

TAXONOMIC CONSIDERATIONS OF THE GENUS RHODOPHYSEMA AND THE RHODOPHYSEMATACEAE FAM. NOV. (RHODOPHYTA, FLORIDEOPHYCIDAE)¹

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Recent investigations of *Rhodophysema*, together with a literature review of the Acrochaetiales-Palmariales complex, indicate that the genus *Rhodophysema* is not closely allied either with the Acrochaetiaceae or the Palmariaceae. Accordingly, a new family, Rhodophysemataceae, is proposed. In this treatment Rhodophysemataceae is differentiated from Acrochaetiaceae by the absence of a carposporophyte and monosporangia, presence of a unique sporangial stalk cell integral to the sexual cycle and an abundance of cellular fusions. Rhodophysemataceae is separated from Palmariaceae by the occurrence of B-phycoerythrin I, presence of *Rhodophysema*-like tetrasporangia and heteromorphic sexual life histories. To date the placement of *Rhodophysema* in the Acrochaetiales or Palmariales has been based either on vegetative morphology and phycoerythrin type or on interpretations of the evolution of the tetrasporangium and life-history type. Further evidence will be required to resolve the ordinal position of this new family. We, therefore, leave Rhodophysemataceae provisionally in the Palmariales while recognizing its uncertain taxonomic position within the Acrochaetiales-Palmariales complex. The Rhodophysemataceae may indeed warrant ordinal status as new taxonomic criteria become established. The genera *Coriophyllum*, *Halosaccicolax*, *Pseudorhododiscus* and *Rhodophysemopsis* are also discussed with respect to their taxonomic placement in the Acrochaetiales-Palmariales complex.

Des études récentes de *Rhodophysema* ainsi qu'une revue des oeuvres publiées du complexe Acrochaetiales-Palmariales démontrent que le genre *Rhodophysema* n'est pas apparenté de près à aucune ordre mentionnée ci-dessus. En conséquence on propose une nouvelle famille, Rhodophysemataceae. De cette façon les Rhodophysemataceae se différencient des Acrochaetiales par l'absence d'un carposporophyte et de monosporanges, ainsi que par la présence d'une seule cellule constituant la tige sporangique et faisant partie intégrante du cycle sexuel, et par une abondance de fusions cellulaires. Les Rhodophysemataceae se séparent des Palmariaceae par la présence de B-phycoérythrine I, de tetrasporanges ressemblant ceux de *Rhodophysema*, et par les développements hétéromorphiques. Jusqu'à présent l'incorporation de *Rhodophysema* dans les Acrochaetiales ou Palmariales a été fondée soit sur la morphologie végétative et le type de phycoérythrine soit sur les interprétations de l'évolution du tetrasporange et du type de cycle biologique. On a besoin de faits nouveaux pour résoudre le placement de cette nouvelle famille dans une ordre quelconque. Nous laissons alors les Rhodophysemataceae provisoirement avec les Palmariales tout en prenant conscience de leur position taxonomique incertaine dans le complexe Acrochaetiales-Palmariales. Il se peut bien que les Rhodophysemataceae méritent un rang ordinal quand de nouveaux critères taxonomiques deviendront établis. On discute aussi des genres *Coriophyllum*, *Halosaccicolax*, *Pseudorhododiscus*, et *Rhodophysemopsis* quant à leur placement taxonomique dans le complexe Acrochaetiales-Palmariales.

Introduction

Kylin (1956) placed *Rhodophysema* Batters (1900) [as *Rhododerms* Crouan frat. ex J. Agardh (1851)] in the family Squamariaceae of the Cryptonemiales. This illegitimate family name was subsequently replaced by Peyssonneliaceae Denizot (1968). Denizot did not include *Rhodophysema* in his new family and left it *incertae sedis* in the

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Florideophycidae. Until recently, most authors either have followed Denizot or have placed *Rhodophysema* in the Peyssonneliaceae.

Guiry (1974) initially proposed the family Palmariaceae to include algae having generative sporangial stalk cells, in which female reproductive structures and the carposporophyte generation were unknown. *Palmaria* Stackhouse, *Halosaccion* Kützing and *Leptosarca* Gepp & Gepp were transferred to Palmariaceae which was retained in the Rhodymeniales. Ganesan and West (1975) suggested that *Rhodophysema elegans* (Crouan frat. ex J. Agardh) P. Dixon be included in the Palmariaceae, as only male and tetrasporangial plants had been reported. In contrast, South and Whittick (1976) suggested that *Rhodophysema* was atypical of Palmariaceae owing to the lack of morphologically distinct stalk cells. Guiry and Irvine (Guiry, 1978) later raised the Palmariaceae to ordinal status. van der Meer and Todd (1980) observed microscopic crusts with sessile carpogonia in cultures of *Palmaria palmata* (Linnaeus) Stackhouse and demonstrated the presence of a type of sexual cycle which lent support to the ordinal status for Palmariales. Subsequently, *Rhodophysema odonthaliae* Masuda & Ohta (as *R. elegans*) was noted as possessing generative stalk cells and sessile carpogonia and was placed in the Palmariaceae, Palmariales by DeCew and West (1982). The type of sexual life history which they reported has been confirmed for Atlantic isolates of *R. elegans* (Saunders et al., 1989), but the proposed homology of the diploid *Rhodophysema*-stalk cell with the morphologically distinct stalk cell of *Palmaria* remains speculative. Silva (1982) disagreed with the placement of *Palmaria* and *Rhodophysema* in the same family or even in the same order. Rather he regarded the putative loss of both tetrasporophyte and carposporophyte in *Rhodophysema* as being a major phylogenetic shift compared to the loss of only the carposporophyte in the Palmariales. Hawkes and Scagel (1986) placed *Rhodophysema* provisionally in the Palmariales and suggested that the genus warranted establishment of a separate family regardless of ordinal position.

Magne (1982) suggested that new taxonomic criteria were required to clarify the affinities of the *Rhodophysema* life history and the taxonomic placement of *Rhodophysema*. Glazer et al. (1982) placed *Rhodophysema* in Acrochaetiales Feldmann (1953, see Garbary and Gabrielson, 1987) based on the presence of B-phycoerythrin. Guiry (1987) strongly opposed placement of *Rhodophysema* in the Acrochaetiales, arguing that the structure and reproduction of the type species, *R. georgii*, is similar to those of the Palmariales. Saunders and Bird (1989), however, did not find a sexual cycle for *R. georgii*, consistent with that of the Palmariales. We have found B-phycoerythrin I to be present in *R. georgii* (unpubl. observ.).

Similarities between Acrochaetiales and Palmariales have often been noted (e.g. Irvine and Guiry, 1983, DeCew and West, 1982, Guiry, 1987). DeCew and West (1982) proposed separating the two orders on the basis of uniseriate vegetative filaments and the absence of secondary pit-connections in Acrochaetiales. Guiry (1987) likewise reported the absence of secondary pit-connections and further noted an absence of cell fusions in the Acrochaetiales. Two exceptions, *Rhodochorton concrescens* Drew and *Rhodochorton spetsbergensis* (Kjellman) Kjellman, to these criteria will be considered in a future publication.

The Rhodophysemataceae fam. nov. is proposed to contain the genera *Rhodophysema*, *Halosacciocolax* Lund and *Rhodophysemaopsis* Masuda. Additional genera of uncertain affinity within this complex are discussed along with a consideration of the taxonomic affinities of Rhodophysemataceae within the Acrochaetiales-Palmariales complex.

Family Rhodophysemataceae fam. nov.

Thallus e filis uniseriatis compositus, aliis erectis aliis prostratis. Fila prostrata fusione cellularum coalescentia, plerumque discum basalem monostromaticum continuum

formantia. Fila erecta singulatim vel fasciculatim surgentia, saepe mucilagine lutinata vel fusione cellularum coalita, pseudoparenchyma formantia. Chloroplasti numerosi, parietales, taeniati vel disciformes, pyrenoidibus carentes, pigmento B-phycoerythrina praediti. Gametophytum monoecum, carpogonia sessilia et spermatangia geminata praebens. Tetrasporophytum continuo e carpogino fecundato ortum, maturum e tetrasporangio cruciatim diviso et cellula suffultoris constitutum. Propagatio non-sexualis bisporis vel tetrasporis mitotice formatis effecta. Galerum obturamenti inter-cellularis distromaticum.

Uniseriate filaments in erect and prostrate axes with prostrate axes adhering laterally by means of cell fusions usually forming a compact monostromatic base. Erect filaments arising individually or in clusters, sometimes becoming adherent and pseudoparenchymatous owing to cell fusions or mucilaginous envelopes or both. Chloroplasts parietal and ribbon-shaped or numerous and discoid; pyrenoids absent; B-phycoerythrin I present. Pit-plug with two cap layers. Gametophyte monoecious with sessile carpogonia and paired spermatangia. Fertilized carpogonium giving rise directly to the tetrasporophytic generation, *in situ* on the gametophytic generation, and consisting of a tetrasporangium subtended by a stalk cell exclusive of the sporangial wall. Asexual life history by formation of mitotic bisporangia or tetrasporangia.

Type genus: **Rhodophysema** Batters (1900, p. 377).

The description for this genus is given by Batters (1900), Irvine and Guiry (1983) and Hawkes and Scagel (1986). Saunders *et al.* (1989) have demonstrated that both sexual and asexual populations occur.

Type species: **Rhodophysema georgii** Batters (1900, p. 377).

This alga has B-phycoerythrin I (Saunders and McLachlan, unpubl.) and a direct life history by mitotic tetrasporangia (Saunders and Bird, 1989). Other species of *Rhodophysema* are discussed elsewhere (Saunders *et al.* 1989).

Other genera: *Rhodophysemopsis laminariae* Masuda (1976a) is composed of loosely adherent erect filaments arising from a compact basal disc. It is very similar to *Rhodophysema* and spermatangia are reported on plants containing *Rhodophysema*-like tetrasporangia. We believe that this species belongs in the Rhodophysemataceae.

Halosaccocolax kjellmanii Lund (1959) which has been variously placed in the Acrochaetiales (Cabiocch and Guiry, 1976) or Palmariales (Pueschel and Cole, 1982) appears to belong in the Rhodophysemataceae. Tetrasporangia seem to be *Rhodophysema*-like (Pueschel and Cole, 1982) and spermatangia are reported to occur on the same crusts as the tetrasporangia (Lund, 1959). Hawkes and Scagel (1986) suggested that this alga may have a *Rhodophysema*-type life history. This plant may (Hawkes and Scagel, 1986) or may not (DeCew, 1983) be the only genus in the family having secondary pit-connections. The ontogeny of connections with host cells requires reinvestigation before this point can be clarified.

Uncertain genera: *Pseudorhododiscus* Masuda (1976b) could be placed in the Rhodophysemataceae based on its original description. Masuda reported an absence of sterile filaments around tetrasporangia, but his figures show the presence of sterile filament-like structures (Masuda, 1976b: Figs. 2 & 3). These filaments may prove to be homologous to the sterile filaments commonly reported in Rhodophysemataceae and Palmariaceae. However, Masuda reported irregular or tetrahedrally divided tetrasporangia and separate male and tetrasporangial plants. This plant needs reinvestigation and may be related to the genus *Coriophyllum* Setchell & Gardner.

Coriophyllum Setchell & Gardner (1903) possesses two-layered pit-plug caps (Pueschel and Cole, 1982) and appears to be allied with the Palmariales. DeCew (1983) suggested that the life history of *C. expansum* is similar to that of *R. elegans*. Guiry (1987), however, described the life history as being intermediate between the *Rhodophysema*-type and the *Palmaria*-type. *C. expansum* has R-phycoerythrin

(Glazer et al. 1982), is vegetatively quite different from *R. elegans*, has a dioecious gametophytic generation and extensive tetrasporophyte development on the female gametophyte (DeCew, 1983). We conclude that *C. expansum* has its closest affinities with the Palmariaceae but requires reinvestigation and may, along with *Pseudorhododiscus*, belong in a new family. For now, *C. expansum* remains *incertae sedis* in the Palmariales as suggested by DeCew (1983).

Taxonomic Placement of the Rhodophysemataceae

We now consider the taxonomic placement of Rhodophysemataceae in relation to the families Acrochaetiaceae and Palmariaceae of the Acrochaetiales-Palmariales complex. The following characters, applicable to diagnoses of Acrochaetiales and Palmariales and Rhodophysemataceae, are discussed below: 1) vegetative morphology; 2) cell fusions and secondary pit-connections; 3) pit-plug ultrastructure; 4) phycoerythrin type; 5) tetrasporangial-type and presence of a generative stalk cell; 6) sessile carpogonia; 7) life-history type and apparent loss of tetrasporophytic and carposporophytic generations.

Vegetative morphology Filamentous Acrochaetiales have been traditionally separated from pseudoparenchymatous Palmariales. Rhodophysemataceae are pseudoparenchymatous, suggesting affinities with Palmariales. However, it is difficult to determine whether the pseudoparenchymatous condition in Rhodophysemataceae is homologous or analogous to that in Palmariales. Reports of intercalary divisions in *Coriophyllum* (DeCew, 1983) and *Rhodophysema* (Saunders et al., 1989) require further investigation.

Cell fusions and secondary pit-connections Occurrence of cell fusions and secondary pit-connections has not previously provided a satisfactory basis for separating Acrochaetiales from Palmariales despite claims to the contrary (e.g. DeCew and West, 1982). Cell fusions have been reported in *Rhodochorton spetsbergensis* and *R. conrescens* (Acrochaetiaceae) and in the Palmariaceae and Rhodophysemataceae. Acrochaetioid algae that exhibit cell fusions are probably related to the Rhodophysemataceae. With the removal of the anomalous species (to be proposed in a future publication), cell fusions become a useful character for distinguishing Acrochaetiaceae from Rhodophysemataceae and Palmariaceae. Cell fusions have probably evolved numerous times in the red algae and this feature does not, in itself, imply close phylogenetic relationships between Rhodophysemataceae and Palmariaceae.

Algae placed in the Acrochaetiales are reported to lack secondary pit-connections (Guiry, 1987), although reported for one species of Palmariales, *Halosaccion americanum* I.K. Lee (Mitman and Phinney, 1985). One of us (GWS) has reinvestigated the *H. americanum* preparations of Mitman and Phinney and observed no evidence of secondary pit-connections, although an abundance of cell fusions was noted. Indeed, all reports of secondary pit-connections may be erroneous for non-parasitic Palmariales. Pueschel (1988) has suggested that algae having two-layered pit-plug caps lack secondary pit-connections and can be separated from a larger group of florideophycean algae based on this combination of characters. Garbary et al. (1983) noted an exceptional case of a secondary pit-connection in the Acrochaetiales, but did not elucidate the ontogeny of the structure and this too may represent a cell fusion. *Halosaccicolax* Lund and *Neohalosaccicolax* Lee & Kurogi were placed in Acrochaetiales and Palmariales respectively owing to the presence of secondary pit-connections in *Neohalosaccicolax* (DeCew, 1983) and their absence in *Halosaccicolax*. This requires clarification as pit-connections between parasite and host cells are included in the description of *Halosaccicolax* (see Hawkes and Scagel, 1986). The ontogeny of connections between *Halosaccicolax* and host cells must be elucidated to determine if these are indeed homologous to those reported for *Neohalosaccicolax* and its host, and whether connections observed in these algae are homologous

to secondary pit-connections observed in the remainder of the Florideo-phycidae.

We consider that the Acrochaetiales and Palmariales are separable, based on the occurrence of cell fusions in only the Palmariales, pending taxonomic placement of the Rhodophysemataceae. Further, we believe that the Acrochaetiales lack, and the Palmariales may lack secondary pit-connections except for analogous structures that link parasite to host tissue. This problem has been discussed recently by Pueschel (1988).

Pit-plug ultrastructure Pueschel and Cole (1982) observed two-layered pit-plug caps in *Palmaria*, which they interpreted as being characteristic of the Palmariales. *Rhodophysema* and *Halosacciocolax* were placed in the Palmariales owing to the presence of pit-plug cap layers similar to those in *Palmaria* (Pueschel and Cole, 1982). However, they also reported two-layered pit-plug caps in Acrochaetiales which they described as being similar in both morphology and development to those in Palmariales. Therefore, this character cannot currently be used for separating Acrochaetiales from Palmariales and does not affect placement of the Rhodophysemataceae.

Phycoerythrin type *Rhodophysema* was placed in Acrochaetiales owing to the presence of B-phycoerythrin observed in *R. elegans*, compared to the Palmariales which possess R-phycoerythrin (Glazer et al., 1982). Guiry (1987) correctly noted that *Rhodophysema* can be moved to the Acrochaetiales only on the basis of features observed in the type species. We investigated *R. georgii*, the type species of *Rhodophysema*, and confirmed the presence of B-phycoerythrin I (unpubl. observ.). Rhodophysemataceae is characterized solely by B-phycoerythrin, as reported for two species of *Rhodophysema*, while Palmariaceae exclusively exhibits R-phycoerythrin (Glazer et al., 1982). The Acrochaetiaceae includes species with either B- or R-phycoerythrin. It is our view that phycoerythrin will eventually prove invaluable for infraordinal classification within Acrochaetiales, probably leading to the establishment of additional families.

Tetrasporangial type Two distinct tetrasporangial types, traditionally recognized in the Acrochaetiales-Palmariales complex, are referred to as the Acrochaetiales-type and the Palmariales-type, the latter probably having evolved from the former (Guiry, 1978). In the Acrochaetiales-type a stalk cell external to the sporangial wall divides, with the terminal daughter cell developing into a primary tetrasporocyte or, if secondary, enlarging within the sporangial wall to form a secondary tetrasporocyte. Repeated tetrasporocyte formation results in continued accumulation of successive wall layers (Hawkes and Scagel, 1986). In the Palmariales-type, the initial divides unequally, yielding a smaller generative stalk cell and a larger terminal tetrasporocyte (Guiry, 1978). Regeneration occurs by growth of the stalk cell into the space occupied by the original sporangial wall, followed by an unequal division. As a result, wall accumulation does not occur and the sporangial wall encloses the stalk cell and tetrasporocyte (Pueschel, 1979). This latter type occurs exclusively in the Palmariaceae. Guiry (1987) suggested that the Acrochaetiales-type stalk cell is the least specialized and is morphologically similar to a vegetative cell.

Based on our recent observations in *Rhodophysema* (Saunders and Bird, 1989; Saunders et al., 1989) we consider tetrasporangia in the Rhodophysemataceae to be different from either of the two previous types as the stalk cell is diploid in sexual populations with a homologous structure present in asexual populations. The presence of intercalary stalk cells and the similarity of stalk cells to vegetative cells in the asexual populations may explain the reported absence (Hawkes and Scagel, 1986) of this structure in some species of *Rhodophysema* (see Saunders and Bird, 1989).

Tetrasporangia of *Rhodophysema*, like those of the Acrochaetiales, are distinct from the Palmariales-type in that the generative stalk cell is external to the sporangial wall and sporangial wall accumulation occurs only in the former (Guiry, 1978; 1987; Hawkes and Scagel, 1986; Poeschel, 1979). G. Mitman (*in verb.*), however, noted an accumulation of sporangial walls in *Halosaccion americanum*, which was confirmed (GWS) by a re-examination of his slides. Nevertheless, both the generative stalk cell and the tetrasporocyte were enclosed within the sporangial wall. In view of Mitman's observations, the only distinguishing character separating tetrasporangia of Acrochaetiales and *Rhodophysema* from those of Palmariales is the inclusion of the generative stalk cell within the tetrasporangial walls in the Palmariales. We consider these three tetrasporangial types as being distinct and useful characters for separating the three families.

Sessile carpogonia Sessile carpogonia are considered to have limited taxonomic value. They are present in Acrochaetiales, Palmariales and Rhodophysemataceae, and as they do not delineate the two orders they cannot be used to determine ordinal placement of Rhodophysemataceae. Although not restricted to these taxa, sessile carpogonia appear to represent an ancestral character and may be useful for recognizing taxa little evolved from the ancestral line of the Florideophycidae.

Life history type and putative loss of carposporophytic or tetrasporophytic generation Life histories are basically isomorphic in Palmariales and both heteromorphic and isomorphic in the Acrochaetiales (Gabrielson and Garbary, 1987). In reality the distinction is less pronounced as a variety of life history patterns occur in the Acrochaetiales: 1) triphasic *Polysiphonia*-type as exemplified by *Colaconema botryocarpa* (see Woelkerling, 1970); 2) an analogue of the *Rhodophysema*-type (see diagnosis) in *Rhodochorton subimmersum* Setchell & Gardner (Lee and Kurogi, 1978); 3) an analogue of the *Palmaria*-type (van der Meer and Todd, 1980) in *Rhodochorton purpureum* (Lightfoot) Rosenvinge and *Rhodothamniella floridula* (Dillwyn) J. Feldmann (Stengenga, 1978). The *Polysiphonia*-type life history in the Acrochaetiales is distinct from the *Rhodophysema* and *Palmaria* analogues. Magne (1982) suggested that the *Rhodophysema* and *Palmaria* patterns represented either phylogenetic relatedness or evolutionary convergencies. Whether the *Rhodochorton* analogues are in fact homologous to the *Palmaria*- and *Rhodophysema*-types remains to be resolved. In any event, Magne was certain that both life histories were derived from the ancestral *Polysiphonia*-type. Magne's view reflects Feldmann's opinion (1952) that a triphasic life history with free-living isomorphic gametophytic, carposporophytic and tetrasporophytic generations was primitive.

West and Hommersand (1981) were uncertain whether biphasic or triphasic life histories were primitive in the Florideophycidae. Guiry (1987) suggested that the biphasic life history noted in the Palmariales and the genus *Rhodophysema* evolved independently of other red algal life histories. He postulated that the ancestral red alga was biphasic and that evolution proceeded through two different modes of zygote amplification: 1) formation of a carposporophytic generation *in situ* on the female gametophyte; 2) the *Palmaria*-type life history. Hence, in Guiry's view, the carposporophyte was never a free-living generation. Guiry, further, was of the opinion that the *Palmaria*- and *Rhodophysema*-type life histories evolved from a biphasic ancestor, not from an alga with the *Polysiphonia*-type life history. Current life-history data are of only limited value for establishing phylogenetic relationships within the Acrochaetiales-Palmariales complex. Attempts to assign Rhodophysemataceae to either order based on life history is speculative and unsupported by factual evidence. All three families are

characterized asexually by the production of mitotic bisporangia and tetrasporangia; however, the production of monosporangia, although not ubiquitous, occurs solely in the Acrochaetiaceae.

Hawkes and Scagel (1986) proposed that algae having a *Rhodophysema*-type life history warrant recognition as a separate family. Silva (1982) remarked that the loss of both the tetrasporophytic and carposporophytic generations in *Rhodophysema* represented a major phylogenetic shift compared to the loss of only the carposporophyte in *Palmaria* and suggested that separate orders are justified.

Considering the evidence, we propose that Rhodophysemataceae; 1) has affinities with the Acrochaetiales-Palmariales complex; 2) is an assemblage distinct from the Acrochaetiaceae and the Palmariaceae; 3) can be placed only provisionally in the Palmariales on the basis of shared derived vegetative characters (which may or may not represent homology) and the lack of monosporangia; 4) that ordinal status may be required to represent the true phylogenetic affinities of the Rhodophysemataceae. We do not believe, that a new order is justified until additional taxonomic criteria are elucidated.

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