

NEW DIAGNOSTIC CHARACTERS FOR THE ORDER SPOROLITHALES (CORALLINOPHYCIDAE, RHODOPHYTA)¹

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The diagnosis of the order Sporolithales is currently restricted to tetrasporangial anatomy. Until recently, there were few reports about gametangial, and more specifically carposporangial material for the Sporolithales. This study provides the first detailed observations of the anatomy of the mature carposporophyte phase from three species of Sporolithales commonly found in rhodolith beds from Brazil: *Sporolithon episporum*, *S. ptychoides*, and *Sporolithon* sp. Using these observations, along with previously published descriptions and illustrations from other representative species in the order, a comparison was made with the other three orders (Corallinales, Hapalidiales, and Rhodogorgonales) of the Corallinophycidae. We amend the diagnosis of the order Sporolithales to include the anatomy of the mature carposporophyte as follows: carposporangial conceptacles that lack a central fusion cell, but instead with numerous, short, one to two-celled, filaments that bear oblong terminal carposporangia that are distributed across the conceptacle chamber floor and walls.

Key index words: anatomy; carposporangial conceptacles; coralline algae; *Sporolithon*; taxonomy

The Sporolithaceae (Sporolithales, Corallinophycidae, Rhodophyta) encompasses those non-geniculate coralline red algae with cruciately divided tetrasporangia produced singly within uniporate, calcified compartments, each bearing an apical plug (Verheij 1993, Le Gall et al. 2010). These compart-

ments most often are arranged in clusters, also called sori (e.g., *Sporolithon ptychoides* Heydrich, see Verheij 1993), or are solitary (e.g., *Heydrichia homalopasta* R.A. Townsend & Borowitzka, see Townsend and Borowitzka 2001). Comprised of two extant genera, *Sporolithon* Heydrich and *Heydrichia* R.A. Townsend, Y.M. Chamberlain & Keats, and two extinct genera, *Hemiphyllum* Me.Lemoine and *Kymalithon* Me.Lemoine & Emberger (see Aguirre et al. 2000), the family was previously included in the order Corallinales (Verheij 1993). Le Gall et al. (2010) elevated the Sporolithaceae to ordinal rank, as the Sporolithales, based on its closer alliance in molecular phylogenies to the Rhodogorgonales rather than the Corallinales and what is now Hapalidiales (Nelson et al. 2015), and characterized by the mode of the tetrasporangial cleavage (cruciate as opposed to simultaneously zonate in the Corallinales and Hapalidiales) and the presence of calcified sporangial compartments formed from the enlarged wall of a tetrasporangial initial (see Cowan 1995, Townsend et al. 1995).

Currently, the characterization of Sporolithales within Corallinophycidae is restricted to tetrasporangial features (Le Gall et al. 2010). Until recently, carposporangial (postfertilized females, thus gametangial) conceptacles were poorly known for the Sporolithales. Heydrich (1899) was the first author to provide a detailed account on carposporangial development in an unspecified species of *Sporolithon*. Since then, among the 23 extant species ascribed to the Sporolithales (Guiry and Guiry 2015) carposporangial material has only been described for seven, with three of those appearing since 2012 (Kaewsuralikhit et al. 2012, Maneveldt and van der Merwe 2012, Bahia et al. 2014). The

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few observations on carposporangial material are likely the reason for characters of this life stage never having been considered as diagnostic for the group.

During large-scale investigations on the Sporolithales from Brazil, we found carposporangial conceptacles on several rhodolith-forming species of *Sporolithon*. Analysis of these specimens as well as data available in the published literature gave us greater insight into carposporangial conceptacle structure at the ordinal level within the Corallinophycidae. Here, we propose characters related to the anatomy of mature carposporophytes that can be used as diagnostic features for the order Sporolithales.

MATERIALS AND METHODS

Carposporangial conceptacles of specimens morpho-anatomically identified (based on Verheij 1993, Bahia et al. 2011, Bahia et al. 2014) as *Sporolithon episporum* (M. Howe) E.Y. Dawson, *S. ptychoides* Heydrich and *Sporolithon* sp. were prepared for histological examination following the method by Maneveldt and van der Merwe (2012). All samples comprised rhodoliths collected by SCUBA diving.

All detailed carposporophyte descriptions and illustrations presented in the published literature for this order were examined and compared with the observations documented herein to determine whether a distinct mature carposporophyte anatomy occurred in all taxa of the Sporolithales. Comparable mature carposporophyte anatomy was documented for the following taxa: *Heydrichia cerasina* Maneveldt & E. van der Merwe (Maneveldt and van der Merwe 2012), *Heydrichia groeneri* Keats & Y.M. Chamberlain (Keats and Chamberlain 1995), *Heydrichia woelkerlingii* R.A. Townsend, Y.M. Chamberlain & Keats (Townsend et al. 1994), *Sporolithon durum* (Foslie) R.A. Townsend & Woelkerling (Townsend et al. 1995, Harvey et al. 2002), *Sporolithon episoredion* (W.H. Adey, R.A. Townsend and Boykins) Verheij (Verheij 1992), *S. ptychoides* (Kaewsuralikhit et al. 2012), *Sporolithon tenue* Bahia, Amado-Filho, Maneveldt & W.H. Adey (Bahia et al. 2014), and other undetermined *Sporolithon* species (Heydrich 1899). The fossil genera *Hemiphyllum* and *Kymalithon* were not included as carposporangial material for these taxa have not been reported. The mature carposporophyte anatomy of Sporolithales species was compared against representative taxa from the other three orders of the subclass Corallinophycidae for which detailed descriptions and illustrations were available (Table 1).

Conceptacle measurements follow Adey and Adey (1973). Typification data follow Woelkerling (1993); botanical descriptive terminology follows Stearn (2004); herbarium abbreviations follow Thiers (2015) (continuously updated).

RESULTS

Sporolithon episporum (M. Howe) Dawson 1960: 40. *Specimen examined*: Brazil, Bahia State, Salvador, Itapuã (12°58' 01" S, 38°22' 13" W), 15 m depth (RG Bahia & GM Amado Filho, 15.iii.2007, RB 547948). Voucher slides deposited in UWC as BR 09/45.

Observations: Carposporangial conceptacles were uniporate, crowded and protruded above the sur-

rounding thallus surface (Fig. 1A). Conceptacle chambers were 160–240 µm in diameter and 170–260 µm in height, with the roof composed of 10–12 layers of cells (Fig. 1A). Chamber floor was located 15–27 cells below the thallus surface. Central fusion cell was absent, and short, one-celled filaments that bear a terminal, oblong carposporangium that at maturity measured 83–111 µm in length and 20–35 µm in diameter, were dorsally distributed across the floor and walls of conceptacle chambers (Fig. 1, A and B).

Confluent thalli bearing carposporangial conceptacles and tetrasporangial sori were found on the same specimen RB 547948. This specimen showed all the features of *S. episporum* (sensu Verheij 1993) including: cells of adjacent filaments joined by both secondary pit connections and cell fusions with a ratio of 4:1; calcified compartments developed on an elongated basal cell layer, and old, empty tetrasporangial compartments that flaked off leaving only a scar(s) visible in the deeper parts of the thallus. Full identification and description of Brazilian *S. episporum* can be found in Bahia (2014).

Sporolithon ptychoides Heydrich 1897: 67–69. *Specimen examined*: Brazil, Espírito Santo State, Itapemirim, Itaipava (21°02' 55" S; 40°17' 49" W), 50 m depth (GM Amado-Filho, 17.vi.2006, RB 579171). Voucher slides deposited in UWC as BR 07/16.

Observations: Carposporangial conceptacles were uniporate and protruded above the surrounding thallus surface (Fig. 1C). Conceptacle chambers were 260–275 µm in diameter and 160–230 µm in height, with the roof composed of 6–8 layers of cells (Fig. 1C). Chamber floor was located 12–16 cells below the thallus surface. Central fusion cell was absent, and short, one-celled filaments that bear a terminal, oblong carposporangium that at maturity measured 90–117 µm in length and 12–25 µm in diameter, were dorsally distributed across the floor and walls of conceptacle chambers (Fig. 1, C and D).

Identification of the examined specimen was based on vegetative features that matched those presented for tetrasporangial specimens of *S. ptychoides* collected at the same sampling site and described in detail by Bahia et al. (2011) and Bahia (2014). These features included collectively: rhodolith-forming thallus with encrusting to warty growth-form; mature thallus with more than 20 cells layers in thickness, monomerous thallus construction; flared epithallial cells, and cells of adjacent filaments joined by both secondary pit connections and cell fusions with a ratio of 2:1, respectively.

Sporolithon sp. *specimen examined*: Brazil, Vitória-Trindade Chain, Davis Seamount (20°34' 36" S; 34°48' 23" W), 50 m depth (GM Amado-Filho, 11.ii.2011, RB 614603).

Observations: Carposporangial conceptacles were uniporate and protruded above the surrounding

TABLE 1. Extant genera of the orders Corallinales, Hapalidiales, and Rhodogorgonales with respective studies considered for comparison of the mature carposporangial anatomy against those known for the Sporolithales listed in the Materials and Methods section.

Order	Family	Subfamily	Genus	Reference(s) considered for the analysis	
Corallinales	Corallinaceae	Corallinoideae	<i>Alatocladia</i>	Murata and Masaki (1978), Akioka et al. (1981)	
			<i>Arthrocardia</i>	Johansen (1971)	
			<i>Bossiella</i>	Johansen (1973), Woelkerling et al. (2008)	
			<i>Calliarthron</i>	Johansen (1976)	
			<i>Chiharaea</i>	Johansen (1971)	
			<i>Corallina</i>	Murata and Masaki (1978)	
			<i>Ellisolandia</i>	Irvine and Chamberlain (1994) (as <i>Corallina elongata</i>)	
			<i>Jania</i>	Srimanobhas et al. (1990) (as <i>Cheilosporum spectabile</i>), Irvine and Chamberlain (1994)	
			<i>Johansenia</i>	Not available	
			<i>Masakiella</i>	Perestenko (1994)	
			Mastophoroideae (sensu lato Harvey et al. 2003)	<i>Hydrolithon/ Porolithon</i>	Maneveldt (2005), Harvey et al. (2006)
				<i>Lesueuria</i>	Woelkerling and Ducker (1987)
				<i>Lithoporella</i>	Turner and Woelkerling (1982)
		<i>Mastophora</i>		Keats et al. (2009)	
		<i>Metamastophora</i>		Woelkerling (1980)	
		<i>Neogoniolithon</i>		Penrose (1992), Kato et al. (2013)	
		<i>Pneophyllum</i>		Penrose and Woelkerling (1991), Chamberlain (1994), Harvey et al. (2006)	
		<i>Spongites</i>		Penrose (1991)	
		Lithophylloideae		<i>Amphiroa</i>	Riosmena-Rodríguez and Siqueiros-Beltrones (1996)
				<i>Ezo</i>	Adey et al. (1974)
			<i>Lithophyllum/ Titanoderma</i>	Woelkerling and Campbell (1992), Harvey et al. (2009)	
			<i>Lithothrix</i>	Borowitzka (1978)	
			<i>Paulsilvella</i>	Torrano-Silva et al. (2014)	
<i>Tenarea</i>	Johansen (1976)				
<i>Austrolithon</i>	Harvey and Woelkerling (1995)				
Hapalidiales	Hapalidiaceae	Austrolithoideae	<i>Boreolithon</i>	Not available	
			<i>Epulo</i>	Townsend and Huisman (2004)	
			Choreonematoideae	<i>Choreonema</i>	Woelkerling (1987)
				<i>Clathromorphum</i>	Lebednik (1977)
				<i>Exilicrusta</i>	Chamberlain (1992)
			Melobesioideae	<i>Kvaleya</i>	Adey and Sperapani (1971)
				<i>Lithothamnion</i>	Wilks and Woelkerling (1995), Harvey et al. (2003)
		<i>Mastophoropsis</i>		Woelkerling (1988)	
		<i>Melobesia</i>		Lee (1970), Wilks and Woelkerling (1991)	
		<i>Mesophyllum/ Melyvonnea</i>		Woelkerling and Harvey (1993), Athanasiadis and Ballantine (2014)	
		<i>Phymatolithon</i>		Wilks and Woelkerling (1994), Van der Merwe and Maneveldt (2014)	
		<i>Synarthrophyton</i>		Maneveldt et al. (2007)	
		Rhodogorgonales	Rhodogorgonaceae	<i>Renouxia</i>	Fredericq and Norris (1995), Lewmanomont and Noiraksa (2010)
				<i>Rhodogorgon</i>	Ogden (1992), Fredericq and Norris (1995), Lewmanomont and Noiraksa (2010)

thallus surface (Fig. 1E). Conceptacle chambers were large, 800–850 µm in diameter and 540–630 µm in height, with the roof composed of 13–20 layers of cells (Fig. 1E). Chamber floor was located 30–45 cells below the thallus surface. Central fusion cell was absent, and short, one-celled filaments that bear a terminal, oblong carposporangium that at

maturity measured 135–210 µm in length and 30–50 µm in diameter, were dorsally distributed across the floor and walls of conceptacle chambers (Figs. 1, E and F).

Confluent thalli bearing carposporangial conceptacles and tetrasporangial sori were found on the same specimen RB 614603. This specimen was

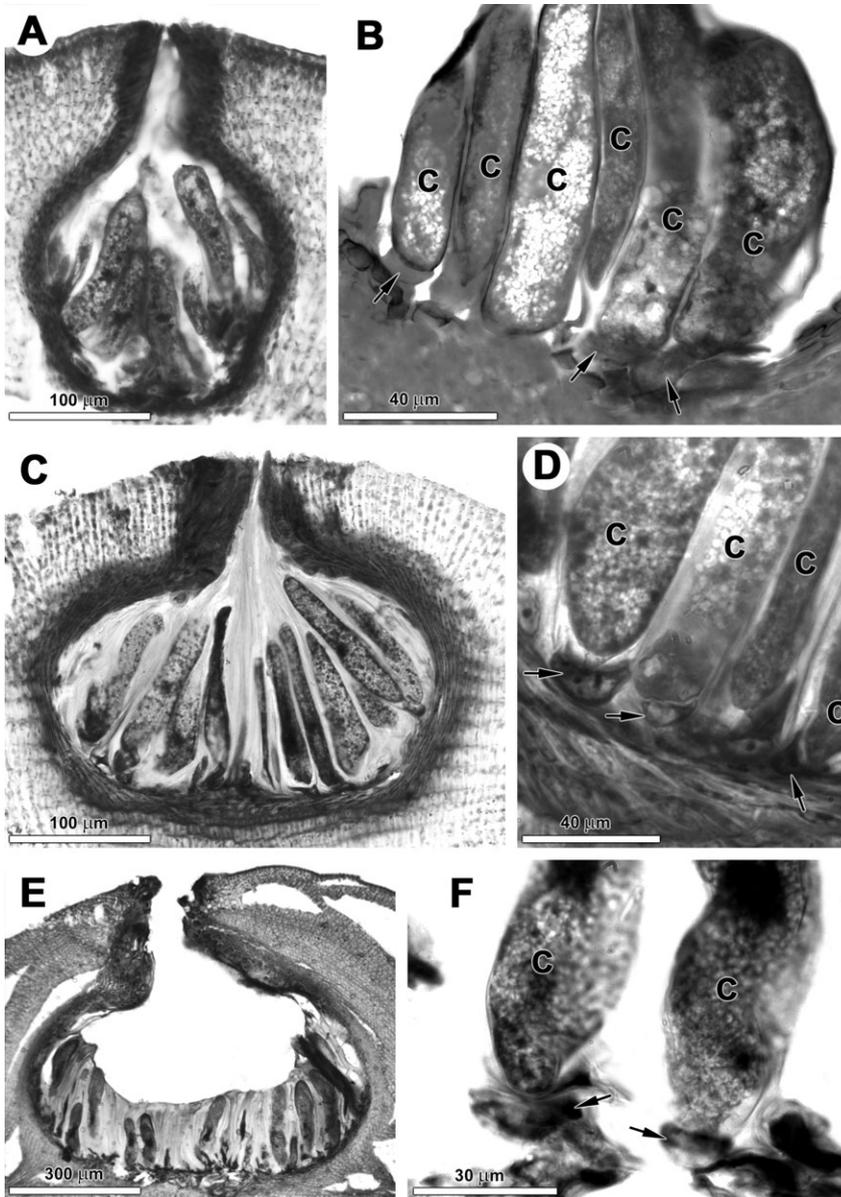


FIG. 1. Carposporangial conceptacle anatomy of three species of *Sporolithon*. (A) Longitudinal section through uniporate conceptacle of *S. episporum* showing oblong carposporangia distributed across floor and walls of conceptacle chamber (RB 547948). (B) Magnified view of carposporangial conceptacle of *S. episporum* showing one-celled filaments (arrows) that bear terminal oblong carposporangia (C). Note absence of central fusion cell (UWC RB 09/45). (C) Longitudinal section through carposporangial conceptacle of *S. ptychoides* showing oblong carposporangia distributed across floor and walls of conceptacle chamber (RB 579171). (D) Magnified view of carposporangial conceptacle of *S. ptychoides* showing one-celled filaments (arrows) that bear terminal, oblong carposporangia (C). Note absence of central fusion cell (RB 579171). (E) Longitudinal section through carposporangial conceptacle of *Sporolithon* sp. showing oblong carposporangia distributed across floor and walls of conceptacle chamber (RB 614603). (F) Magnified view of carposporangial conceptacle of *Sporolithon* sp. showing one-celled filaments (arrows) that bear terminal, oblong carposporangia (C). Note absence of central fusion cell (RB 614603).

identified as belonging to *Sporolithon* as it bore all the features attributable to the genus, including tetrasporangia cruciately divided and borne individually on a single stalk cell within calcified compartments. The determination of this specimen as *Sporolithon* sp. was supported by the combination of the following features: presence of a layer of elongate cells at the base of tetrasporangial compartments, shedding of senescent tetrasporangial compartments with only scars remaining visible in the deeper parts of the thallus, and tetrasporangia 140–180 μm in length (see Bahia et al. 2014, table 1 for a comparison with other *Sporolithon* species). Further investigations, including DNA sequence data, are required to determine if this specimen represents a species new to science.

DISCUSSION

The number of species from the Sporolithales with carposporophyte anatomy described in detail has doubled in the past 3 years. As a result of these recent descriptions (Kaewsuralikhit et al. 2012, Man-eveltdt and van der Merwe 2012, Bahia et al. 2014), as well as those presented herein (including the first record of a carposporangial phase for *S. episporum* and more structural details of carposporophytes for *S. ptychoides*), we now have a better understanding of the distinctive anatomy of the carposporophyte phase in Sporolithales.

The coralline algal orders (Corallinales, Hapalidiales, Sporolithales) all bear gametangia in uniporate conceptacles, whereas gametangia in the remaining

order of Corallinophycidae (Rhodogorgonales) develop on cortical fascicles (Le Gall et al. 2010, Nelson et al. 2015). Generally speaking, before fertilization, the structure of female (carpogonial) conceptacles in Corallinales, Hapalidiales, and Sporolithales are similar and no significant distinction has been reported at the ordinal level. In all these latter orders, carpogonial branches arise from across the conceptacle floor. Mature carpogonial branches are more or less bottle-shaped, consisting of a more or less cylindrical basal carpogonium that extends into a narrow upper trichogyne (Woelkerling 1988). Fully formed carpogonial branches in these orders usually consist of a carpogonium with extended trichogyne and a hypogynous cell that in turn is subtended by one to several supporting cells. Detectable taxonomic differences at ordinal level only appear to take place after fertilization. However, some observations in the pre fertilization development phase should be considered.

Among the few reports documenting prefertilized female conceptacles in Sporolithales (Heydrich 1899, Verheij 1992, Townsend et al. 1994, 1995, Cowan 1995, Harvey et al. 2002, Bahia et al. 2014), mature carpogonial branches were found to be two- to five-celled. Bahia et al. (2014) demonstrated in *S. tenue* that a two-celled filament bearing a carpogonium after fertilization results in a two-celled filament bearing a carposporangium. Similarly, illustrations by Heydrich (1899) (fig. 16) for an unspecified species of *Sporolithon* showed two-celled carpogonial branches that after fertilization result in two-celled filaments bearing a carposporangium that are derived from the remains of the hypogynous cell and the carpogonium (Heydrich 1899: fig. 27). Both studies demonstrated that the formation of the carposporangium occurs directly from the fertilized carpogonium. This pattern of carposporangium development was also observed in *S. episoredion* (Verheij 1992: figs. 13 and 16) and in *H. woelkerlingii* (Townsend et al. 1994). However, in *S. durum* (Townsend et al. 1995, Harvey et al. 2002) a greater number of cells comprising the carpogonial branch (2–5 cells) than in the corresponding filament bearing a carposporangium (one cell plus the carposporangium) has been observed. By all published accounts, irrespective of the number of cells in the carpogonial branch, the postfertilization filaments bearing a carposporangium in Sporolithales comprises of no more than two cells (excluding the terminal carposporangium). In contrast, fertilization of the mostly two-celled carpogonial branches in Corallinales and Hapalidiales (Silva and Johansen 1986), and in Rhodogorgonales (Fredericq and Norris 1995) resulted in filaments bearing a carposporangium that are several-celled (Table 1).

Irrespective of the number of cells in the prefertilized carpogonial branch, in contrast to Corallinales and Hapalidiales, a postfertilization central fusion cell does not appear to develop in either of

the extant Sporolithales genera *Heydrichia* (Townsend et al. 1994, Keats and Chamberlain 1995, Maneveldt and van der Merwe 2012) or *Sporolithon* (Heydrich 1899, Townsend et al. 1995, Harvey et al. 2002, Kaewsuralikhit et al. 2012, Bahia et al. 2014, this study). Although Verheij (1992: 503) reported that “fusion cells are not conspicuous” in *S. episoredion*, Verheij’s (1992) (fig. 16) image depicting these inconspicuous fusion cells is vague and appears to rather depict either a flattened cell from the remains of a modified carpogonial branch or one of the flattened conceptacle floor support cells. Except for this probably incorrectly reported comment (Verheij 1992), no central fusion cell has been reported for any species of Sporolithales.

The pattern of carposporophyte development in Corallinales is generally consistent with that found in Hapalidiales (Table 1). In the Corallinales (which then included the Hapalidiaceae), as suggested by Silva and Johansen (1986), formation of the fusion cell presumably requires only a single fertilization that results in the partial fusion of the fertilized carpogonium with its hypogynous and/or supporting cells. Whether more than one fertilization is effected in each conceptacle is not known, although Penrose (1992; fig. 27), showed what could be two fertilized carpogonia in a conceptacle of *Neogoniolithon* (Corallinales). Probably one or several zygotic nuclei are produced when fertilization occurs. One or more of these nuclei or their derivatives migrates to the subtending supporting cell that may be considered the auxiliary cell (Johansen 1981). The migration of diploid nuclei into supporting cells probably stimulates these cells to fuse with neighboring supporting cells (Johansen 1981). This process then proceeds to include the supporting cells of adjacent unfertilized carpogonial branches as observed for the genus *Metamastophora* by Woelkerling (1980). The resultant diploid zygote nucleus then presumably divides mitotically to make multiple copies of itself that are transferred into the developing fusion cell below (Woelkerling 1980). Sections through fusion cells reveal numerous nuclei, and it has been suggested that both large diploid nuclei as well as small haploid nuclei are included in these cells (Johansen 1981). However, information on diploid zygote nuclear divisions and transfer of the nuclei in Corallinales and Hapalidiales is still hypothetical and requires further investigation.

As additional supporting cells become incorporated, the fusion cell grows progressively larger and extends across much of the conceptacle chamber floor (Woelkerling 1980). Depending on the degree of incorporation of adjoining supporting cells and/or likely the number of fertilized carpogonia, the fusion cell may be conspicuously solid (e.g., *Lithophyllum riosmenae*, Harvey et al. 2009), discontinuous (e.g., *Phymatolithon acervatum*, Van der Merwe and Maneveldt 2014) or even inconspicuous (e.g.,

Phymatolithon repandum, Wilks and Woelkerling 1994). In most genera of the subfamilies Corallinoideae, Mastophoroideae (sensu lato Harvey et al. 2003) and Lithophylloideae of the order Corallinales, a conspicuously solid fusion cell covers nearly the entire fertile area at the base of the carposporangial conceptacle chamber (Lebednik 1977, Johansen 1981). In these taxa the fusion cell is an amalgamated product of only the supporting cells. In most genera of the subfamily Melobesioideae of the order Hapalidiales, a discontinuous fusion cell or several small fusion cells have been reported in which only supporting cells fuse together (Adey and Sperapani 1971, Johansen 1981, Wilks and Woelkerling 1995). In some species of *Clathromorphum* and *Mesophyllum* (Melobesioideae) cortical cells below the supporting cells often also become incorporated into the fusion cell (Lebednik 1977). Despite the observable differences among these taxa, the character of continuous versus discontinuous fusion cell should be considered with caution. The problem here arises in that most of the older literature only included drawings of the fusion cell and did not make the distinction between continuous and discontinuous fusion cells. Even in much of the more recent literature, the state of the fusion cell (continuous vs. discontinuous) is still not reported, but the incorporation of digital microscope images (instead of drawings) have allowed this distinction to be made in hindsight. For example, there are a number of species of *Lithophyllum* (e.g., Harvey et al. 2009) in which the authors did not comment on the type of fusion cell, but their images clearly show a discontinuous central fusion cell, rather than the supposed continuous fusion cell previously reported for the Lithophylloideae by Lebednik (1977). We suspect that completely continuous (solid) fusion cells probably are rare in nature as this would require the incorporation of every single supporting cell of adjacent unfertilized carpogonial branches into the fusion cell. The lack of complete amalgamation of all supporting cells is probably the reason why breaks in the fusion cell are observed when multiple sequential sections through carposporangial conceptacles are made (GW Maneveldt, pers. obs).

It is presumed that the multiple diploid zygote nuclei most often spread laterally within the fusion cell to produce gonimoblast filaments that arise from the margins of the fusion cell (e.g., *Spongites fruticulosus*, Penrose 1991). Alternatively the zygote nuclei produce gonimoblast filaments superficially across the dorsal surface of the fusion cell such as observed in Neogoniolithoideae (e.g., Penrose 1992, Kato et al. 2011, 2013). Detailed descriptions of the postfertilization events and fusion cell formation can be found in Lebednik (1977), Woelkerling (1980), Turner and Woelkerling (1982) and Johansen (1981). Incidentally, although rare, the absence of a fusion cell has been reported for some species from the Hapalidiales (e.g., *Melobesia mediocris*, Lee

1970). In these cases, further studies may reveal that several small fusions do indeed exist. See Lebednik (1977) (table 3) for a summary of the occurrence of fusion cells in the coralline algae.

In the Sporolithales, formation of the carposporangium appears to be directly from the fertilized carpogonium, i.e., the fertilized carpogonium (zygote) becomes the carposporangium (Townsend et al. 1995). Under this scenario, multiple carposporangia can only result from multiple fertilization events. Only some stages in carposporangium formation have been observed for the Sporolithales; further studies are therefore required to confirm carposporangium formation. Lebednik (1977) hypothesized that the production of multiple carposporangia, each from a single separate fertilization event, was an ancestral character. Selection in favor of the formation of greater numbers of carposporangia, needing only a single fertilization event, may initially have led to small scale fusions between the fertilized carpogonium and the adjacent unfertilized carpogonial branches as currently observed in some Hapalidiales (e.g., *Phymatolithon acervatum*, Van der Merwe and Maneveldt 2014), to a more complex and continuous (solid) fusion cell as observed in some Corallinales (e.g., *Lithophyllum riosmenae*, Harvey et al. 2009). This hypothetical evolutionary process is in accordance with the order of appearance of the different coralline algal orders in the fossil record (Aguirre et al. 2010), from the absence of a fusion cell in the oldest order Sporolithales (~130 Ma) to the formation of a mostly discontinuous fusion cell in the more recently derived Hapalidiales (~110 Ma), and a mostly continuous fusion cell in Corallinales (~60 Ma).

Silva and Johansen (1986) considered as a character of ordinal importance of the Corallinales (at that time covering what today is Corallinales, Hapalidiales, and Sporolithales) that postfertilization events involve a cluster of procarpial (a checkered history of the term is provided by Silva and Johansen 1986) filament systems. The resulting carposporophyte was termed a “syncarpium,” implying a compound nature, by which there is the involvement of numerous auxiliary cells rather than multiple fertilizations (Silva and Johansen 1986). However, this condition, now known to be present in the Corallinales and Hapalidiales, cannot be confirmed for the Sporolithales as no auxiliary cells are present in the latter order. Instead, as discussed above, carposporangia likely result from multiple fertilizations. Whereas in Corallinales and Hapalidiales, supporting cells of carpogonial branches function as auxiliary cells in postfertilization development, we hypothesize that supporting cells in Sporolithales function only as a subtending or possibly nutritive role to the developing carpogonial branch.

Carposporangium-bearing filaments of Sporolithales are short, formed by one or two cells

Rhodogorgonales has not been reported for the Sporolithales, Corallinales or Hapalidiales.

We emend the circumscription of the Sporolithales as follows.

Sporolithales L. Le Gall & G.W. Saunders, 2010: 305; emendavit Bahia, Amado-Filho, Maneveldt & Yoneshigue-Valentin

Type family: Sporolithaceae Verheij 1993: 195.

Type species: *S. ptychooides* Heydrich 1897: 67–69

Sporolithales, with the characteristics of the Corallinophycidae (Le Gall and Saunders, 2007); differs from other orders (Corallinales, Hapalidiales, Rhodogorgonales) in producing tetrasporangia singly within calcified sporangial compartments, in having tetrasporangia that undergo cruciate cleavage, in having carposporangial conceptacles that lack a central fusion cell, in bearing short (one to two-celled) filaments that bear a terminal carposporangium that are distributed across the conceptacle chamber floor and walls, and in possessing oblong carposporangia.

The characters considered of taxonomic significance within the Corallinophycidae are summarized in Table 2.

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