

A chronicle of the convoluted systematics of the red algal orders *Palmariales* and *Rhodymeniales* (Floriideophyceae, Rhodophyta)

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Introduction

A review of the taxonomic history and turmoil surrounding the red algal orders *Palmariales* and *Rhodymeniales* is presented. The text starts with an outline of the early history of the *Rhodymeniales* and travels through a progression of published taxonomic opinions on intraordinal relationships that led to recognition of *Palmaria* as a genus distinct from *Rhodymenia*, to a distinct family Palmariaceae, and ultimately to a new order, *Palmariales*. Although the *Palmariales* was generally well received, there was reluctance to accept that this new order was an ally of the putatively 'primitive' *Acrochaetiales* and *Nemaliales* rather than the 'advanced' *Rhodymeniales* and *Ceramiales* (*cf.* Guiry 1987). This uneasy paradigm shift forms a recurrent theme in the current review.

The focus then shifts from the *Palmariales sensu stricto* to consider a series of publications concerning the uncertain taxonomic position of *Rhodophysema*, variously considered a member of the *Gigartinales* (including *Cryptonemiales*), *Acrochaetiales*, and *Palmariales*. The resolution of this conundrum finds *Rhodophysema* positioned in a new family, Rhodophysemataceae, only provisionally included in the *Palmariales*. Following recognition of the Rhodophysemataceae, a more contentious debate ensued regarding the taxonomic affinities of anomalous species of the *Acrochaetiales*. In one case, that of *Rhodochorton spetsbergense* (Kjellman) Kjellman, a move to a new genus, *Meiodiscus*, was recommended with this genus transferred to the Rhodophysemataceae. *Rhodothamniella*, a second genus of the *Acrochaetiales* with affinities to the *Palmariales*, is then considered. Although a few phycologists of the time discussed the possibility of an alliance of this genus with the *Palmariales* rather than the *Acrochaetiales*, the controversial issues surrounding the phylogenetic affinities of this genus were not critically addressed until the modern tools of molecular biology were brought to bear on red algal systematics.

Molecular data were strong in their support of a monophyletic *Palmariales* that includes the Palmariaceae, *Meiodiscus* and *Rhodophysema* of the Rhodophysemataceae, and *Rhodothamniella*, which was assigned to its own family. Subsequent molecular work indicated that additional species, originally placed in *Ballia* of the *Ceramiales*, also required

transfer to the Rhodothamniellaceae. As a result, the contemporary Palmariales is a melting pot of species once considered so diverse that they were distributed among five of the six orders recognized by Kylin, but that are nevertheless united by commonality of their anatomical, ultrastructural, biochemical and molecular features. Ironically, included among the unifying features are aspects of the female reproductive structures and postfertilization development - the cornerstones of Kylin's taxonomic system. For all of the species currently included in the Palmariales, however, their life histories were not elucidated in Kylin's day, and some of the species are still only known to reproduce asexually. The palmarialean species were, therefore, distributed among the red algal orders on the basis of superficial vegetative similarities to species in families and orders whose life histories were known.

The review closes with a summary of intraordinal advancements in the Rhodymeniales *sensu stricto*. Although a few key manuscripts were published on this important aspect of red algal taxonomy, phylogenetic thought in this order had reached an impasse. Recent molecular investigations have breached the blockade and have certainly opened the doors to future challenges of intraordinal taxonomy in the Rhodymeniales.

Discussion

An early history of the Rhodymeniales

Rhodymeniales from inception to 1926

The Rhodymeniales was one of the original four orders proposed by Schmitz (1889) according to the patterns of zygote formation and subsequent development. Species included in this order were procarpic, i.e., the female gamete (carpogonium) is positioned in close proximity to the 'auxiliary cell' from which zygote development is ultimately initiated. Schmitz included six families, Bonnemaioniaceae, Ceramiaceae, Delesseriaceae, Rhodomelaceae, Rhodymeniaceae, and Sphaerococcaceae, in the Rhodymeniales. Schmitz's emphasis on aspects of female reproductive anatomy marked a fundamental redirection in red algal systematics, one that still exerts deserved influence on contemporary taxonomy and phylogenetic thought (Saunders & Kraft, 1997). Despite the immensity of his contribution, it was inevitable that time would witness modifications and improvements to the system that Schmitz presented more than a century ago.

Meticulous observation by Oltmanns (1904) resulted in the Bonnemaioniaceae, Ceramiaceae, Delesseriaceae and Rhodomelaceae being relocated to a new order, Ceramiales, because the auxiliary cells in some members (and by extension all) form only after, rather than before or in the absence of, fertilization. This left only the Rhodymeniaceae and Sphaerococcaceae in the Rhodymeniales.

Sjöstedt (1926) erected the Sphaerococcales for the Sphaerococcaceae and the genus *Plocamium*, which was until that time included in the Rhodymeniaceae. Species in this new order had the supporting cell of the carpogonial branch (the branch that bears the carpogonium) or the basal cell of this filament itself function as the auxiliary cell. For a comprehensive history of the Sphaerococcaceae as a member of the contemporary Gigartinales, the demise of the Sphaerococcales and the positioning of *Plocamium* in a new family, and subsequently a new order, the reader is referred to Saunders & Kraft (1994). Sjöstedt's 1926 account resulted in a relatively monophyletic Rhodymeniales containing the single family, Rhodymeniaceae, defined by auxiliary cells formed prior to or in the absence of fertilization and generally terminating a two-celled filament borne on the carpogonial branch supporting cell.

Establishing intraordinal classification: 1928-1957

Bliding (1928) confirmed the reproductive uniformity, in essence overall monophyly, of the Rhodymeniales as inherited from Sjöstedt. During his observations, Bliding recognized two natural groups of species in the Rhodymeniales and a second family, Champiaceae, was proposed. Species of the Rhodymeniaceae had solidly constructed thalli, or in the

case of a hollow medulla lacked longitudinal filaments lining the cavity, cruciate tetrasporangial division, three-celled carpogonial branches, and carposporophytes in which most gonimoblast cells differentiate as carposporangia. Species in the Champiaceae, on the other hand, had hollow thallus portions lined by longitudinal medullary filaments, tetrahedral tetrasporangial division, generally four-celled carpogonial branches, and usually only the terminal gonimoblast cells forming carposporangia. Bliding's familial distinctions held virtually unchanged until the 1970s, all efforts from 1928 to that time focused on intrafamilial levels of taxonomy.

Kylin (1931) provided additional observations for species of the Rhodymeniales and designated subfamilies for both the Rhodymeniaceae and Champiaceae. In the former he recognized the Faucheoideae (as Faucheeae), Hymenocladioideae (as Hymenocladieae) and Rhodymenioideae (as Rhodymeneae), whereas for the latter he had the Champioideae (as Champieae) and Lomentarioideae (as Lomentarieae). The Faucheoideae included species with terminal cruciate tetrasporangia and a distinctive network of filaments (*tela arachnoidea*) surrounding the mature carposporophyte, whereas species of the Hymenocladioideae lacked such filaments and had intercalary tetrahedral tetrasporangia. Diverse species lacking a *tela arachnoidea*, but with terminal cruciate tetrasporangia were lumped in the Rhodymenioideae. The Champioideae and Lomentarioideae differed by four versus three-celled carpogonial branches, terminal versus most gonimoblast cells forming carposporangia, intercalary scattered versus terminal tetrasporangia aggregated in sunken sori, and regularly spaced single-layered versus multilayered septa traversing the hollow medulla, respectively. In 1956, Kylin abandoned the formal taxonomic category of subfamily in favor of a number of informal groups. The only substantial change from his 1931 treatment was the segregation of three new groups from the Rhodymenioideae. For a detailed review see Saunders *et al.* (1999).

Sparling (1957): negating intrafamilial classification

Sparling (1957) reconsidered the work of Bliding and Kylin and, although she accepted the two families Rhodymeniaceae and Champiaceae, rejected their criteria to separate and subsequently subdivide the two families. Sparling argued that characters such as presence or absence of a *tela arachnoidea*, tetrasporangial division pattern, and carpogonial branch cell number were too ambiguous or variable to have taxonomic utility. In separating the Rhodymeniaceae from the Champiaceae Sparling considered vegetative construction to be the only useful feature. Species of the former were solid or if hollow lacked longitudinal filaments lining the cavities, whereas species of the latter were hollow with the cavities lined by longitudinal medullary filaments. Sparling additionally rejected the six groups of Kylin and recognized only the Rhodymenioideae (cruciate and terminal tetrasporangia) and Hymenocladioideae (tetrahedral and intercalary tetrasporangia) in the Rhodymeniaceae.

This was essentially where rhodymenialean taxonomy rested until the 1970s when two divergent paths of investigation emerged. The first challenged the implicit belief that the Rhodymeniales was largely monophyletic and ultimately led to the new and diverse order Palmariales. The second was a continued quest to define intraordinal taxonomy for the Rhodymeniales *sensu stricto*. These two directions form the themes for the two major sections of this manuscript.

I. Palmariales: origin, evolution and maturation of an order

Palmariaceae: initiating a paradigm shift

Kylin had largely codified red algal systematics by 1932 and recognized six orders in the Florideophyceae. The Nemaliales and Gelidiales lacked auxiliary cells and the carposporophyte was considered to develop directly from the fertilized carpogonium with the orders characterized by haplobiontic and diplobiontic life histories, respectively. The Nemaliales contained the Acrochaetiaceae, a family of filamentous reds whose simple vegetative construction and elementary reproductive features prompted Kylin to consider them the 'primitive' florideophytes (Fig. 1a).

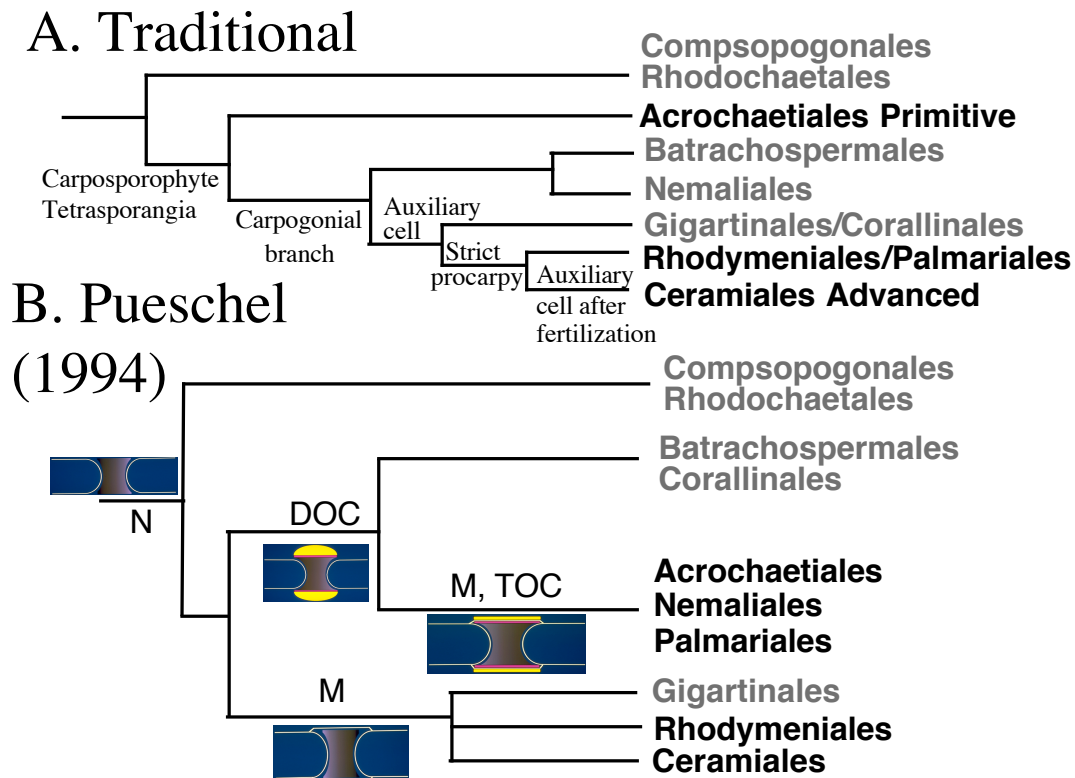


Fig. 1. Schematic representations of phylogenetic hypotheses for the Rhodophyta. A) A system derived from the views of Kylin with Florideophyceae evolving from the 'primitive' Acrochaetiaceae to the 'derived' Ceramiales. The origins of key reproductive features are noted along branches of the phylogram. B) An alternative system devised by Pueschel on the basis of pit-plug ultrastructure indicating the putative origin of pit plug associated features. N = naked pit plug condition; DOC = domed outer cap; TOC = thin outer cap; M = membrane.

The Cryptonemiales, Gigartinales and Rhodymeniales had generative auxiliary cells that were produced prior to, or in the absence of, fertilization. The Cryptonemiales was considered to have auxiliary cells formed in accessory filaments in contrast to the Gigartinales for which they were intercalary in normal vegetative filaments, whereas the Rhodymeniales had a characteristic procarpy with auxiliary cells terminating two or three-celled filaments borne on the carpogonial branch supporting cell. Finally, the Ceramiales were distinct in producing auxiliary cells from the carpogonial-branch supporting cell only after fertilization. This unique tactic for conserving resources led Kylin to speculate that the Ceramiales was the apogee of red algal evolution (Fig. 1a). Kylin's system faced few serious challenges in the subsequent 40 years, at least none that swayed the momentum of popular opinion. The proposals for revision are summarized by Saunders & Kraft (1997) and will not be reiterated here. Kylin's system worked so well for the majority of red algae that had been investigated to that point in time that it provided a logical and practical framework for the classification of the Florideophyceae. Regrettably, the comfort manifested from Kylin's system led to a universal acceptance and loyalty that impeded efforts for reform and improvement despite the accumulation of detailed investigations that challenged the classical model.

The tide of change was initiated with a seemingly minor revision by Guiry (1974), one that, in the opinion of this author, opened the doors to reform in red algal systematics. This strong statement derives from two perspectives: 1) Guiry proposed a taxonomic revision

that was not based on the axiomatic features of female reproductive anatomy and postfertilization; and, 2) he challenged the Rhodymeniales, an order whose monophyly seemed absolute considering the highly conservative nature of the procarp and postfertilization development. Guiry (1974) emphasized that certain species of the Rhodymeniaceae have tetrasporangia composed of a tetrasporocyte with a subtending generative stalk cell (Fig. 2). He also noted that these same species had an apparent absence of females in the field, only males and tetrasporophytes being reported. Guiry proposed a new family, Palmariaceae, for these anomalous species and included it only provisionally in the Rhodymeniales. Guiry (1978) later argued that there was little save cruciate tetrasporangia, a state reported for some species in all six of Kylin's orders, to ally the Palmariaceae to the Rhodymeniales, and the Palmariales Guiry et Irvine was proposed. Hence, the first order to disregard the system established by Schmitz (1889), and subsequently codified by Kylin (1932, 1956), entered red algal taxonomy.

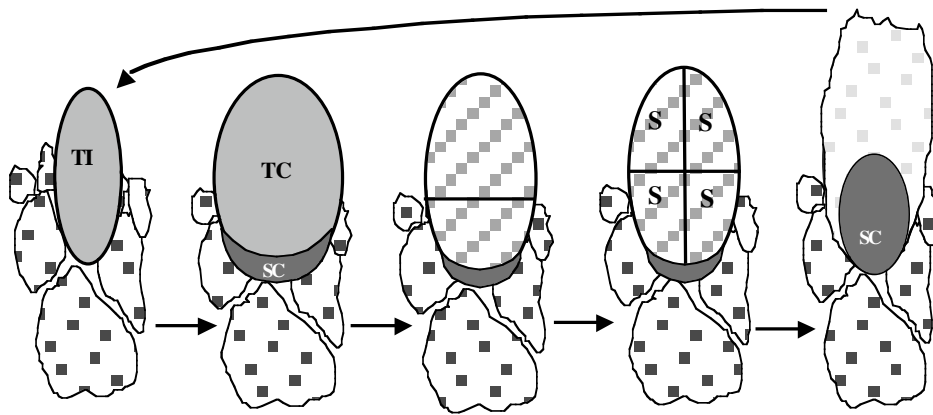


Fig. 2. Diagrammatic presentation of tetrasporangial development in species of the Palmariaceae. The tetrasporangial initial (TI) undergoes a mitotic division to yield a diploid tetrasporocyte (TC) and subtending stalk cell (SC). The tetrasporocyte then undergoes meiosis with subsequent cytokinesis to yield four haploid tetraspores (S) in a cruciate pattern. After the spores are released the stalk cell expands into the empty sporangial sheath to produce a new tetrasporangial initial.

Life history investigations: classical support for the Palmariales

Observations that provided Kylinian evidence for the Palmariales, viz., female reproductive anatomy and postfertilization development soon followed Guiry's proposal. Van der Meer & Todd (1980) published an important study outlining a new life history type for the Rhodophyta and solving the enigma of male and tetrasporophyte prevalence with contrasting female absence in the field for species of Palmariaceae (Fig. 3). The life history involves an alternation of isomorphic generations with reference to tetrasporophytes and

males, but with sexual dimorphism between the latter and the greatly reduced females. Tetraspores are released from sporangia on the erect blades of the tetrasporophyte generation and develop into small crustose females that become sexually mature within a few days to weeks of germination, as well as other crusts that produce erect blades that require many months to produce male gametangia (spermatangia). Female crusts produce sessile carpogonia (i.e., lacking a carpogonial branch) that are fertilized by spermatia (male gametes) from previously established males. The resulting zygote develops *in situ* on, and eventually overgrows, the diminutive female crust – the carposporophyte of a ‘typical’ florideophycean life history is completely absent. These observations provided unequivocal support for recognition of *Palmaria* as distinct from *Rhodymenia*, as well as for the familial and ordinal proposals of Guiry (1974, 1978).

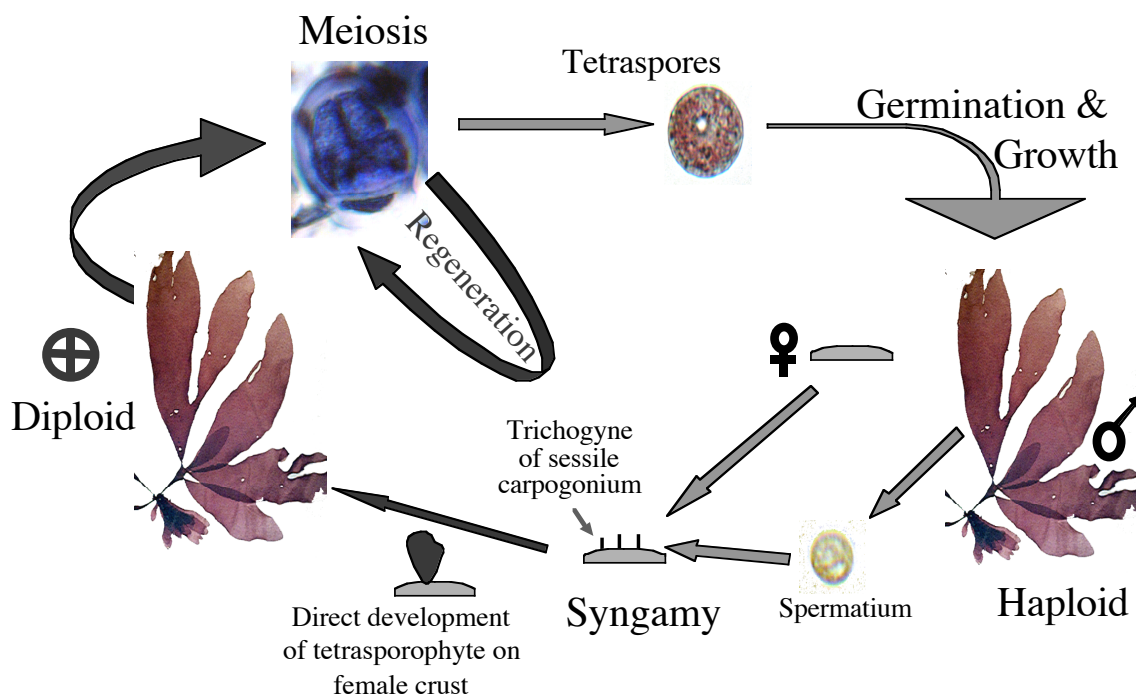


Fig. 3. Life history of the Palmariaceae. See text for a description of events.

Phylogenetic affinities of Palmariales

The life history results of 1980 were soon augmented by ultrastructural investigations. Pueschel & Cole (1982) observed that representatives of the Rhodymeniales had pit plugs covered at their cytoplasmic faces by a membrane, whereas species of the Palmariaceae had the membrane sandwiched between an inner and plate-like outer cap layer. Pueschel & Cole (1982) stated that “The number of plug cap layers ... (is)... a taxonomically reliable character when tested against a recent revision of the Rhodymeniales which established the order Palmariales”. In fact, a number of previous, largely rejected, taxonomic recommendations derived support from the pit plug data and completely new orders were proposed on this non-Kylinian feature (Pueschel & Cole, 1982; *cf.* Saunders &

Kraft, 1997). Pueschel & Cole's publication marked a major advance in the field of red algal systematics.

A further significant observation by Pueschel & Cole (1982) was that the Palmariaceae were characterized by pit plugs essentially identical to those found in representatives of the Acrochaetales and Nemaliales, and quite distinct from the Rhodymeniales and its allies in the Ceramiales and Gigartinales. Pueschel & Cole only briefly discussed this phylogenetic unorthodoxy, however, Pueschel (1994) later published a detailed phylogenetic scheme for the red algae (Fig. 1b). He posited, along with other hypotheses, that all orders whose species were characterized by two pit-plug cap layers shared a common ancestor. He further contended that the dome-like morphology of the outer cap layer, e.g., as in the Batrachospermales, was ancestral to the plate-like outer cap. In effect, this forced the Acrochaetales, Nemaliales and Palmariales into a close alliance as a recently derived group within the two cap-layer assemblage (Fig. 1b), a view in sharp contrast to the established system (Fig. 1a). Saunders & Bailey (1997, 1999) have tested the proposals of Pueschel (1994) and uncovered strong congruence between his proposals and phylogenies derived from small-subunit ribosomal DNA. All evidence unequivocally recognized the Palmariales as distinct and only remotely related to the parental Rhodymeniales, as well as resolving the former as a close ally to the Acrochaetales and Nemaliales (Fig. 1b).

Palmariales: expanding an ordinal concept

An additional observation of Pueschel & Cole (1982) is pertinent to the current discussion. They reported that *Rhodophysema* ssp. have pit plugs equivalent to those characteristic of the Palmariales and should be transferred to this order from the Gigartinales (as Cryptonemiales) where they were included with a diverse assortment of other red crusts in the Peyssonneliaceae. The uncertainty surrounding the taxonomic affinities of *Rhodophysema* relative to the Palmariaceae started with the life history investigations of Ganesan & West (1975). Ganesan & West noted that tetrasporophytes in culture reproduced only via mitotic tetrasporangia, and reviewed literature that indicated that only males and tetrasporophytes occurred in the wild for species of this genus. This was reminiscent of the Palmariaceae *sensu* Guiry (1974), or previous to the work of van der Meer & Todd (1980). Ganesan & West argued for a transfer of *Rhodophysema* to the Palmariaceae, which was still tentatively positioned in the Rhodymeniales. Considerable disagreement followed, notably, South & Whittick (1976) considered that tetrasporangia in *Rhodophysema* ssp. lacked the diagnostic generative stalk cell of the Palmariaceae (Fig. 2). Debate followed in the literature as to the presence or absence of stalk cells in *Rhodophysema* and, in the event of the former, whether such stalk cells were analogues or homologues of structures in the Palmariaceae. *Rhodophysema* was generally retained in the Gigartinales for lack of a better taxonomic repository and because inclusion of this genus from the Gigartinales in the same order, let alone family, as *Palmaria* seemed at that time absurd (*cf.* Silva, 1982).

DeCew & West (1982) completed life history investigations for a species of *Rhodophysema* (*cf.* Saunders *et al.*, 1989) from the Northeast Pacific (Fig. 4). The results of this study had an impact on *Rhodophysema* systematics equivalent to that manifested by life history observations in *Palmaria* (van der Meer & Todd, 1980). Prior to the work of DeCew & West, *Rhodophysema* was regarded as a presumably tetrasporophytic crust recycling itself by mitotic bisporangia and/or tetrasporangia with gametophytes absent in the field (Ganesan & West, 1975; South & Whittick, 1976; *cf.* Saunders *et al.*, 1989). The crustose phase, however, was recognized as a monoecious gametophyte with male gametes released from spermatangia [these had been observed earlier, but were afforded no significance in the life history of this genus, *cf.* Saunders *et al.* (1989)] eventually adhering to the trichogynes of sessile carpogonia. The resultant zygote then initiated development directly from the remnant carpogonium (i.e., no auxiliary cell) by undergoing a single mitotic division to produce a larger, diploid tetrasporocyte initial subtended by a smaller generative

stalk cell (DeCew & West, 1982). The tetrasporocyte then enlarged and underwent meiotic division with cytokinesis to form four haploid tetraspores. The released spores germinated to establish the monoecious crustose gametophyte generation. The generative stalk cell would then enlarge through the evacuated tetrasporangial sheath, undergo a mitotic division, and thus generate a new tetrasporocyte initial subtended by a smaller generative stalk cell (Fig. 4).

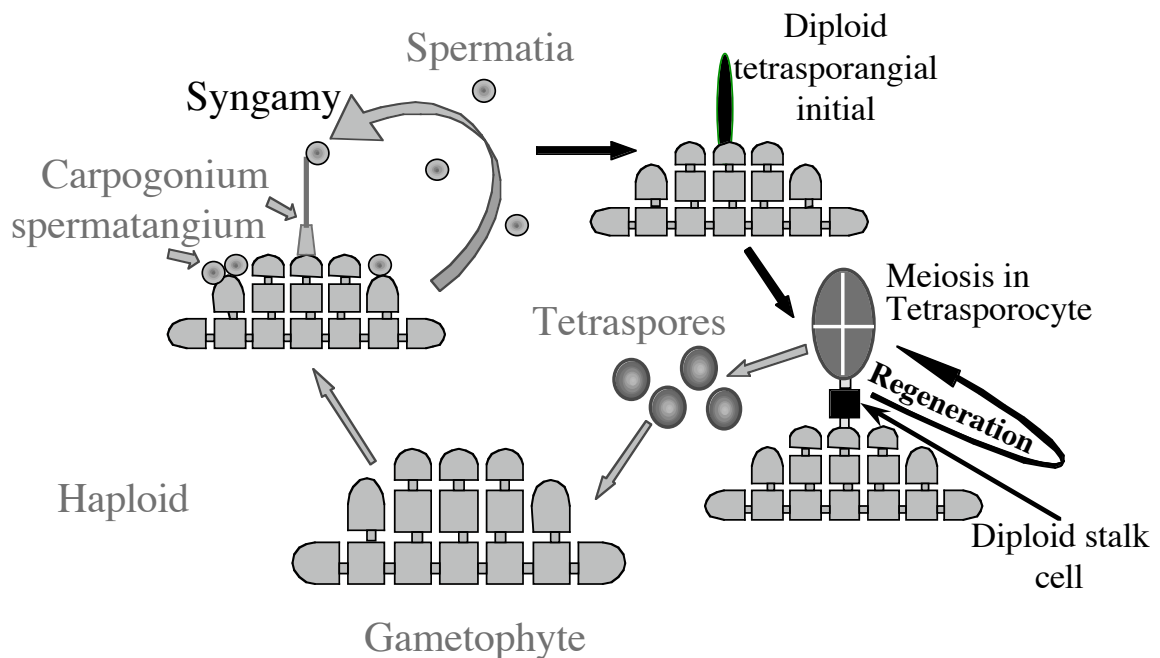


Fig. 4. Life history of the Rhodophysemataceae. See text for a description of events.

Again a new life history was uncovered for the Florideophyceae (lacking both carposporophytes and tetrasporophytes), one considered by DeCew & West to be related to the Palmariaceae type rather than the 'typical' florideophycean type. DeCew & West suggested that *Rhodophysema* should be included in the Palmariaceae by displaying sessile carpogonia and generative stalk cells, and for the absence of the carposporophyte generation in the life history, a view argued forcefully by Guiry (1987). Their taxonomic conclusions were in agreement with those of Pueschel & Cole (1982) on the basis of pit plug ultrastructure, but the taxonomic affinities of *Rhodophysema* were far from settled. In the same year, Glazer *et al.* (1982) noted that the Acrochaetiales was the only order of the Florideophyceae to include species with B-phycoerythrin, a state also observed for *Rhodophysema*. Glazer *et al.* argued for placement of *Rhodophysema* in the Acrochaetiales rather than in the Palmariales, for which all tested species had R-phycoerythrin. This presented an interesting dilemma because the Acrochaetiales share sessile carpogonia and pit plug ultrastructure with the Palmariales and *Rhodophysema*, and regenerative sporangia, some possibly with distinct stalk cells, are reported in the Acrochaetiales (Guiry, 1978, 1990). Thus, an alliance for *Rhodophysema* to the

Palmariales was reduced to a single feature, absence of a carposporophyte in the life history (an attribute shared with a member of the Acrochaetiales, discussed below), whereas the Acrochaetiales and *Rhodophysema* were linked by the presence of B-phycoerythrin. It was, therefore, a matter of conjecture at that time as to which order *Rhodophysema* had affinities; nevertheless, it was certain that it was not a member of the Gigartinales. The objective now became one of defining the ordinal affinities of *Rhodophysema*.

Rhodophysemataceae & Rhodothamniellaceae: additional families of the Palmariales
Saunders & McLachlan (1989) emphasized the evidence in favor of an association between the Acrochaetiales and Palmariales, and used the term Acrochaetiales-Palmariales complex when discussing this group of taxa (Fig. 5). They were particularly concerned with the taxonomic affinities of *Rhodophysema* and argued for provisional inclusion in the Palmariales owing to the absence of a carposporophyte in the life history, absence of monosporangia, occurrence of a generative stalk cell associated with tetrasporangia, and the presence of cellular fusions. Furthermore, Saunders & McLachlan argued that the absence of a tetrasporophyte in the life history, as well as the occurrence of B-phycoerythrin rather than R-phycoerythrin, were sufficient grounds for recognition of a second family, Rhodophysemataceae, in the Palmariales (Fig. 5).

Acrochaetiales-Palmariales Complex

	Acrochaetiales	Palmariales	
	Acrochaetiaceae	Palmariaceae	Rhodophysemataceae
Pit plug (2 cap/mem)	yes	yes	yes
Sessile carpogonia	yes	yes	yes
Carposporophyte	yes	no	no
Stalk cell with generative sporangia	No?	Yes	yes
Monosporangia	yes	no	no
Cellular fusions	absent*	present	present
Phycoerythrin	B & R	R	B
Tetrasporophyte	yes	yes	no

*except for two species, *Rhodochorton spetsbergense* & *R. concrescens*

Fig. 5. Tabular presentation of the features pertinent to taxonomy in the Acrochaetiales-Palmariales Complex. The first two features (enclosed by solid black line) serve to unite all three families. The subsequent four features define the Palmariales (enclosed by dashed line). The final two features (dotted line) distinguish the two families within the Palmariales.

The justification for only provisional placement of Rhodophysemataceae in the Palmariales was that there were also certain species of the Acrochaetiales that lack carposporophytes in their life history, that arguably have stalk cells associated with tetrasporangia, that lack monosporangia and in a few cases that have cell fusions. To resolve this conundrum, Saunders & McLachlan (1989, 1991) argued that the Acrochaetiales was too broadly defined and included anomalous members whose phylogenetic affinities were with the Palmariales rather than the Acrochaetiales.

Saunders & McLachlan (1991) published the first of what were expected to be two papers in a series that would clarify ordinal boundaries for the Acrochaetiales and Palmariales. In the first manuscript they addressed the phylogenetic affinities of *Rhodochorton spetsbergense* (Kjellman) Kjellman, an alga included in the Acrochaetiales. In light of the life history investigations on *Rhodophysema* and the profound taxonomic changes occurring in the Florideophyceae in the early 1980s, a few systematists suggested that perhaps *Rhodochorton spetsbergense* was more closely related to *Rhodophysema* than the Acrochaetiales (Woelkerling, 1983; Stegenga, 1985; Saunders *et al.*, 1989). This species has only male gametangia and tetrasporangia reported in the field, spore germination as a disc rather than a filament, putative stalk cells subtending the generative tetrasporangia, an absence of monosporangia, is one of the few acrochaetes with B-phycoerythrin, and is the only acrochaete (*R. condescens* Drew is included in synonymy for simplicity; *cf.* Guiry, 1975) to have cell fusions (Saunders & McLachlan, 1991). Saunders & McLachlan (1991) established a new genus, *Meiodiscus*, for this species and considered it a member of the Rhodophysemataceae, Palmariales (Fig. 5). The notion of including acrochaetes in the Palmariales was not greeted with enthusiasm and publication of this research was protracted. The second paper in this series was, therefore, not prepared for publication. The intended publication was to move a second acrochaete to the Palmariales (Saunders, 1987). *Rhodothamniella floridula* (Dillwyn) J. Feldmann was the only member of the Acrochaetiales to have a strictly Palmariaceae-type life history (Fig. 3), furthermore it lacks monosporangia and it has generative sporangia (*cf.* Stegenga, 1978; Guiry, 1987). Guiry (1987) in particular emphasized the functional equivalence of the life history in *Rhodothamniella* to that of the Palmariaceae. Saunders (1987) argued that *R. floridula* should be transferred to the Palmariales, however, the occurrence of B-phycoerythrin (as in Rhodophysemataceae) and a tetrasporophyte in the life history (as in Palmariaceae), as well as the absence of cellular fusions (unique to the order) prompted a proposal for a distinct family, Rhodothamniellaceae (Fig. 6).

Saunders *et al.* (1995) provided a molecular test of the earlier proposals of Saunders & McLachlan (1989, 1991). Saunders *et al.* provided strong evidence for inclusion of *Rhodophysema* in the Palmariales (rather than Acrochaetiales or Gigartinales) and showed that it was relatively distant from *Devaleraea*, *Halosaccion* and *Palmaria*, Palmariaceae, thus supporting recognition of the Rhodophysemataceae (Fig. 7). Strong support was acquired for the segregate genus *Meiodiscus* for *Rhodochorton spetsbergense*, and for its inclusion in the Palmariales rather than the Acrochaetiales. The molecular results were equivocal on the inclusion of *Meiodiscus* in Rhodophysemataceae, but hypotheses on the life history and reproductive features prompted Saunders *et al.* (1995) to retain provisionally this genus in Rhodophysemataceae. *Meiodiscus spetsbergensis* is reported to produce spermatangia on the same plant as tetrasporangia, a situation that recalls the life history of *Rhodophysema*, and also shares the character of intercalary divisions in cells of the basal layer with *Rhodophysema*. This taxonomic decision is, therefore, in need of further supporting evidence either through elucidation of the life history in *Meiodiscus* or (preferably both) stronger molecular data. Investigations of the large-subunit of the ribosomal cistron have been initiated in an effort to resolve this conundrum (Saunders & Clayden, unpubl.). Saunders *et al.* (1995) also produced strong molecular support for inclusion of *Rhodothamniella* in the Palmariales rather than the Acrochaetiales. Consistent with the proposals of Saunders (1987), this genus formed an early and distinct lineage in this order

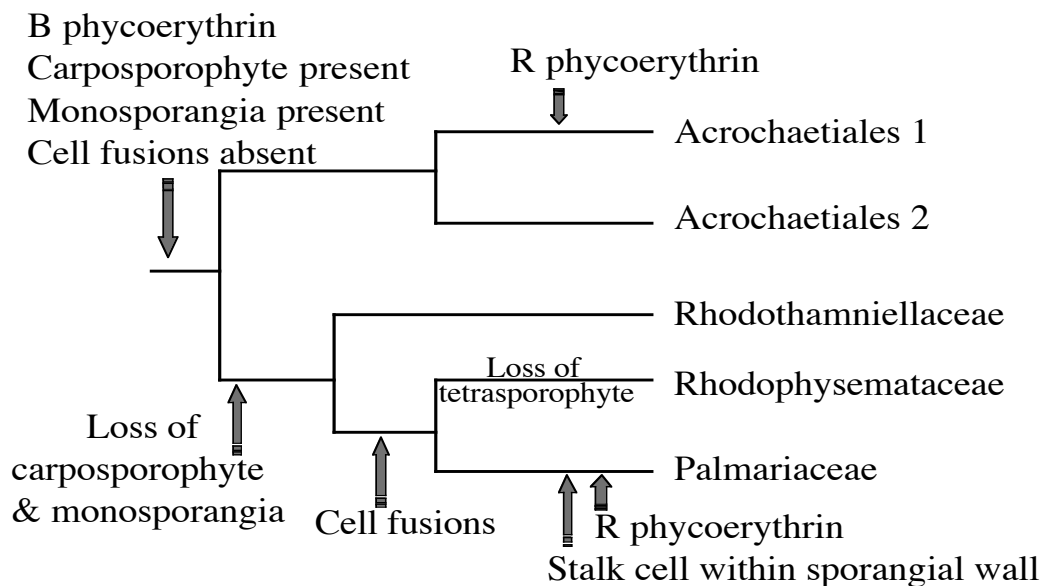


Fig. 6. A phylogenetic summary of the proposals of Saunders (1987) and Saunders & McLachlan (1989, 1991). The putative evolution of key features is indicated along the branches of the phylogram.

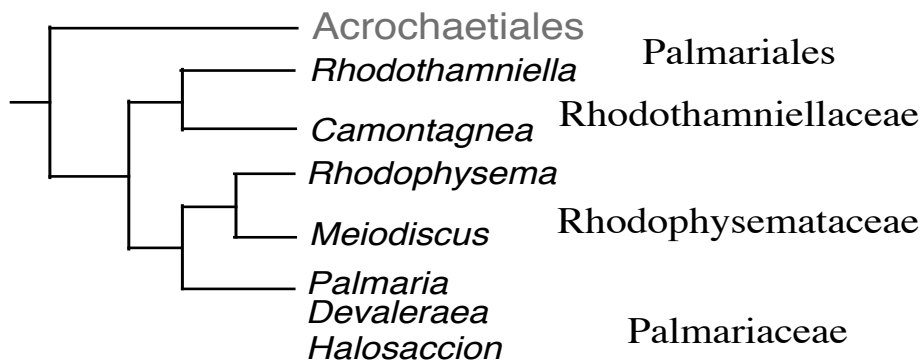


Fig. 7. A phylogram for all genera included in the Palmariales based on the molecular trees of Harper & Saunders (1998).

(Figs 6 & 7) and the Rhodothamniellaceae was formally proposed at that time (Saunders *et al.*, 1995). The proposals for character evolution (Fig. 6) in Saunders & McLachlan (1989, 1991) are similarly consistent with the molecular results (Fig. 7), with the caveat that inclusion of *Meiodiscus* in the Rhodophysemataceae is based on speculative arguments that this genus has, or evolved from an ancestor with the *Rhodophysema* life-history type. As noted above, the resolution of this issue awaits the input of new data.

A final (to date) interesting step in the maturation of the Palmariales from 1978 to 2000 stems from a publication by Pujals (1981) in which she moved *Ballia scoparia* (Hooker et Harvey) Harvey [subsequently joined by *Ballia hirsuta* Wollaston (Woelkerling & Womersley, 1994)] from the Ceramiales to a new genus, *Camontagnea*, considered closely related to *Rhodothamniella* in the Acrochaetiales. This decision was largely based on the presence of multiple stellate plastids, each with a central pyrenoid, in *Camontagnea* and *Rhodothamniella*, a feature not known for any other Florideophyceae. Harper & Saunders (1998) included a representative of *Camontagnea oxyclada* (Montagne) Pujals (= *B. scoparia*) in their molecular analyses of the Acrochaetiales and furnished unequivocal evidence that this genus was allied to *Rhodothamniella*, Rhodothamniellaceae, in the Palmariales (Fig. 7).

II. Rhodymeniales *sensu stricto*

Intraordinal taxonomy in turmoil

The second path of events to evolve out of the 1970s is related to the Rhodymeniales *sensu stricto*. At the same time Guiry (1978) had removed the Palmariaceae to its own order rendering the Rhodymeniales largely monophyletic and with two families, Rhodymeniaceae and Champiaceae, Lee (1978) was directing his attention at diversity among the remaining elements. In his work Lee argued that the Champioideae and Lomentarioideae should be recognized as distinct at the familial level. Thus the Rhodymeniales entered the 1980s with three families: Champiaceae, hollow cavities with longitudinal filaments and traversed by single-layer diaphragms, four-celled carpogonial branches, and intercalary, scattered tetrahedral tetrasporangia; Lomentariaceae, hollow cavities with longitudinal filaments and traversed by multilayer diaphragms, three-celled carpogonial branches, and terminal tetrahedral tetrasporangia in sunken sori; and, Rhodymeniaceae, plants solid or with hollow portions lacking longitudinal filaments (Fig. 8). The Rhodymeniaceae was generally regarded to have terminal tetrasporangia, but Lee (1978) argued that this feature was variable within species and of little taxonomic value. Thus, the two subclasses still recognized by Sparling (1957) – Rhodymenioidae with terminal cruciate versus Hymenocladieae with intercalary and tetrahedral tetrasporangia – were considered by Lee to differ only in the division pattern of their tetrasporangia. Although Lee did not formalize taxonomic revision, he indicated that this single character was insufficient for recognition of the intrafamilial groupings in the Rhodymeniaceae (Fig. 8).

The careful division of rhodymenialean species into these three families, however, remained controversial. Specific problems included the placement *Chrysymenia* and *Coelothrix*, whose species have hollow portions lined by longitudinal filaments, in the Rhodymeniaceae (*cf.* Guiry & Irvine, 1981), and inclusion of *Hymenocladia* and *Hymenocladopsis* in the Rhodymeniaceae owing to their solid construction, but despite the occurrence of tetrahedral tetrasporangia as in the Champiaceae and Lomentariaceae (Moe, 1986; Womersley, 1996). *Semnocarpa* has a fusion cell in the mature carposporophyte similar to that of the Rhodymeniaceae (component cells retain their original outline), but has hollow fronds and sunken sori of tetrahedral tetrasporangia as in the Lomentariaceae (Huisman *et al.*, 1993). On the other hand, *Ceratodictyon* and *Gelidiopsis* have the solid axes and cruciate tetrasporangia of the Rhodymeniaceae, but the columnar fusion cell in mature carposporophytes typical of the Lomentariaceae (Price & Kraft, 1991). *Dictyothamnion* has such a mix of features diagnostic of both the Champiaceae and

Lomentariaceae that Millar (1990) left it *incertae sedis* in the Rhodymeniales. Finally, although the Rhodymeniaceae was long considered to be characterized by terminal tetrasporangia, and subsequently a mix of terminal and intercalary tetrasporangia, recent investigations have indicated that most species have exclusively intercalary positioning of these structures (Huisman, 1996; Womersley, 1996).

Rhodymeniales *sensu stricto*

Kylin (1931)	Lee (1978)	Saunders <i>et al.</i> (1999)
<ul style="list-style-type: none"> ■ Rhodymeniaceae: solid <ul style="list-style-type: none"> – Cruciate terminal tetrasporangia <ul style="list-style-type: none"> ■ Rhodymenieae - Lack <i>tela arachnoidea</i> ■ Faucheae - Have <i>tela arachnoidea</i> – Tetrahedral intercalary tetrasporangia <ul style="list-style-type: none"> ■ Hymenocladieae ■ Champiaceae: hollow, longitudinal filaments <ul style="list-style-type: none"> – Champieae <ul style="list-style-type: none"> ■ Cavities traversed by single-layered diaphragms ■ 4-celled carpogonial branches ■ Intercalary, scattered, tetrahedral tetrasporangia – Lomentarieae <ul style="list-style-type: none"> ■ Cavities traversed by multi-layered diaphragms ■ 3-celled carpogonial branches ■ Terminal, tetrahedral tetrasporangia in sunken sori 	<ul style="list-style-type: none"> ■ Rhodymeniaceae: solid <ul style="list-style-type: none"> – Cruciate, terminal & intercalary tetrasporangia <ul style="list-style-type: none"> ■ Rhodymenieae (including Faucheae) – Tetrahedral & intercalary tetrasporangia <ul style="list-style-type: none"> ■ Hymenocladieae Doubtfully distinct, single feature of tetrasporangial division pattern. ■ Champiaceae <ul style="list-style-type: none"> – Same features. ■ Lomentariaceae <ul style="list-style-type: none"> – Same features. 	<ul style="list-style-type: none"> Group 1 <ul style="list-style-type: none"> ■ Rhodymeniaceae <ul style="list-style-type: none"> – Cruciate, intercalary tetrasporangia – 4-celled carpogonial branches Group 2 <ul style="list-style-type: none"> ■ Faucheaceae <ul style="list-style-type: none"> – Cruciate, terminal tetrasporangia – 3-celled carpogonial branches ■ Hymenocladieae <i>incertae sedis</i> <ul style="list-style-type: none"> – tetrahedral, intercalary tetrasporangia – 4-celled carpogonial branches ■ Champiaceae <ul style="list-style-type: none"> – tetrahedral, intercalary tetrasporangia – 4-celled carpogonial branches ■ Lomentariaceae <ul style="list-style-type: none"> – tetrahedral, terminal tetrasporangia – 3-celled carpogonial branches

Fig. 8. A representation of taxonomic changes in the Rhodymeniales *sensu stricto* from Kylin (1931) to Saunders *et al.* (1999).

The initial molecular trees contributed additional strife to rhodymenialean systematics (Saunders & Kraft, 1996). Most notably, Kylin's Faucheae, included by Sparling (1957) and Lee (1978) in the Rhodymenioideae, was allied strongly to the Champiaceae and Lomentariaceae rather than Rhodymeniaceae. This seemingly confounding molecular tree, in addition to the increasingly untenable classical taxonomy of Rhodymeniales in light of new species being described from the Southern Hemisphere, prompted Saunders *et al.* (1999) to complete a comprehensive molecular survey of the Rhodymeniales. These preliminary trees (Saunders & Kraft, 1996) did, however, serve to establish that the Rhodymeniales is a distinct lineage and should not be subsumed into a broadening concept of the Gigartinales as was suggested by some workers (Kraft & Robins, 1985; Garbary & Gabrielson, 1990).

Molecular survey of the Rhodymeniales

Saunders *et al.* (1999) completed an extensive survey of the Rhodymeniales considering ca. 60% of the included genera, with ca. 60% of these represented by their type species.

They considered the Rhodymeniales to consist of two major lineages, a restricted Rhodymeniaceae and a second group including expanded concepts for the Champiaceae and Lomentariaceae, Kylin's Faucheae, and a number of genera of unresolved affinities that were previously included in the Rhodymeniaceae (Fig. 8).

Saunders *et al.* (1999) disputed the paradigm initiated by Bliding and demoted vegetative construction as a useful feature for delineating families in the Rhodymeniales. They argued that the Rhodymeniaceae *sensu stricto* was defined by intercalary (rarely terminal) positioning of the exclusively cruciate tetrasporangia and four-celled [occasionally three, a single report of two (Lee, 1978)] carpogonial branches (*cf.* Saunders *et al.*, 1999, fig. 6). The Champiaceae was defined as genera with intercalary positioning of the tetrahedral tetrasporangia and four-celled carpogonial branches. *Dictyothamnion* was included in their expanded concept of the Champiaceae and it was suggested that *Hymenocladia* (and the closely related *Erythrymenia*), an anomalous member of earlier concepts for the Rhodymeniaceae in having tetrahedral tetrasporangia, would ultimately join this family (Fig. 8; *cf.* Saunders *et al.*, 1999). The Lomentariaceae was considered to include species with terminal positioning of tetrahedral tetrasporangia and three-celled carpogonial branches. This essentially equated to the Lomentariaceae *sensu* Huisman *et al.* (1993), but was not defined on vegetative criteria and included the solid *Ceratodictyon* and *Gelidiopsis* [these having secondarily reverted to cruciate tetrasporangial division in the hypothesis of Saunders *et al.* (1999)] from the Rhodymeniaceae. Finally, a new family, Faucheaceae, was erected that corresponded roughly to Kylin's Faucheae. Faucheaceae was not, however, defined on the presence of a *tela arachnoidea* (although this structure is present in the cystocarps of many species in the family), but rather included genera with terminal cruciate tetrasporangia and three-celled carpogonial branches.

The Rhodymeniales, therefore, presently includes four families: Champiaceae, Faucheaceae, Lomentariaceae and Rhodymeniaceae (Fig. 8). The molecular trees were equivocal on the relative affinities of these families, as well as the phylogenetic positioning of *Fryeella*, *Hymenocladopsis* and *Erythrymenia* and *Hymenocladia*. Further research is required to resolve these remaining issues and to test the phylogenetic and taxonomic hypotheses proposed by Saunders *et al.* (1999). Only through continued anatomical observation and molecular investigation, always with an open mind to change, will the systematics of the Rhodymeniales *sensu stricto* be resolved.

Summary

The tale of systematic change in the Rhodymeniales is long and convoluted. The research of the 20th century in shaping this saga includes abrupt transitions in emphasis and technique, from the meticulous anatomical observations still practiced today (unfortunately by too few), to the detailed life history investigations so prevalent during the seventies and eighties, through the ultrastructural wave (itself suffering from too few practitioners in contemporary science) to the revolutions of molecular systematics in the nineties. All of these techniques have contributed valuable data towards elucidating the phylogenetic affinities and diversity of species that constituted the Rhodymeniales circa 1970.

Recognition of the Palmariales marked the first major revision, and this order has subsequently grown to form a melting pot including species from five of the six orders recognized by Kylin (1932, 1956). For the Rhodymeniales *sensu stricto*, the familial complement has grown from two to three, and recently four, but more importantly the most recent system marks a paradigm shift in placing no weight on vegetative construction at the familial level. Rather, emphasis is placed on tetrasporangial division pattern and position in the vegetative filaments (intercalary versus terminal), and on the number of cells in the carpogonial branch. There can be little doubt that the future will be equally exciting as systematists test the current systems of taxonomy in the Palmariales and Rhodymeniales, as well as strive to resolve the many remaining conundrums.

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