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CHOREONEMA (CORALLINALES, RHODOPHYTA): 18S rDNA PHYLOGENY AND RESURRECTION OF THE HAPALIDIACEAE FOR THE SUBFAMILIES CHOREONEMATOIDEAE, AUSTROLITHOIDEAE, AND MELOBESIOIDEAE[1]

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Phylogenetic analyses of 18S rDNA gene data for *Choreonema thuretii* (Corallinales, Rhodophyta) and available data for other coralline red algae indicated that *Choreonema* belongs to the same lineage as other taxa of Corallinales possessing tetra/bisporangial conceptacles with multiporate plates. These results, when integrated with extant morphological/anatomical data, ultrastructural data, and taxonomic data led to the conclusion that all taxa of Corallinales possessing multiporate conceptacles belong to a distinct family, the Hapalidiaceae. Recognition of the Hapalidiaceae as a distinct family was supported both phylogenetically and phenetically. The Hapalidiaceae includes those taxa of Corallinales whose tetrasporangia produce zonately arranged spores and whose tetra/bisporangia are borne in conceptacles, produce apical plugs, and develop beneath multiporate plates. The Hapalidiaceae includes the subfamilies Choreonematoideae, Melobesioideae, and Austrolithoideae, formerly placed in the Corallinaceae *sensu lato*. The Choreonematoideae lack cell connections between adjacent vegetative filaments and have a multiporate plate that is acellular at maturity, consisting only of a calcium carbonate matrix. The Austrolithoideae and Melobesioideae both have cellular pore plates; taxa of Melobesioideae have cell fusions between cells of adjacent vegetative filaments, whereas taxa of Austrolithoideae lack cellular connections between adjacent vegetative filaments. Inclusion of the Austrolithoideae in the Hapalidiaceae was based entirely on morphological/anatomical evidence; molecular evidence currently is lacking. Relevant historical and nomenclatural data are included.

Key index words: **18S rDNA phylogeny; Austrolithoideae; *Choreonema*; Choreonematoideae; Corallinaceae; Corallinales; Hapalidiaceae; Melobesioideae; Sporolithaceae**

Abbreviations: **ML, maximum likelihood; MP, maximum parsimony**

This article deals with the 18S rDNA (small subunit rDNA) phylogeny of *Choreonema thuretii* and the placement of *Choreonema* and subfamilies Choreonematoideae, Melobesioideae, and Austrolithoideae in a separate family of Corallinales (Rhodophyta), the earliest available name for which is Hapalidiaceae (Gray 1864, p. 22). The recognition of the Hapalidiaceae as a distinct family of Corallinales is supported both phenetically and phylogenetically by evidence from LM, SEM, TEM, and molecular biology.

Our understanding of the phenetic relationships or overall similarity of *Choreonema* to other members of the Corallinales has evolved over time, as reflected in the various classification proposals. Woelkerling (1987a) summarized the earlier history of these classification proposals and formally established the subfamily Choreonematoideae within the family Corallinaceae. The Choreonematoideae, which includes a single genus and species (*Choreonema thuretii*) was characterized (Woelkerling 1987a, p. 125, 1988, p. 88) by three features: 1) absence of cell fusions and secondary pit-connections between cells of contiguous vegetative filaments, 2) tetrasporangia possessing apical plugs, and 3) tetrasporangia occurring in uniporate conceptacles. Subsequently, the Choreonematoideae was recognized by various authors, including Adams (1994), Irvine and Chamberlain (1994), Womersley (1996), Babbini and Bressan (1997), Bailey and Chapman (1998), and Yoshida (1998).

Before 1996, hypotheses concerning the possible phylogeny or evolutionary history of taxa within the Corallinales were based exclusively on evidence from comparative morphology and anatomy gleaned almost entirely from LM. In the absence of gene sequence data, however, it was difficult to determine which character states were the result of common ancestry, which the result of parallel evolution, and which the result of convergent evolution, and this problem led to differing classification proposals (e.g. compare Johansen 1969 with Cabioch 1972). The possible phylogenetic relationships of *Choreonema* remained especially problematic, as

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evidenced by its placement either in one of several different subfamilies of Corallinaceae (summarized in Woelkerling 1987a, pp. 112–113, 1988, p. 92) or placement in its own subfamily (Woelkerling 1987a, 1988), all characterized by the presence of uniporate tetrasporangial conceptacles.

The molecular-based phylogenetic studies of the Corallinales (using 18S rDNA data) by Bailey and Chapman (1996, 1998) and Bailey (1999) have provided a new perspective on the evolutionary history within the Order. Unfortunately, however, the absence of 18S rDNA data for *Choreonema* has precluded any consideration of its evolutionary history from a molecular viewpoint.

Meanwhile, in an abstract for the 1998 meeting of the Phycological Society of America, Broadwater et al. (1998) announced the discovery of a deeply sunken multiporate plate in tetrasporangial conceptacles of *Choreonema*, and they suggested that the genus was a reduced member of the Corallinaceae, subfamily Melobesioideae. The Melobesioideae and Austrolithoideae are the only two subfamilies of Corallinaceae (and Corallinales) in which tetrasporangial conceptacles have a multiporate plate associated with the conceptacle roof (Johansen 1969, Cabioch 1972 [as the Lithothamnioideae], Woelkerling 1988, p. 158, Irvine and Chamberlain 1994, p. 159, Harvey and Woelkerling 1995). More recently, Broadwater et al. (2002) provided a detailed light and ultrastructural account of the multiporate plate in *Choreonema* demonstrating its unique structure. The pore plate is acellular and recessed within the conceptacle rim that curves over the plate nearly enclosing it, thus creating the false impression that the conceptacle is uniporate. The presence of a multiporate plate clearly supports the hypothesis that *Choreonema* is most closely related to other taxa of Corallinales with multiporate plates.

In this article, this hypothesis is further tested with newly obtained 18S rDNA data for *Choreonema*, and the taxonomic implications for multiporate taxa of Corallinales are fully considered.

MATERIALS AND METHODS

DNA extraction, PCR amplification, and sequencing. *Choreonema thuretti* (LTB 17968) on *Jania micrarthrodia* Lamouroux used in the molecular analyses was collected by A. Harvey on 1 December 1999 from Smiths Beach, Phillip Island, Victoria, Australia. This material is currently housed at Department of Botany Herbarium, La Trobe University, Bundoora, Victoria, Australia but will eventually be transferred to the National Herbarium of Victoria, Royal Botanic Gardens, South Yarra, Victoria, Australia.

Samples for DNA extraction were air dried in the field and placed in plastic bags with silica gel. Techniques modified from Goff and Moon (1993) were used for DNA extraction. Fine forceps and a dissecting microscope were used to remove 5–10 conceptacles, which were then placed into sterile 1.5 mL Eppendorf tubes with 200 μL of Chelex 100 resin (Biotechnology grade, Bio-Rad, Hercules, CA, USA) extraction buffer (5% Chelex resin w/v in a sterile solution of 90 mM Tris-HCl [pH 8.0] and 50 μM EDTA). The material was ground for approximately 3 min with a sterile Kontes 1.5 mL pellet pestle (Kontes Glass Company, Vineland, NJ, USA) and incubated on ice for 15–30 min; tubes were capped, boiled for 10 min, and then immediately placed on ice. Chelex resin and cellular debris were spun down for 2 min at 12,500*g* and the supernatant transferred to a new tube. The DNA extract was stored at −20° C until required for PCR amplification.

Oligonucleotide primers used for PCR amplification are given in Saunders and Kraft (1994). For each PCR amplification 50 μL reactions included 7–15 μL DNA template (from Chelex extraction), 1 μL DMSO (5% solution), 1 μL forward primer (10 μM), 1 μL reverse primer (10 μM), 1.5 μL $MgCl_2$ (50 mM), 1 μL dNTP mixture (10 mM), 5 μl PCR buffer (10×) (Gibco, Invitrogen Australia Pty Limited, Mt. Waverley, Australia), 0.5 μL Taq DNA polymerase recombinant (Gibco), and sterile water to 50 μL.

The thermocycling profile used for the PCR amplification was as follows: 3 min initial denaturing at 95° C, followed by 27 cycles of 30 s at 95° C, primer annealing for 30 s (at variable temperatures dependent on primer pairs used), and extension for 1 min at 72° C; with a final single extension step of 10 min at 72° C. To increase the final amount of target DNA, 7–15 μL of PCR reaction products were reamplified under the same conditions.

The PCR product was purified by separating the DNA fragments on a 1% agarose gel, excising the appropriate molecular weight band with a razor blade and eluting the DNA on a diatomaceous earth bead column according to standard methods (Hansen et al. 1995). The purified DNA was then sequenced using the ABI PRISM Big Dye Terminator Cycle Sequencing Ready Reaction Kit (PE Biosystems Pty Ltd, Foster City, CA, USA) following manufacturer's instructions, and ETOH/NaOAc precipitated to remove residual dye terminators. The sequencing products were sent to a DNA Sequencing facility (Monash University, Clayton, Australia) for sequence determination.

Sequence alignment and tree rooting. Sequences from both DNA strands of the three gene fragments were assembled using Gene Jockey (version 1.31, Taylor 1991). In an attempt to ensure that the 18S rDNA sequence for *C. thuretii* was not contaminated by the host, the assembled sequence was compared with published 18S rDNA sequences for both *Jania crassa* (U62113) and *Jania rubens* (U61259). The sequence for *C. thuretii* was first aligned automatically with 42 published sequences, obtained from GenBank (Table 1) using CLUSTAL W (Thompson et al. 1994) at BioNavigator by eBioinformatics Pty Ltd (http://www.eBioinformatics.com) and then edited manually with regard to secondary structure (Van de Peer et al. 1999) using SeqPup (Gilbert 1995). Sequence regions of the data matrix that could not be unambiguously aligned were excluded from the phylogenetic analyses. An alignment of 1555 bases out of a total of approximately 1800 bases was used for the final analyses. The 18S rDNA data for *C. thuretii* were analyzed with published sequences of 38 other coralline red algae together with four additional noncoralline red algae taxa (Table 1) used as the outgroup. These additional taxa were added to the data matrix because in recent analyses they were included in the sibling clade to that containing both the Corallinales and Rhodogorgonales (Choi et al. 2000).

Previous molecular investigations of coralline algae had used *Rhodogorgon carriebowensis* J. N. Norris and Bucher as the outgroup species (Bailey and Chapman 1998, Bailey 1999), and division-wide analyses suggest the Rhodogorgonales forms a sibling clade to the Corallinales (Saunders and Bailey 1997). Because the placement of *R. carriebowensis* within the Rhodophyta remains unresolved (Harvey et al. 2002) and the primary interest is to investigate phylogenetic relationships between *Choreonema* and other coralline red algal (Corallinales) taxa, *Rhodogorgon* was not included in the molecular analyses shown.

Phylogenetic analyses of 18S rDNA sequences included maximum parsimony (MP) and maximum likelihood (ML) approaches using the PAUP* computer package (beta version 4.0b, Swofford 2001). All characters were unordered and equally weighted, and alignment gaps were treated as missing data.

For MP analyses, trees were retrieved using the heuristic search option, tree-bisection-reconnection branch swapping, random stepwise addition of taxa and 100 replicates. Support for the resultant phylogeny was assessed using bootstrap analyses (based on 1000 resamples of the data) (Felsenstein 1985).

TABLE 1. List of species and 18S rDNA GenBank accession numbers used in the present study.

Order, family, subfamily, and species	GenBank accession number
Corallinales	
Corallinaceae	
Corallinoideae	
Arthrocardia filicula (Lamarck) H.W. Johansen	U61258
Bossiella californica ssp. *schmittii* (Manza) H.W. Johansen	U60945
Bossiella orbigniana ssp. *dichotoma* (Manza) H.W. Johansen	U60746
Calliarthron cheilosporioides Manza	U60943
Calliarthron tuberculosum (Postels and Ruprecht) E.Y. Dawson	U60944
Cheilosporum sagittatum (Lamouroux) J. Areschoug	U60745
Corallina elongata Ellis and Solander	U60946
Corallina officinalis Linnaeus	L26184
Haliptilon roseum (Lamarck) Garbary and H.W. Johansen	U60947
Jania crassa Lamouroux	U62113
Jania rubens (Linnaeus) Lamouroux	U61259
Serraticardia macmillanii (Yendo) Silva	U62114
Lithophylloideae	
Amphiroa sp. (Australia)	U62115
Amphiroa sp. (South Africa)	U62116
Amphiroa fragilissima (Linnaeus) Lamouroux	U60744
Lithophyllum incrustans Philippi	093410
Titanoderma pustulatum (Lamouroux) Nägeli	093409
Lithophyllum kotschyanum (Unger) Foslie	U62117
Lithothrix aspergillum J.E. Gray	U61249
Mastophoriodeae	
Spongites yendoi (Foslie) Chamberlain	U60948
Metagoniolithoideae	
Metagoniolithon chara (Lamarck) Ducker	U60743
Metagoniolithon radiatum (Lamarck) Ducker	U61250
Metagoniolithon stelliferum (Lamarck) Weber-van Bosse	U61251
Hapalidiaceae	
Choreonematoideae	
Choreonema thuretii (Bornet) Schmitz	AY221254
Melobesioideae	
Clathromorphum compactum (Kjellman) Foslie	U60742
Clathromorphum parcum (Setchell and Foslie) Adey	U61252
Lithothamnion glaciale Kjellman	U60738
Lithothamnion tophiforme Unger	U60739
'Leptophytum acervatum'[a]	U62119
'Leptophytum ferox'[a]	U62120
Mastophoropsis canaliculata (W.H. Harvey) Woelkerling	U62118
Mesophyllum engelhartii (Foslie) Adey	U61256
Mesophyllum erubescens (Foslie) Lemoine	U61257
Phymatolithon laevigatum (Foslie) Foslie	U60740
Phymatolithon lenormandii (Areschoug) Adey	U60741
Synarthrophyton patena (J.D. Hooker and W.H. Harvey) Townsend	U61255
Sporolithaceae	
Heydrichia woelkerlingii Townsend, Chamberlain and Keats	U61253
Heydrichia homalopasta Townsend and Borowitzka	AF411629
Sporolithon durum (Foslie) Townsend and Woelkerling	AF411626
Acrochaetiales	
Acrochaetiaceae	
Audouinella dasyae (Collins) Woelkerling	L26181
Batrochospermales	
Batrochospermaceae	
Psilosiphon scoparium Entwisle	AF026041
Nemaliales	
Liagoraceae	
Nemalion helminthoides (Velley) Batters	L26196
Palmariales	
Palmariaceae	
Meiodiscus spetsbergensis (Kjellman) G.W. Saunders and McLachlan	U23814

[a] Use of quotation marks follows Bailey and Chapman (1998, p. 694, Table 1, footnote b); *Leptophytum* has been reaffirmed to be a heterotypic synonym of *Phymatolithon* by Woelkerling et al. (2002a). The taxonomic status of the 'Leptophytum' species included in Bailey and Chapman (1998) and this study remains uncertain. Pending further studies and nomenclatural changes that are beyond the scope of this study, we have continued to use quotation marks for 'Leptophytum' to reflect the unresolved taxonomy.

For ML analyses, the program MODELTEST (Posada and Crandall 1998) was used to establish the model of DNA evolution that best fits the data. ML analyses were replicated 10 times, and support for the resultant phylogeny was assessed using bootstrap analyses (based on 50 resamples of the data).

RESULTS AND DISCUSSION

Phylogenetic analyses. Of 1555 included characters, the alignment contained 250 parsimony-informative characters, 96 variable but parsimony-uninformative charac-

ters, and 1209 constant characters. A strict consensus of 60 equally most parsimonious trees is presented in Figure 1, with MP derived bootstrap values presented at the nodes of the tree. The ML tree reconstruction is presented in Figure 2, with ML derived bootstrap values presented at the nodes of the tree. The ML substitution model corresponded to the general time reversible model with rates (for variable sites) assumed to follow a gamma distribution with shape parameter 0.55 and an estimated proportion of invariable sites of 0.59. This combination of parameters produced the tree with the highest log-likelihood score.

In both reconstruction methods the Sporolithaceae was the earliest diverging group. These taxa consistently diverged before a strongly supported (MP bootstrap = 100%, ML bootstrap = 100%) monophyletic clade that included the Hapalidiaceae and Corallinaceae. Although MP analyses resolved the Sporolithaceae as a monophyletic group, bootstrap support for this clade was weak (Hillis and Bull 1993) (MP bootstrap = 73%) and ML analyses did not resolve the Sporolithaceae as monophyletic. Moreover, although MP analyses resolved the *Heydrichia* taxa as a monophyletic group, ML analyses did not. In previous mo-

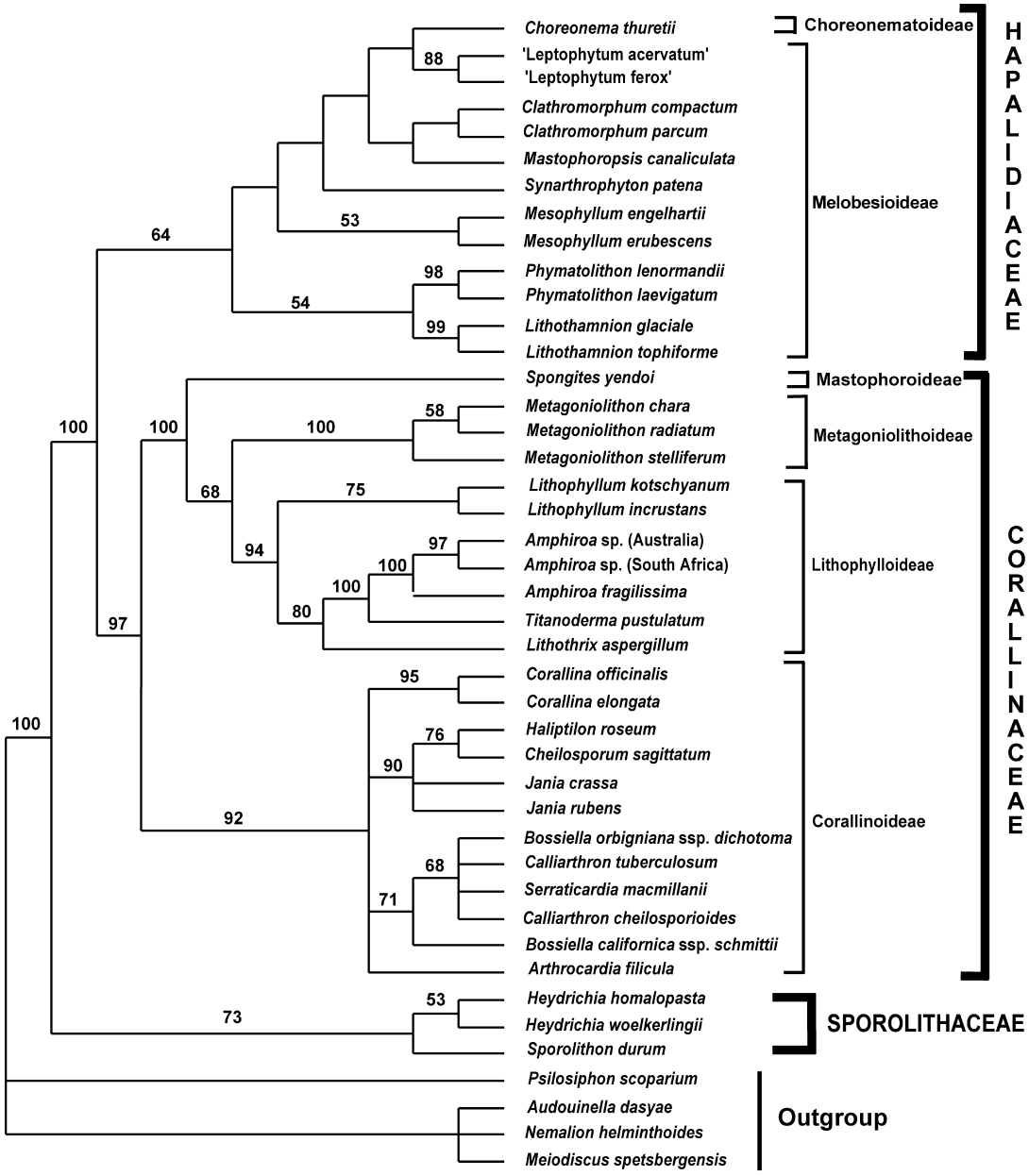

FIG. 1. Strict consensus of 60 equally most parsimonious trees. Values are percentage bootstrap replicates derived from MP analysis (>50%). Quotation marks indicate that *Leptophytum* is not a valid genus name (see footnote in Table 1).

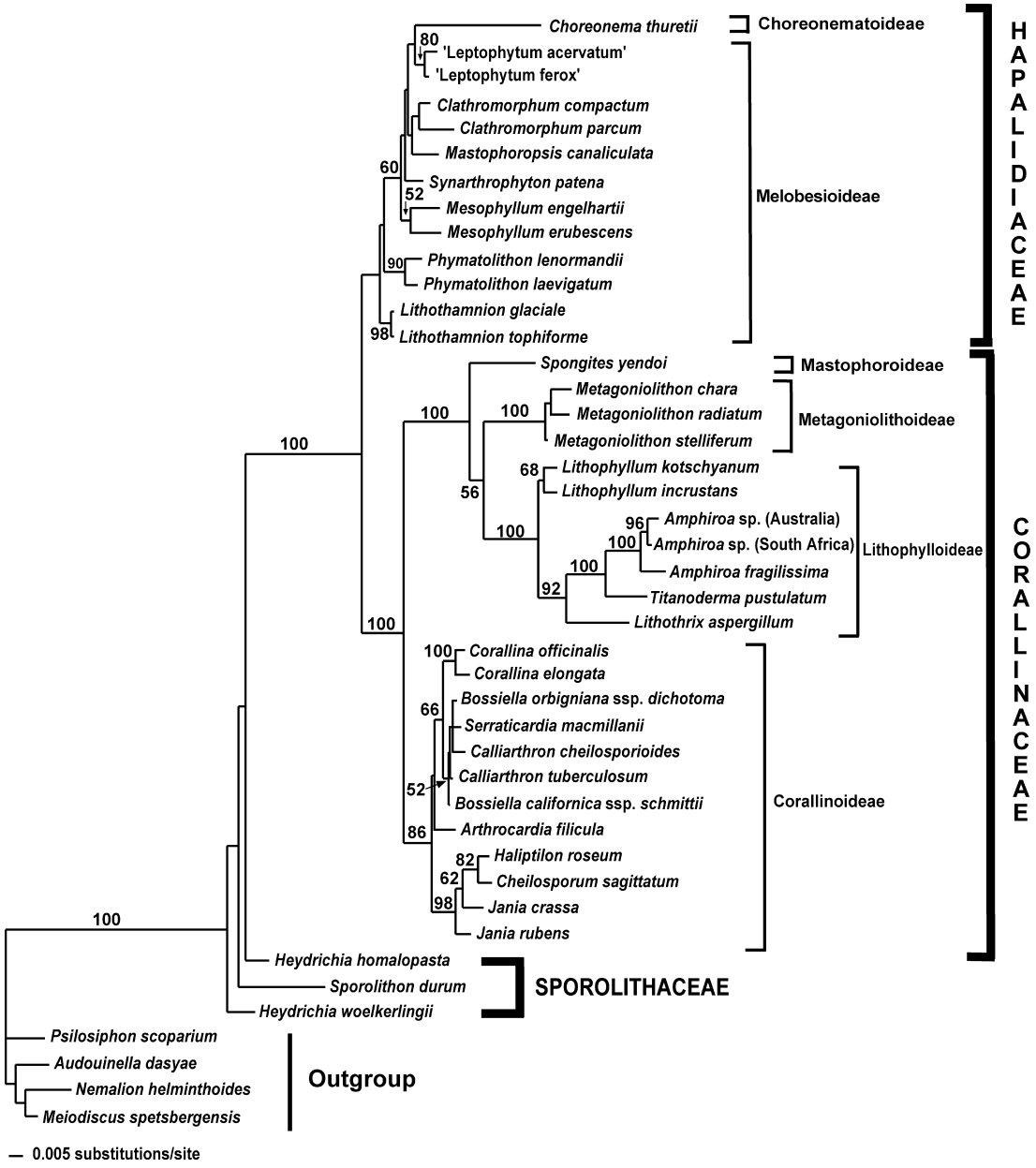

FIG. 2. Maximum likelihood phylogram. Values are percentage bootstrap replicates derived from ML analysis (>50%). Quotation marks indicate that *Leptophytum* is not a valid genus name (see footnote in Table 1).

lecular analyses (Harvey et al. 2002), both ML and MP analyses resolved *H. homalopasta* and *H. woelkerlingii* as a monophyletic clade separate from *Sporolithon durum.* Further work using sequences from additional taxa of Sporolithaceae are needed to clarify these relationships further, a task beyond the scope of the present study. In both reconstruction methods, *Choreonema* formed part of a monophyletic group that also contained the included taxa of Melobesioideae. Bootstrap support for this clade, however, was weak (MP bootstrap = 64%, ML bootstrap = <50%). Analyses suggested that the Choreonematoideae is most closely related to the melobesioid taxa designated by Bailey and Chapman (1998, p. 694) as 'Leptophytum acervatum' and 'Leptophytum ferox' (use of quotation marks follows Bailey and Chapman [1998, p. 694, Table 1, footnote b]; *Leptophytum* has been reaffirmed to be a heterotypic synonym of *Phymatolithon* by Woelkerling et al. 2002a). Most interrelationships within this clade, however, were poorly resolved, including the relationship between *Choreonema* and the Melobesioideae taxa, and drawing firm conclusions from these data is not possible because of lack of 18S sequence variation within this group (Bailey and Chapman 1998, Bailey 1999). Both MP and ML analyses showed strong support (MP bootstrap = 97%, ML bootstrap = 100%), however,

for the clade containing the remaining members of the Corallinaceae.

Phylogenetic analyses were also conducted inclusive of *Rhodogorgon carriebowensis* (GenBank accession number AF006089) for completeness (data not shown). In both ML and MP analyses, *Choreonema* formed part of a monophyletic group that also contained the included taxa of Melobesioideae, but resolution of most relationships within this clade was weak.

Taxonomic implications, family classification in the Corallinales. The Corallinales Silva and Johansen (1986) constitutes one of the most distinctive and easily recognized orders of Rhodophyta, and 18S rDNA data (Saunders and Bailey 1997) show it to be monophyletic. It is the only Order in which most or all vegetative cell walls are impregnated with calcium carbonate as calcite. Other features common to all Corallinales and shared with some (but not all) other Orders of Rhodophyta are discussed by Silva and Johansen (1986) and Woelkerling (1988, pp. 83–84). In formally establishing the Corallinales, Silva and Johansen (1986) also reviewed the history of family-level taxonomy in the group. Silva and Johansen (1986) chose to recognize a single family, the Corallinaceae Lamouroux (1812, p. 185, as "Corallineae") and suggested further (p. 252) that any elevation of subfamilies to the rank of family should be approached with caution. Woelkerling (1988, p. 84) supported this view, pointing out the need for significant new data as a basis for further reappraisal of classification at genus, subfamily, and family levels within the Corallinales.

Since 1988, a considerable body of new significant data has emerged not only from a spectrum of microscopy studies (Campbell and Woelkerling 1990, Chamberlain 1992, Penrose and Woelkerling 1992, Verheij 1993, Townsend et al. 1994, Wilks and Woelkerling 1994, Harvey and Woelkerling 1995) but also from molecular biology (Bailey and Chapman 1996, 1998, Bailey 1999), and taxonomic history (Woelkerling 1993, Woelkerling and Verheij 1995, Woelkerling and Lamy 1998), all of which have led to a better understanding of the concepts of a number of species, genera, and subfamilies; clarification of their associated nomenclature; and the recognition of new taxa. The new data for *Choreonema* (Broadwater and LaPointe 1997, Broadwater et al. 2002, present study), taken together with other information now available, ultimately have led us to reappraise family- level taxonomy within the Corallinales. We have concluded that three families with living representatives should be recognized, each with a distinct set of morphological/anatomical features. Two of the three (Hapalidiaceae and Corallinaceae) constitute monophyletic groups based on both MP and ML analyses. The third group (Sporolithaceae) was monophyletic in the MP tree but not in the ML tree.

Table 2 contains a summary of the characters and character states considered diagnostic of each of the three families. All four characters are associated with diploid reproductive structures, and each family possesses a unique combination of these. Moreover, the character states for all four characters are invariant within each family: no exceptions are known. Each family shares at least one character state with one but not both of the other two families, and at least two characters separate each family from the other two. Each family also has at least one character state not found in the other two.

None of the three families is newly described, but several previous family concepts require emendation. Data published since 1986 also has led to changes at subfamily level and generic level. These aspects are considered for each family below.

1. Sporolithaceae Verheij (1993, p. 195). The Sporolithaceae includes those taxa of Corallinales whose tetrasporangia produce cruciately arranged spores and whose tetrasporangia/bisporangia are borne individually in calcified sporangial compartments and produce apical plugs but do not develop beneath multiporate plates and are not produced within conceptacles.

Verheij (1993) originally established the Sporolithaceae for the genus *Sporolithon*, which hitherto had been placed in the Corallinaceae. A second genus, *Heydrichia*, was described by Townsend et al. (1994), but separate subfamilies have not been established. Phylogenetic studies involving both genera of Sporolithaceae have been published by Bailey and Chapman (1998), Bailey (1999), and Harvey et al. (2002); all are restricted to 18S rDNA data. These analyses indicate that the Sporolithaceae are a distinct lineage separate from the Corallinaceae and Hapalidiaceae on molecular grounds, and this is supported by the existing morphological/anatomical data (Harvey et al. 2002). Although further work using sequences from additional taxa of Sporolithaceae is needed to clarify the phylogenetic relationships within the Sporolithaceae, taxa of *Heydrichia* clearly differ from taxa of *Sporolithon* on morphological/anatomical grounds (Harvey et al. 2002).

2. Corallinaceae Lamouroux (1812, p. 185, as "Corallineae"), emendavit A. Harvey, S. Broadwater, W.

TABLE 2. Characters and character states considered diagnostic of the families of Corallinales with living representatives.

Character	Corallinaceae	Sporolithaceae	Hapalidiaceae
Arrangement of spores within tetrasporangia	Zonate	Cruciate	Zonate
Tetra/bisporangia producing apical plugs	No	Yes	Yes
Tetra/bisporangia produced beneath multiporate plates	No	No	Yes
Tetra/bisporangia borne within conceptacles or calcified compartments	Conceptacles	Calcified compartments[a]	Conceptacles

[a] See Townsend et al. (1995) for further information on calcified sporangial compartments in the Sporolithaceae.

Woelkerling, and P. Mitrovski. As emended here, the Corallinaceae is restricted to those taxa of Corallinales whose tetrasporangia produce zonately arranged spores and whose tetrasporangia/bisporangia are borne in uniporate conceptacles but do not produce apical plugs, do not develop beneath multiporate plates, and are not borne individually within calcified sporangial compartments.

The most significant change from the recent concept of the Corallinaceae (Verheij 1993), as followed by Irvine and Chamberlain (1994), Woelkerling (in Womersley 1996), and Yoshida (1998) and Bailey (1999), is the removal of those taxa (including *Choreonema*) whose tetrasporangia/bisporangia produce apical plugs and develop beneath multiporate plates to the Hapalidiaceae (see below).

The number and circumscription of subfamilies within the Corallinaceae has varied since 1969 (Johansen 1969, 1976, 1981, Cabioch 1972, Woelkerling 1988, Woelkerling in Womersley 1996). In the context of the emended family circumscription above, available morphological/anatomical data, and available 18S rDNA data, four subfamilies of Corallinaceae can be recognized: the Metagoniolithoideae, the Corallinoideae, the Mastophoroideae, and the Lithophylloideae. Table 3 contains a summary of the diagnostic features of each subfamily and associated references.

Currently recognized genera of Corallinaceae with living representatives are listed by subfamily in Table 4. The Metagoniolithoideae contains one genus with three species (for detailed accounts see Ducker 1979 and Womersley and Johansen 1996a). The genera of Corallinoideae include the 12 recognized by Johansen (1976, 1981) and the more recently described *Masakia* (Kloczcova 1987, 1996). The eight genera of Mastophoroideae are those recognized by Woelkerling (1996a). *Goniolithon*, recently used in Macintyre et al. (2001, p. 97) for a species of Mastophoroideae, is a genus of Lith-

TABLE 3. Characters and character states considered diagnostic of the subfamilies of Corallinaceae, Sporolithaceae, and Hapilidiaceae with living representatives.

Family	Subfamily	Summary of diagnostic characters of subfamily	Notes
Corallinaceae	Corallinoideae	Cells of contiguous vegetative filaments linked by cell fusions; secondary pit-connections unknown; genicula composed of one tier of cells	Subfamily concept follows Irvine and Chamberlain (1994) and Womersley and Johansen (1996b); 18S rDNA data provided by Bailey and Chapman (1996, 1998) and Bailey (1999)
	Metagoniolithoideae	Cells of contiguous vegetative filaments linked by cell fusions; secondary pit-connections unknown; genicula composed of untiered multicellular filaments	Subfamily concept follows Womersley and Johansen (1996a); 18S rDNA data provided by Bailey and Chapman (1996, 1998) and Bailey (1999)
	Mastophoroideae	Cells of contiguous vegetative filaments linked principally or exclusively by cell fusions; secondary pit-connections known only in one genus (*Metamastophora*); genicula absent	Subfamily concept follows Woelkerling (1988, 1996a); 18S rDNA data provided by Bailey and Chapman (1996, 1998) and Bailey (1999)
	Lithophylloideae	Cells of contiguous vegetative filaments linked principally or exclusively by secondary pit-connections; cell fusions reported for only one species; genicula (when present) composed of one or more tiers of cells	Subfamily concept follows Cabioch (1972); 18S rDNA data provided by Bailey (1999)
Hapalidiaceae	Austrolithoideae	Cells of contiguous vegetative filaments not linked by cell fusions or secondary pit-connections; genicula absent; multiporate plate composed of cells at maturity	Subfamily concept follows Harvey and Woelkerling (1995) and Woelkerling and Harvey (1996); no current 18S rDNA data
	Choreonematoideae	Cells of contiguous vegetative filaments not linked by cell fusions or secondary pit-connections; genicula absent; multiporate plate acellular at maturity, composed only of a calcium carbonate matrix	Subfamily concept modified here from Woelkerling (1987a) to take account of data in Broadwater et al. (2002); 18S rDNA data provided in present study
	Melobesioideae	Cells of contiguous vegetative filaments linked by cell fusions; secondary pit-connections unknown; genicula absent; multiporate plate composed of cells at maturity	Subfamily concept follows Woelkerling (1996b); 18S rDNA data provided by Bailey and Chapman (1996, 1998) and Bailey (1999)
Sporolithaceae			Not currently divided into subfamilies; 18S rDNA data provided by Bailey and Chapman (1998), Bailey (1999), and Harvey et al. (2002)

TABLE 4. Currently recognized genera with living representatives in each family and subfamily of Corallinales. The Sporolithaceae is not currently divided into subfamilies (see text).

Family and subfamily	Genera[a]
Corallinaceae	
Metagoniolithoideae	*Metagoniolithon*
Corallinoideae	*Alatocladia*, *Arthrocardia*, *Bossiella*, *Calliarthron*, *Cheilosporum*, *Chiharaea*, *Corallina*, *Haliptilon*, *Jania*, *Marginosporum*, *Masakia*, *Serraticardia*, *Yamadaea*
Mastophoroideae	*Hydrolithon*, *Lesueuria*, *Lithoporella*, *Mastophora*, *Metamastophora*, *Neogoniolithon*, *Pneophyllum*, *Spongites*
Lithophylloideae	*Amphiroa*, *Ezo*, *Lithophyllum/Titanoderma*, *Lithothrix*, *Paulsilvella*, *Tenarea*
Hapalidiaceae	
Austrolithoideae	*Austrolithon*, *Boreolithon*
Choreonematoideae	*Choreonema*
Melobesioideae	*Clathromorphum*, *Exilicrusta*, *Kvaleya*, *Lithothamnion*, *Mastophoropsis*, *Melobesia*, *Mesophyllum*, *Phymatolithon*, *Synarthrophyton*
Sporolithaceae	*Heydrichia*, *Sporolithon*

[a]Included genera and generic concepts follow: Metagoniolithoideae, Womersley (1996); Corallinoideae, Johansen (1976), Kloczcova (1987); Mastophoriodeae, Woelkerling and Penrose *in* Womersley (1996); Lithophylloideae, Woelkerling et al. (2002b); Austrolithoideae, Harvey and Woelkerling (1995); Choreonematoideae, present study; Melobesioideae, Chamberlain (1992), Woelkerling (1996b), Düwel and Wegeberg (1996); Sporolithaceae, Harvey et al. (2002).

ophylloideae requiring further evaluation (Woelkerling 1988, p. 216, Babbini and Bressan 1997, p. 306); the species mentioned, *G. improcerum* Foslie and Howe in Foslie, belongs to *Hydrolithon* (Penrose 1996, p. 258). The name *Paragoniolithon*, also used in Macintyre et al. (2001), is a heterotypic synonym of *Neogoniolithon*, based on evidence provided by Woelkerling (1987b).

The Lithophylloideae includes two geniculate genera (*Amphiroa*, *Lithothrix*) formerly placed in a separate subfamily (the Amphiroideae) and four or five nongeniculate genera, including the recently described *Paulsilvella* (Woelkerling et al. 2002b). *Lithophyllum* and *Titanoderma* are clearly distinct based on 18S rDNA data but presently cannot be unequivocally separated on morphological/anatomical grounds (Bailey 1999, Woelkerling et al. 2002b). The name *Pseudolithophyllum*, recently used in Desikachary et al. (1998) and in Adey and Steneck (2001), is a heterotypic synonym of *Lithophyllum* based on evidence provided by Woelkerling (1988, p. 103).

3. Hapalidiaceae J. E. Gray (1864, p. 22), emendavit A. Harvey, S. Broadwater, W. Woelkerling, and. P. Mitrovski. As emended here, the Hapalidiaceae includes those taxa of Corallinales whose tetrasporangia produce zonately arranged spores and whose tetrasporangia/bisporangia are borne in conceptacles, produce apical plugs, develop beneath multiporate plates, but are not borne individually within calcified sporangial compartments.

Gray (1864) originally established the Hapalidiaceae for a single genus, *Hapalidium* (Kützing 1843, p. 385), in turn, based on the single species *H. roseolum* Kützing (1843, p. 385). Gray's diagnosis ("Frond plain, hyaline, composed of cells"; Gray 1864) was extremely general and made no mention of calcification; with one exception (Gray 1867), the family was not recognized by subsequent authors.

Chamberlain (1983, p. 300) determined that the type of *H. roseolum* was conspecific with and thus a heterotypic synonym of *Melobesia membranacea* (Esper) Lamouroux, the type species of *Melobesia*. Consequently, *Hapalidium* is a heterotypic synonym of *Melobesia*. Nevertheless, as noted by Woelkerling (1988, p. 86), the family name Hapalidiaceae is legitimate and thus available for a family that includes the genus *Melobesia*. In the context of the present proposal to place all genera of Corallinales (including *Melobesia*) whose tetrasporangia/bisporangia produce apical plugs and develop beneath multiporate plates in a separate family, the family name Hapalidiaceae becomes the oldest available name for the group.

The Hapalidiaceae includes three subfamilies (Choreonematoideae, Austrolithoideae, Melobesioideae) that originally were placed in the Corallinaceae *sensu lato*. Table 3 contains a summary of the diagnostic features of each subfamily and associated references. None of these subfamilies possesses taxa with genicula and none possesses taxa that produce secondary pit-connections between cells of contiguous vegetative filaments. The subfamilies are separated on the presence/absence of cell fusions and the structure of the multiporate plate. The Choreonematoideae lack fusions between cells of contiguous vegetative filaments and have an acellular multiporate plate that consists only of a calcium carbonate matrix at maturity. Taxa of Austrolithoideae also lack fusions between cells of contiguous vegetative filaments, but they have a multiporate plate that at maturity is composed of cells. Taxa of Melobesioideae possess fusions between cells of contiguous vegetative filaments and also have a multiporate plate that at maturity is composed of cells.

The 18S rDNA data presented here indicate that *Choreonema*, the only known genus of Choreonematoideae, and all genera of the Melobesioideae for which data are available form a monophyletic group, thus supporting the recognition of the family Hapalidiaceae. The recognition of three subfamilies within the Hapalidiaceae is based largely on morphological/anatomical evidence. The inclusion of the Austrolithoideae in the Hapalidiaceae is based entirely on morphological/anatomical evidence. Although Bailey and Chapman (1998, p. 703) suggested the possibility that the Melobesioideae and Austrolithoideae are sister taxa, 18S rDNA data for the Austrolithoideae are presently

lacking. Similarly, although the relationship of *Choreonema*, and thus the Choreonematoideae, to the Melobesioideae remains equivocal on molecular grounds, the situation is clear-cut on morphological/anatomical grounds. The character states for the characters used to separate the subfamilies are invariant within the subfamilies; no exceptions are known.

Currently recognized genera of Hapalidiaceae with living representatives are listed by subfamily in Table 4. The Choreonematoideae contains a single genus with a single species. The Austrolithoideae contains two genera, each with a single species (for detailed accounts of the species see Harvey and Woelkerling 1995). The Melobesioideae contains nine extant genera and hundreds of described species, most of which remain poorly known (see comments in Woelkerling 1988 under individual genera). *Leptophytum* is a heterotypic synonym of *Phymatolithon*, as proposed by Düwel and Wegeberg (1996). None of the criteria used by Adey et al. (2001) to reinstate *Leptophytum* as a distinct genus were found to be reliable by Woelkerling et al. (2002a; see also Alongi et al. 2002). Although the possibility of a second genus separate from *Phymatolithon* was suggested by molecular data (Bailey and Chapman 1998), no firm conclusions based on these data were possible, and there are currently no known reliable morphological or anatomical features that can be used to delimit such a genus (Woelkerling et al. 2002a).

Comparisons with a two-family proposal based on presence/absence of genicula. The segregation of coralline red algae into two families based on the presence or absence of genicula was first proposed by Kützing (1843, pp. 385–389) but did not gain general acceptance and apparently was not used by any author since Daveau (1884) until 1998. Then, in the second part of their red algal flora of India, Desikachary et al. (1998) placed all geniculate taxa of Corallinales into one family, the Corallinaceae, and all nongeniculate taxa into a second family, the Spongitaceae, a legitimate family name (Woelkerling 1988, p. 86) proposed by Kützing (1843, p. 385).

We have not followed this proposal for various reasons. Desikachary et al. (1998) provide no supporting evidence for their proposal, and they do not explain why sporolithoid algae are best considered a tribe of the subfamily Melobesioideae rather than a distinct family of Corallinales as proposed by Verheij (1993). Their proposal also implies, contrary to existing morphological/anatomical data (e.g. significant differences in the formation and composition of genicula in the Lithophylloideae, Metagoniolithoideae, and Corallinoideae [Bailey 1999, p. 214]), that genicula arose only once during the evolution of the Corallinales. Finally, their proposal does not reflect the evolutionary history of the Corallinales as suggested by available 18S rDNA data (Bailey and Chapman 1996, 1998, Bailey 1999).

Although the name Spongitaceae (Kützing 1843) predates the name Hapalidiaceae (Gray 1864), it cannot be used for a family characterized by the occurrence of multiporate plates and the occurrence of apical plugs on tetrasporangia/bisporangia because *Spongites*, the genus upon which the family name is based, lacks both features (for an account of the original collections upon which *Spongites* is based, see Woelkerling 1985).

Extinct families associated with the Corallinales. Two families known only from the fossil record have been associated with the Corallinales. No molecular data are available, but neither seems closely related to the Hapalidiaceae.

The Graticulaceae Brooke and Riding (2000), first described under the invalid name Craticulaceae Brooke and Riding (1998), is known only from the middle of the Silurian (439–409 million years ago) and is characterized by the production of sporangial compartments like those in the Sporolithaceae. According to Brooke and Riding (1998), however, the earliest confirmed record for the Sporolithaceae is in the Early Cretaceous (which began about 145 million years ago). Brooke and Riding (1998) also characterize the Graticulaceae by the occurrence of trichocytes and irregular sori but suggested (pp. 189–190) that these criteria are unlikely to be sufficient to distinguish the two families should future work demonstrate that included taxa are contemporaneous in time in the fossil record.

The systematic position of the Solenoporaceae Pia (1927), a family that has been associated in various ways with taxa of Corallinales (Woelkerling 1988, p. 85, Brooke and Riding 1998, p. 186), remains unclear (Brooke and Riding 1998, p. 186, Aguirre and Barattolo 2001, p. 1113). The name Solenoporaceae is derived from the type genus, *Solenopora* (Dybowski 1878), whose type species, *S. spongioides* Dybowski, is known only from sterile material (Aguirre and Barattolo 2001). Woelkerling (1988, p. 85) suggested *incertae sedis* placement of the family within the Corallinales, whereas Aguirre and Barattolo (2001) consider the Solenoporaceae to be an *incertae sedis* group of algae.

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