Mediterranean Sea, the type locality of *Spongites fruticulosus*. Their COI sequence diverge up to 12%, which usually indicates distinct species (Clarkston and Saunders 2010, Rueness 2010, Yang et al. 2013) and, consequently, these two Mediterranean clades likely need to be recognized as two independent species. We tried to obtain a DNA sequence from the lectotype (Rijksherbarium, Leiden, Netherlands L943.8.134), but the results were only very short DNA fragments of poor quality that were not useful. As the type locality of Kützing's original material is the "Mediterranean Sea" with no further precision, we establish here as epitype (Art. 9.8, ICN, McNeill et al. 2012) the specimen with the herbarium voucher GDA61338 from the Eastern coast of Spain (see collection details in Table 1 and Fig. 2), because it matches best with the protologue of *S. fruticulosus*. The conspecific specimen PC0142664 from Greece was treated in Peña et al. (2014). The lectotype was described by Woelkerling (1985) as monomerous, with a non-coaxial ventral core, a multistratose dorsal region, and a unistratose layer of epithallial rounded or transversely compressed cells. Cell fusions were common in the dorsal region and occasional in the ventral core, absent between epithallial cells. Solitary trichocytes occurred occasionally at the thallus surface but did not become buried. Uniporate tetrasporangial conceptacles possessed more or less ovoid chambers up to 385 μm in diameter and 220 μm in height. The selected epitype possesses the same morpho-anatomical features, although the tetrasporangial conceptacle chambers of GDA61338 have dimensions slightly smaller than the lectotype, maximal chamber diameter 370 μm, height 195 μm. The epitype establishes a reference for future taxonomic studies.

Sample GDA61373 (Fig. 3), assigned to *Pneophyllum confervicola*, and the sample named "Corallinales sp. Madeira" comprise very thin epilithic dimerous thalli (max 100 μm) with frequent cell fusions and occasional trichocytes. *P. confervicola* is morphologically very similar to the type species of *Pneophyllum*, *P. fragile* Kützing. Tetrasporangial conceptacles of the analyzed specimen of *P. confervicola* are uniporate, with an external diameter of 100–150 μm; the specimen from Madeira is nonfertile. *Pneophyllum* has been described as possessing tetrasporangial conceptacle roofs formed either by filaments surrounding or surrounding and interspersed among sporangial initials (Chamberlain 1983, 1994). Woelkerling (1988) understood *Spongites* and *Pneophyllum* as one group that lacks "derivate" characters of other mastophoroids sensu Woelkerling (1987a), such as a coaxial ventral core, haustoria, trichocyte fields, or rows, massive cell fusions, and pit connections. It is possible that many thin laminar taxa represent pedomorphic forms of more complex coralline algae (Chamberlain 1983) and may belong to several subfamilies despite the lack of morphological evidence. Samples identified in GenBank as *Pneophyllum* occur in different clades of the Corallinaceae and, therefore, should be reassessed in future research, especially with DNA sequences. Our results imply the inclusion of a *Pneophyllum* species morphoanatomically similar to the type species of the genus in one of the clades in the subfamily Neogoniolithoideae. This species shows the ancestral type of conceptacle roof formation within Corallinaceae, built only by filaments surrounding the fertile area. Nevertheless, analysis of the molecular affinities of the type species is required for a confident assignment of *Pneophyllum* to Neogoniolithoideae.

(4) Subfamily Hydrolithoideae A. Kato & M. Baba in Kato et al. 2011: 8

Description: The outline of cell filaments is entirely lost in large portions of the thallus due to pervasive and extensive cell fusions, giving it a distinctive and unique appearance in cross-section. Although monomerous organization can occur,
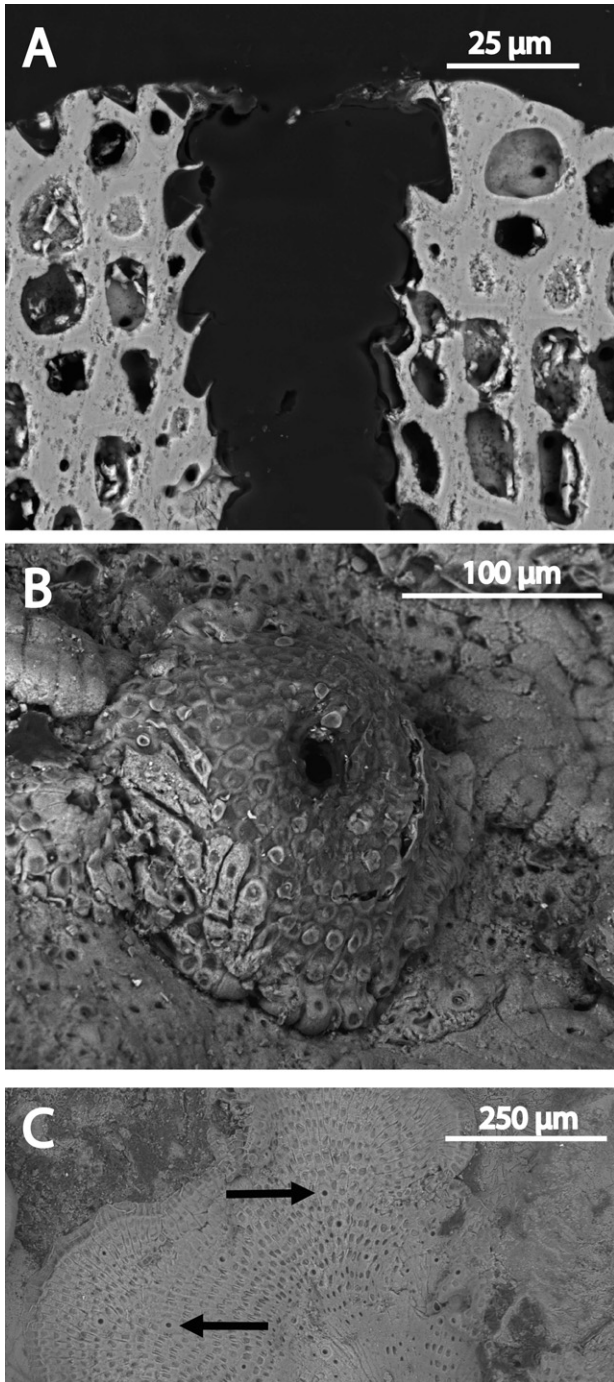
FIG. 3. SEM images of *Pneophyllum confervicola* GDA61373. Cala de Plomo, Almería, SE Spain. (A) Detail of a cross-section of conceptacle pore, cells lining pore canal partly protruding into canal. (B) Surface view of uniporate conceptacle. (C) Surface view of thallus showing solitary trichocytes (arrows).

thallus organization is primarily dimerous. The tetra/bisporangial conceptacle roof is formed by filaments surrounding and interspersed among sporangial initials (Kato et al. 2011). Pore canals of uniporate tetra/bisporangial conceptacles are lined by a ring of elongate cells that do not protrude into

the canal and are oriented more or less perpendicularly to the roof surface (Penrose and Woelkerling 1992, Verheij 1994).

Type genus: *Hydrolithon* (Foslie) Foslie 1909: 55

Remarks: The two studied living members of this subfamily, *Hydrolithon boergesenii* and *H. reinboldii*, could not be discriminated with any single marker or combinations of them in our molecular analysis. As shown in Figure 1, specimens collected in the Caribbean Sea (L15 and L16, from La Desirade, Lesser Antilles) and identified as *H. boergesenii* cannot be separated from the specimens attributed to *H. reinboldii* from Indo-Pacific localities (Figs. 1 and 4). The type locality of *H. boergesenii* is St. Croix, Caribbean Sea (Woelkerling 1993: 40), whereas the type locality of *H. reinboldii* is in the Indo-Pacific (lectotype locality: Muaras Reef, East Kalimantan, Indonesia, Silva et al. 1996: 239). In the original publications, Foslie (1901a,b) already considered the two species very similar and stated that *H. reinboldii* (as *Lithophyllum Reinboldi*) stands near *H. boergesenii* (as *L. Børgesenii*). According to Foslie (1901a,b), Penrose and Woelkerling (1992), and Mendoza-González et al. (2009), the tetra/bisporangial thalli of the two species cannot be morphologically distinguished. Athanasiadis et al. (2013) also showed that characters such as habitat, substratum, thallus size and organization, tetrasporangial chamber diameter, and height and sporangia size of Caribbean and Indo-Pacific specimens overlap. Both molecular and morphological data indicate that this is a single species. According to Woelkerling (1993), *H. boergesenii* was first described as *Goniolithon Börgesenii* in 1901, before the publication of *Lithophyllum reinboldi* Weber-van Bosse & Foslie later in the same year. Therefore, *H. reinboldii* is a younger heterotypic synonym of *H. boergesenii* (which is the only living representative of the subfamily Hydrolithoideae included in our molecular analysis). The morphological characters of other taxa such as *Hydrolithon breviclavium* (Foslie) Foslie and *Hydrolithon abyssophila* Athanasiadis, D.L.Ballantine & H.Ruiz seem to be close to those of *H. boergesenii*, and can probably be attributed to *Hydrolithon* within this subfamily, but this cannot be fully ascertained until DNA sequences are available. Molecular data were also not available for some species attributed to *Hydrolithon* in the last decades, especially those with thin laminar thalli (such as *H. farinosum* (J.V.Lamouroux) Penrose & Y.M.Chamberlain). The generic and subfamily assignment of these species will remain doubtful as long as DNA sequences are not available.

(5) Subfamily Metagoniolithoideae (H.W.Johansen) emendavit A.Rösler, Perfectti, V.Peña & J.C.Braga

Description: Thallus either geniculate with conspicuous mucilaginous caps, genicula of many-celled untiered filaments, or nongeniculate and monomerous, lateral cell fusions present, secondary pit con-
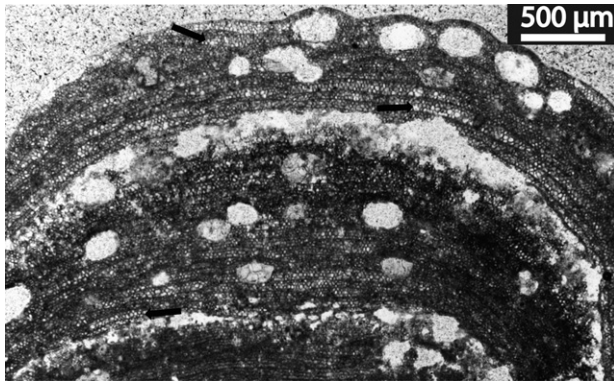
Fig. 4. Light micrograph of cross-section of *Hydrolithon boergesenii*. Lizard Island, Queensland, NE Australia. Note outline of peripheral filaments fully lost in large portions of thallus due to extensive cell fusions (arrows).

nections absent, trichocytes occurring singly or in horizontal fields. Tetrasporangial uniporate conceptacle roofs are formed by filaments peripheral to the fertile area and interspersed among tetrasporangial initials. Spermatangia develop on the floor of the male conceptacle.

Type genus: *Metagoniolithon* Weber-van Bosse 1904: 86, 101

Remarks: No single diagnostic morphoanatomical character separates this subfamily from other clades with conceptacle roofs formed by filaments peripheral to and interspersed among tetrasporangial initials. Subfamily Metagoniolithoideae, however, is a strongly supported clade (PP = 1.0; Fig. 1) that comprises two monophyletic clades (5.1 and 5.2). Clade 5.1 is here assigned to *Porolithon*, and includes all specimens attributed to *P. onkodes*, *P. pachydermum*, *P. gardineri*, and coralline algae attributed to *Porolithon.* sp. in Bittner et al. (2011). Clade 5.2 includes three subclades: a: *Metagoniolithon*, b: *Harveylithon*, and its sister group c: "*Pneophyllum*" *conicum* group.

The geniculate corallines included in *Metagoniolithon* are grouped in a derived subclade within a clade of nongeniculate corallines. A similar relationship with nongeniculate corallines was shown for *Amphiroa* by Bailey (1999) with DNA sequence data, confirming the inclusion of this geniculate genus in the subfamily Lithophylloideae, a relationship proposed by Cabioch (1972) based on the presence of secondary pit connections. Cabioch (1972) also pointed to the similarity of thallus development in *Metagoniolithon* and branched species of *Porolithon*. According to the ICN, article 11.3 (McNeill et al. 2012), the name Metagoniolithoideae H.W.Johansen 1969 has priority over Porolithoideae A.Kato & M.Baba in Kato et al. (2011).

(5.1) *Porolithon* Foslie emend. A.Kato & M.Baba in Kato et al. 2011: 8

Diagnosis: Nongeniculate Metagoniolithoideae with common horizontal fields of trichocytes becoming buried in the thallus, usually not interspersed
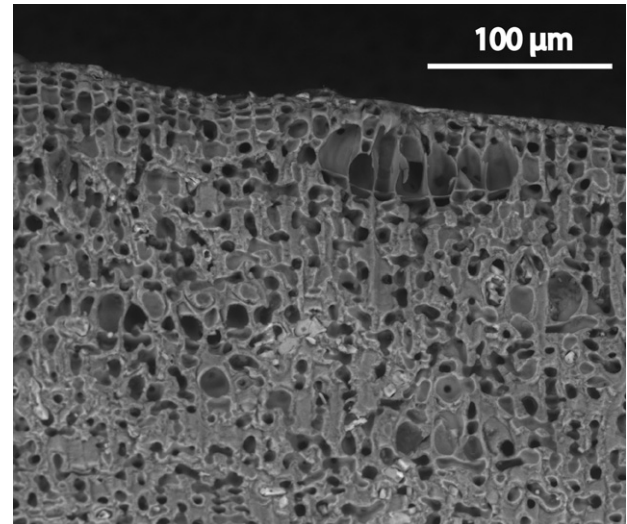

Fig. 5. SEM image of cross-section of *Porolithon onkodes* GDA61359. One Tree Island, Queensland, NE Australia. Note horizontal field of tightly packed trichocytes buried in upper part of thallus (arrow).

with vegetative cells and consisting of three or more cells in a cross-sectional row (Kato et al. 2011, Fig. 5).

Type species: *Porolithon onkodes* (Heydrich) Foslie

Distribution: Tropical and subtropical, widely reported in the Atlantic, Indian, and Pacific Oceans based on morphoanatomical identification (Maneveldt and Keats 2014). Sequenced specimens of the genus from New South Wales and Puerto Rico (Bailey et al. 2004), Ryukyu Islands (Japan) and Hawai'i (Kato et al. 2011), and New Caledonia and Fiji (Bittner et al. 2011).

Remarks: *Hydrolithon craspedium* (Foslie) P.C.Silva is anatomically very similar to *P. onkodes* (Johnson 1957), and will most likely be assigned to *Porolithon*. *H. cymodoceae* shows features shared with Metagoniolithoideae (horizontal fields of trichocytes and uniporate tetrasporangial conceptacle roof development and pore canal cell orientation) but, on the other hand, a dimerous (and monomerous) thallus organization that does not occur in other members of the subfamily (Penrose 1996a). The semiendophytic *Hydrolithon braganum* Woelkerling, D.Bassi & Iryu, which was to date only found as fossil, also shows horizontal fields of trichocytes. The generic and subfamily position of these species will remain unclear as long as no sequences are available. In addition, molecular data for *Hydrolithon improcerum* were available in GenBank (Kato et al. 2011) but they were excluded during the sequence filtering process to improve the phylogenetic accuracy of our analyses (see Material and Methods section). In the analysis of Nelson et al. (2015), *H. improcerum* and *P. onkodes* grouped together but were not resolved as monophyletic.

(5.2a) *Metagoniolithon* Weber-van Bosse 1904: 86, 101

Diagnosis: Metagoniolithoideae with geniculate thalli. Branch apices covered by caps of mucilaginous material. Genicula with filaments formed by many cells not arranged in tiers (Womersley and Johansen 1996b).

Type species: *Metagoniolithon charoides* (J.V.Lamouroux) Weber-van Bosse (= *M. radiatum* (Lamarck) Ducker

Distribution: Reported from Western Australia, across southern Australia to New South Wales and Tasmania (Womersley and Johansen 1996b, Huisman 2000). Old reports in checklists from outside Australia were rejected by Ducker (1979), but the genus was afterwards listed in the Seychelles (Silva et al. 1996) and Mariana Islands (Tsuda 2003). Sequenced specimens are from Australia (Bailey and Chapman 1998, Bittner et al. 2011).

(5.2b) *Harveylithon* A.Rösler, Perfectti, V.Peña & J.C.Braga **gen. nov.**

Diagnosis: Nongeniculate Metagoniolithoideae with monomerous thallus organization and a plumose ventral core. Trichocytes usually occur singly and may become buried in the thallus. Cells lining the pore canal of tetrasporangial conceptacles are oriented perpendicular to the thallus surface.

Etymology: *Harveylithon* honors the Australian botanist Dr. Adele Harvey, who has published numerous, decisive, far-reaching articles on coralline algae since the 1990s, significantly contributing to the knowledge of these organisms.

Type species: *Harveylithon rupestre* (Foslie) A.Rösler, Perfectti, V.Peña & J.C.Braga **comb. nov.**

Basionym: *Lithophyllum rupestre* Foslie 1907. *Det Kongelige Norske Videnskabers Selskabs Skrifter* 1906:26.

Homotypic synonyms: *Mesophyllum rupestre* (Foslie) W.H.Adey 1970: 26, *Hydrolithon rupestris* (Foslie) Penrose 1996a: 265.

Type locality: Ocean Beach, Phillip Island, Victoria (Woelkerling and Campbell 1992: 100). Holo-

type: C. J. Gabriel; April 1905; TRH A3-149 (Penrose 1996a: 266).

Description: Thallus encrusting to warty, which can form rhodoliths; construction monomerous, not coaxial. Filaments composed of small cells (5–8 × 5–15 μm, diameter × height). Cell fusions present; trichocytes, when present, occurring singly or in horizontal rows or fields at the thallus surface, not becoming buried within the thallus. Tetrasporangial conceptacles uniporate, up to 110 μm in diameter and up to 55 μm high (Fig. 6A). Conceptacle pore canals lined by cells orientated perpendicularly to the thallus surface and not protruding into the pore canal. *H. rupestre* can be distinguished from other *Harveylithon* species by the small size of its tetrasporangial conceptacle chambers (maximum 110 μm in diameter; see Fig. 6A). More details and illustrations in Penrose (1996a) (as *Hydrolithon rupestris*, p. 265) and Harvey et al. (2006) (as *Hydrolithon rupestre*, p. 402). The specimen of *H. rupestre* analyzed (GDA 61360, Fig. 6A) was collected in Westernport Bay (Victoria, Australia), the type locality of *Lithophyllum rupestre.*

Distribution: *Harveylithon rupestre* was reported as *Hydrolithon rupestre* from Western Australia, across southern Australia to New South Wales (Penrose 1996a, Harvey et al. 2006), southern Wallis Islands (N'Yeurt and Payri 2004), French Polynesia (N'Yeurt and Payri 2010), and the St. Peter and St. Paul Archipelago (Mid Atlantic Ridge, Crespo et al. 2014) based on morphoanatomical examination.

Other species transferred to *Harveylithon* are:

Harveylithon canariense (Foslie) A.Rösler, Perfectti, V.Peña & J.C.Braga **stat. nov.**

Basionym: *Goniolithon accretum f. canariensis* in Foslie (1906a). *Det Kongelige Norske Videnskabers Selskabs Skrifter* 1905 (10): 19.

Description: Encrusting to warty thallus, shiny surface, up to 1 mm thick, plumose ventral region and
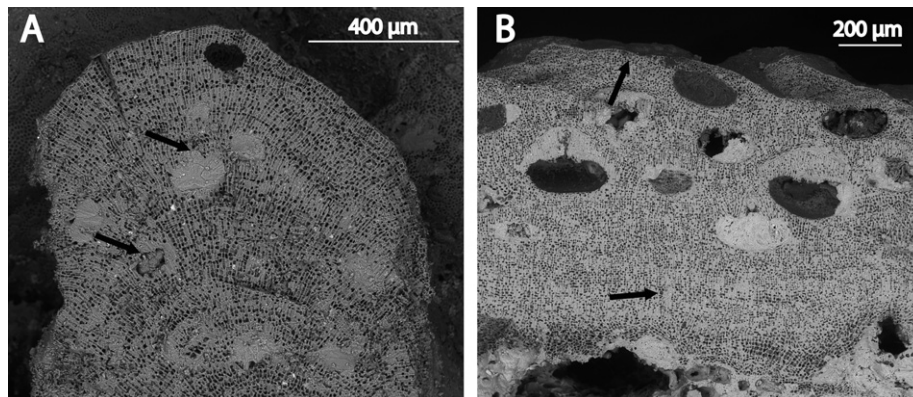

FIG. 6. SEM images of representatives of *Harveylithon*, (A) *Harveylithon rupestre* GDA61360. Westernport Bay, Victoria, Australia. Section of protuberance showing small buried uniporate tetrasporangial concetacles. Arrows point to buried conceptacle pores. (B) *Harveylithon munitum* GDA61348. One Tree Island, Queensland, NE Australia. Section of thallus showing plumose ventral core, buried uniporate tetrasporangial conceptacles and scarce trichocytes both buried and at thallus surface (arrows).

single trichocytes on the dorsal surface. Cell fusions common, sporangial conceptacle chambers uniporate, 250–400 µm inner diameter (Foslie 1906a: 20). Trichocytes in *H. canariense* do not become buried in the thallus.

Type locality: Puerto Orotava, Tenerife, Canary Islands

Remarks: *Goniolithon accretum* Foslie & M.Howe was originally described by Foslie and Howe (1906) from Sand Key, Florida. Setchell and Mason (1943) transferred it to *Neogoniolithon* due to the presence of a coaxial ventral region. According to our DNA sequence data and non-coaxial character of the ventral core of the type specimen of the forma *canariensis* already reported by Foslie (1906a), *G. accretum f. canariensis* cannot be attributed either to *Neogoniolithon* or to *Goniolithon accretum*. Here, the subspecific (forma) name is raised to the species rank. Another specimen of this species from a different locality in the Canary Islands was described by Lemoine (1929, p. 35). Tetrasporangial conceptacles were not found in the type specimen of *H. canariense.*

Distribution: *Harveylithon canariense* has only been recorded in the Canary Islands.

Two more members of this genus, not identified to species, were collected on La Desirade, Lesser Antilles, and Vanuatu, southern Pacific Ocean, respectively. Furthermore, specimens morphoanatomically attributable to *H. munitum* and *Hydrolithon samoënse* are grouped in clade 5.2b. These specimens share with *H. rupestre* and *H. canariense* a monomerous organization with a plumose ventral core, occasionally having trichocytes that usually occur only on the surface and do not become buried, except in some cases in *H. munitum*, but never as horizontal rows/fields. As the attempts to obtain a diagnostic DNA sequence from the isotype of *H. munitum* failed, the proposed inclusion of this species in *Harveylithon* is exclusively based on the morphoanatomical characters of the holotype of this species in the New York Botanical Garden herbarium: NY Howe no. 4023.

Harveylithon munitum (Foslie & M.Howe) A.Rösler, Perfectti, V.Peña & J.C.Braga **comb. nov.**

Basionym: *Lithophyllum munitum* Foslie & M.Howe 1906. *Bulletin of the New York Botanical Garden* 4, p. 132, plates 86, 88, 89.

Homotypic synonyms: *Neogoniolithon munitum* (Foslie & M.Howe) Adey 1970: 9, *H. munitum* (Foslie & M.Howe) Penrose 1996b: 263.

Type locality: Cave Cays, Exuma Chain, Bahamas (Woelkerling 1998: 319).

Description: Growth form encrusting to warty, thallus monomerous, ventral core plumose, trichocytes not in common horizontal rows/fields of trichocytes, at the thallus surface and/or buried within the thallus. Uniporate tetrasporangial conceptacle chambers 220–300 µm in diameter and 100–150 µm high (see Fig. 6B).

Distribution: Based on morphological features, *Harveylithon munitum* was reported as *H. munitum* from the tropical and subtropical Western Atlantic (Wynne 2011) and from Western Australia, across southern Australia to Queensland (Penrose 1996a, Harvey et al. 2006, Bostock and Holland 2010) far from its type locality in the Bahamas.

Harveylithon samoënse (Foslie) A.Rösler, Perfectti, V.Peña & J.C.Braga **comb. nov.**

Basionym: *Lithophyllum samoënse* Foslie 1906b. *Det Kongelige Norske Videnskabers Selskabs Skrifter* 1906(2): 20.

Homotypic synonyms: *Pseudolithophyllum samoënse* (Fosley) Adey 1970: 13, *Hydrolithon samoënse* (Foslie) Keats and Chamberlain 1994: 15.

Type locality: Satana, Savai'i Island, Western Samoa

Description: Thallus encrusting and smooth, monomerous, ventral core plumose, trichocytes common, single or in small vertical rows at the surface or buried in the thallus (Maneveldt et al. 2015). *Harveylithon samoënse* is morphologically separate from other species of the genus due to its distinctive (tetrasporangial and carposporangial) uniporate conceptacle roof filaments, which comprise an epithallial cell subtended by a characteristic columnar cell and, usually, a smaller basal cell. Recently, Maneveldt et al. (2015) described the lectotype designated by Woelkerling (1993: 193). Based on morphoanatomical features, Maneveldt et al. (2015) consider *Neogoniolithon caribaeum* (Foslie) W.H.Adey (type locality in US Virgin Islands), *Neogoniolithon erosum* (Foslie) W.H.Adey (type locality in US Virgin Islands), and *Neogoniolithon rugulosum* W.H.Adey, R.A.Townsend & Boykins (type locality in Oahu, Hawaii) as heterotypic synonyms of *H. samoënse.* As in other cases of taxa described from distant type localities, analysis of the molecular affinities of type material is required for a confident assessment.

Distribution: Based on morphoanatomical characters, the species was reported as *Hydrolithon samoënse* in many localities in the Indian and Pacific oceans (Keats and Chamberlain 1994, Maneveldt et al. 2015), from southern Australia to Queensland (Harvey et al. 2006), the Canary Islands, Atlantic coasts of Spain and France, and the British Isles (Chamberlain and Irvine 1994). The only sequenced specimen attributed to *Harveylithon samoënse* was collected in South Australia (Bailey et al. 2004, as *Hydrolithon samoënse*).

(5.2b) "*Pneophyllum*" *conicum* (E.Y.Dawson) Keats, Y.M.Chamberlain & M.Baba group

Description: Thallus nongeniculate, monomerous with predominantly coaxial ventral core. Cell fusions are abundant in peripheral filaments. Trichocytes occur singly or in horizontal fields at the surface but do not become buried; within the fields, they may all be contiguous or occur in clusters, with vegetative subepithallial initials and epithallial cells

among them. Tetrasporangial conceptacles are raised and low conical, with an internal diameter of 220–400 μm. Old conceptacles are usually shed, sometimes leaving a distinctive, rimmed scar on the surface (Keats et al. 1997). The uniporate tetrasporangial conceptacle roof is formed by filaments surrounding and interspersed between sporangial initials with cells lining the pore canal oriented oblique to the pore wall (or to the roof surface) and slightly projected into the canal. This feature separates "*P.*" *conicum* from other Metagoniolithoideae. A vegetative distinction from *Porolithon* is that trichocyte fields do not become buried.

Homotypic synonyms: *Hydrolithon conicum* Dawson 1960: 27 (basionym); *Neogoniolithon conicum* (E.Y.Dawson) Gordon et al. 1976, : 259; *Paragoniolithon conicum* (E.Y.Dawson) W.H.Adey, R.A.Townsend & Boykins 1982: 13; *Porolithon conicum* (E.Y.Dawson) M.Baba in Keats et al. 1997: 264 (nom. inval.).

Remarks: Mariath et al. (2012) reported that all of the holotype material of "*Pneophyllum*" *conicum* (E.Y.Dawson, 19.xi.1953, US Dawson 12148), collected from the intertidal reef at Binners Cove, Isla Socorro, Revillagigedo Archipelago, Mexico (Pacific), is now housed in the Herbarium UC (University of California), while an isotype preserved in the A. Hancock Foundation was transferred to United States. This isotype is described in Keats et al. (1997), and it was sequenced for our molecular studies, unfortunately without results.

The species grouped in this clade (Fig. 1) do not include any coralline algae, showing morphological characters similar to *Pneophyllum fragile*, the type species of *Pneophyllum*, except the orientation of the cells lining the pore canal in tetrasporangial conceptacles and other characters shared by many genera of Corallinaceae. As stated above, the current circumscription of *Pneophyllum* itself is questionable and needs reassessment. Before being transferred to *Pneophyllum* by Keats et al. (1997), the species was assigned to the genus *Paragoniolithon* which was established by Adey et al. (1982) for coralline algae with the following attributes: (i) ventral core multilayered, thick, and weakly to strongly coaxial, multilayered peripheral region, (ii) cell fusions common, (iii) trichocytes loosely grouped into horizontal fields composed of 2–3 cells, and (iv) spermatangia restricted to the floor of the male conceptacle. Woelkerling (1987b) questioned the occurrence of the morphoanatomical characters separating *Paragoniolithon* and *Neogoniotlihon* since generitypes of the two genera (*Paragoniolithon solubile* (Foslie & M.Howe) W.H.Adey, R.A.Townsend & Boykins and *Neogoniolithon fosliei* (Heydrich) Setchell & L.R.Mason) possessed a coaxial ventral core and trichocytes. In agreement with Kato et al. (2011), the separation of "*Pneophyllum*" *conicum* from the genus *Neogoniolithon* is well established according to our results. In addition, spermatangia in *Neogoniolithon* occur on both the floor and roof of the male conceptacle but only on the floor in "*Pneophyllum*" *conicum* (Kato et al. 2011). On the other hand, recent molecular results based on *psb*A sequences group coralline algae from the Atlantic coast of Mexico with morphoanatomical characters of *Goniolithon solubile* Foslie (type locality Culebra, Puerto Rico) with other *Neogoniolithon* species (Mateo-Cid et al. 2014), although no type or topotype material was analyzed. Due to the great geographical distance between sequenced specimens and the type locality of "*Pneophyllum*" *conicum*, we leave this species with an uncertain genus assignment until unambiguous attribution of DNA sequences to type material or epitypes from the type locality are designated.

Distribution: Based on morphoanatomy, "*Pneophyllum*" *conicum* was reported in the tropical and subtropical Pacific (Adey et al. 1982, Keats et al. 1997, Yoshida 1998, Tsuda 2003, as *Paragoniolithon conicum*, South and Skelton 2003, N'Yeurt and Payri 2010, Xia 2013a,b, Tsuda and Walsh 2013), and in Mauritius, Indian Ocean (Antonius and Afonso-Carrillo 2001), and in Brazil, southwest Atlantic (Mariath et al. 2012). Previously sequenced specimens of "*Pneophyllum*" *conicum* were collected in Vanuatu and Fiji (Bittner et al. 2011), and Hawaii and Japan (Kato et al. 2011).

(6) The Southern Hemisphere group

The sixth clade, the Southern Hemisphere group, contains OTUs attributed to *Spongites yendoi* (Foslie) Y.M. Chamberlain (New Zealand and South Africa), *Pneophyllum coronatum* (Rosanoff) Penrose and *P. fragile* (New Zealand), *Spongites hyperellus* (Foslie) Penrose (southern Australia), and *Spongites sp.* (Chile). Morphologically, this group is difficult to delimit from other genera or even subfamilies of Corallinaceae. All members possess monomerous and/or dimerous but thin thalli. Uniporate tetrasporangial conceptacle roofs in *Spongites yendoi* and *S. hyperellus* develop from peripheral filaments, whereas in species attributed to *Pneophyllum* from the Southern Hemisphere, they are formed either by filaments surrounding sporangial initials or by filaments peripheral to and interspersed among sporangial initials (Penrose 1996b). These species assigned to *Spongites* can be monomerous and dimerous, whereas *Pneophyllum* from southern Australia has been described as dimerous (Penrose 1996b) or as monomerous and dimerous (Harvey et al. 2006). In species attributed to both genera, the cells lining the pore canal are oriented parallel to oblique to the thallus surface and partly protruding into the canal. A taxonomic treatment of this clade is beyond the scope of this paper. Further research is necessary to identify morphological traits delimiting the group, the possible internal subdivision, and the relationships of the Southern Hemisphere species comprising this clade with European or Northern Hemisphere species that have been attributed to the same genera. Nelson et al. (2015) found a similar

clade forming a sister group to a branch containing *Porolithon onkodes*, member of Metagoniolithoideae. As indicated in the clade name, all the specimens analyzed here were collected in the Southern Hemisphere: New Zealand, Southern Australia, South Africa, and Chile. The formation of subclades of specimens from New Zealand can also be observed in lithophylloids, which indicates a high degree of genetic differentiation of corallines from this region. Nelson et al. (2015) reported an unexpectedly great diversity of coralline algae from the New Zealand region. Endemism in the Southern Hemisphere was also mentioned for the genus *Spongites* (Vidal et al. 2008) and is found as well in other red algal orders in New Zealand, for example, in Bangiales and Gigartinales (Nelson et al. 2005, 2011). This group needs a profound analysis of molecular and morphological affinities of a larger number of specimens and a revision of the generic and specific attribution of the component species.

(7) Subfamily Lithophylloideae Setchell 1943: 134
Type genus: *Lithophyllum* Philippi 1837: 387

Remarks: This clade corresponds to the subfamily Lithophylloideae, and contains: (i) several paraphyletic branches of specimens assigned to *Lithophyllum kotschyanum* Unger and morphologically related species (Pacific and Indian ocean); (ii) one clade composed of algae identified by Farr et al. (2009) as different *Lithophyllum* species from New Zealand (*L. stictaeforme* (Areschoug) Hauck, *L. johansenii* Woelkerling & S.J. Campbell, *L. corallinae* (P.L. Crouan & H.M. Crouan) Heydrich, *L. carpophylli* (Heydrich) Heydrich, *L. pustulatum* (J.V. Lamouroux) Foslie) and specimens attributed to *L. insipidum* W.H.Adey, R.A.Townsend & Boykins from Hawaii (Sherwood et al. 2010); (iii) a group consisting of specimens attributed to Mediterranean taxa such as *L. racemus* (Lamarck) Foslie, *L. incrustans* Philippi, and *L. dentatum* (Kützing) Foslie, together with coralline algae attributed to *L. kotschyanum* from Pacific and Indian Ocean localities; (iv) one paraphyletic group of algae attributable to *L. pustulatum* and morphologically similar species (=*Titanoderma auctorum*); and (v) one monophyletic group of *Amphiroa* with taxa from Belize, Guadeloupe, Fiji, Philippines, and the Mediterranean Sea. Morphologically, the members of this subfamily can be easily distinguished from all other groups of Corallinaceae by possessing secondary pit connections instead of cell fusions between cells of adjacent filaments (Woelkerling 1988, Chamberlain and Irvine 1994). As shown by recent research (Hernandez-Kantun et al. 2015), the taxonomy of the group needs to be reassessed by a combination of molecular and morphoanatomical studies.

CONCLUDING REMARKS

This study reassessed the phylogenetic relationships of Corallinaceae based on molecular data from recent collections and type material. Hydrolithoideae, Metagoniolithoideae, and Lithophylloideae share the evolutionary novelty of the development of the tetra/bisporangial conceptacle roofs by filaments surrounding and interspersed among the sporangial initials, whereas tetra/bisporangial conceptacle roofs in Mastophoroideae, Corallinoideae, and Neogoniolithoideae formed by filaments peripheral to the fertile area. The subfamilies Neogoniolithoideae and Metagoniolithoideae were amended. *Spongites fruticulosus* was included in Neogoniolithoideae. As stated by Hind and Saunders (2013), no morphoanatomical characters are useful to separate this subfamily from Corallinoideae. As already suggested by morphological comparison (Mendoza-González et al. 2009), *Hydrolithon reinboldii* is a younger, heterotypic synonym of *H. boergesenii* since the two species could not be separated in our molecular analysis. Besides *Metagoniolithon,* Metagoniolithoideae includes the genus *Porolithon* and the newly described genus *Harveylithon.* Porolithoideae was rejected as an independent subfamily. *Harveylithon* is distinguished from other Metagoniolithoideae by the combination of nongeniculate monomerous thallus organization with plumose ventral core and absence of buried horizontal trichocyte fields. In addition to the type species, *Harveylithon rupestre,* the genus includes the species *H. canariense,* and *H. munitum,* and *H. samoënse* transferred from *Hydrolithon.* Another clade within Metagoniolithoideae comprises specimens assigned to "*Pneophyllum*" *conicum.* The formal definition of this clade requires the analysis of type material of this species. Our results also pointed out the necessity of profound reassessment of members of the subfamily Lithophylloideae and of coralline taxa from the Southern Hemisphere assigned to *Pneophyllum* and *Spongites.*

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1. List of taxa extracted from GenBank that were included in our analyses, arranged alphabetically.