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TIMING OF THE EVOLUTIONARY HISTORY OF CORALLINACEAE (CORALLINALES, RHODOPHYTA)[1]

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The temporal dimension of the most recent Corallinaceae (order Corallinales) phylogeny was presented here, based on first occurrence time estimates from the fossil record. Calibration of the molecular clock of the genetic marker SSU entailed a separation of Corallinales from Hapalidiales in the Albian (Early Cretaceous ~105 mya). Neither the calibration nor the fossil record resolved the succession of appearance of the first three emerging subfamilies: Mastophoroideae, Corallinoideae, and Neogoniolithoideae. The development of the tetra/bisporangial conceptacle roofs by filaments surrounding and interspersed among the sporangial initials was an evolutionary novelty emerging at the Cretaceous–Paleogene boundary (~66 mya). This novelty was shared by the subfamilies Hydrolithoideae, Metagoniolithoideae, and Lithophylloideae, which diverged in the early Paleogene. Subclades within the Metagoniolithoideae and Lithophylloideae diversified in the late Oligocene–middle Miocene (~28–12 mya). The most common reef corallinaceans (*Hydrolithon*, *Porolithon*, *Harveylithon*, "*Pneophyllum*" *conicum*, and subclades within Lithophylloideae) appeared in this interval in the Indo-Australian Archipelago.

Key index words: **calibrated phylogenetic tree; Corallinaceae; fossil record; paleobiogeography; SSU marker**

***Abbreviations*: mya, million years ago; myr, million years; OTU, operational taxonomic unit**

Coralline red algae (Corallinophycidae, Rhodophyta) constitute the major extant group of calcareous algae and are important components of shallow-water marine hard and sediment bottoms in areas of low siliciclastic influx from subpolar regions to the Equator (Adey and Mcintyre 1973, Adey 1986). The nongeniculate species have entirely calcified thalli with high preservation potential and therefore have an excellent and continuous fossil record since the Early Cretaceous (136 mya; Aguirre et al. 2000, Chatalov et al. 2015). Coralline algae are common components in sedimentary rocks, especially in Cenozoic shallow-water carbonates. The latter include coral reefs and other biogenic structures of which corallines are major builders (Adey 1986, Bosence 1991). Because of their common occurrence, coralline algae have been used in paleoenvironmental interpretations of ancient deposits, using the ecological distribution of living algae to interpret the sedimentary environments of the rocks in which they appear (Adey and Mcintyre 1973, Adey 1979, 1986, Bosence 1983, 1991, Braga and Aguirre 2001, 2004, Webster et al. 2009). In the last decade, the calcified thalli of coralline algae have also been used as archives of climatic and environmental changes, especially in middle and high latitudes, combining sclerochronological and geochemical techniques (Halfar et al. 2008, McCoy and Kamenos 2015).

Although not all morpho-anatomical characters used to discriminate among extant taxa are preserved, many

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diagnostic characters at the subfamily level are discernible in fossil nongeniculate corallines (Braga et al. 1993). The feasibility of identifying fossil corallines at the generic rank depends on the extent to which morpho-anatomical characters allow researchers to distinguish living genera. In any case, the first appearance of many individual taxa (especially subfamilies and genera) can be pinpointed in geological time (Aguirre et al. 2010, Rösler et al. 2015). By contrast, geniculate taxa that possess alternating calcified and uncalcified segments (named intergenicula and genicula, respectively) have a poor fossil record, as noncalcified genicula decay after death, and calcified segments disperse as sand and gravel grains. The isolated segments have a low preservation potential and are difficult to identify. Despite the unevenness created by the limited record of geniculate taxa and gaps in the available information from specific time intervals and geographic areas, the fossil record of coralline algae can be considered one of the most continuous and complete of living groups of organisms and, by far, the best record among algae (Aguirre et al. 2000, 2010). The excellent fossil record, together with a reliable molecular phylogeny, is an important tool for understanding the evolutionary history of the group. Recently, a time-calibrated phylogeny was employed to estimate divergences of the major lineages in the class Florideophyceae (Yang et al. 2016); according to the fossil data set that encompassed Proterozoic taxa considered the oldest known fossil Rhodophyta (*Bangiomorpha pubescens* N.J.Butterfield) and potential noncalcified ancestors of modern coralline red algae (genera *Thallophyca*, *Paramecia*), it was estimated that the subclass Corallinophycidae lineage early diverged at 579 (543–617) mya.

Members of the family Corallinaceae (order Corallinales), the subject of this work, are the main corallines in both modern and fossil low- to mid-latitude shallow-water algal assemblages at least since the Miocene (Adey et al. 1982, Bosence 1983, 1991, Littler and Littler 1984, Braga et al. 2010, Mallela 2013). They are major builders in modern coral reefs, contributing significantly to reef health and biodiversity (Morse et al. 1996, reviewed in Nelson 2009, Vermeij et al. 2011) and have been the dominant coralline algae in shallow reefs since the Oligocene (Bosence 1991, Braga et al. 2010). Therefore, understanding the evolutionary history of this group is crucial to comprehend the history of the most valued marine ecosystems in the world.

Herein, we provided a temporal dimension for the molecular phylogeny of the family Corallinaceae (order Corallinales), recently established with a set of five DNA markers (SSU, LSU, *psb*A, COI and 23S; Rösler et al. 2016). We sought to understand the evolutionary history of Corallinaceae by combining the results of molecular analysis with data of first occurrences in the fossil record of representatives of major clades in the phylogenetic tree of the family.

MATERIALS AND METHODS

The phylogenetic tree for the family Corallinaceae by Rösler et al. (2016; Fig. 1) showed a paraphyletic grouping of seven well-supported monophyletic clades that corresponded to: (i) the subfamily Mastophoroideae Setchell emend. A.Kato & M.Baba; (ii) the subfamily Corallinoideae (Areschoug) Foslie; (iii) the subfamily Neogoniolithoideae A.Kato & M.Baba emend. A.Rösler, Perfectti, V.Peña & J.C.Braga, comprising *Neogoniolithon* Setchell & L.R.Mason, the generitype species of *Spongites* Kützing, *S. fruticulosus* Kützing and thin encrusting algae with morpho-anatomical characters of corallines attributed to *Pneophyllum* Kützing; (iv) the subfamily Hydrolithoideae A.Kato & M.Baba; (v) the subfamily Metagoniolithoideae H.W.Johansen emend. A.Rösler, Perfectti, V.Peña & J.C.Braga comprising *Metagoniolithon* Weber-van Bosse, *Porolithon* Foslie, *Harveylithon* A.Rösler, Perfectti, V.Peña & J.C.Braga and specimens attributed to *"Pneophyllum" conicum* (E.Y.Dawson) Keats, Y.M.Chamberlain & M.Baba; (vi) a clade named the Southern Hemisphere group including taxa from New Zealand, southern Australia, Chile, and South Africa attributed to *Pneophyllum* Kützing and *Spongites*, and (vii) the subfamily Lithophylloideae Setchell 1943 sensu Bailey (1999).

We added a temporal dimension to this phylogenetic tree using the software BEAST (Drummond et al. 2012). The evolution model was found with MrModeltest (Nylander 2004), software that use Modeltest algorithms (Posada and Crandall 1998). The GTR+I+G evolutionary model was selected under the Akaike information criteria for all partitions (SSU, LSU, *psb*A, COI, and 23S). The five-marker data set was tested to follow a strict molecular clock, and the result was negative: the harmonic mean of marginal likelihood resulted −42,234.66 (without clock), −43,243.25 (strict clock), and −43,274.13 (relaxed clock, exponential by default). A reduced one-marker data set of 126 sequences, including all OTUs with SSU sequences, was used to calibrate the molecular clock. Several reasons led to this decision: (i) SSU was by far the most represented marker in the data matrix, (ii) its resulting phylogenetic tree was representative of the topology of the phylogeny of the five-marker data set, and (iii) SSU shows a constant evolution rate as it is under purifying and concerted evolution (Meagher et al. 1989, Ganley and Kobayashi 2007). Tests with different combinations of markers showed that divergence times and rate variations were not identical among different loci, and no other marker or marker combination showed lower variance in the resulting time trees. When various markers were combined, dating attempts led to high uncertainty in the resulting trees. In addition, when the same age calibration points were applied, contradicting bifurcation ages resulted from dating the SSU and *psb*A phylogenies. The plastid gene *psb*A is a faster-evolving marker (Wolfe et al. 1987, Broom et al. 2008), leading to younger root age of the tree compared to the SSU phylogeny. The random local clock model with branch-specific rate variation was selected for this data set (Drummond and Suchard 2010). A representative of the order Hapalidiales, *Mesophyllum lichenoides* (J.Ellis) Me.Lemoine, was selected as outgroup. Four tree nodes with temporal information, or with first occurrence age available from fossil material, were set as time points to calibrate the molecular clock. Confidence intervals, giving indications of the certainty of the age of the fossil's first occurrence, were calculated following Marshall (1990, 1998), who developed a mathematical equation that requires the number of occurrences of the fossil taxon in question:

$$r_c = a \times R$$

where r_c is the confidence interval, a is a constant (see below), and R is the observed stratigraphic range.

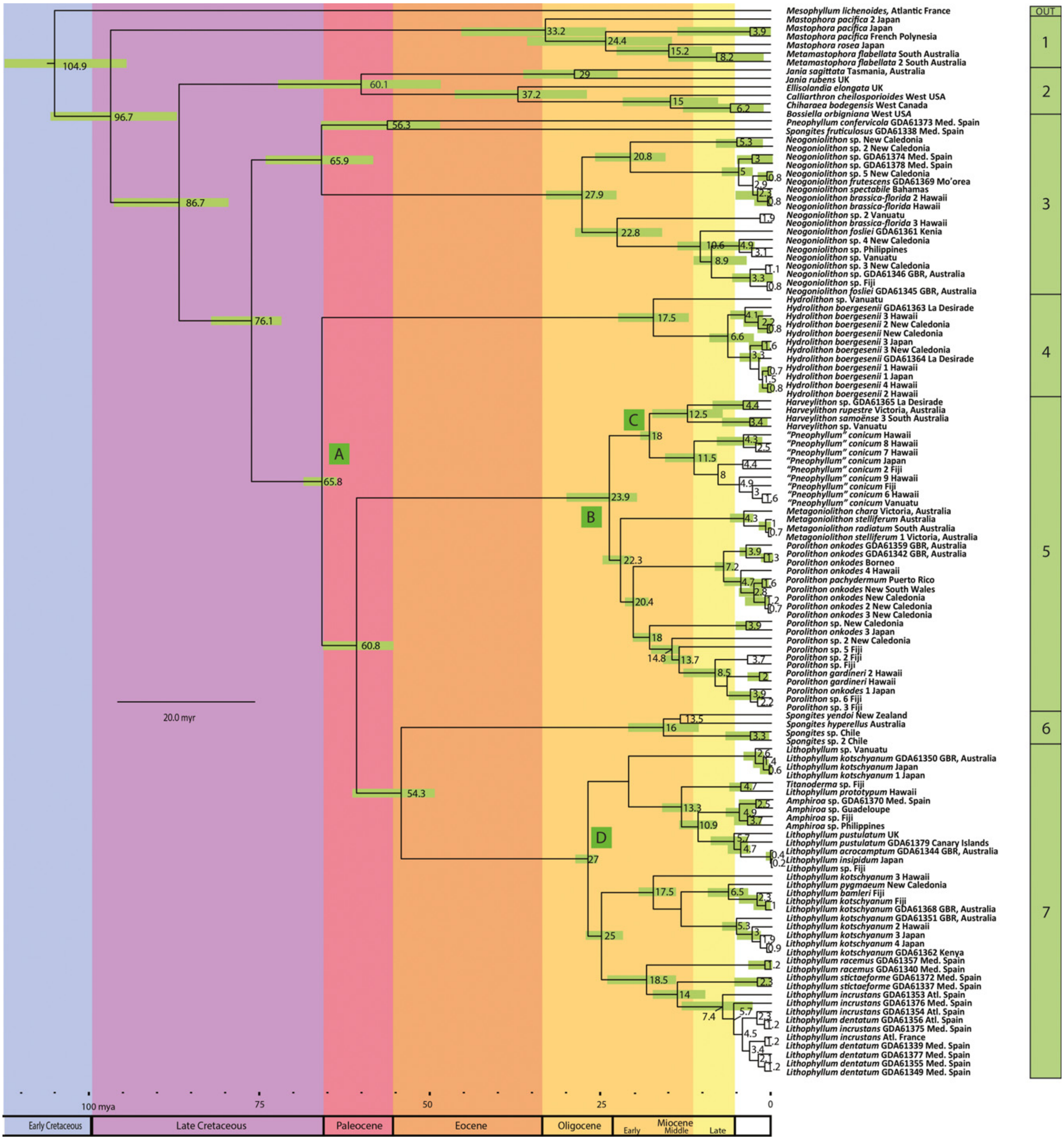

FIG. 1. SSU time tree inferred with BEAST including 126 OTUs. Numbers at nodes indicate ages in million years. Bars on internal nodes represent Bayesian probability intervals. Squares (A–D) indicate nodes used for calibration. Numbering on right side indicates following clades: (1) Mastophoroideae; (2) Corallinoideae; (3) Neogoniolithoideae; (4) Hydrolithoideae; (5) Metagoniolithoideae; (6) Southern Hemisphere group; and (7) Lithophylloideae. [Color figure can be viewed at wileyonlinelibrary.com]

The constant a was calculated as:

$$a = [(1 - \mathrm{C})^{-1/(H-1)}] - 1$$

where C is the confidence level (here 0.95) and H is the number of stratigraphic levels with occurrence of the taxon.

The resulting confidence intervals (Table 1) were converted to standard deviations that were incorporated into BEAST as soft boundaries of the prior distribution of the "time to the most recent common ancestor" ("tMRCA"; Drummond et al. 2012). Numbers of citations of the taxa treated and the resulting confidence intervals are listed in Table S1 in the Supporting Information. The MCMC output analysis was performed with TreeAnnotator (version 1.7.5), and trees were visualized in FigTree (version 1.3.1; Drummond et al. 2012).

In addition to data retrieved from the literature, we included in our analysis the oldest known fossil record of Metagoniolithoideae (see below). This specimen, "82,40 18" (drill hole S4, Pindaï peninsula, Chapeau Chinois sector, New Caledonia), was cut in one ultra-thin section (48 × 28 mm, 10–15 μm thick) and subsequently studied and photographed (software AxioVision, version 4.6) with a light microscope. Thallus and algal growth-form terminology follow Woelkerling (1988) and Woelkerling et al. (1993).

RESULTS

Calibrating nodes were established using the following groups:

(1) Hydrolithoideae (bifurcation "A" in Fig. 1). This group is characterized by a primarily dimerous thallus organization and pervasive cell fusions that make the outline of cell filaments indistinct. The living representative is *Hydrolithon boergesenii* Foslie (Foslie) that encompasses the taxon *H. reinboldii* (Weber-van Bosse & Foslie) Foslie, considered a younger heterotypic synonym by Rösler et al. (2016). Fossil records of this group comprise the extinct taxon *Karpathia* Maslov (also cited as *Peyssonnelia antiqua* J.H.Johnson, see Bassi et al. 2005) and *H. boergesenii* itself (as *H. reinboldii*). *Karpathia* shows characters typical of Hydrolithoideae: (i) a primarily dimerous thallus organization, (ii) outline of cell filaments entirely lost in large portions of the thallus due to pervasive and extensive cell fusions, and (iii) pore canals of uniporate sporangial conceptacles are lined by cell filaments perpendicular to the roof surface. The presumably oldest fossil of this group, *Karpathia sphaerocellulosa* Maslov, was found in deposits of the Cretaceous–Paleogene boundary 66 mya (Aguirre et al. 2007), with a confidence interval of 2.23 mya.

(2) *Porolithon* group (bifurcation "B" in Fig. 1). The occurrence of buried horizontal fields of trichocytes has been taken as a reliable character attesting to the record of some members of this clade. This character, when present, is diagnostic for the genus *Porolithon* (subclade 5.1 in Rösler et al. 2016, Fig 2B). Horizontal fields of trichocytes occur at the thallus surface in specimens of the *"Pneophyllum" conicum* subclade (5.2c in Rösler et al. 2016, Kato et al. 2011, Bittner et al. 2011). Confident identification of fossil *Metagoniolithon* is difficult due to the very low preservation potential of diagnostic features (genicula of many-celled untiered filaments and mucilaginous caps; Womersley and Johansen 1996). Nevertheless, the origination of clades with buried horizontal fields of trichocytes must have been coeval with, or predate, *Metagoniolithon* (see Fig. 1). The oldest known coralline showing buried horizontal fields of trichocytes (Fig. 2A) was found in limestones in New Caledonia dating as late Chattian–Aquitanian (23.94 ± 0.13 mya to 23.18 ± 0.19 mya; Maurizot et al. 2016). This indicates a calibration of the ancestor node of this group to 23.94 mya (±4.65 myr confidence interval).

(3) *Harveylithon* group (bifurcation "C" in Fig. 1). This genus comprises nongeniculate monomerous corallines with plumose ventral core. Trichocytes usually occur singly and may become buried in the thallus. Cell filaments lining the pore canal of uniporate tetrasporangial conceptacles are perpendicular to the thallus surface. Fossils of this group have been found mainly in Pleistocene limestones (Table S1), but the earliest representatives occurred in late Burdigalian reefs (18 mya) in East Kalimantan (Rösler et al. 2015, as *Hydrolithon rupestre* (Foslie) Penrose). The node aggregating this group was calibrated to 18 mya (±8.4 myr confidence interval).

(4) *Lithophyllum pustulatum* (J.V.Lamouroux) Foslie group (bifurcation "D" in Fig. 1). Here, we use the generic concept of *Lithophyllum* proposed by Woelkerling and Campbell (1992). *Lithophyllum pustulatum* is the type species of *Titanoderma*, a genus name used by many authors for corallines with bistratose dimerous thallus margin and a ventral layer of palisade cells (Chamberlain and Irvine 1994, Merwe and Maneveldt 2016). They supposedly constitute a clade independent of other lithophylloid species (Bailey 1999). A recent phylogenetic analysis, however, showed that corallines with typical *Titanoderma* morphology group with corallines with morpho-anatomy typical of lithophylloids without a ventral layer of palisade cells and, consequently "generic boundaries between *Lithophyllum* and *Titanoderma* remain unresolved"

TABLE 1. Calculation of the confidence intervals.

	H (citations/number of beds)	C	R	a	r_c	SD
Hydrolithoideae	91	0.95	66.0	0.0338	2.2338	0.58
Porolithon group	44	0.95	23.8	0.0722	1.7244	0.45
Lithophyllum pustulatum group	40	0.95	26.8	0.0798	2.1397	0.56
Harveylithon group	29	0.95	18.0	0.1129	2.0326	0.53

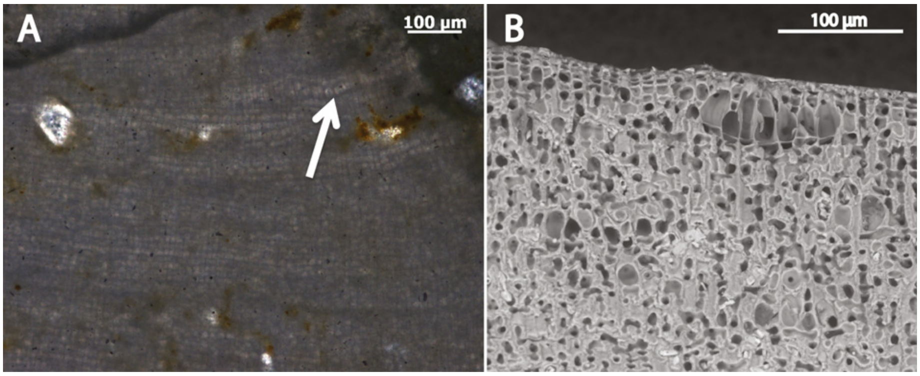

FIG. 2. Porolithoideae. (A) Light-microscope image of thin slide of fossil sample of oldest member of Porolithoideae; arrow shows horizontal row of trichocytes, (B) SEM image of cross-section of extant *Porolithon onkodes* GDA61359. [Color figure can be viewed at wileyonlinelibrary.com]

(Richards et al. 2014). The oldest record of this group is reported from Oligocene rocks (26.8 mya) in the Central Pacific (Bassi et al. 2009). The node in which all OTUs of *L. pustulatum* group members divide from the other Lithophylloideae (the first bifurcation of this subfamily) was calibrated to an age of 26.8 mya ± 5.1 myr confidence interval.

Based on the known age of these four nodes, calibrated in the phylogenetic tree, the separation between Hapalidiales (Hapalidiaceae) and Corallinales (Corallinaceae) was estimated to have occurred at about 105 mya ± 15 myr, in the Albian (late Early Cretaceous). Mastophoroideae separated from the rest of Corallinales at 97 mya (±12 myr) in the early Late Cretaceous; and Corallinoideae separated from the clade grouping Neogoniolithoideae, Hydrolithoideae, Metagoniolithoideae, Lithophylloideae, and the Southern Hemisphere clade at 87 mya (±8 myr, early Late Cretaceous). The next branching event at about 76 mya separated Neogoniolithoideae from the remaining clades of the Corallinaceae studied. The estimated error bars (Bayesian probability intervals) of the appearances of Mastophoroideae, Corallinoideae, and Neogoniolithoideae overlap, and the fossil record does not resolve clearly the succession (see below).

After the first occurrence of Hydrolithoideae at the Cretaceous–Paleogene boundary (66 mya), different groups began to diversify in the Oligocene (~34–23 mya): the modern representatives of the subfamily Metagoniolithoideae including *Porolithon*, the *"Pneophyllum" conicum* clade and *Harveylithon*, the Southern Hemisphere group, and finally the separation of the clades within the subfamily Lithophylloideae with the appearance of the *L. pustulatum* species group about 27 mya. The diversification of major subclades at the generic level continued during the early and middle Miocene (~23–12 mya).

DISCUSSION

Age of appearance of major clades. Our time-calibrated tree (Fig. 1) suggests the appearance of corallines (order Corallinales, family Corallinaceae) with uniporate sporangial conceptacles in the late Early Cretaceous (105 ± 15 mya). This result is similar to the appearance time proposed for this order (117.5 mya) by Aguirre et al. (2010) and, more recently, by Yang et al. (2016) in the tree for the class Florideophyceae (119–114 mya). The lineage of Mastophoroideae diverged about 97 ± 10 mya; potential fossil records of this group have probably been reported as *Lithoporella* given that no vegetative characters separate this genus from *Mastophora*. The oldest record of *Lithoporella*, as *L. melobesioides* (Foslie) Foslie, is from Aptian–Albian (~125–100 mya) rocks of SW France (Poignant 1968). Late Jurassic (~163–145 mya) records of *Lithoporella* were considered doubtful both in terms of identification and age attribution (Lemoine 1970, 1977, Moussavian 1991, Aguirre et al. 2000). The first reliable records of *Mastophora* are Pleistocene in age (Iryu et al. 2010). According to Yang et al. (2016; Fig. 1), the lineage of *Mastophora rosea* diverged at a similar time estimation as the one obtained here for Mastophoroideae. Further results concerning the remaining Corallinaceae lineages cannot be compared because they are absent or poorly resolved in Yang et al. (2016).

Presumed members of Corallinoideae were described by Lemoine (1970) from Albian (113–100 mya) rocks from southern France and northern Spain, as *Corallina* sp. 1. One of the reported fragments preserved a conceptacle and the remains of a genicula. Misra et al. (2006) reported *Amphiroa guatemalense* J.H.Johnson & Kaska, *Amphiroa foliacea* J.V.Lamouroux and *Amphiroa kaskaella* J.H.Johnson & Kaska from Aptian–Albian limestones from the Cauvery Basin in southern India. Descriptions and illustrations of the latter fossils suggest that they correspond to intergenicula of geniculate corallines, although the presence of cell fusions rules out the attribution to *Amphiroa*. As no conceptacles were observed, the assignment to Corallinoideae remains uncertain.

The earliest occurrences of presumed representatives of nongeniculate Corallinaceae with monomerous organization were reported in the late Early

Cretaceous (Lemoine 1939, Elliott 1959, Misra et al. 2004, 2006). *Lithophyllum shebae* was described from lower Cretaceous sediments in Iraq (Elliott 1959), and *L. antiquum* from Aptian–Albian rocks in Algeria (Lemoine 1939). However, the descriptions and illustrations shown in the original publications and published records of these species (Lemoine 1939, Elliott 1959, Rey 1972, Poignant 1981) do not warrant an unequivocal assignment to Corallinaceae. A sexual (gametangial) character of the preserved conceptacle cannot be disregarded due to its small reported size in the case of *L. shebae.* This taxon has even been considered attributable to *Marinella* Pfender, a fossil genus with unknown reproductive structures, included in Solenoporaceae Pia 1927 (Barattolo and Del Re 1985) or in Ellianellaceae Granier and Dias-Britto 2016 (a term proposed to replace Pia's name, Granier and Dias-Britto 2016), a group of extinct red algae. In the *L. antiquum* case, Lemoine (1939) indicated that the morphology corresponds to a spermatangial conceptacle. The corallines illustrated by Misra et al. (2004, 2006) from the Aptian–Albian Kallakudi Limestone in the Cauvery Basin as *Lithophyllum* sp. and *Lithophyllum* sp. 2 show cell fusions and are probably sporangial plants of Corallinaceae but a gametangial or carposporangial nature of the conceptacles cannot be fully dismissed, and therefore these records might correspond to Hapalidiales or Sporolithales. This is also true for a Cenomanian (~100–94 mya) record of potential sporangial plants of Corallinaceae with cell fusions in Romania (*Lithophyllum* sp. in Bucur and Baltres 2002). The values obtained in the dated tree, however, suggest that all these fossil records fall into the range of error of the appearance of Corallinaceae and the successive appearance of the subfamilies Corallinoideae and Neogoniolithoideae. Other early presumed representatives of early nongeniculate corallinaceans, such as *Lithophyllum* (?) *venezuelaensis* J.H.Johnson, from Aptian–Albian rocks of Venezuela (Johnson 1965), also reported from the Aptian–Albian of SW France (Poignant 1967, 1968), *Lithophyllum* (?) *maximum* S.F.Conti and *Lithophyllum montalti* S.F.Conti from the Cretaceous of northern Italy (Conti 1949) and Cenomanian to Coniacian (~100–86 mya) rocks of the Pyrenees (Poignant 1981), and *Lithophyllum senonicum* Maslov from Maastrichtian (~72–66 mya) deposits in Georgia (Maslov 1956) and Corsica (Poignant and Chaffaut 1970) are also disputable due to the lack of reproductive structures and scant descriptions.

Fossil corallines showing morpho-anatomical characters similar to the *Spongites* lectotype (Woelkerling 1985) and epitype (Rösler et al. 2016, momomerous organization, noncoaxial core and sporangial pore canal lined by cells filaments orientated parallel to the thallus surface) are known from Thanetian (~59–56 mya) deposits in the Pyrenees (Aguirre et al. 2007). The oldest fossil attributed to *Neogoniolithon, N. montainvillense* Poignant, is from the middle Paleocene (Poignant 1977), but this species lacks diagnostic features to be doubtlessly assigned to *Neogoniolithon.* Diversification within the group of the sequenced *Neogoniolithon* species, however, did not start until the Oligocene, which may explain the scarcity of fossil representatives of the genus in older deposits.

Considering the oldest record of *Karpathia* as the first occurrence of the subfamily Hydrolithoideae, the sporangial conceptacle formation from filaments surrounding and interspersed within the fertile area first appeared at the Cretaceous–Paleogene boundary (66 mya). This evolutionary novelty characterizes the most derived clades of Corallinaceae that separated in the early Paleogene.

The oldest known coralline showing the diagnostic characters of Metagoniolithoideae was found in Chattian–Aquitanian (Oligocene–Miocene boundary) deposits in New Caledonia yielding a Sr-isotope age of 23.9 ± 0.13 myr (Maurizot et al. 2016, Fig. 2A). Our time-calibrated tree (Fig. 1) predicts the first diversification events within this subfamily to have occurred in the very late Oligocene–early Miocene. Rösler et al. (2015) illustrated the first representative in the fossil record of *Harveylithon*, found in a late Burdigalian patch reef (~16 mya). These very late Oligocene to early Miocene Metagoniolithoideae, indicate the onset of the typical reef coralline flora in Indonesia. Nevertheless, most fossil representatives of Metagoniolithoideae are cited from Pleistocene and younger deposits (Table S1). This is the case of *"Pneophyllum" conicum*, the oldest records of which are only Pleistocene (for example, Braga and Aguirre 2004, as *Neogoniolithon conicum*, Iryu et al. 2010, as *P. conicum*). Potential oldest members of this subclade have probably been identified as *Neogoniolithon* in the paleontological literature due to the coaxial ventral core shown by most plants.

According to our results, the differentiation of the Southern Hemisphere group took place 54 ± 3 mya, but no reliable or distinct fossil records of the group are known. Merwe et al. (2015) recently recorded representative taxa of this sister group of Lithophylloideae (*Spongites decipiens* (Foslie) Y.M.Chamberlain and *S. tumidus* (Foslie) K.A. Miller, P.W.Gabrielson, Miklasz, E.van der Merwe & Maneveldt) along the NE Pacific coast, expanding the biogeographical distribution of the subclade, which in the analysis of Rösler et al. (2016) only included species from southern latitudes.

Aguirre et al. (2010) proposed *Distichoplax biserialis* W.O.Dietrich as a direct ancestor of the modern Lithophylloideae. Another possible candidate mentioned is *Lithophyllum premoluccense* var. *cretacicum* Maslov from Late Cretaceous sediments in Georgia (Braga et al. 2005). The lithophylloid affinity of *Distichoplax* has been questioned, and an affinity with *Mastophora* or *Lithoporella* has been suggested (Athanasiadis 1995). In the case of *L. premoluccense* var.

cretacicum, although no cell fusions between cells of adjacent filaments are present, no secondary pit connections characteristic of lithophylloids can be observed in the only known specimen. The last occurrence of *D. biserialis* (Priabonian, ~38–34 mya; Bucur et al. 1984) took place several million years before the first records of modern lithophylloids (26.8 mya; Bassi et al. 2009), and the time gap (>38 myr) from the record of *L. premoluccense* var. *cretacicum* (Late Cretaceous) to the first occurrence of modern lithophylloids is very long. However, if the lithophylloid affinity of *D. biserialis* is not rejected, these two kinds of fossil corallines might represent early lithophylloids that lived before the diversification of the modern members of the subfamily. The oldest known records of thick lithophylloids similar to living representatives were described by Johnson (1964b) as *Lithophyllum alternicellum* J.H.Johnson, from the early–middle Miocene Bonya Limestone in Guam. Thick lithophylloid species were reported in the early Langhian (middle Miocene) of the Czech Republic (Hrabovský et al. 2015, as *Lithophyllum* sp.1 and *Lithophyllum* sp.2) and in the Langhian of southern Spain (Braga and Aguirre 1995, as *L. incrustans* Philippi). The deposits in which the latter record was found were originally attributed to the early Miocene but subsequent biostratigraphic analysis revealed a younger, middle Miocene age (Martín et al. 2009).

Paleobiogeography of first records of major groups of Corallinaceae. The paleogeographic reconstructions for the middle Cretaceous (~100 mya) indicate that the oldest records of Mastophoroideae and Corallinoideae (Poignant 1968, Lemoine 1970) come from areas at latitudes from 30° to 35° in the Northern Hemisphere at the transition from the Tethys Ocean to the North Atlantic (Fig. 3). Roughly coeval Corallinoideae and the first putative monomerous nongeniculate Corallinaceae were found in the Cauvery Basin in southern India (Misra et al. 2004, 2006), located in the middle Cretaceous at intermediate latitudes in the Southern Hemisphere. However, the low chronostratigraphic resolution of all records, dated as Aptian–Albian or Albian, precludes the establishment of a spatiotemporal sequence of appearance. The few younger Cretaceous reports of Corallinaceae are dispersed in the Tethys Ocean. The scarcity, ambiguity, and the poor age constraint of the records prevent any attempt to understand the paleobiogeography of the early corallinaceans.

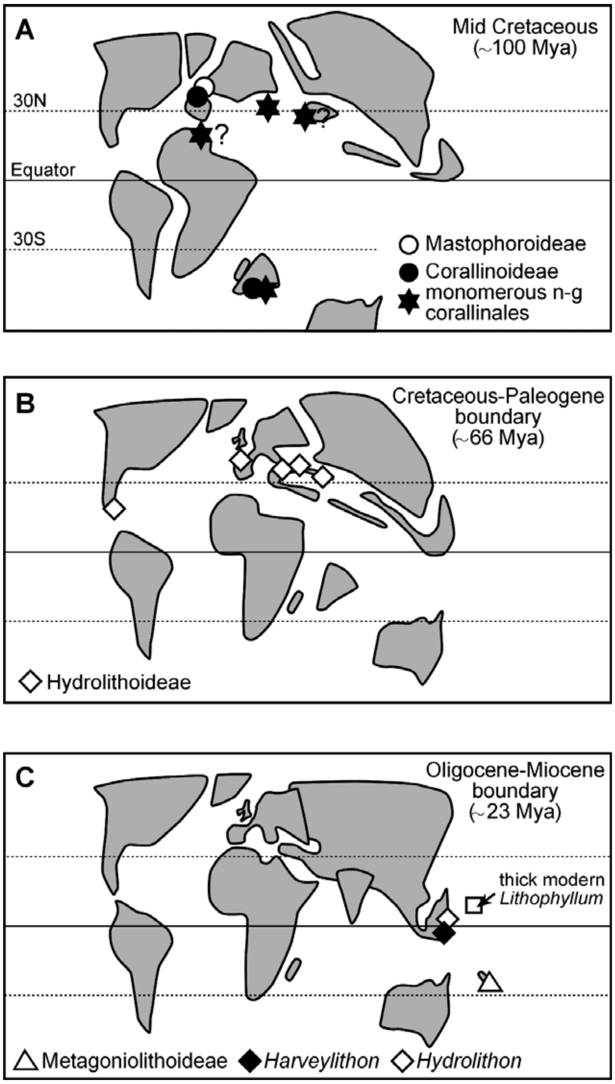

FIG. 3. Paleogeographic locations of oldest fossil records of recent coralline algal groups. Paleogeographic sketches based on Cowman and Bellwood (2013). [Color figure can be viewed at wileyonlinelibrary.com]

The earliest reports of Hydrolithoideae at the Cretaceous–Paleogene boundary (~66 mya) come from low to intermediate latitudes in the Northern Hemisphere, both in the western Tethys Ocean and North Atlantic Ocean (as *P. antiqua*, Johnson 1964a, Johnson and Kaska 1965, Moussavian 1988, Stockar 2001, as *Peyssonnelia preantiqua* Moussavian and *Peyssonnelia taeniforme* Moussavian, Moussavian 1988, as *Karpathia*, Maslov 1962, Aguirre et al. 2007). By contrast, the earliest fossils attributable to modern *Hydrolithon* were recorded in lower Miocene reef deposits in SE Asia near the Equator (Rösler et al. 2015).

The oldest Paleocene (~66–56 mya) records of *D. biserialis*, a potential Lithophylloideae, are distributed along the northern margin of the Tethys Ocean, North Atlantic and the Caribbean Sea (from Borneo, Keij 1963, Johnson 1966, to Cuba, Beckmann and Beckmann 1966). *Lithophyllum premoluccense* var. *cretacicum* was found in intermediate latitudes at the northern margin of the Tethys Ocean (Braga et al. 2005). The main diversification of Metagoniolithoideae and Lithophylloideae took place during the late Oligocene–middle Miocene interval (~28–12 mya). In this time interval, the genera within Metagoniolithoideae (*Harveylithon*, *Metagoniolithon*, *Porolithon*) and the *"Pneophyllum" conicum* group diverged, together with the main subclades within Lithophylloideae (Fig. 1). The earliest records of *Harveylithon* and *Porolithon*, and thick multistratose *Lithophyllum* similar to the modern members of the genus were found in reefs in the Indo-Australian Archipelago (Johnson 1964b, Rösler et al. 2015). A substantial increase in the number of tropical coral-reef sites and volume of tropical coral-reef deposits at a global scale, which was especially marked in the Indo-Pacific (Perrin and Kiessling 2010), took place during this interval of major diversification of typical reef coralline algae (*Porolithon*, *Harveylithon*, *Hydrolithon*, *"Pneophyllum" conicum*, and subclades within lithophylloids), suggesting a potential relationship between the two processes. According to the limited data set available, the Indo-Australian Archipelago was the center of origination of reef corallines. Similar patterns of increased diversification during the latest Oligocene–early Miocene in the Indo-Australian Archipelago have been recognized for coral reef fishes (Cowman and Bellwood 2013), reef-building corals (Wilson and Rosen 1998, McMonagle et al. 2011, Santodomingo et al. 2015), seagrass associated mollusks (Reich et al. 2014), and larger benthic foraminifera (Renema et al. 2008).

CONCLUSIONS

According to our time-calibrated tree, the order Corallinales (family Corallinaceae) separated from Hapalidiales in the Early Cretaceous (~105 mya). The subfamilies Mastophoroideae, Corallinoideae, and Neogoniolithoideae were the first three emerging clades, but neither the calibration nor the fossil record resolves the succession of appearance. The earliest fossil representatives of these groups are dispersed from low to intermediate latitudes in both hemispheres. The evolutionary novelty of the development of the tetrasporangial conceptacle roofs by filaments surrounding and interspersed among the sporangial initials emerged at the Cretaceous–Paleogene boundary and branching of the major clades (Hydrolithoideae, Metagoniolithoideae, and Lithophylloideae) took place in the early Paleogene. The main diversification within the Metagoniolithoideae and Lithophylloideae clades occurred in the late Oligocene–middle Miocene (~28–12 mya). The main reef corallinaceans (*Hydrolithon*, *Porolithon*, *Harveylithon*, *"Pneophyllum" conicum*, and subclades within Lithophylloideae) appeared in this interval in the Indo-Australian Archipelago.

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Adey, W. H. 1979. Crustose coralline algae as microenvironmental indicators in the Tertiary. *In* Gray, J. & Boucot, A. J. [Eds.] *Historical Biogeography, Plate Tectonics and the Changing Environment.* Oregon State University Press, Corvallis, Oregon, pp. 459–64.

Adey, W. H. 1986. Coralline algae as indicators of sea-level. *In* van de Plassche, O. [Ed.] *Sea-Level Research: A Manual for the Collection and Evaluation of Data.* Free University of Amsterdam, Amsterdam, The Netherlands, pp. 229–79.

Adey, W. H. & Mcintyre, I. G. 1973. Crustose coralline algae: a reevaluation in the geological sciences. *Geol. Soc. Am. Bull.* 84:883–904.

Adey, W. H., Townsend, R. A. & Boykins, W. T. 1982. The crustose coralline algae (Rhodophyta: Corallinaceae) of the Hawaiian Islands. *Smith. Contr. Mar. Sci.* 15:1–74.

Aguirre, J., Baceta, J. I. & Braga, J. C. 2007. Recovery of marine primary producers after the Cretaceous-Tertiary mass extinction: Paleocene calcareous red algae from the Iberian Peninsula. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 249:393–411.

Aguirre, J., Perfectti, F. & Braga, J. C. 2010. Integrating phylogeny, molecular clocks, and the fossil record in the evolution of coralline algae (Corallinales and Sporolithales, Rhodophyta). *Paleobiology* 36:519–33.

Aguirre, J., Riding, R. & Braga, J. C. 2000. Diversity of coralline red algae: origination and extinction patterns from the Early Cretaceous to the Pleistocene. *Paleobiology* 26:651–67.

Athanasiadis, A. 1995. Morphology, anatomy and reproduction of the eastern Mediterranean coralline *Tenarea tortuosa* and its relationship to members of the Lithophylloideae and Mastophoroideae (Lithophylloideae, Corallinales). *Nordic J. Bot.* 15:655–63.

Bailey, J. C. 1999. Phylogenetic position of *Lithophyllum incrustans* and *Titanoderma pustulatum* (Corallinaceae, Rhodophyta) based on 18S rRNA gene sequence analysis, with a revised classification of the Lithophylloideae. *Phycologia* 38:208–16.

Barattolo, F. & Del Re, M. C. 1985. Alghe rosse Solenoporacee del Cenomaniano dei dintorni di Caserta (Appennino meridionale, Italia). *Boll. Soc. Nat. Napoli* 93:203–55.

Bassi, D., Braga, J. C. & Iryu, Y. 2009. Palaeobiogeographic patterns of a persistent monophyletic lineage: *Lithophyllum pustulatum* species group (Corallinaceae, Corallinales, Rhodophyta). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 284:237–45.

Bassi, D., Braga, J. C., Zakrevskaya, E. & Petronova-Radionova, E. 2005. Re-assessment of the type collections of corallinalean genera (Corallinales, Rhodophyta) described by V. P. Maslov. *Palaeontology* 48:929–45.

Beckmann, J. P. & Beckmann, R. 1966. Calcareous algae from the Cretaceous and Tertiary of Cuba. *Schweiz. Paleont. Abh.* 85:1–45.

Bittner, L., Payri, C. E., Maneveldt, G., Couloux, A., De Reviers, B. & Le Gall, L. 2011. Evolutionary history of the Corallinales (Coralinophycidae, Rhodophyta) inferred from nuclear, plastidial and mitochondrial genomes. *Mol. Phylog. Evol.* 61:697–713.

Bosence, D. W. J. 1983. The occurrence and ecology of recent rhodoliths – a review. *In* Peryt, T. M. [Ed.] *Coated Grains.* Springer-Verlag, Berlin, pp. 225–42.

Bosence, D. W. J. 1991. Coralline algae: mineralization, taxonomy, and palaeoecology. *In* Riding, R. [Ed.] *Calcareous Algae and Stromatolites.* Springer-Verlag, Berlin, pp. 98–113.

Braga, J. C. & Aguirre, J. 1995. Taxonomy of fossil coralline algal species: Neogene Lithophylloideae (Rhodophyta, Corallinaceae) from southern Spain. *Rev. Palaeobot. Palynol.* 86:265–85.

Braga, J. C. & Aguirre, J. 2001. Coralline algal assemblages in upper Neogene reef and temperate carbonates in Southern Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 175:27–41.

Braga, J. C. & Aguirre, J. 2004. Coralline algae indicate Pleistocene evolution from deep, open platform to outer barrier reef environments in the northern Great Barrier Reef margin. *Coral Reefs* 23:547–58.

Braga, J. C., Bassi, D. & Piller, W. E. 2010. Palaeoenvironmental significance of Oligocene–Miocene coralline red algae – a review. *In* Mutti, M., Piller, W. E. & Betzler, C. [Eds.] *Oligocene–Miocene Carbonate Systems. Inter. Ass. Sedimentol. Spec. Publ.*, Vol. 42, pp. 165–82.

Braga, J. C., Bassi, D., Zakrevskaya, E. & Petrovna Radionova, E. 2005. Reassessment of the type collections of Maslov's species of Corallinales (Rhodophyta). I. Species originally attributed to *Lithophyllum* and *Melobesia*. *Rev. Esp. Paleontol.* 20:207–24.

Braga, J. C., Bosence, D. W. J. & Steneck, R. S. 1993. New anatomical characters in fossil coralline algae and their taxonomic implications. *Palaeontology* 36:535–47.

Broom, J. E. S., Hart, D. R., Farr, T. J., Nelson, W. A., Neil, K. F., Harvey, A. S. & Woelkerling, W. J. 2008. Utility of *psb*A and nSSU for phylogenetic reconstruction in the Corallinales based on New Zealand taxa. *Mol. Phylog. Evol.* 46:958–73.

Bucur, I. I. & Baltres, A. 2002. Cenomanian microfossils in the shallow water limestones from Babadag Basin: biostratigraphic significance. *St. Univ. Babeș-Bolyai Geol. Sp. Iss.* 1:79–95.

Bucur, I. I., Mészáros, N., Polikronopoulus, K. & Karagianis, H. 1984. Algues floridées dans les calcaires de l'Eocene supérieur de Lecta et Răstoci (NW du Bassin de Transilvanie). *Muzeul Brukenthal Studii Comunicări* 26:7–13.

Chamberlain, Y. M. & Irvine, L. M. 1994. Lithophylloideae Setchell. *In* Irvine, L. M. & Chamberlain, Y. M. [Eds.] *Seaweeds of the British Isles, Rhodophyta. Part 2B Corallinales, Hildenbrandiales*, vol. 1. HMSO, London, pp. 58–112.

Chatalov, A., Bonev, N. & Ivanova, D. 2015. Depositional characteristics and constraints on the mid-Valanginian demise of a carbonate platform in the intra-Tethyan domain, Circum-Rhodope Belt, northern Greece. *Cretac. Res.* 55: 84–115.

Conti, S. 1949. Alghe corallinacee cretacee nelle Argille Scagliose di Montalto. *Publ. dell'Istit. Geol. Univ. Genova Ser. A Paleontol.* 3:3–9.

Cowman, P. F. & Bellwood, D. R. 2013. The historical biogeography of coral reef fishes: global patterns of origination and dispersal. *J. Biogeogr.* 40:209–24.

Drummond, A. & Suchard, M. A. 2010. Bayesian random local clocks, or one rate to rule them all. *BMC Biol.* 8:114.

Drummond, A. J., Suchard, M. A., Xie, D. & Rambaut, A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Mol. Biol. Evol.* 29:1969–73.

Elliott, G. F. 1959. New calcareous algae from the Cretaceous of Iraq. *Rev. Micropaleontol.* 1:217–22.

Ganley, A. R. D. & Kobayashi, T. 2007. Highly efficient concerted evolution in the ribosomal DNA repeats: total rDNA repeat variation revealed by whole-genome shotgun sequence data. *Gen. Res.* 17:184–91.

Granier, B. & Dias-Brito, D. 2016. On the fosil alga *Marinella lugeoni* Pfender, 1939, nom. cons., and its seven unfortunate avatars. Revision of the Juliette Pfender collection. Part 2. Revision of the Jesse Harlan Johnson collection. Part 2. *Carnets Geol.* 16:231–45.

Halfar, J., Steneck, R. S., Joachimski, M., Kronz, A. & Wanamaker, A. D. Jr 2008. Coralline red algae as high resolution climate recorders. *Geology* 36:463–6.

Hrabovský, J., Basso, D. & Doláková, N. 2015. Diagnostic characters in fossil coralline algae (Corallinophycidae: Rhodophyta) from the Miocene of southern Moravia (Carpathian Foredeep, Czech Republic). *J. Syst. Palaeontol.* 14:499–525.

Iryu, Y., Takahashi, Y., Fujita, K., Camoin, G., Cabioch, G., Matsuda, H., Dato, T., Sugihara, K., Webster, J. M. & Westphal, H. 2010. Sealevel history recorded in the Pleistocene carbonate sequence in IODP Hole 310-M0005D, off Tahiti. *Island Arc.* 19:690–706.

Johnson, J. H. 1964a. Paleocene calcareous red algae from northern Iraq. *Micropaleontology* 10:207–16.

Johnson, J. H. 1964b. *Fossil and Recent Calcareous Algae from Guam.* Geol. Surv. Prof. Paper 403-G, U.S. Gov. Print. Off., Washington, 40 pp.

Johnson, J. H. 1965. Three Lower Cretaceous algae new to the Americas. *J. Paleontol.* 39:719–30.

Johnson, J. H. 1966. Tertiary red algae from Borneo. *Bull. Br. Mus. (Nat. Hist.) Geol.* 11:255–80.

Johnson, J. H. & Kaska, H. V. 1965. Fossil algae from Guatemala. *Prof. Contr. Col. Sch. Mines* 1:1–152.

Kato, A., Baba, M. & Suda, S. 2011. Revision of the Mastophoroideae (Corallinales, Rhodophyta) and polyphyly in nongeniculate species widely distributed on Pacific coral reefs. *J. Phycol.* 47:662–72.

Keij, A. J. 1963. *Distichoplax* in Sarawak and north Borneo. *Bull. Br. Borneo Geol. Surv.* 4:153–60.

Lemoine, M. 1939. Les Algues calcaires fossiles de l'Algérie. *Matér. Carte Géol. Algér 1ère sér. Paléontol.* 9:1–131.

Lemoine, M. P. 1970. Les algues floridées calcaires du Crétacé du sud de la France. *Archives du Muséum Nationale d'Histoire Naturelle Paris série 7* 10:129–240.

Lemoine, M. P. 1977. Les difficultés de la philogénie chez les algues Corallinacées. *Bul. Soc. Géol. Fr.* 19:1319–25.

Littler, M. M. & Littler, D. S. 1984. Models of tropical reef biogenesis: the contribution of algae. *Prog. Phycol. Res.* 3:323–55.

Mallela, J. 2013. Calcification by reef-building sclerobionts. *PLoS ONE* 8:e60010.

Marshall, C. R. 1990. Confidence intervals on stratigraphic ranges. *Paleobiology* 16:1–10.

Marshall, C. R. 1998. Determining stratigraphic ranges. *In* Donovan, S. K. & Paul, C. R. C. [Eds.] *The Adequacy of the Fossil Record.* Wiley, New York, pp. 23–53.

Martín, J. M., Braga, J. C., Aguirre, J. & Puga-Bernabéu, A. 2009. History and evolution of the North-Betic Strait (Prebetic Zone, Betic Cordillera): a narrow, early Tortonian, tidal-dominated, Atlantic-Mediterranean marine passage. *Sed. Geol.* 216:80–90.

Maslov, V. P. 1956. Fossil calcareous algae of USSR. *Trudy Geolo. Inst. Akad. Nauk. SSSR* 160:1–301.

Maslov, V. P. 1962. Fossil red algae of USSR and their connections with facies. *Trudy Geolo. Inst. Akad. Nauk. SSSR* 53:1–222.

Maurizot, P., Cabioch, G., Fournier, F., Leonide, P., Sebih, S., Rouillard, P., Montaggioni, L. et al. 2016. Post-obduction carbonate system development in New Caledonia (Népoui, Lower Miocene). *Sed. Geol.* 331:42–62.

McCoy, S. J. & Kamenos, N. A. 2015. Coralline algae (Rhodophyta) in a changing world: integrating ecological, physiological, and geochemical responses to global change. *J. Phycol.* 51:6–24.

McMonagle, L. B., Lunt, P., Wilson, M. E. J., Johnson, K. G., Manning, C. & Young, J. 2011. A reassessment of age dating of fossiliferous limestones in Eastern Sabah, Borneo: implications for understanding the origins of the Indo-Pacific marine biodiversity hotspot. *Palaeogeog. Palaeoclimatol. Palaeoecol.* 305:28–42.

Meagher, R. B., Berry-Lowe, S. & Rice, K. 1989. Molecular evolution of the small subunit of ribulosebisphosphate carboxylase: nucleotide substitution and gene conversion. *Genetics* 123:845–63.

Merwe, E. V. D. & Maneveldt, G. W. 2016. A modern account of the South African non-geniculate Lithophylloideae (Corallinales, Corallinophycidae, Rhodophyta). *S. Afr. J. Bot.* 103:247–67.

Merwe, E. V. D., Miklasz, K., Channing, A., Maneveldt, G. W. & Gabrielson, P. W. 2015. DNA sequencing resolves species of *Spongites* (Corallinales, Rhodophyta) in the Northeast Pacific and South Africa, including *S. agulhensis* sp. nov. *Phycologia* 54:471–90.

Misra, P. K., Jauhri, A. K., Singh, S. K., Kishore, S. & Rajanikanth, A. 2006. Non-geniculate coralline algae from the Uttatur Group (Early Cretaceous), south India. *Palaeobotanist* 55:29–40.

Misra, P. K., Rajanikanth, A., Jauhri, A. K., Kishore, S. & Singh, S. K. 2004. Albian limestone building algae of Cauvery Basin, South India. *Curr. Sci.* 87:1516–8.

Morse, A. N. C., Iwao, K., Baba, M., Shimoike, K., Hayashibara, T. & Omori, M. 1996. An ancient chemosensory mechanism brings new life to coral reefs. *Biol. Bull.* 191:149–54.

Moussavian, E. 1988. Die Peyssonneliaceen (auct.: Squamariaceae; Rhodophyceae) der Kreide und des Paläogen der Ostalpen. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie* 28:89–124.

Moussavian, E. 1991. New aspects of the phylogeny of coralline red algae (Rhodophyta): Cretaceous-Recent. V Int. Sym. Fossil Algae, Capri, Italy, Abstract Book, pp. 72–3.

Nelson, W. A. 2009. Calcified macroalgae – critical to coastal ecosystems and vulnerable to change: a review. *Mar. Freshwater Res.* 60:787–801.

Nylander, J. A. A. 2004. MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, 2.

Perrin, C. & Kiessling, W. 2010. Latitudinal trends in Cenozoic reef patterns and their relationship to climate. *In* Mutti, M., Piller, W. E. & Betzler, C. [Eds.] *Carbonate Systems During the Oligocene-Miocene Climatic Transition.* Wiley, New York, pp. 17–24.

Poignant, A. F. 1967. Les algues du Crétacé inférieur de Tercis (Landes). *C. R. Acad. Sci. Paris* 264:1145–7.

Poignant, A. F. 1968. Les algues des calcaires Aptiens et Albiens d'Aquitaine méridionale. *Rev. Micropaléontol.* 10:271–6.

Poignant, A. F. 1977. Une nouvelle algue Corallinacée *Neogoniolithon montainvillense* nov. sp. dans le paléocène du Bassin Parisien. *Geobios* 10:129–33.

Poignant, A. F. 1981. Sur des forms nouvelles d'algues rouges crétacées. *Cret. Res.* 2:187–95.

Poignant, F. & Chaffaut, S. A. 1970. Les algues des formations transgressives maestrichtiennes, paléocènes et yprésiennes de la cote sud-orientale de la Corse. *Rev. Micropaleontol.* 12:202–8.

Posada, D. & Crandall, K. A. 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics* 14:817–8.

Reich, S., Wesselingh, F. P. & Renema, W. 2014. A highly diverse molluscan seagrass fauna from the early Burdigalian (early Miocene) of Banyunganti (south-central Java, Indonesia). *Ann. Nat. Hist. Mus. Vienna Ser. A* 116:5–129.

Renema, W., Bellwood, D. R., Braga, J. C., Bromfield, K., Hall, R., Johnson, K. G., Lunt, P. et al. 2008. Hopping hotspots: global shifts in marine biodiversity. *Science* 321:654–7.

Rey, J. 1972. Recherches géologiques sur le Crétacé inférieur de l'Estremadura (Portugal). *Mem. Ser. Geol. Port.* 21:1–477.

Richards, J. L., Gabrielson, P. W. & Fredericq, S. 2014. New insights into the genus *Lithophyllum* (Lithophylloideae, Corallinaceae, Corallinales) from deepwater rhodolith beds offshore the NW Gulf of Mexico. *Phytotaxa* 190:162–75.

Rösler, A., Perfectti, F., Peña, V. & Braga, J. C. 2016. Phylogenetic relationships of corallinaceae (Corallinales, Rhodophyta): taxonomic implications for reef-building corallines. *J. Phycol.* 52:412–31.

Rösler, A., Pretković, V., Novak, V., Renema, W. & Braga, J. C. 2015. Coralline algae from the Miocene Mahakam Delta (East Kalimantan, SE Asia). *Palaios* 30:83–93.

Santodomingo, N., Novak, V., Pretkovic, V., Marshall, N., Di Martino, E., Capelli, E. L. G., Rösler, A., Reich, S., Braga, J. C., Renema, W. & Johnson, K. G. 2015. A diverse patch reef from turbid habitats in the middle Miocene (east Kalimantan, Indonesia). *Palaios* 30:128–49.

Setchell, W. A. 1943. *Mastophora* and the Mastophoreae: genus and subfamily of Corallinaceae. *Proc. Natl. Acad. Sci. USA* 29:127–35.

Stockar, R. 2001. *Polystrata alba* (Pfender) Denizot and *Peyssonnelia antiqua* Johnson: two peyssonneliacean algae (Rhodophyta) from the Paleocene of the Tobiago Formation (Montorfano Member type-section, Como, northern Italy). *Gol. Insbr.* 6: 15–22.

Vermeij, M. J. A., Dailer, M. L. & Smith, C. M. 2011. Crustose coralline algae can suppress macroalgal growth and recruitment on Hawaiian coral reefs. *Mar. Ecol. Prog. Ser.* 422:1–7.

Webster, J. M., Braga, J. C., Clague, D. A., Gallup, C., Hein, J. R., Potts, D. C., Renema, W., Riding, R., Riker-Coleman, K., Silver, E. & Wallace, L. M. 2009. Coral reef evolution on rapidly subsiding margins. *Global Planet. Change* 66:129–48.

Wilson, M. E. J. & Rosen, B. R. 1998. Implications of paucity of corals in the Paleogene of SE Asia: plate tectonics or centre of origin? *In* Hall, R. & Holloway, J. D. [Eds.] *Biogeography and Geological Evolution of SE Asia.* Backburys Publ, Leiden, The Netherlands, pp. 165–95.

Woelkerling, W. J. 1985. A taxonomic reassessment of Spongites (Corallinaceae, Rhodophyta) based on studies of Kützing's original collections. *Br. Phycol. J.* 20:123–53.

Woelkerling, W. J. 1988. *The Coralline Red Algae: An Analysis of the Genera and Subfamilies of Nongeniculate Corallinaceae.* Oxford University Press, Oxford, and British Museum (Natural History), London, UK, 268 pp.

Woelkerling, W. J. & Campbell, S. J. 1992. An account of the southern Australian species of *Lithophyllum* (Corallinaceae, Rhodophyta). *Bull. Brit. Mus. (Nat. Hist.) Bot.* 22:1–107.

Woelkerling, W. J., Irvine, L. M. & Harvey, A. S. 1993. Growth-forms in non-geniculate coralline red algae (Corallinales, Rhodophyta). *Aust. Syst. Bot.* 6:277–93.

Wolfe, K. H., Li, W. H. & Sharp, P. M. 1987. Rates of nucleotide substitution vary greatly among plant mitochondrial, chloroplast, and nuclear DNAs. *Proc. Natl. Acad. Sci. USA* 84:9054–8.

Womersley, H. B. S. & Johansen, H. W. 1996. Subfamily metagoniolithoideae. *In* Womersley, H. B. S. [Ed.] *The Marine Benthic Flora of Southern Australia–Part IIIB. Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales.* Australian Biological Resources Study, Canberra, Australia, pp. 317–23.

Yang, E. C., Boo, S. M., Bhattacharya, D., Saunders, G. W., Knoll, A. H., Fredericq, S., Graf, L. & Yoon, H. S. 2016. Divergence time estimates and the evolution of major lineages in the florideophyte red algae. *Sci. Rep.* 6:21361.

Supporting Information

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

Table S1. Citations of fossils to calculate the constant *H* for the calculation of the confidence interval.