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Radiation of the coralline red algae (Corallinophycidae, Rhodophyta) crown group as inferred from a multilocus time-calibrated phylogeny

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Running title: Evolutionary history of coralline red algae

Abstract:

The subclass Corallinophycidae is the only group of red algae characterized by the presence of calcite crystals in their cell walls. Except for the Rhodogorgonales, the remaining orders - collectively called corallines - are diverse and widely distributed, having calcified cell walls and highly variable morphology. Corallines constitute the group with the richest fossil record among marine algae. In the present study, we investigate the evolutionary history of the subclass Corallinophycidae and provide a time-calibrated phylogeny to date the radiation of the crown group and its main lineages. We use a multi-locus dataset with an extensive taxon sampling and comprehensive collection of fossil records, carefully assigned to corallines, to reconstruct a time-calibrated phylogeny of this subclass. Our molecular clock analyses suggest that the onset of crown group diversification of Corallinophycidae started in the Lower Jurassic and sped up in the Lower Cretaceous. The divergence time of the oldest order Sporolithales is estimated in the Lower Cretaceous followed by the remaining orders. We discuss the long period of more than 300 million years between the early Paleozoic records attributed to the stem group of Corallinophycidae and the radiation of the crown group. Our inferred phylogeny yields three highly-supported suprageneric lineages for the order Corallinales; we confirm the family Mastophoraceae and amend circumscription of the families Corallinaceae and Lithophyllaceae. These three families are distinguished by a combination of vegetative and reproductive features. In light of the phylogeny, we discuss the evolutionary trends of eleven morphological characters. In addition, we also highlight homoplasious characters and selected autapomorphies emerging in particular taxa.

Key words: Corallinales; evolution; diversification; Florideophyceae; fossil records; taxonomy.

1. Introduction

In the course of red algal evolution, calcification of cell walls with calcite crystals only evolved within the subclass Corallinophycidae (Borowitzka et al., 1974; Le Gall and Saunders, 2007),

which encompasses four extant orders: the Rhodogorgonales with calcification limited to calcite husks excreted in a mucilaginous cell wall (Pueschel et al., 1992; Fredericq and Norris, 1995), and Sporolithales, Hapalidiales and Corallinales. These last three orders are collectively known as coralline algae (corallines). In this group calcification either covers the entire plant or is interrupted by genicula which consist of non-calcified parts mechanically working as ball joints allowing some flexibility of the plant (reviewed in Johansen, 1981). Coralline algae are very diverse and taxonomic studies led to the recognition of more than 750 species (Guiry and Guiry, 2020). They have a global distribution, and occur from the intertidal to the extreme limit of the photic zone (>250 m, Littler et al., 1985). They have been considered as an exclusively marine group, although the recent discovery of a genuine freshwater species, *Pneophyllum cetinaensis* (Žuljević et al., 2016), has challenged this paradigm.

Coralline red algae have perplexed naturalists since the beginning of the 18th century. Their calcified nature rendered them enigmatic and they were studied along with other marine calcified metazoans, such as corals. It was not before 1837 that they became recognized as photosynthetic organisms (Philippi, 1837). Their variable morphology together with the difficulty of the anatomical study of calcareous organisms led to the description of more than 1600 taxa of specific and infraspecific rank; however, uncertainty still prevails with respect to the global diversity of coralline algae and many species remain unnamed or are putatively recognized as synonyms of previously described taxa (Woelkerling and Lamy, 1998, Fig. 1). The recent application of molecular characters to coralline red algal systematics has yielded a better understanding of their phylogenetic affinities within Florideophyceae and a separate monophyletic subclass, the Corallinophycidae, allied to Rhodogorgonales was proposed (Le Gall and Saunders, 2007). The subclass Corallinophycidae differs from other Florideophyceae subclasses by the presence of calcite and by having pit plugs with two cap layers characterized by dome outer cap and without cap membrane (Le Gall and Saunders, 2007).

Within the Corallinophycidae, phylogenetic analyses have revealed substantial diversity and two lineages were successively elevated to ordinal level, i.e. the Sporolithales (Le Gall et al.,

2010) and Hapalidiales (Nelson et al., 2015). At lower rank, recent phylogenetic studies have provided a better resolution for subfamilies of all orders (Harvey et al., 2003; Bittner et al., 2011; Kato et al., 2011; Rösler et al., 2016; Caragnano et al., 2018); and within the order Corallinales, Townsend & Huisman (2018) have recently proposed six families based on polyphyly inferred from literature and newly generated data.

Diagnostic features distinctive of Sporolithales are based on the occurrence within calcified compartments of tetrasporangia that undergo cruciate cleavage (Le Gall et al., 2010). In contrast, in Hapalidiales, zonate sporangia are developed in conceptacles with multiporate roofs and each sporangium possesses an apical plug, while in Corallinales the zonate sporangia are developed in uniporate conceptacles (Harvey et al., 2003; Nelson et al., 2015). Further features considered diagnostic at different taxonomic levels are mostly related to the type of connection between adjacent cells (cell fusions or secondary pit-connections), structure of spermatangial and carposporangial conceptacles, type of formation of sporangial roof conceptacles, and the presence and arrangement of trichocytes (reviewed in Johansen, 1981; Woelkerling, 1988; Irvine and Chamberlain, 1994; Harvey et al., 2003; Kato et al., 2011; Rösler et al., 2016; Caragnano et al., 2018).

Since the establishment of Corallinophycidae, several studies have addressed the evolutionary history of coralline red algae focusing on different morpho-anatomical characters. Before the era of molecular systematics, classifications of coralline were mostly based on vegetative and reproductive features (i.e. Cabioch, 1972; Johansen, 1972; Lebenik, 1977; Bailey and Chapman, 1998). However, the high phenotypic plasticity of coralline red algae led to morphological convergences between distant phylogenetic taxa (reviewed in Johansen, 1981). For instance, Bittner et al. (2011) analysed five characters related with the type of sporangial conceptacle (uniporate/multiporate), presence or absence of apical pore plug, type of cell connection (cell fusions, secondary pit-connections), and occurrence of genicula, and came to the conclusion that these features were subject to a high degree of homoplasy. In particular, the taxonomic value traditionally attributed to the genicula to separate non-articulated (non-

geniculate) from articulated (geniculate) taxa (tribes Melobesieae and Corallineae; Areschoug, 1852) is no longer accepted. The latter are thought to be derived from the former, and later reversals to the ancestral state have also occurred (Bailey and Chapman, 1998; Martone et al., 2012; Hind and Saunders, 2013; Hind et al., 2016, 2018). As evolutionary novelty within the order Corallinales (subfamilies Hydrolithoideae, Metagoniolithoideae and Lithophylloideae), Rösler et al. (2016) pointed out the type of development of sporangial conceptacle roofs involving filaments surrounding and interspersed among the sporangial initials. In addition, Yang et al. (2016) showed evolutionary innovations in the carposporophyte stage within the class Florideophyceae that have been acquired by most of the Corallinophycidae lineages.

The calcareous nature of coralline red algae contributes to their preservation in fossil deposits. The oldest fossil record confidently assigned to a Corallinophycidae is attributed to *Sporolithon* from the Lower Cretaceous (Valanginian, ca. 136 Mya., *Sporolithon* sp. (?), Chatalov et al., 2015). However, the affinity of earlier taxa resembling coralline red algae and with scarce fossil record is subject to debate in the literature. Notably, the Neoproterozoic taxa *Thallophyca* and *Paramecia* (ca. 600 Mya.) are considered non-calcified ancestors of modern coralline red algae based on the resemblance in vegetative structure (Xiao et al., 2004). Additional taxa, both calcified and non-calcified forms, gathered from Paleozoic and Triassic rocks have been claimed to be related with modern corallines or to be included within the order Corallinales (Brooke and Riding, 1998, 2000; Riding et al., 1998; Senowbary-Daryan et al., 2002; Riding and Braga, 2005; Senowbary-Daryan and Velledits, 2007; Smith and Butterfield, 2013; Teichert et al., 2019). Nonetheless, whether these taxa belong to the stem group of the modern corallines or are true corallines requires an indepth evaluation (see Discussion).

During the Upper Cretaceous, coralline red algae were diverse in shallow tropical reefs in the Tethyan realm; then, from the Cretaceous to Miocene coralline red algae showed a geographic and bathymetric range expansion, although they also suffered episodes of extinction followed by evolutionary radiations and occupation of new available habitats (i.e. Aguirre et al., 2000a, 2000b, 2007). In addition, from the Upper Cretaceous to the Pleistocene, the species richness of

Corallinales and Hapalidiales increased while Sporolithales declined along with the progressive cooling of the Earth (Aguirre et al., 2000a).

Corallines, with the most abundant fossil record among marine benthic algae, have been extensively used to calibrate phylogenies with molecular clock dating to estimate the time of origin of this group and the main lineages of Rhodophyta. Based on 18rDNA sequences of the three fully calcified orders (Sporolithales, Hapalidiales and Corallinales), Aguirre et al. (2010) confirmed that the order Sporolithales (as Sporolithaceae) was the first diverging group in the Lower Cretaceous (*ca.* 136 Mya). Recently, Rösler et al. (2017) estimated the separation between the orders Hapalidiales and Corallinales at *ca.* 105 Mya, and subsequent Corallinales subfamilies between *ca.* 97-54 Mya. On the other hand, Yang et al. (2016) - using a seven-gene concatenated dataset of florideophycean taxa and earlier, non-calcified records from the Late Neoproterozoic (*Thallophyca* and *Paramecia*, Xiao et al., 2004) - concluded that the subclass Corallinophycidae diverged at *ca.* 579 Ma, about 241 Ma older than estimated by Aguirre et al. (2010). Nonetheless, they also pointed out that the crown group diversification appears to occur later, in the Lower Cretaceous.

In this study, we aim to provide a comprehensive evolutionary history of the subclass Corallinophycidae, focusing on the radiation of the crown group and its main lineages. To this end, we reconstruct the phylogeny of the subclass using a multi-locus dataset with an extensive taxon sampling including representatives of the four orders (Rhodogorgonales, Sporolithales, Hapalidiales and Corallinales). The resulting phylogeny was time-calibrated using comprehensive datasets of fossil records attributed to Corallinophycidae corresponding to the three orders with fully calcified skeleton (Sporolithales, Hapalidiales and Corallinales). In light of the phylogenetic tree, we discuss evolutionary trends of morphological characters.

2. Material and methods

2.1 DNA extractions, PCR amplifications and sequencing of own collections

To reassess the great diversity of coralline algae, we collected specimens of different growth-forms (crustose, unattached as maerl/rhodolith, geniculate, etc), all over the world from tropical to temperate regions, from intertidal to depth of *ca.* 30 m. (Table S1). Prior to DNA extraction, material was observed under a stereomicroscope to select tissues from a single species which were ground with a drill bit of 2 mm in diameter for DNA extraction. Genomic DNA was extracted using a NucleoSpin® 96 Tissue kit (Macherey-Nagel, GmbH and Co. KG, Germany) or QIAamp® DNA Micro Kit (Qiagen S.A.S., France) following the manufacturer protocol for tissues. PCR reactions followed Peña et al. (2015). The mitochondrial gene *cox1* and the plastid gene *psbA* were amplified according to Peña et al. (2015), while the nuclear gene LSU rRNA was PCR amplified as three overlapping fragments using primers T01N/T20, T04/T08 and T05/T15 (Harper and Saunders, 2001) according to the thermal profile that included an initial denaturation at 95°C for 3 min followed by 38 cycles of 40 s denaturation at 95°C, 40 s annealing at 55°C and 1 min of extension at 72°C followed by an additional 7 min at 72°C and storage at 12°C. PCR products were purified and sequenced by Eurofins (Eurofins Scientific, France). Sequences were assembled and aligned with the assistance of CodonCode Aligner® (CodonCode Corporation, USA) and adjusted by eye using SeaView version 4 (Gouy et al., 2010). Sequences were submitted to the Barcode of Life Data Systems (project 'NGCOR', BOLD, <http://www.boldsystems.org>; Ratnasingham and Hebert, 2007) and GenBank (accession numbers listed in Table S1). Collections are deposited in the herbaria PC, GENT and SANT (Muséum National d'Histoire Naturelle, Ghent University and Universidade de Santiago de Compostela, respectively; acronyms follow Thiers (2020)).

2.2 Phylogenetic analyses

Novel molecular data were generated from selected collections and complemented with sequences from GenBank. First, a database of 422 taxa representing all lineages of the subclass Corallinophycidae and the outgroups Rhodymeniophycidae and Ahnfeltiophycidae was built using 1032 GenBank accessions and novel molecular data for at least one of the following seven genes: *cox1* (from the mitochondrial genome), *psbA*, *rbcL* and 23S rRNA (from the plastid

genom), and SSU rRNA, LSU rRNA and EF2 (from the nuclear genome). Among those 422 taxa, we further selected the taxa to be included in the phylogenetic analysis with the following priorities: generitypes, taxa for which multiple molecular markers were obtained from the same voucher and taxa represented by one gene but distant from other taxa had priority for building the alignment. We also selected chimeras (n=20) which grouped taxa with less than 4% divergence estimated in Mega 6.06 (Tamura et al., 2013) for the *cox1* and *psbA* databases (the most comprehensive for Corallinophycidae with more than 2000 and 1000 publicly available sequences, respectively). From this initial dataset, 132 taxa were finally selected for the analyses of which 22 were newly included for this study. In addition, for another 21 specimens preserved in the herbaria PC and SANT with previous GenBank records, new sequences corresponding to additional markers (e.g. *rbcL*) were also generated (Table S1). Prior to concatenation, each alignment has been checked and their length has been reduced using Mega 6.06 to obtain at least 75% of coverage on the gene level. Gap-rich regions in both SSU rRNA and LSU rRNA alignments were deleted using GBlocks with options for a less stringent final alignment (Castresana, 2000). Thus, the final length of each resulting alignment was: 556 bp for the *cox1* alignment, 589 bp for the *psbA*, 1387 bp for the *rbcL*, 370 bp for 23S rRNA, 2087 bp for the SSU rRNA, 4717 bp for the LSU rRNA and 1623 bp for the EF2). Phylogenetic analyses of the seven-gene concatenated alignment of 11329 bp were inferred using maximum likelihood (RAxML 8.1.11; Stamakis, 2014) and Bayesian inference (BI) using MrBayes 3.2.3 (Ronquist and Huelsenbeck, 2003), both available from CIPRES Science Gateway (Miller et al., 2010). For both analyses, PartitionFinder (Lanfear et al., 2012) was performed to estimate the best-fitting partitioning scheme (seven partitions: (i) 23S, (ii) *cox1*, (iii) EF2, (iv) LSU rRNA, (v) *psbA*, (vi) *rbcL* and, (vii) SSU rRNA) and model of molecular evolution (GTR).

2.3 Calibration methods

A database of fossil coralline red algae based on a literature survey was compiled by Juan C. Braga and Julio Aguirre. The database comprises 4550 reports of species attributed to groups that can be included in Corallinophycidae. The accuracy of every single record was checked and

those records without sufficient description and/or illustration were removed from the database. For the final calibration, 2350 fossil records identified at the genus or subfamily level were selected. Six calibration nodes (*Harveylithon* (A), *Porolithon* (B), '*Lithophyllum pustulatum*' (C), Hydrolithoideae (D) groups, and Hapalidiales (E) and Sporolithales (F) orders) were set as time points based on these fossil records, to calibrate the molecular clock. These six calibration nodes were strategically placed in disparate regions of the tree. The absolute age attributed to each record was calculated as the midpoint of the absolute age range of the stratigraphic interval from which the taxon was reported, according to the International Chronostratigraphic Chart (Cohen et al., 2015). Records reported from long, imprecise stratigraphic intervals were discarded.

In order to reconstruct the time-calibrated phylogeny, we used the seven genes (LSU, SSU, 23S, *cox1*, EF2, *psbA*, *rbcL*) concatenated alignment consisting of 8000 higher up bp. Nine outgroups sequences were added to the 123 Corallinophycidae taxon alignment. Divergence times were estimated using Bayesian inference through Markov chain Monte Carlo (MCMC), as implemented in BEAST v1.10.0 (Suchard et al., 2018) under a fixed local clock model (Worobey et al., 2014), using BEAGLE 3 (Ayres et al., 2019) for computational efficiency. We opted for a fixed local clock model because our molecular data consists of distinct clusters of sequences and the fixed local clock specifically allows to assign each cluster its own evolutionary rate. Relaxed molecular clock models are not able to properly deal with such multi-modal rate distributions, and have been shown to yield incorrect topologies in such cases (Worobey et al., 2014). The tree prior was specified as a Yule process prior (Yule, 1924). Convergence was assessed through visual inspection whereas proper statistical mixing was assessed through estimating effective sample sizes (ESS) in Tracer v1.7.1 (Rambaut et al., 2018). Except for the ribosomal genes, all markers (*cox1*, EF2, *psbA*, *rbcL*) were presumed to evolve independently under a GTR + Γ model for each codon position, using empirical base frequencies. Ribosomal genes were presumed to evolve under a GTR with no site heterogeneity model. The MCMC chain length was set to 250 million iterations and parameter values were

sampled at each 5000th iteration. After discarding 25% of the trees as burn-in, a maximum clade credibility (MCC) tree was constructed using TreeAnnotator v1.10.0, which was subsequently visualized using Figtree v1.4.2 (Rambaut, 2014). Six calibration priors were used, four within the Corallinales, in addition to the Hapalidiales (E) and Sporolithales (F) crown groups (see Supplementary Data 1 for BEAST XML input). Within the Corallinales, the most recent common ancestor (MRCA) of *Harveyolithon* group (A) was set to 18 ± 8.4 Ma; the MRCA of the *Porolithon* group (B) to 23 ± 4.65 Ma; the MRCA of the '*Lithophyllum pustulatum*' group (C) to 26.8 ± 5.1 Ma; the MRCA of the Hydrolithoideae group to 66 ± 2.23 Ma (see Rösler et al., 2017); the MRCAs of the order Hapalidiales and Sporolithales to 116.66 ± 0.66 Ma and 137.63 ± 1.23 Ma, respectively (see Aguirre et al., 2010). In addition, we constrained the monophyly for these six groups and for the Corallinophycidae according to the phylogenetic results.

Among the different methods used to contrast the quality of node ages in a phylogenetic tree, Warnock et al. (2015) suggested that the most effective one is "*a priori evaluation of the intrinsic paleontological, stratigraphic, geochronological and phylogenetic data*". That is, tree nodes can be accurately established using the first appearance dates of particular taxa in the rock record when such a group of organisms shows a complete fossil record (high coverage). In contrast, when the fossil record of the organisms under study is poor or deficient (low coverage), the age calibration of nodes requires the application of cross-validation methods to evaluate the consistency of age estimations based on fossil occurrences, and the inconsistent ones discarded. Taking into consideration our database, which is based on hundreds of carefully checked references, strong evidence supports that the fossil record of the clades used to date nodes in our coralline algal phylogeny (Sporolithales, Hapalidiales, *Harveyolithon* group, *Porolithon* group, *Hydrolithon* group, and *L. pustulatum* group) is reasonably complete (high coverage), as demonstrated in previous papers (Aguirre et al., 2010; Rösler et al., 2016, 2017). By using confidence intervals (95%) (see Marshall, 1990, 1998), we accurately and reliably established the minimum age ranges for those nodes to calibrate the tree since they are based on a very rich and complete fossil record.

3. Results

3.1. Phylogeny of Corallinophycidae

In agreement with previous studies, our phylogenetic analyses consistently resolve the four orders currently recognized in the subclass Corallinophycidae as monophyletic lineages (Figs. 2, 3). Likewise, the genus *Corallinapetra* recently discovered in New Zealand (Nelson et al., 2015) is resolved as a sister lineage to the one encompassing the orders Corallinales and Hapalidiales. A summary of diagnostic features for each order (excluding Rhodogorgonales because of their distinct morphology and calcification restricted to husks, Table 1) is provided according to literature review for the 59 genera currently accepted taxonomically within the subclass Corallinophycidae. Within the order Corallinales three suprageneric, monophyletic lineages are highly supported: i) one lineage containing species assigned to *Mastophora* and *Mastophora/Lithoporella*, ii) a second lineage comprising taxa pertaining to the subfamilies Neogonolithoideae and Corallinoideae, and iii) a third lineage including the subfamilies Hydrolithoideae, Metagoniolithoideae, Lithophylloideae, Chamberlainoideae as well as the lineage containing two taxa of *Parvicellularium* (*P. leonardi*, *P. sp.*), a recently described genus as *incertae sedis* (Caragnano et al., 2018). Within this third lineage, maximum likelihood (Fig. 2) and Bayesian (Fig. 3) reconstruction methods led to well-supported alternative topologies among subfamilies (see also Fig. S1).

3.2. Divergence time estimation of the crown group of Corallinophycidae

The time-calibrated molecular clock analyses reveal that the divergence time of the common ancestors of the orders Sporolithales, Rhodogorgonales, Corallinales and Hapalidiales is estimated in the Early Jurassic, at 179.88 Ma (171.47 – 188.24 Ma based on 95% highest posterior densities, HPD; Fig. 4). The divergence time of the oldest order among the Corallinophycidae, the Sporolithales, is estimated at 137.03 Ma (134.43 – 139.24 Ma HPD). The divergence times of the three other orders occur almost simultaneously in the second half of

the Lower Cretaceous (Rhodogorgonales 114.87 Ma (100.99 – 128.88 Ma HPD); Hapalidiales

116.73 Ma (115.25 – 117.84 Ma HPD); Corallinales 112.86 Ma (106.09 – 119.21 Ma HPD)

(Fig. 4). Our analyses show clearly distinct evolutionary rates among clades, supporting the use of the fixed local clock model (Fig. S2). The Hapalidiales and Sporolithales were the only calibration nodes to present indistinguishable marginal prior and posterior age distributions, indicating that for these nodes and regions of the tree the signal largely results from prior beliefs rather than from the data.

3.3. Taxonomic proposal for *Corallinophycidae*

According to our results, and in an effort towards a classification closer to the natural systems in compliance with the International Code of Nomenclature for algae, fungi, and plants (Shenzhen code, Turland et al., 2018), we propose the following classification scheme of the order Corallinales with three families: Corallinaceae, Lithophyllaceae and Mastophoraceae. For each family, a detailed description is provided together with a comparative summary of vegetative and reproductive features compiled from the literature and pertaining to different phases of the life cycle (gametangial, carposporangial and sporangial, Tables 2-4).

Order Corallinales P.C. Silva & H.W.Johansen (1986) (Table 1)

Family Mastophoraceae (Setchell) R.A.Townsend & Huisman (2018) (Table 2, Figs. 2, 3)

Subfamily Mastophoroideae (Setchell) A.Kato & M.Baba *in* Kato et al. (2011)

Type genus: *Mastophora* Decaisne 1842

Description of the family Mastophoraceae: Non-geniculate, arborescent, encrusting or unattached plants. Rhizoids absent or present. Dorsiventral organization, dimerous construction. Cell fusions or secondary pit-connections (occasional). Trichocytes single or in horizontal groups. Gametangial, carposporangial and sporangial conceptacles uniporate. Spermatangial filaments unbranched, on the chamber floor. Carpogonial branches arising from the chamber

floor. Carposporophyte with a conspicuous fusion cell and marginal gonimoblast filaments. Sporangial conceptacle roofs formed by filaments surrounding sporangial initials, with pore canals lined by cells oriented more or less parallel to roof surface and protrude slightly into the canal; central columella present. Sporangium with zonate division, lacking an apical plug; bisporangia unknown.

Remarks: We confirmed the circumscription of family Mastophoraceae proposed in Townsed and Huisman (2018). According to our results, the family Mastophoraceae only encompasses the subfamily Mastophoroideae, which is restricted to the genera *Mastophora* and *Metamastophora* and possibly *Lithoporella* for which no reliable sequences are available.

Despite similarities in vegetative anatomy, the genus *Lithoporella* is distinguished by having: i) tetrasporangial conceptacle roofs formed by filaments surrounding and interspersed amongst sporangial initials, ii) a pore canal lined by cells that are orientated more or less perpendicularly to the roof surface and does not protrude into the canal, and iii) the tetrasporangial conceptacles lacking a central columella. In addition, the carposporophyte of *Lithoporella* is composed of a thin fusion cell with gonimoblast filaments arising from its ventral surface, while in *Mastophora* and *Metamastophora* the fusion cell is described as compact, thick with marginal gonimoblast filaments (Woelkerling, 1980; Turner and Woelkerling, 1982a). Further detailed studies involving genuine *Lithoporella* collections are needed to elucidate the phylogenetic affinities of this genus. Molecular information is also needed to resolve the taxonomic position of *Lesueuria*, an endophytic genus which shares the development of tetrasporangial conceptacle roofs (only by filaments surrounding sporangial initials), the disposition of cells lining the pore canal of tetrasporangial conceptacles (parallel to roof surface) and the arising type of gonimoblast filaments from the fusion cell of the carposporophyte (marginal) with the remaining Mastophoraceae genera. *Lesueuria* differs however by the presence of haustoria (Woelkerling and Ducker, 1987).

Family Corallinaceae Lamouroux *emendavit* V.Peña, J.C.Braga, J.Aguirre, A.Rösler, De Clerck & L.Le Gall (Table 2, Figs. 2, 3)

Subfamilies: Corallinoideae (Areschoug) Foslie (1908) and Neogoniolithoideae (A.Kato & M.Baba) A. Rösler, Perfectti, V.Peña & J.C.Braga *in* Rösler et al. (2016) (Table 3)

Type genus: *Corallina* Linnaeus 1758

Description of the family Corallinaceae: Non-geniculate encrusting or unattached, to geniculate plants. Rhizoids absent. Organization dorsiventral, radial, multiaxial. Construction monomerous or dimerous, non-coaxial to coaxial, without palisade cells. Cell fusions present, secondary pit-connections absent. Trichocytes single or arranged in horizontal groups or vertical rows, becoming buried or not. Gametangial, carposporangial and sporangial conceptacles uniporate. Spermatangial filaments unbranched, confined to the chamber floor, or on floor and walls, or on floor, walls and roof. Carpogonial branches arising from the chamber floor. Carposporophyte with fusion cell present or absent, gonimoblast filaments marginal or dorsal. Tetra/bisporangial conceptacle roofs formed by filaments surrounding sporangial initials; central columella present or absent; sporangium with zonate division, lacking apical plug.

Remarks: The family Corallinaceae encompasses the subfamilies Corallinoideae and Neogoniolithoideae. Diagnostic features of both subfamilies are summarized in Table 3. Non-geniculate, encrusting genera are represented in both subfamilies with recent descriptions of the NE Pacific genus *Crusticorallina* and two *Bosiella* for Corallinoideae (Hind et al., 2016, 2018). Our family circumscription differs from Townsend and Huisman (2018) who recently upgraded the subfamily Neogoniolithoideae (genera *Neogonolithon* and *Spongites*) to family rank (fam. Spongitaceae). In this respect, our phylogenetic analyses resolved both subfamilies Neogoniolithoideae and Corallinoideae as paraphyletic (Figs. 2, 3). Further detailed studies are needed to elucidate the phylogenetic affinities of both subfamilies.

Family Lithophyllaceae Athanasiadis *emendavit* V.Peña, J.C.Braga, J.Aguirre, A.Rösler, De Clerck & L.Le Gall (Table 2, Figs. 2, 3)

Subfamilies: Lithophylloideae Setchell (1943), Hydrolithoideae A. Kato & M. Baba *in* Kato et al. (2011), Metagoniolithoideae (H.W.Johansen) A.Rösler, Perfectti, V.Peña & J.C.Braga *in* Rösler et al. (2016), and Chamberlainoideae Caragnano, Foetisch, Maneveldt & Payri *in* Caragnano et al. (2018). It also includes the genus *Parvicellularium* as *incertae sedis* in Caragnano et al. (2018) (Table 4)

Type genus: *Lithophyllum* Philippi 1837

Description of the family Lithophyllaceae: Non-geniculate, encrusting to unattached, to geniculate plants. Pseudoparenchymatous to unconsolidated. Organization dorsiventral, radial, isobilateral, multiaxial. Construction monomerous to dimerous, non-coaxial to coaxial. Palisade cells present or absent. Cell fusions or secondary pit-connections. Trichocytes present or absent, single or arranged in horizontal groups, or in bands near intergenicula, becoming buried or not. Gametangial, carposporangial and sporangial conceptacles uniporate. Spermatangial filaments unbranched, on the chamber floor. Carpogonial branches arising from the chamber floor. Carposporophyte with a conspicuous fusion cell and gonimoblast filaments dorsal to marginal, peripheral. Tetra/bisporangial conceptacle roofs formed from filaments surrounding and interspersed amongst sporangial initials, or only surrounding; cells lining the pore canal perpendicular or parallel to the surface, protruding laterally or not into the canal (papillae); surface of the pore surrounded or not by papillae or coronas; central columella present or absent; sporangium with zonate division, lacking apical plug.

Remarks: The family Lithophyllaceae encompasses four subfamilies: Lithophylloideae, Metagoniolithoideae, Hydrolithoideae, and Chamberlainoideae and the genus *Parvicellularium* as *incertae sedis*. Diagnostic features are summarized in Table 4. Taxonomic remarks and descriptions of the recent subfamilies Metagoniolithoideae, Hydrolithoideae and

Chamberlainoideae are provided in Kato et al. (2011), Rösler et al. (2016) and Caragnano et al. (2018). Our proposal emended the circumscription of the family Lithophyllaceae first proposed by Athanasiadis (2016), and later by Townsend and Huisman (2018) that only encompassed the subfamilies Lithophylloideae and Chamberlainoideae, with descriptions of two further families (Porolithaceae and Hydrolithaceae) for the remaining subfamilies included herein.

4. Discussion

4.1. Radiation of the crown group of Corallinophycidae

Our time-calibrated phylogeny obtained through a fixed local molecular clock analysis suggests that the onset of crown group diversification of Corallinophycidae started in the Lower Jurassic (179.88 ± 8.41 Ma) with the divergence of the common ancestor of the orders Sporolithales, Rhodogorgonales, Corallinales and Hapalidiales. Within this subclass, the divergence time of the oldest order Sporolithales is estimated in the Lower Cretaceous (137.03 ± 2.6 Ma) followed by the remaining orders that occurred around same time in the second half of the Lower Cretaceous: Hapalidiales (116.73 ± 1.48 Ma), Rhodogorgonales (114.87 ± 14.01 Ma) and Corallinales (112.86 ± 6.77 Ma). For the three calcified orders, these estimations are relatively older than the divergence times provided in Aguirre et al. (2010, Fig. 2) except for Hapalidiales (115 Ma). In addition, our results suggest that the divergence time of the common ancestors of the Hapalidiales and the Corallinales (139.59 ± 15.02 Ma) is older than estimations provided in Aguirre et al. (2010, 117.52 Ma), Yang et al. (2016, 117 Ma) and in Rösler et al. (2017, 105 Ma).

Using earlier, non-calcified records from the Precambrian Late Neoproterozoic as stem group of coralline algae, Yang et al. (2016) estimated a much earlier divergence of the subclass Corallinophycidae than Aguirre et al. (2010, *ca.* 579 versus 338 Ma). However, both studies agreed that the radiation of the crown group took place in the Lower Cretaceous, which coincides with our analyses. The consistent diversification during the Lower Cretaceous

requires a reappraisal of the nature and classification of a number of fossil red algae ranging from the Neoproterozoic to the Triassic that have been considered as either possibly related to modern corallines or as true corallines (Riding et al., 1998; Brooke and Riding, 1998, 2000; Senowbari-Daryan et al., 2002; Cózar and Vachard, 2003; Smith and Butterfield, 2003; Riding and Braga, 2005; Senowbari-Daryan and Velledits, 2007; Teichert et al., 2019) (Figure 5). While modern day Corallinophycidae are described with pseudoparenchymatous tissue showing cell walls impregnated by high-Mg calcite (Borowitzka et al, 1974; Le Gall and Saunders, 2007), the fossil taxa *Paramecia* and *Thallophyca*, from the Neoproterozoic, as well as *Nematothallopsis gotlandii*, from the late Silurian, are non-calcified organisms. Other Paleozoic and Triassic coralline-like taxa are calcified and present pseudoparenchymatous tissue. Some of them have been included in the fossil family Archaeolithophyllaceae (Chuvashov et al., 1987; Cózar and Vachard, 2003). Specimens of the type genus *Archaeolithophyllum* show conical structures, which can correspond to uniporate conceptacles (Johnson, 1956; Wray, 1977, fig. 73). However, *Archaeolithophyllum* as well as other genera in the family Archaeolithophyllaceae possess aragonite skeletons (James et al., 1988; Kirkland et al., 1993). Other pseudoparenchymatous Paleozoic to Miocene algae probably formed their skeletons as calcite but lack reproductive structures, which would link them unequivocally to the Corallinophycidae. These taxa were collectively included in the fossil family Solenoporaceae Pia 1927. Since Riding (2004) demonstrated that the type genus *Solenopora* is a chaetetid sponge rather than a red alga, Granier (in Granier and Dias-Brito, 2016) proposed the new family Elianellaceae to embrace the algal fossils. Two such calcified Paleozoic fossils show structures that can be interpreted as reproductive structures. The so-called *Solenopora richmondensis* by Blackwell et al. (1982) was originally described as a sponge (*Stromatocerium richmondense*, Miller, 1882). This late Ordovician fossil consists of relatively large tubes (about 50 µm in diameter) with poorly defined transverse partitions which may be interpreted as primary cell walls and an external layer of large structures (200 µm long x 90 µm wide) that recall sporangial compartments in Sporolithales but most have an irregular shape different from sporangial chambers (Fig. 5). The other fossil, *Graticula gotlandica* (Rothpletz) Brooke and

Riding 1998, from the Silurian of Gotland, shows ovoid cavities (150 μm long x 100 μm wide) irregularly distributed in the organism that were interpreted as sporangial compartments similar to those of the present-day Sporolithales (Brooke and Riding, 1998). These structures, however, are dispersed in the organism and not arranged in sori (Fig. 5).

Recently, Teichert et al. (2019) described the new genus and species *Aguirrea fluegelii*, from the mid-Silurian of Gotland, as a representative of the order Corallinales based on the vegetative anatomy and the claimed presence of uniporate sporangial conceptacles (Teichert et al., 2019: figs 2-3). Nonetheless, both the vegetative features and the alleged nature of the observed cavities as conceptacles are questionable. First, the isotype is described as an “encrusting thallus” attached to “a calcified host, probably a graticulacean alga” (Teichert et al., 2019: fig. 3A). The image of the isotype is in fluorescent light and *Aguirrea* crust is separated from the host by a bright luminescent boundary, which would define the limit between *Aguirrea* and the substrate. The fluorescent light impedes a clear observation of the cell filaments and other vegetative features. Nonetheless, a detailed observation of the central part of the isotype shows that filaments in the substrate continue into the *Aguirrea* thallus. That is, it seems that both *Aguirrea* and the host substrate form parts of the same organism. Regarding the supposed conceptacles, the base of the cavity shown in the isotype of *A. fluegelii* (Teichert et al., 2019: fig. 3) clearly obliquely cuts the cell filaments and the outline of the feature shown in the holotype of *A. fluegelii* (Teichert et al., 2019: fig. 2) is highly irregular and poorly defined. This suggests that they are not structures developed by changes in cell filaments, typical of Corallinales, but rather a later void due to bioerosion breakage of the cell filaments. In addition, the supposed conceptacle pore in the holotype opens to an irregular and steep surface obliquely cutting the filaments instead of opening to a defined surface perpendicular to filaments indicative of the thallus surface at the time of conceptacle development, typical of buried conceptacles in living corallines and preserved conceptacles in fossils. On the other hand, the isolated cavities in the *Aguirrea* type interpreted as microborings by Teichert et al. (2019: fig. 2A) show cell filaments surrounding each cavity. They actually are similar to the structures

observed in *Graticula gotlandica* (Rothpletz) Brooke and Riding, interpreted by previous authors (Rothpletz, 1908; Wood, 1944; Brooke and Riding, 1988) as sporangial compartments (Fig. 5). In our opinion *Aguirrea fluegelii* must be considered a heterotypic synonym of *Graticula gotlandica*.

In addition to the anatomical issues commented above, molecular phylogenies consistently depict an earlier divergence of the order Sporolithales compared to Corallinales. Therefore, accepting *Aguirrea* as a true representative of the order Corallinales implies a different evolutionary history to those obtained with molecular analyses (e.g. Nelson et al. 2015; Yang et al. 2016; Lee et al. 2018; this study).

Even assuming that cavities of *Solenopora richmondensis* and *Graticula* are true reproductive structures, there is a significant time gap between the fossil records attributed to coralline red algae and the first fossil records of modern coralline algae in the Lower Cretaceous (Fig. 5). Pushing back the origin of Sporolithales (*Solenopora richmondensis* and *Graticula*) to the Ordovician and Silurian means that representatives of this order existed for nearly 300 million years in the marine environment with no record as fossils. Contradicting this arguable scenario, the Cretaceous-Cenozoic history of coralline algae is demonstrably well represented in the fossil record (Aguirre et al., 2000, 2010; Rösler et al., 2017) and representatives of the three fully calcified orders (Sporolithales, Hapalidiales, and Corallinales) are continuously recorded in different sedimentary rocks since the Lower Cretaceous up to the recent. Taking into consideration the abundance of calcareous algae during the late Paleozoic and other geological periods between the Ordovician and the Lower Cretaceous, it is difficult to assume that modern corallines were occurring without leaving any traces in the fossil records; however, the recent description of *Proterocladus antiquus*, a new fossil species dating from the Tonian and ascribed to siphonocladalean chlorophytes (Tang et al., 2020) constitutes another example of a long gap in the fossil records between the oldest and a more continuous record.

In summary, pre-Lower Jurassic examples claimed to be coralline algae could be indeed rhodophytes, since they show characteristic pseudoparenchymatous tissue, and they might correspond to the stem group of the modern Corallinophycidae (Xiao et al., 2004).

Yang et al. (2016) related the diversification of Corallinophycidae with the event known as Mesozoic Marine Revolution in which shell-forming clades evolved different strategies against radiation of predators (Vermeij, 1977). Herbivory has also been proposed as a significant force in coralline algae diversification, particularly in the promotion of thicker, unbranched growth-forms under intense grazing (Steneck, 1990). Although the evolutionary histories of herbivores and coralline algae are not well correlated (Aguirre et al., 2000a), some anatomical and reproductive characters observed in corallines (e.g. cell fusions that allow translocation of photosynthates to heal damaged areas, conceptacles beneath the surface) have been interpreted as evolutionary novelties against grazing that favoured their radiation (Steneck, 1992). In addition, our results indicate that the diversification for most of the clades analyzed continued during the Oligocene and middle Miocene (~ 15 Ma), a pattern similarly to that observed by Rösler et al. (2017) for the order Corallinales.

Diversification of corallines roughly shows an inverse correlation with global paleotemperatures (Aguirre et al., 2000a). These authors stated that during the evolutionary history of corallines major extinction events that eliminated up to 67% of coralline species took place in the Late Cretaceous and late Miocene-Pliocene. These extinction events were followed by episodes of radiation favoured by the availability of empty habitats (i.e. Aguirre et al., 2007), and also shaped by the environmental affinities of each order (mainly related to water temperature) and evolutionary events in another marine groups such as the scleractinian corals for reef-building corallines (Aguirre et al. 2000a).

4.2. *Phylogeny of Corallinophycidae*

Our phylogenetic analyses of the subclass Corallinophycidae corroborated that the four currently recognised orders (Rhodogorgonales, Sporolithales, Hapalidiales and Corallinales)

corresponded to monophyletic lineages, together with the genus *Corallinapetra*, which is resolved as a distant sister taxon to the lineage encompassing the orders Corallinales and Hapalidiales. The monophyly of these four orders is congruent with phylogenomic analyses performed on mitochondrial and plastid genome data from five coralline taxa, in which the earlier divergence of both Rhodogorgonales and Sporolithales, or Rhodogorgonales first or Sporolithales are proposed as the most likely evolutionary scenarios that agree with fossil record (Lee et al., 2018). While the order Sporolithales (*Sporolithon*, *Heydrichia*) produces individual sporangial compartments separated from each other by paraphyses when grouped in sori (Harvey et al., 2002), the genus *Corallinapetra* produced individual sporangial compartments resembling multiporate sporangial conceptacles (Nelson et al., 2015), the latter is characteristic of the order Hapalidiales. The genus *Corallinapetra* (type species *C. novaezealandiae*) is only known from a single collection in New Zealand. According to Nelson et al. (2015), further studies are required to better resolve the phylogenetic position of this taxon within the subclass Corallinophycidae. Another entity pending to be further studied is the recently described genus *Rhodenigma* J.A.West, Verbruggen & Loiseaux in the order Rhodogorgonales. This monospecific genus (*R. contortum* J.A.West, Verbruggen & Loiseaux) consists of microscopic, uncalcified filaments growing on coral rubbles in Australia, and is phylogenetically resolved as a sister lineage of *Renouxia* (West et al., 2016). According to these authors, detailed observations are needed to elucidate structural similarities with remaining Corallinophycidae, such as the pit plug ultrastructure. In addition, this entity was interpreted as a microscopic life stage of an unknown Rhodogorgonales species (West et al., 2016), which would imply the occurrence of heteromorphic life histories within the subclass Corallinophycidae.

For the order Corallinales, our phylogenetic inferences resolved three highly supported suprageneric lineages. These lineages correspond to the families Mastophoraceae, Corallinaceae and Lithophyllaceae. We amend here the circumscription of the two latter families proposed in recent taxonomical studies (Athanasiadis, 2016; Townsend and Huisman, 2018). At lower taxonomic rank, our phylogenetic analyses showed paraphyletic subfamilies within the family

Corallinaceae (Corallinoideae and Neogoniolithoideae), and also provided alternative topologies with high support, particularly among subfamilies of Lithophyllaceae (order Corallinales), that differed from previous phylogenies inferred from a lower number of markers (4-5 genes sequences, e.g. Bittner et al., 2011; Rösler et al., 2016; Caragnano et al., 2018). Those discrepancies are beyond the scope of the present study, and further analyses are needed to clarify those phylogenetic relationships.

The three delineated families of the order Corallinales can be distinguished through a combination of vegetative features related to their internal structure (i.e. organization, presence of palisade cells, type of cell connections, trichocytes), reproductive features related with spermatangial conceptacles (location of spermatangial branches), carposporophyte (type of the fusion cell -conspicuous or not- and the arising type of gonimoblast filaments), and sporangial conceptacles (roof formation, cells lining pore canal, type of sporangia, presence of columella). Additional characters such as the development of rhizoids (exclusive for Mastophoraceae), presence of geniculate taxa, or reports of unattached growth-form were also considered. Within the family Corallinaceae, the arrangement of trichocytes together with reproductive characters related with spermatangial and carposporangial conceptacles are diagnostic among subfamilies. Within Lithophyllaceae, internal structure (organization, presence of palisade cells) and type of cell connection became diagnostic together with reproductive features of the sporophyte.

4.3. Evolutionary trends in Corallinophycidae, homoplasious characters and selected autapomorphies

Our literature review for the subclass Corallinophycidae suggested distinctive characters that, in light of the evolutionary history of these lineages, can be considered evolutionary novelties, or at least evolutionary trends, for this subclass. In addition, homoplasious characters and selected autapomorphies emerging in particular calcified groups/taxa are also discussed.

4.3.1. Evolutionary trends

- *Calcification of cell wall*. In contrast to some other Florideophyceae orders (i.e. Nemaliales, Peyssonneliales) that excrete calcium carbonate as an extracellular skeleton of aragonite, coralline red algae deposit high-Mg calcite in their cell walls (reviewed in Johansen, 1981). In the subclass Corallinophycidae, the calcification of cell walls is a homoplasious character recorded in Sporolithales, Hapalidiales and Corallinales. However, the calcification in the order Rhodogorgonales is limited to calcite husks (known as calciferous cells, Norris and Bucher, 1989; Pueschel et al., 1992), with unknown role although they appear to be related with the production of rhizoidal filaments in *Renouxia* (Fredericq and Norris, 1995). This character might be considered an ancestral trait that evolved to a continuous calcification of their cell walls throughout the sister group (Sporolithales) and following lineages (Fig. S3A). The physiological process of calcification is still poorly known. Borowitzka (1977) proposed that calcification is controlled by a protein-polysaccharide matrix (“Organic Matrix Theory”) but more recently, Nash et al. (2019) argued that calcification is likely bioinduced. These latter authors also described two types of cell wall calcification (primary and secondary) that are found among different cells of both geniculate and non-geniculate taxa (Nash et al. 2019). The three fully calcified orders show inner wall crystals or blade-like crystals perpendicular to cell surface and interfilament calcite crystals elongate and tangentially oriented to the cell surface (Flajs, 1977) that are particularly conspicuous in the cold-water *Clathromorphum* (Adey et al., 2013); by contrast, the crystals of calcite husks reported in Rhodogorgonales are small and rhombohedral (Pueschel et al., 1992). The degree of calcification is however variable among taxa of the same lineage (i.e. unconsolidated filaments reported in some *Pneophyllum* taxa). In addition, Smith et al. (2012) found that magnesium content is variable among New Zealand taxa belonging to different orders, and between growth forms. The highest content of magnesium was found in the order Corallinales followed by Sporolithales and Hapalidiales, and is higher in erect, geniculate coralline than in crustose ones. By contrast, the geographical location of collections did not show a significant effect despite that the saturation state of seawater for carbonate minerals varies with latitude (generally lower at high latitudes than at low latitudes, Andersson et al., 2008). In this regard, the highly significant correlations between Mg/Ca ratio

deposited by coralline algae and seawater temperature has been used to estimate paleoclimatic variations in the last centuries (i.e. Halfar et al., 2000, Kamenos et al., 2008).

- *Emergence of trichocytes*. Related with the formation of non-calcified hairs on the surface, trichocytes are very rare in Sporolithales (single record, Townsend et al., 1995), occasional in Hapalidiales (e.g. Sissini et al., 2014; Townsend and Huisman, 2018), but they are frequently reported in the order Corallinales (e.g. reviewed in Johansen, 1981) (Fig. S3B). For the three families of the order Corallinales (Mastophoraceae, Corallinaceae and Lithophyllaceae), the disposition of trichocytes can be variable, occurring individually or arranged in horizontal/vertical rows, and becoming buried or not within the thallus.

Colourless, unicellular, hair cells are reported in other Florideophyceae lineages (e.g. Nemaliophycidae, Rhodymeniophycidae, reviewed in Fristch, 1945; Pueschel, 1990; Delivopoulos, 2002), and also in Rhodogorgonales (basal hair cells in *Rhodogorgon*, Norris and Bucher, 1989). However, the structure commonly referred as trichocyte in coralline algae are initially formed by the division of a meristematic cell that generates a support cell and the hair-bearing cell (the true trichocyte); the overlying epithallial cell is lost or the hair can grow through it, and after trichocyte formation, a large cell (called megacell) can be potentially developed (reviewed in Johansen, 1981). Cabioch (1971) recognized three types of complexity mainly focused on processes after hair has been shed: (i) a simple type where trichocytes persisted with the same morphology and having a pore or neck at hair scar; (ii) an intermediate type where meristematic activity of support cell is reactivated with consequent lost of trichocyte, and (iii) the most complex type where trichocytes are transformed into megacells that persisted within the thallus, and even became buried. The simple type occurs in the family Mastophoraceae (Turner and Woerlkerling, 1982b), and an evolutionary reversal to this type occurred in thin, encrusting taxa of the family Lithophyllaceae (*Pneophyllum*, and taxa currently attributed to *Lithophyllum* -as *Dermatolithon litorale*-, and *Hydrolithon* -as *Fosliella farinosa*-; Cabioch, 1971; Chamberlain, 1985). The most complex trichocytes occur in reef coralline taxa of the families Corallinaceae (*Neogoniolithon*), and Lithophyllaceae (*Porolithon*). Finally, the intermediate type is reported for geniculate taxa in the family Corallinaceae (*Corallina*, *Jania*),

and for geniculate and non-geniculate Lithophyllaceae (*Metagoniolithon* and *Lithophyllum*, respectively) (Cabioch, 1971; Basso and Caragnano, 2014). In addition, Garbary and Johansen (1982) reported two subtypes for the geniculate *Corallina* and *Jania* according to their base morphology at the surface (C-type as rounded, slightly raised in *Corallina* versus J-type as elongated with excentric pore in *Jania*). While in *Dawsoniolithon* (Lithophyllaceae), Caragnano et al. (2018) reported a combined trichocyte development between the intermediate and complex types. Interestingly, megacells corresponding to the complex type have been also reported in cultured young plants of Hapalidiales, but they are obliterated by renew meristematic activity in older plants (Walker, 1984). In addition, terminal trichocytes resembling to the simple type have been reported in *Melyvonnea* and *Rhizolamellia* (Verheij, 1993; Athanasiadis and Ballantine, 2014; Sissini et al., 2014, Townsend and Huisman, 2018). In Sporolithales, the exceptional record of one trichocyte in *Sporolithon durum* illustrated in Townsend et al. (1995) as terminal with a short hair on surface without an overlying epithallial cell could be assigned to an early stage of the simple type where the trichocyte does not persist.

Despite the occasional report of trichocytes in Hapalidiales, only the complex trichocytes (type iii) giving way to megacells have a high preservation potential to be recognized in fossil corallines. The oldest trichocytes in fossils were found much later in *Neogoniolithon* in the middle Eocene in SE Spain (J.C. Braga and J. Aguirre, unpublished data), and in *N. raripunctatum* Mastrorilli in the late early Oligocene (Braga and Bassi, 2011). These records corresponded to preserved structures disposed in mostly columns although some of them occur in rows in longitudinal section of filaments, which are to the most complex type described in extant *Neogoniolithon* (order Corallinales).

Although the role of the trichocytes is still unclear, the literature attributed them a protective role against excessive insolation, or as an alternative to increase surface area for nutrient assimilation (reviewed in Basso and Caragnano, 2014). In the remaining Florideophyceae lineages, their occurrence was related to environmental conditions (e.g. nutrient uptake) and with sexual reproduction as initial attachment site for spermatia (reviewed in Cole and Sheat, 1990).

- *Simplification of spermatangial filaments and restriction of their location within the conceptacle chamber.* While branched (dendroid) or unbranched spermatangial filaments occur in the orders Sporolithales and Hapalidiales, only relatively simple, unbranched filaments are developed in Corallinales (but see Masaki, 1968, Table 2, Fig. S3C). In Rhodogorgonales, spermatangia are produced in subterminal clusters (Fredericq and Norris, 1995); and in the remaining Florideophyceae lineages, spermatangial branches are commonly reported (reviewed in Fristch, 1945; Cole and Sheath, 1990), with exceptions such as terminal spermatangia in Ahnfeltiophycidae (e.g. Milstein and Saunders, 2012).

Regarding the location of spermatangial filaments within the conceptacle chamber, in both orders Sporolithales and Hapalidiales spermatangial filaments are produced on the floor, walls and roof. In the order Corallinales, an evolutionary trend towards the production confined to the floor occurred in Mastophoraceae and in Lithophyllaceae, while in Corallinaceae reversed to ancestral states appearing in floor and walls (Corallinoideae) and floor, walls and roof (Neogoniolithoideae) (Fig. S3D). The location of spermatangial filaments in the conceptacle chamber is employed as taxonomical support at genus and subfamily levels (e.g. Lebednik, 1978). Spermatangial filaments are very rare in the fossil record, and are observed only in a few cases of exceptional preservation (Braga, 2006).

- *Restriction of carpogonial branches location within the female conceptacle chamber.* The carpogonial branches in Sporolithales occur on the chamber floor and walls, while in both Hapalidiales and Corallinales the carpogonial branches are restricted to the chamber floor (Fig. S4A). According to a review by Johansen (1981), reproductive cells are derived from all the meristematic cells forming the conceptacle disc, although only those located in the central part appeared to have fully developed carpogonial filaments. Peripheral cells remain undeveloped or immature (i.e. lack of trichogynes, hypogynous cells). Based on the centrifugal pattern of development of disc filaments examined in some genera belonging to Hapalidiales, Lebednik (1977) distinguished a carpogonial complex located in the disc centre and an auxiliary complex in the peripheral disc area involved in post-fertilization processes. Coralline algal ancestors formed disc filaments with fully developed mature carpogonial branches (polycarpogonial

type), which would allow independent events of carposporangial formation (Lebednik, 1977). Subsequently, coralline algae evolved to favour a higher number of carpospores requiring a single fertilization and the specialization of filament disc. The ancestral condition is observed in Sporolithales and Hapalidiales (Lebednik, 1977).

- *Presence of auxiliary cells in post-fertilization event.* Auxiliary cells and connecting filaments are absent only in the non-calcified order Rhodogorgonales (Fredericq and Norris, 1995); for the remaining Corallinophycidae orders (Sporolithales, Hapalidiales, Corallinales), auxiliary cells are reported in the literature (Fig. S4B). The migration of the zygotic nuclei to the auxiliary cell through fused cells was described in different taxa belonging to Hapalidiales and Corallinales (reviewed in Johansen, 1981). An alternative mechanism involving transfer tubes from carpogonium to supporting cells was proposed by Lebednik (1977) but later questioned (Woelkerling, 1980). In this regard, Lebednik (1977) also proposed that some Hapalidiales taxa were not procarpial based on the fusion of gonimoblast filaments with surrounding supporting cells that would act as auxiliary cells. This interpretation is refuted by authors such as Townsend (1979) who observed gonimoblast filaments in *Synarthrophyton* (Hapalidiales) that simply fuse with other cells before producing carposporangia.

- *Fusion cell in the carposporophyte.* An evolutionary shift towards a coherent development of the fusion cell is observed within the Corallinophycidae subclass, but this trend is irregular among lineages, particularly within the family Corallinaceae. According to the literature examined, in Sporolithales (and Rhodogorgonales) the fusion cell is absent or inconspicuous while in Hapalidiales is described as discontinuous or inconspicuous. For the order Corallinales, the fusion cell is conspicuously present in two clades corresponding to the families proposed here: Mastophoraceae and Lithophyllaceae. However, within the family Corallinaceae there is a high variability in size and aspect of fusion cells: from absent, discontinuous or thin and flattened fusion cells in the subfamily Neogoniolithoideae, to thick and compact or thin and flattened in Corallinoideae (Fig. S4C). In a recent study of the evolutionary history of the class Florideophyceae, Yang et al. (2016) related evolutionary changes in the carposporophyte stage

with maximization of spore production after fertilization. According to these authors, the subclass Corallinophycidae would encompass taxa corresponding to both states.

- *Development of gonimoblast filaments in the carposporophyte stage.* While in the non-calcified order Rhodogorgonales the gonimoblast filaments are diffusely branched (Fredericq and Norris, 1995), in the order Sporolithales they can be present or absent, the latter producing carposporangia directly from the fertilized carpogonium. For subsequent Corallinophycidae orders (Hapalidiales and Corallinales), the gonimoblast filaments are always reported, produced from a fusion cell more or less conspicuous (Fig. S4D). The literature also reported variation in the arising type of gonimoblast filaments from the fusion cell: from a dorsal position in Sporolithales to variable position in the orders Hapalidiales and Corallinales.

- *Development of sporangia in conceptacles.* While in the order Sporolithales each sporangium occurs in a calcified compartment isolated or grouped in a fertile area (sori) separated by paraphyses (Harvey et al., 2002), the genus *Corallinapetra* produced individual sporangial compartments resembling multiporate sporangial conceptacles in sunken areas (Nelson et al., 2015), the remaining orders produced sporangia in conceptacles: multiporate in Hapalidiales and uniporate in Corallinales (Fig. S5A). Interestingly, the occurrence of sporangial conceptacles is only shared with another Florideophyceae subclass –Hildenbrandiophycidae– that emerged earlier (*ca.* 781 Ma, Yang et al., 2016). However, the ontogeny of conceptacles differed significantly between both subclasses since they derived from intercalary cells in Corallinophycidae, and from superficial cells in Hildenbrandiophycidae (Pueschel, 1982).

Similar observations of fused sporangial compartments were recorded in the Cretaceous taxon *Sporolithon rude* (Lemoine) Ghosh and Maithy (Tomás et al., 2007), suggesting this extinct species as evolutionary linkage between Sporolithales and Hapalidiales. According to Tomás et al. (2007), the sori are ancestral characters that early evolved into multiporate conceptacles in the evolutionary history of Corallinophycidae. On the other hand, both Sporolithales and Hapalidiales have apical plugs in common that block the canal pore prior to spore release, which are lacking in Corallinales (Harvey et al., 2002, 2003).

If multiporate sporangial conceptacles are considered an evolutionary novelty for the order Hapalidiales (Tomás et al., 2007), the development of uniporate sporangial conceptacles represents another evolutionary novelty shared by all taxa belonging to the order Corallinales. Within Corallinales, Johansen (1981) cited two out of four types of sporangial conceptacle roof development. Rösler et al. (2016) pointed out that the sporangial roof development involving surrounding and interspersed filaments among sporangial initials (detected in the family Lithophyllaceae, type 2 in Johansen, 1981) is a character novelty in relation to the development only restricted to surrounding filaments shared among taxa of the families Mastophoraceae and Corallinaceae (type 1 in Johansen, 1981). Apart from filaments involved in roof formation of sporangial conceptacles, Johansen (1981) mentioned the formation of the chamber and the formation of the pore and canal as criteria to establish four types of sporangial conceptacles in Corallinophycidae (type 3 and 4 are Hapalidiales and Sporolithales, respectively). Based on the literature compiled for the order Corallinales, the families Mastophoraceae and Corallinaceae have in common cells lining the pore canal of sporangial conceptacles parallel to the roof surface and protruding into the canal, while in Lithophyllaceae they acquire another disposition rather than parallel (perpendicular to roof surface, protruding or not into the canal) and pores can be surrounded in surface view by coronas of filaments. These features could represent additional evolutionary novelties emerged in the family Lithophyllaceae. The first occurrence of corallines of this group is recorded at the Cretaceous-Paleogene boundary, with the appearance of the oldest known Hydrolithoideae (*Karpathia* Maslov, i.e. Rösler et al., 2017). Likewise, the detection in the subfamily Chamberlainoideae (fam. Lithophyllaceae) of an alternative mode of formation of sporangial conceptacle roofs by filaments surrounding sporangial initials and the disposition of cells lining the canal pore parallel to roof surface could represent reversals to the ancestral states recorded in Mastophoraceae and Corallinaceae.

- *Zonate division of sporangia*. Although it was occasionally observed in Sporolithales (i.e. Cabioch, 1972), this type of division is recorded in Hapalidiales and Corallinales (Fig. S5B). While in the non-calcified genus *Renouxia* (Rhodogorgonales), carposporangia occasionally divided into an irregularly zonate arrangement and may function as tetraspores (Fredericq and

Norris, 1995). The zonate division of sporangia is reported in different Florideophyceae lineages, for example in *Hildenbrandia* or *Peyssonnelia*, which develop analogous reproductive structures such as conceptacles and sori (Denizot, 1968; Irvine and Chamberlain, 1994). Zonate sporangia are assumed to be present since early records of Hapalidiales in the Aptian. Lemoine (1977) claims that they are visible in late Eocene-Oligocene specimens of *Lithothamnion redovisense* from Macedonia and clear examples were found in the early Miocene of Indonesia (Rösler et al, 2015).

- *Occurrence of bisporangia.* Bisporangia are frequent in Florideophyceae (reviewed in Cole and Sheath 1990) and they are also recorded in the order Hapalidiales and the families Corallinaceae and Lithophyllaceae (order Corallinales). However, in the order Sporolithales and the family Mastophoraceae (Corallinales) only tetrasporangia are reported (Fig. S5C). Reproduction by uninucleate bisporangia was related with an altered life-history that produce self-perpetuating, diploid plants observed in *Hydrolithon*, *Pneophyllum* and *Lithophyllum* (reviewed in Irvine and Chamberlain, 1994). The report of bisporangial populations as well as plants producing together gametangial and sporangial conceptacles (i.e. *Mesophyllum sphaericum*, Peña et al., 2011) conferred a wide range of reproductive strategies to the Corallinophycidae (reviewed in Irvine and Chamberlain, 1994). These events would affect their ploidy level and further studies are needed. Kapraun and Freshwater (2012) estimated that geniculate taxa have larger nuclear genomes than non-geniculate species, and Kapraun and Bailey (2003) correlated them with independent, polyploid events that occurred in the different articulated lineages observed in Corallinales.

4.3.2. Homoplasious characters

- *Genicula.* Absent in the orders Sporolithales and Hapalidiales, and in the family Mastophoraceae (Corallinales), the occurrence of uncalcified segments more or less corticated known as genicula is reported in different Corallinales taxa belonging to the families Corallinaceae (subfamily Corallinoideae) and Lithophyllaceae (subfam. Lithophylloideae and Metagoniolithoideae) (Fig. S6A). Since the genicula evolved independently in these lineages,

they are considered non-homologous structures for the subclass Corallinophycidae (Johansen, 1969; Bailey and Chapman, 1998; Bittner et al., 2011). In the subfamily Corallinoideae, the records of non-geniculate taxa within the genus *Bossiella* and the non-geniculate genus *Crusticorallina* that evolved from geniculate ancestors corroborated the loss and gain events of this character throughout the evolutionary history of this group (Hind et al., 2016, 2018). Genicula confer flexibility to resist intense hydrodynamic conditions (Denny et al., 2013), and the increase of the number of joints (Corallinaceae) or variation in their size (Lithophyllaceae) have been used for these geniculate lineages to reduce bending stress (Janot and Martone, 2018). Similar to the emergence of geniculate taxa in different lineages, non-geniculate taxa producing arborescent canopy forming plants with erect stipes are reported in the order Hapalidiales (i.e. *Mastophoropsis*) and the order Corallinales (i.e. *Metamastophora*), but they are absent in Sporolithales (Woelkerling, 1988; Harvey et al., 2002). The oldest geniculate coralline is reported in the late Aptian in the French Pyrenees as *Amphiroa* sp. 2 (Lemoine, 1970). No illustration of the specimens is given but according to other fossil corallines attributed by the author to *Amphiroa*, this name refers to geniculate corallines not necessarily matching the modern concept of the geniculate lithophylloid.

- *Filamentous structure*. This type of structure occurs in several non-geniculate taxa belonging to Hapalidiales (i.e. subfamilies Choreonematoideae, Austrolithoideae) and Corallinales (i.e. Chamberlainoideae). In contrast with the common pseudoparenchymatous structure composed of contiguous filaments, these taxa produced unconsolidated filaments. It mainly occurs on endophytic/semi-endophytic taxa (i.e. *Austrolithon*, *Choreonema*, *Lesueuria*), and on epiphytic taxa (i.e. *Pneophyllum*) (Chamberlain, 1983; Woelkerling and Ducker, 1987; Woelkerling, 1988; Harvey and Woelkerling, 1995).

- *Dimerous construction*. This second type of internal organization occurs in several non-geniculate taxa belonging to the orders Hapalidiales and Corallinales. In the order Sporolithales, and presumably in the genus *Corallinapetra* (i.e. figure 4, Nelson et al., 2015), only monomerous plants are reported. In the dimerous pattern, two groups of filaments are distinguished, one involved in the lateral/longitudinal growth (primigenous filaments), and the

other in plant thickening (postigenous filaments) (Woelkerling, 1988). Dimerous construction was reported in the oldest “*Lithoporella*”, described as *L. melobesiodes* by Poignant (1968) in Aptian-Albian (Lower Cretaceous) rocks in SW France, although it is not well documented.

- *Palisade cells*. These are elongated vegetative cells belonging to the primigenous filaments observed in the dimerous construction. Palisade cells are recorded only in the order Corallinales, but occur in several taxa of the families Mastophoraceae (i.e. *Mastophora*) and Lithophyllaceae (i.e. “*Tenarea*”, *Lithophyllum*) as well as in *Lithoporella* (i.e. Woelkerling, 1988) (Fig. S6B).

Palisade cells were recorded in the first “*Lithoporella*” with dimerous construction, described as *Lithoporella melobesiodes* by Poignant (1968) mentioned above.

- *Type of cell connections between cells of contiguous filaments*. Both types of cell connections described for Corallinophycidae (cell fusions, secondary pit-connections) are present in the order Sporolithales. In remaining Corallinophycidae taxa, cell fusions appear to be the only type of connection in the genus *Corallinapetra*, the order Hapalidiales and several lineages of the order Corallinales (family Corallinaceae, and subfamilies Hydrolithoideae, Metagoniolithoideae and Chamberlainoideae of the family Lithophyllaceae) (Fig. S6C). Secondary pit-connections are however the only type of connections present in the subfamily Lithophylloideae, and occasionally in the family Mastophoraceae. By contrast, other Corallinophycidae taxa did not present any cell connections, such as the Hapalidiales taxa belonging to subfamilies Austrolithoideae and Choreonematoideae and with endophytic/semi-endophytic habit.

According to the fossil record, cell fusions appeared with the first report of *Sporolithon* in Valanginian (Chatalov et al., 2015). Pit connections are assumed to be the connections of not fused cells in the same specimens but they are never clear in fossils, even when they are the only type of adjacent cell connection.

- *Flared epithallial cells*. This particular shape of epithallial cells is characteristic for Sporolithales genera (*Sporolithon*, *Heydrichia*), the genus *Corallinapetra* and the Hapalidiales genus *Lithothamnion* (Fig. S6D). The remaining Corallinophycidae taxa produced epithallial cells of different shapes (i.e. domed, flattened, etc). Epithallial cells have uncalcified upper walls and derived from transverse division of subtending meristematic cells known as

subepithallial (initials) cells (reviewed in Johansen, 1981). They are usually disposed in a single layer, but some Corallinophycidae species from cold and temperate regions produce several layers (i.e. up to 14 cell layers in *Clathromorphum*, Adey et al., 2015). An additional cuticle of different thickness is also reported in different Corallinophycidae taxa (reviewed in Johansen, 1981) which is produced by the secretory activity of epithallial cells (Giraud and Cabioch, 1976). The number of epithallial cell layers and the cuticle thickness were related with a protective strategy against grazing (reviewed in Steneck, 1986). Tomás et al. (2007) claim that trapezoidal features at the top of perithallial filaments observed in *Sporolithon rude* in the late Hauterivian (Lower Cretaceous) from eastern Spain might be the remains of flared epithallial cells.

-*Unattached growth-form (maerl/rhodolith)*. This type of growth-form is recorded for the three calcified Corallinophycidae orders (Sporolithales, Hapalidiales and Corallinales), while in *Corallinapetra* only crusts overgrowing pebbles and small stones were hitherto reported (Nelson et al., 2015). Previous phylogenetic studies of Hapalidiales and Corallinales genera observed that the unattached habit is characteristic of some lineages, but in others (i.e. *Lithophyllum*) appears to be influenced by environment (Hernandez-Kantun et al., 2015). Deposits of unattached growth-forms known as maerl/rhodolith beds are worldwide distributed (reviewed in Riosmena-Rodríguez, 2017), and are common in the fossil record (Aguirre et al., 2017). Recently, Tâmega et al. (2017) reported deposits of free-living geniculate taxa (*Amphiroa*, *Jania*) forming beds in Brazil. In the fossil record, *Sporolithon rude* and *S. phylloideum* in upper Hauterivian reef-related deposits (Lower Cretaceous, Tomás et al., 2007) showed unattached growth-forms and encrusting habit around bioclastic nuclei, respectively.

4.3.3. Selected autapomorphies emerged in particular group/taxa

- *Rhizoids in Mastophora (Mastophoraceae, Corallinales)*. Except for some taxa belonging to *Mastophora*, and more rarely in *Lithoporella* (Turner and Woelkerling, 1982b), the remaining lineages of Corallinales as well as the rest of the calcified Corallinophycidae orders (Sporolithales, Hapalidiales) have attached growth-forms devoid of rhizoids. Thus, the

attachment is produced by cell adhesion of the lower surface, presumably by secretion of adhesive mucilage (reviewed in Irvine and Chamberlain, 1994). In non-geniculate taxa with stipe-like upright axes (e.g. *Metamastophora*) and geniculate species, the adhesion to the substrate usually occurs by a holdfast. The attachment by rhizoids is present in other Florideophyceae clades with crustose growth-forms such as *Peyssonnelia* (i.e. Denizot, 1968). -*Isobilateral organization in Tenarea (Lithophyllaceae, Corallinales)*. This type of dimerous construction occurs only in the genus *Tenarea*, hitherto recognized as a distinct genus in the subfamily Lithophylloideae (Guiry and Guiry, 2020). It involves the development of two central rows of primigenous filaments composed of palisade cells instead of a single layer described in remaining lineages with dimerous construction (Woelkerling, 1988). The fossil taxon *Distichoplax biserialis* W.O. Dietrich undoubtedly shows isobilateral organization in longitudinal section, similar in geometry to the one of *Tenarea*. *Distichoplax biserialis* was reported in the Upper Cretaceous (the oldest one is Coniacian, Poignant, 1981), nonetheless reliable records first appeared in the Paleocene (Elliott, 1960; Johnson, 1966; Dieni et al., 1979; Aguirre et al., 2007). The nature of *Distichoplax*, however, is arguable. It was considered as a direct ancestor of the modern Lithophylloideae by Aguirre et al. (2010), but the lithophylloid affinity of *Distichoplax* was questioned by Athanasiadis (1995), who suggested an affinity with *Mastophora* or *Lithoporella*. Recently illustrated material from India seems to support the latter interpretation, although the author (Sarkar, 2018) maintained *Distichoplax* as a member of Lithophylloideae.

- *Mucilaginous caps*. These are present over the branch apices of the geniculate genus *Metagoniolithon* (fam. Lithophyllaceae, Corallinales). Interestingly, these apical parts do not present epithallial cells which appear to be pushed up by the mucilaginous caps (Ducker, 1979).

- *Several stalk cells subtending mature tetrasporangia in Heydrichia (Sporolithales)*: Present from the early stages of the sporangial development, they remained small in subsequent stages (reviewed in Johansen, 1981). It is considered diagnostic within the order Sporolithales to distinguish the genus *Sporolithon* from *Heydrichia* (1 vs. 1-5 stalk cells, respectively, Harvey et al., 2002). For the remaining Corallinophycidae orders and for *Corallinapetra*, one stalk cell

subtending each sporangium is usually reported or illustrated but is not further mentioned as diagnostic (e.g. Suneson, 1937, 1943; Woelkerling and Campbell, 1992; Irvine and Chamberlain, 1994; Harvey and Woelkerling, 1995; Harvey et al., 2003, Nelson et al., 2015). In the fossil record, material described as *Agardhiellopsis cretacea* Lemoine by Lemoine (1970) in the late Aptian of SW France (Early Cretaceous) seems to show several stalked cells at the base of the sporangial compartments.

- *Sterile cells (“involucre”) surrounding sporangial compartments in Heydrichia (Sporolithales)*. Together with the different number of stalk cells, it is considered a diagnostic feature to distinguish it from the remaining Sporolithales genus *Sporolithon* (Harvey et al., 2002). The presence of this group of sterile cells within the tetrasporangial compartments in *Heydrichia* is unique for the whole subclass Corallinophycidae. The specific role of this group of cells is not precisely indicated in the literature, but the enlargement of these cells observed in old sporangial compartments (Harvey et al., 2002) might be related with infilling processes of old conceptacles recorded in other Corallinophycidae lineages. Woelkerling et al. (2014) report their occurrence in structures that they identify as sporangial compartments in fossils from which they established the taxon *Heydrichia (?) poignantii* Woelkerling, Granier & Dias-Brito, in the Albian (Lower Cretaceous) of Brazil. The illustrated structures, however, clearly correspond to sponge bioperforations affecting both core and peripheral filaments in thalli of fossil plants.

5. Conclusions

Our phylogenetic analyses resolved the four orders currently recognized in the subclass Corallinophycidae as monophyletic lineages, together with *Corallinapetra* resolved as a distant sister to the lineage encompassing the orders Corallinales and Hapalidiales. Within the order Corallinales, we corroborate the family Mastophoraceae and amend the circumscription of the families Corallinaceae and Lithophyllaceae. At lower taxonomic rank, our phylogenetic

analyses showed paraphyletic subfamilies (Corallinoideae and Neogoniolithoideae), and discrepancies among subfamilies of Lithophyllaceae. Further analyses are needed to clarify those phylogenetic relationships.

Our time-calibrated molecular clock analyses suggest that the diversification of the crown group of Corallinophycidae started in the Lower Jurassic and sped up in the Lower Cretaceous; the divergence time of the oldest order Sporolithales is Lower Cretaceous, followed by the remaining orders that occurred around the same time in the second half of the Lower Cretaceous. The onset of the crown group radiation in the Lower Jurassic implies a long period of more than 300 million years since the early Paleozoic records attributed to the stem group of Corallinophycidae. Our estimations are relatively older than those provided in the literature (except for Hapalidiales), and an older divergence time of the Hapalidiales and the Corallinales (139.59 Ma *versus* 105 or 117 Ma). However, our analyses agreed with previous studies in suggesting the crown group diversification in the Lower Cretaceous.

Eleven morphological characters have been highlighted as evolutionary trends in Corallinophycidae. Homoplasious characters and selected autapomorphies have been also examined. They consisted on vegetative or reproductive features pertaining to the three stages of the life-history of Corallinophycidae, with variable trace in the fossil record.

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Figure legends

Fig. 1. Discovery/description rate of coralline red algae species over time. The red line represents all names described, the blue line those taxa currently accepted taxonomically (basionym).

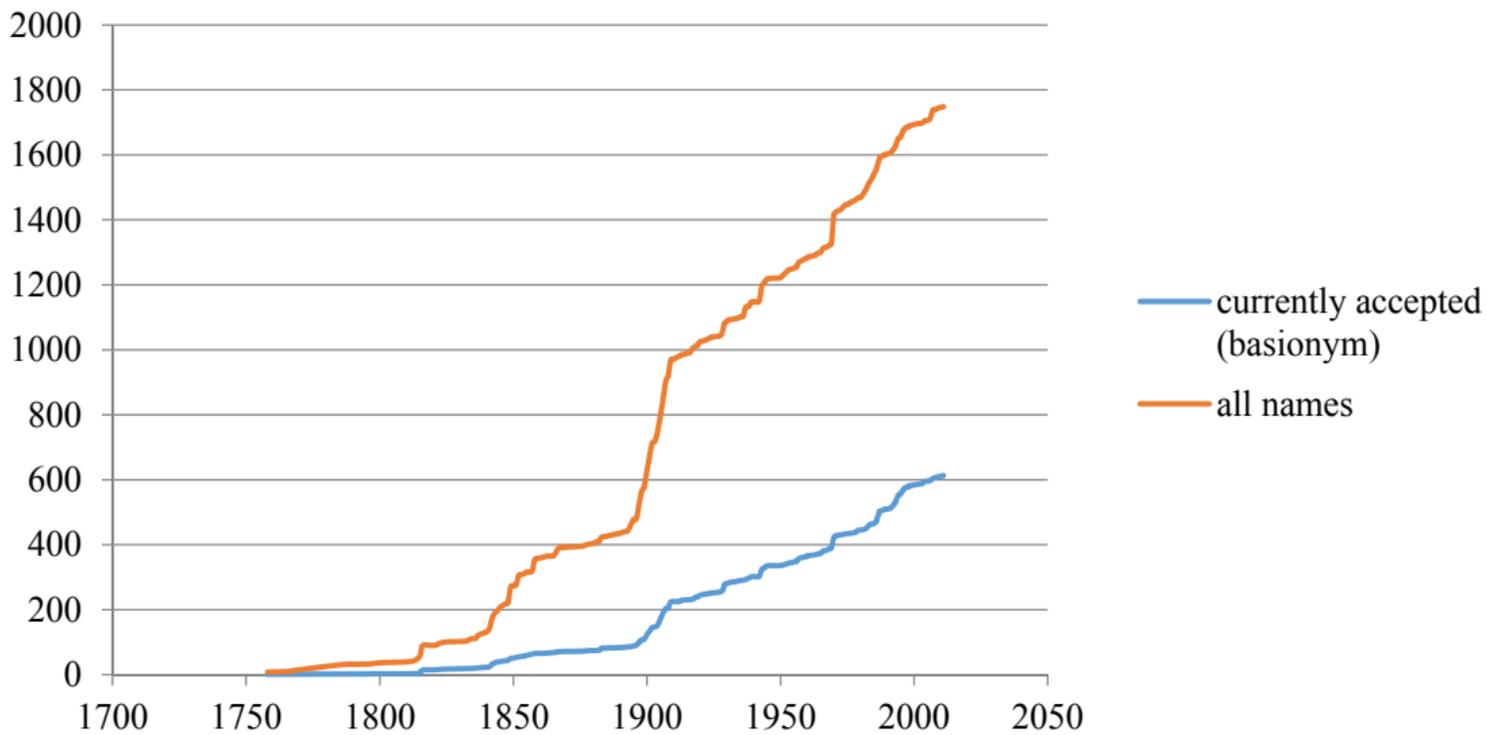
Fig. 2. Phylogenetic tree inferred from maximum likelihood (RAxML) analysis. Bootstrap ML values >60% shown for each node. In red colour, discrepancies with Bayesian inference (see also Fig. S1). Paraphyletic subfamilies Corallinoideae and Neogoniolithoideae marked with asterisk.

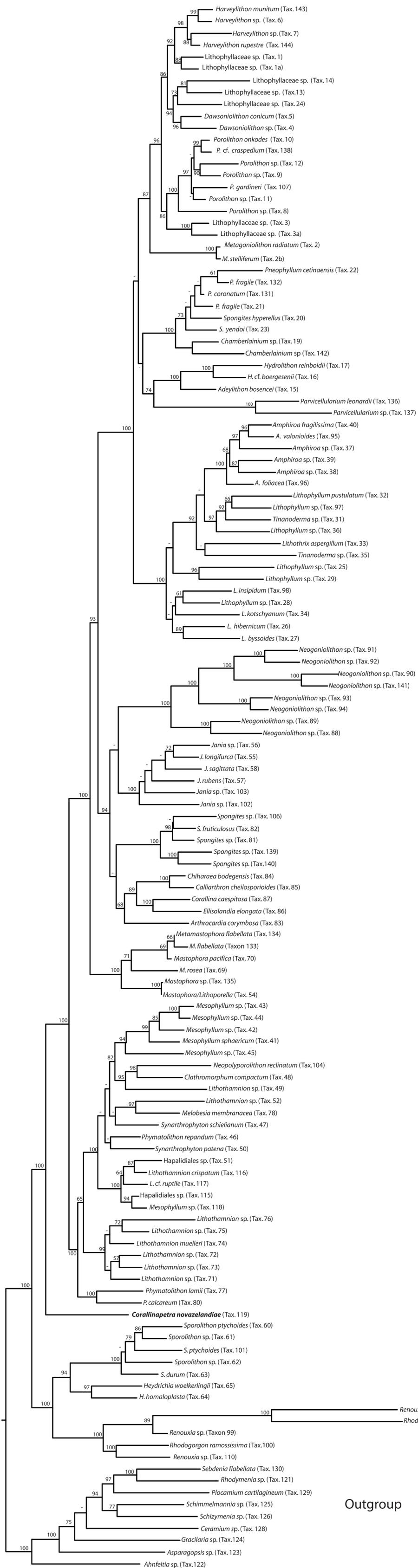
Fig. 3. Phylogenetic tree inferred from Bayesian (MrBayes) analysis. Bootstrap ML values >60% and posterior probabilities >0.60 from Bayesian inference shown for each node. In red colour, discrepancies with ML inference (see also Fig. S1). Paraphyletic subfamilies Corallinoideae and Neogoniolithoideae marked with asterisk.

Fig. 4. Time-calibrated phylogenetic tree of Corallinophycidae resulting from a BEAST v1.10.0 analysis with seven genes (LSU, SSU, 23S, *cox1*, EF2, *psbA*, *rbcL*), under a fixed local clock, and a Yule process model. Posterior probabilities values above 0.95 are represented by grey circles, and fully supported nodes by black circles. Six time constraints are indicated by the red letters, A: *Harveyolithon* (18 ± 8.4); B: *Porolithon* (23 ± 4.65), C: *Lithophyllum pustulatum* (26.8 ± 5.1); D: Hydrolithoideae (66 ± 2.23); E: Hapalidiales (116.66 ± 0.66).

Fig. 5. The fossil record of pseudoparenchymatous calcitic red algae. Red bars indicate the raw number of pseudoparenchymatous fossil species with no reproductive structures known in the fossil record. a-d) Original pictures of fossil pseudoparenchymatous algae with alleged reproductive structures. a) *Solenopora richmondensis*, the small arrow (lower left) points to a cavity similar to a sporangial compartment in a sorus-like structure according to Blackwell et al. (1982). b) *Graticula gotlandica* showing sporangial compartments (white arrows) according to Brooke and Riding (1998). c) Holotype of *Aguirrea fluegelii* from the same formation and age

from Gotland (Sweden) as *Graticula gotlandica*, showing according to Teichert et al. (2019) a uniporate conceptacle (black arrow) with a sporangium (arrowhead) and elongate cavities interpreted as micro-borings (white arrows). In our opinion the latter cavities are similar to those interpreted as sporangial compartments in *Graticula gotlandica* (b) by Brooke and Riding (1998). The supposed uniporate conceptacle is most probably a bioerosion cavity (see text for detailed explanation). *Aguirrea fluegelii* is a younger heterotypic synonym of *Graticula gotlandica*. d) Sporangial compartments in sori in *Sporolithon rude*. The arrow point to the remains of a stalk cell at the base of a sporangial compartment according to Tomás et al. (2007). Green lines mark the occurrence of *S. richmondensis* in the Ordovician (Ordov) and of *G. gotlandica* plus *A. fluegelii* in the Silurian (Sil). The asterisk indicates the onset of crown group diversification of the Corallinophycidae according to our calibration. Note the long time gap between the alleged reproductive structures in pseudoparenchymatous red algae in the Silurian (Sil, 430 Mya) and the initiation of the continuous fossil record of modern corallines with reproductive structures (140 Mya). During this long time, however, there are records of pseudoparenchymatous calcitic algae and other calcareous algae.



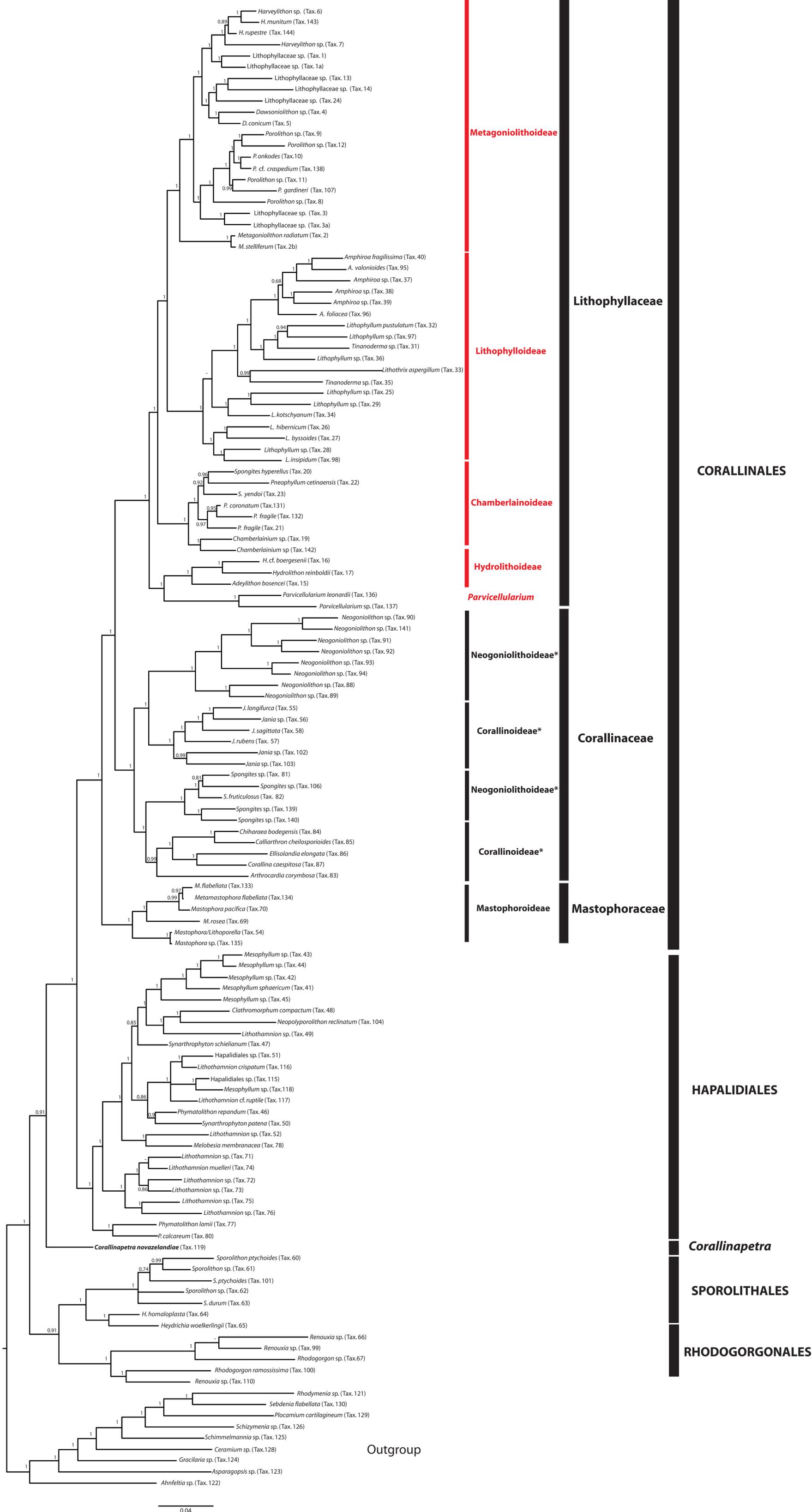


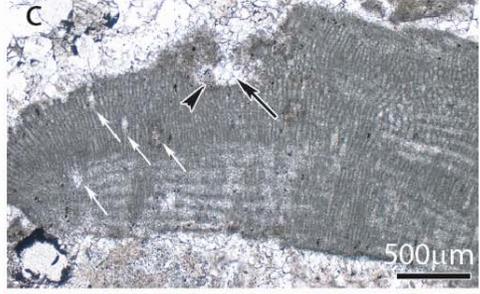
Metagonioliθοideae
Chamberlainoideae
Hydrolithoideae
Parvicellularium
Lithophylloideae
Neogonioliθοideae*
Corallinoideae*
Neogonioliθοideae*
Corallinoideae*
Mastophoroideae

Lithophyllaceae
CORALLINALES
Corallinaceae
Mastophoraceae
HAPALIDIALES
Corallinapetra
SPOROLITHALES
RHODOGORGONALES

Outgroup

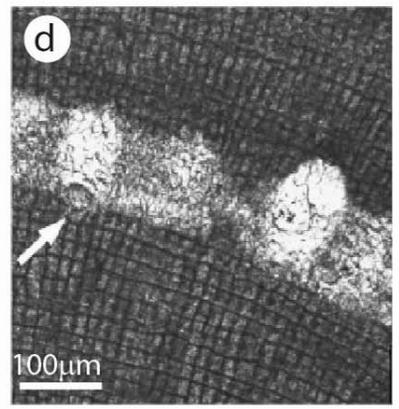
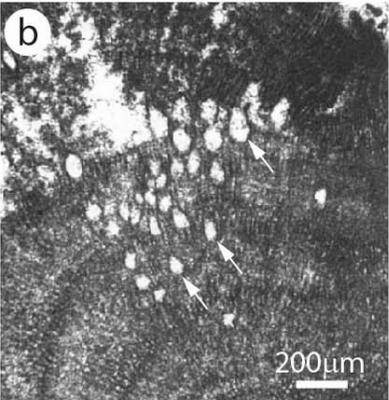
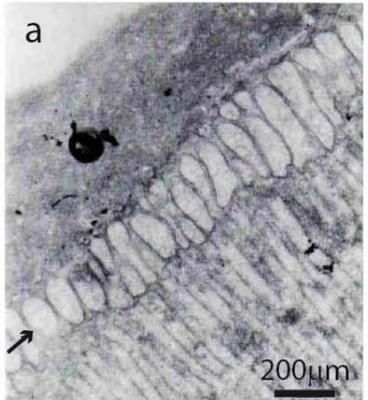
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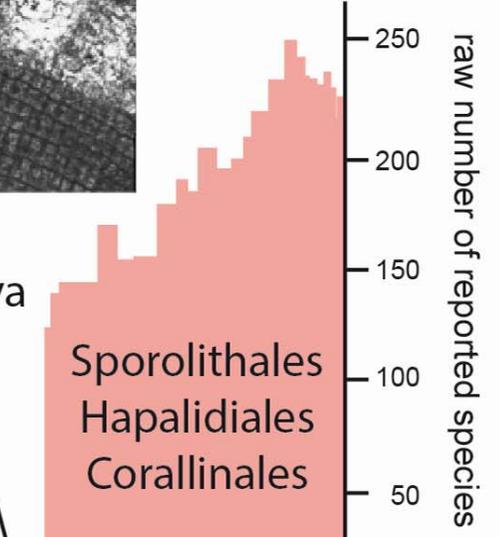
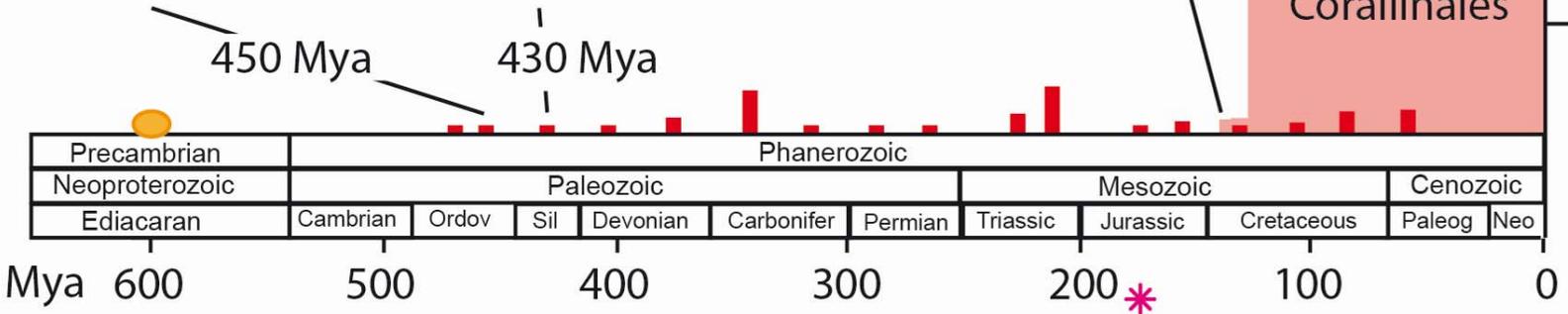


sorus-like structures

structures similar to sporangial compartments



sporangial compartments



phosphatized pseudoparenchymatous algae
 calcitic pseudoparenchymatous algae
 290 Myr
 continuous record of fossil corallines with reproductive structures

Table 1. Subclass Corallinophycidae: summary of diagnostic features for the calcified orders Sporolithales, Hapalidiales and Corallinales, excluding genus *Corallinapetra* (Corallinophycidae ord. *incertae sedis*). Type of conceptacle roof formation followed Johansen (1981).

		Sporolithales	Hapalidiales	Corallinales
	Geniculate growth-form	-	-	+/-
	Unattached growth-form (rhodolith/maerl)	+/-	+/-	+/-
	Rhizoids	-	-	+
	Internal structure	Pseudoparenchymatous	Pseudoparenchymatous to filamentous	Pseudoparenchymatous to filamentous
	Internal organization	Dorsiventral, radial. Monomerous	Dorsiventral, radial, diffuse. Monomerous, dimerous	Dorsiventral, radial or isobilateral, multiaxial. Monomerous, dimerous
	Type of connection	Cell fusions and secondary pit-connections (both)	Cell fusions or no connections.	Cell fusions/secondary pit-connections
	Trichocytes	- ¹	+ occasional ²	+
	Haustoria	-	+/-	+/-
	Epithallial cells flared	+	+	-
Gametophyte (male)	Spermatangial filaments and location on chamber	Unbranched/branched (dendroid), on floor, walls and roof	Unbranched/branched (dendroid), on floor, walls and roof.	Unbranched ³ , on floor/floor+walls/floor+walls+roof
Gametophyte (female)	Carpogonial branch	Chamber floor and walls	Chamber floor	Chamber floor
Carposporophyte	Fusion cell	Absent/inconspicuous	+/- (discontinuous, inconspicuous)	+/-

Sporophyte	Gonimoblast filaments	-/+ (dorsal)	+ (marginal/peripheral)	+ (dorsal/marginal/peripheral)
	Sporangia	Solitary/aggregated into sori	Conceptacles	Conceptacles
	Conceptacle roof	-	Multiporate	Uniporate
	Sporangia division	Cruciate ⁴	Zonate	Zonate
	Apical plug	+	+	-
	Sporangia	Tetrasporangia	Tetra/Bisporangia	Tetra/Bisporangia
	Stalk cells	1-5	1	1
	Conceptacle roof formation	- Type 4	Multiporate, from filaments surrounding and interspersed among sporangial initials. Type 3	Uniporate, from filaments surrounding, or surrounding and interspersed among sporangial initials. Types: 1-2
Columella	-	-	+	

¹Report of one trichocyte in *Sporolithon durum* (Foslie) R.A.Townsend & Woelkerling, Townsend et al. et al. (1995)

²Reported in cultured young plants (Walker, 1984), and in *Melyvonnea* and *Rhizolamellia* (Verheij, 1993; Athanasiadis and Ballantine 2014; Sissini et al. et al., 2014; Townsend and Huisman, 2018)

³Masaki (1968) reported dendroid spermatangial filaments in *Neogoniolithon accretum* (Foslie & M.Howe) Setchell & L.R.Mason.

⁴Cabioch (1972) reported cruciate and zonate tetrasporangia in *Sporolithon* sp.

Table 2. Order Corallinales: summary of diagnostic features for the families Mastophoraceae, Corallinaceae and Lithophyllaceae.

		Mastophoraceae	Corallinaceae	Lithophyllaceae
	Geniculate taxa	- ¹	+/-	+/-
	Unattached growth-form (rhodolith/maerl)	-	+/-	+/-
	Rhizoids	+	-	-
	Internal structure	Pseudoparenchymatous	Pseudoparenchymatous	Pseudoparenchymatous to unconsolidated filaments
	Internal organization	Dorsiventral. Dimerous	Dorsiventral, radial, multiaxial. Monomerous, dimerous	Dorsiventral, radial, isobilateral, multiaxial. Monomerous, dimerous
	Palisade cells	+	-	+/-
	Type of connection	Cell fusions/secondary pits (occasional)	Cell fusions	Cell fusions/ secondary pit connections
	Trichocytes	Single, and/or in horizontal groups	Single, horizontal groups, vertical rows	Single, horizontal groups, or bands on intergenicula
Gametophyte (male)	Spermatangial branches and location on chamber	Unbranched, on floor	Unbranched, on floor/floor+walls/floor+walls+roof	Unbranched ² , on floor
Carposporophyte	Fusion cell	+	+/-	+
Sporophyte	Gonimoblast filaments	Marginal	Dorsal/Marginal	Dorsal/Marginal/Peripheral
	Conceptacle roof formation	Formed only by filaments surrounding sporangial initials	Formed only by filaments surrounding sporangial initials	Formed from surrounding or surrounding and interspersed amongst sporangial initials
	Cells lining pore canal	Parallel to roof cells, protruding into the canal	Parallel to thallus surface, protruding into canal	Perpendicular to more or less parallel to the thallus surface, protruding or not into the

canal. Papillae
present/absent. Pores
surrounded or not by coronas
Tetra/bisporangia
+/-

Sporangia
Columella

Tetrasporangia
+

Tetra/bisporangia
+/-

¹It comprised arborescent taxa with stipe-like, upright axes (e.g. *Metamastophora*, Woelkerling, 1980)

²Masaki (1968) reported dendroid spermatangial filaments in *Neogoniolithon accretum*.

Table 3. Family Corallinaceae: summary of diagnostic features for the subfamilies Corallinoideae and Neogoniolithoideae.

		Corallinoideae	Neogoniolithoideae
	Geniculate taxa	+/-	-
	Unattached growth-form (rhodolith/maerl)	+ ¹	+
	Trichocytes	+/- Single, with pore central or excentric. Not becoming buried within the thallus	+/- Single, horizontal groups, vertical rows Sometimes becoming buried within the thallus
Gametophyte (male)	Spermatangial filaments and location on chamber	Unbranched (or usually without branchlets), on the floor and walls	Unbranched ² , confined to floor ³ , or floor, walls and roof
Carposporophyte	Fusion cell	Thin, broad to thick and compact	-/discontinuous, thin, flattened
	Gonimoblast filaments	Dorsal/Marginal	Dorsal/Marginal
Sporophyte	Conceptacle roof formation	Formed from filaments surrounding sporangial initials	Formed from filaments surrounding sporangial initials
	Sporangia	Tetra/Bisporangia	Tetra/bisporangia
	Columella	-	+/-

¹Tâmegea et al. (2017) reported free-living Corallinoideae taxa.

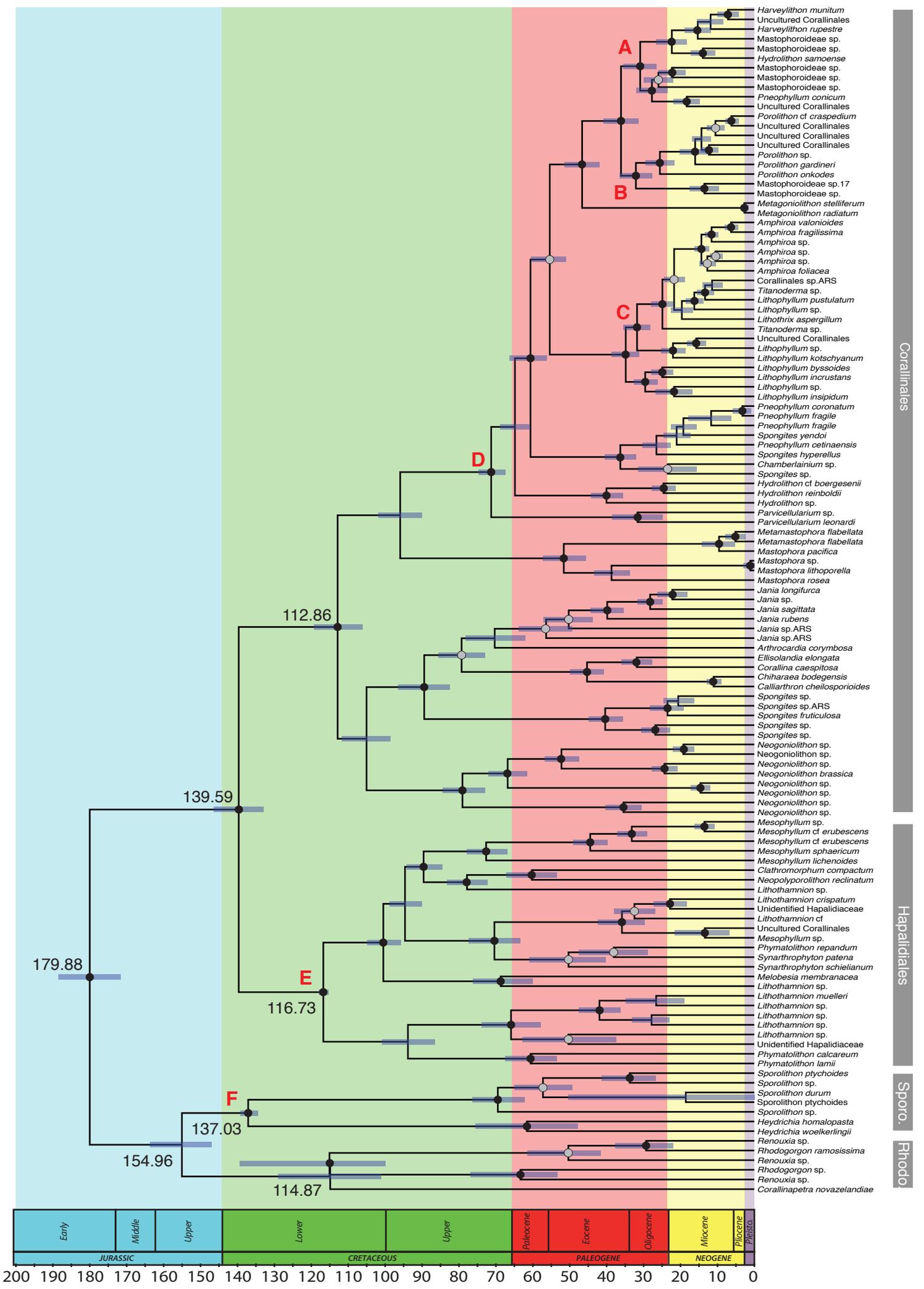
²Masaki (1968) reported dendroid spermatangial filaments in *Neogoniolithon accretum* (Foslie & M.Howe) Setchell & L.R.Mason.

³Penrose (1991) and Basso and Rodondi (2006) reported spermatangial filaments confined to chamber floor in the genus *Spongites*

Table 4. Family Lithophyllaceae: summary of diagnostic features for the subfamilies Hydrolithoideae, Metagoniolithoideae, Lithophylloideae, Chamberlainoideae and the genus *Parvicellularium* (subfam. *incertae sedis*)

		Hydrolithoideae	Metagoniolithoideae	Lithophylloideae	Chamberlainoideae	<i>Parvicellularium</i>
	Geniculate taxa	-	+/-	+/-	-	-
	Unattached growth-form (rhodolith/maerl)	+	+	+	-	-
	Internal organization	Dorsiventral, radial. Usually dimerous (predominant monomerous <i>Adeylithon</i>)	Dorsiventral, radial, multiaxial. Monomerous/dimerous	Dorsiventral, radial, isobilateral, multiaxial. Monomerous/dimerous	Dorsiventral. Monomerous/dimerous	Dorsiventral. Monomerous
	Palisade cells	-	-	+/-	-	-
	Type of connection	Cell fusions (pervasive/alternate layers)	Cell fusions	Secondary pit connections	Cell fusions	Cell fusions
	Trichocytes	Single, in horizontal groups, not becoming buried within thallus	Single, in horizontal groups, becoming or not buried within thallus	Single, becoming buried within thallus	+/-, single, paired, horizontal groups, not becoming buried within the thallus	Rare. Single vertical rows
Carposporophyte	Gonimoblast filaments	Marginal/Peripheral	Marginal/Peripheral	Dorsal/Marginal/Peripheral	Marginal/Peripheral	ND
Sporophyte	Conceptacle roof formation	Formed from filaments	Formed from filaments surrounding	Formed from filaments surrounding	Formed from filaments	ND

	surrounding and interspersed amongst initials	and interspersed amongst initials	and interspersed amongst initials	surrounding and interspersed, or only surrounding, amongst initials	
Cells lining pore canal	More or less perpendicularly to the roof surface, not protruding into the canal	More or less perpendicular to the thallus surface, not protruding into canal	Protruding or not into the canal. Enlarged cells occluding partially or totally canal can be present	More or less parallel to conceptacle roof, protruding into the canal. Pore canal surrounded or not by papillae	More or less parallel to conceptacle roof, protruding into the canal. Pore canal not surrounded by papillae
Sporangia	Tetra/bisporangia	Tetrasporangia	Tetra/bisporangia	Tetra/bisporangia	Tetra/bisporangia
Columella	+/-	+/-	+/-	+	+ (poor developed)



Corallinales

Hapalidiales

Sporolithales

Rhodolithales

