

ASSESSING RED ALGAL SUPRAORDINAL DIVERSITY AND TAXONOMY IN THE CONTEXT OF CONTEMPORARY SYSTEMATIC DATA¹

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The wondrously diverse eukaryotes that constitute the red algae have been the focus of numerous recent molecular surveys and remain a rich source of undescribed and little known species for the traditional taxonomist. Molecular studies place the red algae in the kingdom Plantae; however, supraordinal classification has been largely confined to debate on subclass vs. class level status for the two recognized subgroups, one of which is widely acknowledged as paraphyletic. This narrow focus has generally masked the extent to which red algal classification needs modification. We provide a comprehensive review of the literature pertaining to the antiquity, diversity, and systematics of the red algae and propose a contemporary classification based on recent and traditional evidence.

Key words: Bangiophyceae; Compsopogonophyceae; Cyanidiophyta; Eurhodophytina; Florideophyceae; Metarhodophytina; Rhodophyta; Rhodoplantae.

The biological significance of red algae is only beginning to be appreciated. Even among professional biologists, knowledge of these organisms is often minimal and based on cursory information contained in general botany textbooks (Woelkerling, 1990, p. 1).

Macroalgal systematics traces its “modern” era to rather humble beginnings, the multitude of diverse species assigned to a few genera in a subdivision (Algae) of the class Cryptogamia, which also included the ferns, mosses and fungi, positioned among 23 classes of cone-bearing and flowering plants in the plant kingdom (Linnaeus, 1753). This early classification clearly underrepresented macroalgal diversity and substantial taxonomic refinements inevitably followed. Lamouroux (1813) was the first to use color to segregate algal assemblages when he removed certain red algae from their respective associations with species of like morphology to the Floridées. Harvey (1836) took the “biochemical” marker further and established the Chlorospermae, Melanospermae, and Rhodospermae for green, brown, and red algae, respectively; in essence establishing the three major groups of macroalgae that are recognized today.

Numerous taxonomic changes were implemented in the ensuing decades, but the relatively recent advent of ultrastructural and molecular systematic data in particular have uncovered the bewildering diversity, as well as evolutionary affinities of the chlorophytic and chromophytic lineages. Recent taxonomic treatments vary, but schemes including as many as 10 classes in two phyla are now presented for the chlorophytic line (cf. Lewis and McCourt, 2004). The brown algae are included in a larger chromophytic lineage, Heterokontophyta,

including a wide diversity of lineages distributed among some 15 classes (cf. Andersen, 2004). The Rhodophyta have not experienced a similar explosion in taxonomic breadth with our current perspective on supraordinal relationships virtually unchanged since ca. 1900 and confined to a continuing debate as to whether the two constituent lineages, Bangiophyceae and Florideophyceae, should be recognized as distinct classes or subsumed as subclasses within a single class Rhodophyceae (cf. Dixon, 1973).

The current system of red algal classification creates the illusion that this lineage is relatively limited in its diversity when compared to chlorophytes and chromophytes; this despite the wide range of morphology observed among red algae and a wealth of contemporary ultrastructural and molecular data that speak to the antiquity and diversity within Rhodophyta. This review sets as its aim to amass the available information on red algal phylogeny, diversity, and antiquity and to use this to reform red algal taxonomy. It is not our intent to deal with the broader issue of red algal affinities relative to the other major eukaryotic lines. The reader is directed to an overview of that topic by Keeling (2004) in this issue.

FOSSILS AND ANTIQUITY OF THE RED ALGAE

The red algae are a study in extremes. Morphologically more diverse than any other group of algae, they range from single cells to large ornate multicellular plants . . . Uniquely among (nonfungal) eukaryotes they lack both flagella and centrioles . . . and exhibit a remarkable, often bizarre range of reproductive strategies (Butterfield, 2000, p. 386).

The earliest putative red algal fossils date to ca. 2 billion years before present and are superficially similar to the extant taxa of the Porphyridiales, Bangiophyceae (Tappan, 1976). Although the evolutionary scenario presented by Tappan, in which the red algae represent a direct link between the prokaryotic cyanophytes and other eukaryotes, is widely rejected in light of recent phylogenetic hypotheses (e.g., Ragan and Gutell, 1995), the possibility that unicellular red algae did exist at such an early stage (Fig. 1) is compatible with the fossils

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A Red Perspective on the Geological Time Scale

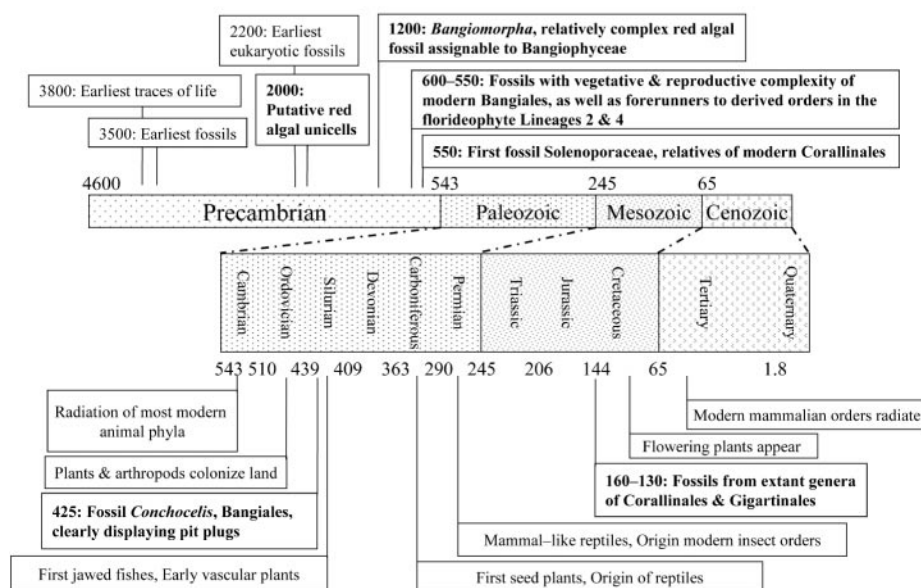


Fig. 1. Geological time scale from a general biology text (Campbell and Reece, 2002), modified to place red algal fossils in context with other major evolutionary events.

observed by Tappan and other scientists. Most notable in this regard is the old (1.2 billion years) and relatively advanced fossil taxon *Bangiomorpha* (Butterfield, 2000). *Bangiomorpha pubescens* Butterfield (2000) was described from the 1200-million-year-old Hunting Formation in the Canadian Arctic and represents the earliest putative record for sex and taxonomically resolvable complex multicellularity among eukaryotes. Thus its likeness to taxa currently included in the red algal order Bangiales is truly remarkable (Butterfield et al., 1990; Butterfield, 2000).

Zhang et al. (1998) considered that at least eight of the fossil species described from the terminal Proterozoic (600–550 million years ago [Ma]) Doushantuo Formation, China, were red algae (also see Xiao et al., 1998), and their observations may provide a unique window into the vegetative and reproductive diversity of red algae prior to the Paleozoic (Fig. 1). In addition to a variety of parenchymatous species, the fountain-type filamentous construction with differentiated medullary and cortical filaments was reported for some species. This pattern is characteristic of some extant Florideophyceae. Tetrads noted for *Paratetraphycus* are reminiscent of carposporangial production in *Porphyra*, Bangiales, whereas cavities and clusters of spheroidal cells in *Thallophyca* were considered as a link between this taxon and later fossil Solenoporaceae, which are considered a stem group to extant Corallinales (lineage 2, Fig. 2). Moreover, *Thallophyca* lacked calcification (Zhang et al., 1998), indicating that this attribute derived relatively recently within lineage 2, a result consistent with the SSU (small subunit ribosomal DNA) molecular trees for florideophyte taxa (Saunders and Kraft, 1997). In this same formation were other fossil algae, e.g., *Paramecia*, with embedded clusters of carposporophyte-like structures considered similar to those in lineage 4 orders (Fig. 2) such as the Ceramiales and Gigartinales (Zhang et al., 1998).

If the interpretations of these fossils are correct, then the Bangiales, as well as the four major lineages of florideophytes

(Saunders and Kraft, 1997; Fig. 2), were established and differentiated by 600–550 Ma, at the end of the Proterozoic Eon and prior to the Cambrian explosion. In further support of the antiquity of these various groups, Campbell (1980) reported on a 425-million-year-old endolithic microfossil from Poland clearly identifiable as a *Conchocelis* stage of the Bangiales, for which pit plugs (proteinaceous plugs deposited in the pores resulting from incomplete furrowing following cell division in red algae) were clearly documented. This same formation also contained red solenoporacean algae, considered to be the stem lineage from which the Corallinales evolved (Campbell, 1980), which differ from the earlier *Thallophyca* in being calcified. In fact, the calcareous Solenoporaceae first appear in the fossil record ca. 550 Ma and disappear around 60 Ma (Johnson, 1960; Wray, 1977). Fossil red algae directly assignable to extant genera of the Corallinales (lineage 2, Fig. 2) show up in the Cretaceous (130 Ma), whereas fossils identifiable with genera of the Peyssonneliaceae, Gigartinales (lineage 4, Fig. 2), are recovered from the late Jurassic (160 Ma) providing solid evidence (Wray, 1977) for a relatively early divergence among orders within the major florideophyte lineages.

Naturally, the more recent the fossil, the more easily assignable to extant taxa, whereas the earliest records (e.g., Tappan, 1976) are the most difficult to assign unambiguously to taxonomic lineages. Perhaps the unexpected antiquity of the earliest putative red algal unicells is sufficient to cause controversy over their identification. However, when all of the fossil evidence is considered in combination, both the relative and absolute chronological series of events is logical and consistent with molecular data on both the antiquity and phylogenetic relationships of red algae (Figs. 1 and 2).

MOLECULAR SYSTEMATICS AND DIVERSITY

Red algae clearly constitute one of the major radiations of eukaryotes. Measured by divergence of SSU rDNA sequences within

Contemporary Phylogeny for the Rhodophyta

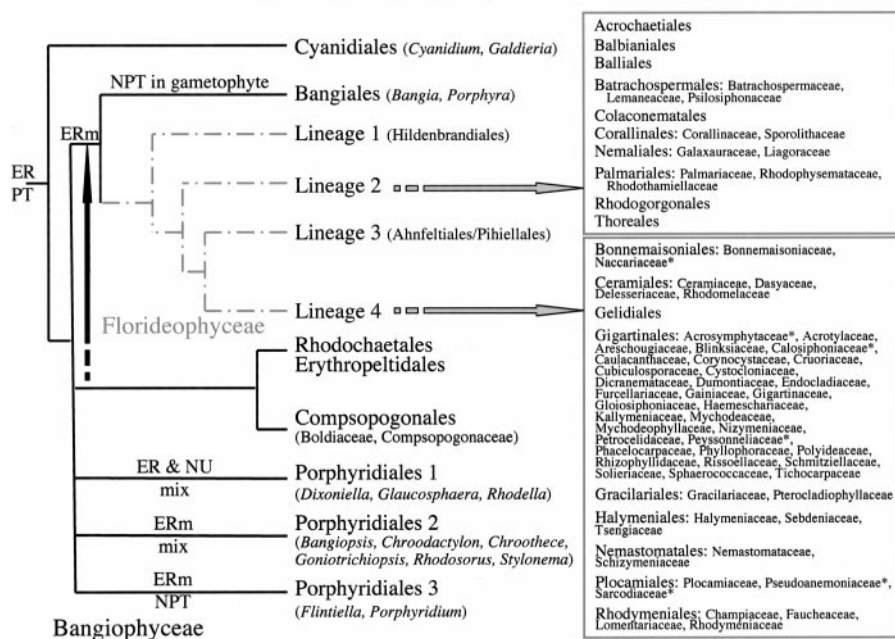


Fig. 2. Phylogenetic hypothesis for the red algae based on a compilation of molecular results from Saunders and Bailey (1997, 1999), Oliveira and Bhattacharya (2000), Müller et al. (2001), and Yoon et al. (2002b). The black arrow indicates an association (albeit not supported) for an alliance of the Compsopogonales et al. with the Bangiales/Florideophyceae lineage. For orders with more than one family (excepting Porphyridiales), the familial composition is provided (* indicates a family of equivocal taxonomic affinity). Lineages 1–4 of the Florideophyceae follow Saunders and Kraft (1997). Putative evolutionary scenarios for the type of Golgi association (ER = exclusively ER; ERm = ER and mitochondrial; NU = nuclear) and presence vs. absence (PT, NPT, respectively, or Mix for both) of peripheral encircling thylakoids are provided. Only those porphyridial genera included in molecular systematic studies are listed.

the most conservative regions, Rhodophyta are more divergent among themselves than are (i) fungi or (ii) green algae and green plants together (Ragan et al., 1994, p. 7278).

Although it is known that homologous genes can evolve at unequal rates in different lineages and, therefore, that direct comparisons of levels of divergence can be misleading as to the relative age of a group, the red algae display consistently high diversity across a variety of genes including actin and the nuclear and plastid small subunit ribosomal (SSU) genes (cf. Ragan et al., 1994; Medlin et al., 1997).

Lim et al. (1986) published the first study to consider red algae in a broader eukaryotic context and to estimate their divergence dates from molecular data. They used the 5S ribosomal RNA and concluded: red algae diverged from other eukaryotes at an early stage, ca. 1400 Ma; the split between the Bangiales and Florideophyceae was relatively early in red algal evolution (ca. 1000 Ma); and, the florideophytes included in their analyses (representatives of the contemporary lineages 2 and 4, Fig. 2) were phylogenetically remote from one another relative to taxa within other eukaryote lines. The brown algae, in contrast, were considered a recent divergence, only ca. 200 Ma, consistent with later estimates based on additional molecular data (Saunders and Druehl, 1992) but in strong contrast to their putative fossil record and taxonomic framework (cf. Saunders et al., 1992).

Yoon et al. (2004) used a six-gene data set to generate the most robust molecular clock estimates to date for the divergence of photosynthetic lineages. Their results echo the findings of earlier studies that used single molecules and inferred great antiquity for the red algae (e.g., Lim et al., 1986; Ragan et al., 1994). According to the estimates of Yoon et al. (2004),

the red and green lines diverged ca. 1500 Ma; the Cyanidiales diverged soon after, ca. 1370 Ma, and prior to the secondary endosymbiosis event (ca. 1270 Ma) that seeded the chromophytic line; the remaining bangiophycean lines had largely diverged by the time the chlorophytes had separated from the charophycean-land plant line (ca. 1200 Ma); the Florideophyceae and Bangiales diverged prior to the split between the charophytes and land plants (ca. 800 Ma); and the major florideophycean groups had diverged prior to the first appearance of land plants (ca. 460 Ma; Yoon et al., 2004).

Clearly, the molecular data are consistent with the fossil record in recognizing the red algae as a relatively early lineage of eukaryotes, with the component lineages also the result of early divergence events. However, the task of resolving adequately the composition and relative relationships among these same red algal lineages receives limited support from the fossil record. Molecules, on the other hand, have provided considerable insight in this regard. The first molecular investigations to consider red algal phylogeny at and above the ordinal level were published back-to-back in 1994 and used the nuclear SSU (Ragan et al., 1994) and the plastid *rbcL* (Freshwater et al., 1994). These studies suffered the inevitable consequence of being first viz. low, and underrepresentative taxon sampling (cf. Saunders and Kraft, 1997). This was particularly true for the Bangiophyceae, which were represented by only four to six genera in these reports. Regardless, both studies set the foundations for future molecular phylogenetic research in the Rhodophyta and were consistent in resolving the Bangiophyceae as paraphyletic to the Florideophyceae.

The paucity of published molecular data for the Bangiophyceae was soon remedied by a series of ordinal-level taxonomic

nomic studies. Oliveira et al. (1995) enhanced representation for the Bangiales in SSU trees, while Holton et al. (1998) added the first representatives of the freshwater family Bolidiaceae, Compsopogonales. Rintoul et al. (1999) expanded representation for the Compsopogonales in the SSU and *rbcL* alignments and uncovered support for a monophyletic lineage including the freshwater families Bolidiaceae and Compsopogonaceae, as well as the marine Erythrotrichiaceae (assigned to a segregate order in some treatments; cf. Silva, 1996). The following year, the Rhodochaetales were added to the molecular framework (Zuccarello et al., 2000). This monogeneric order was considered by many to be of pivotal importance in understanding red algal evolution (e.g., Chadeaud, 1965; Pueschel and Magne, 1987; Garbary and Gabrielson, 1990), but they were later shown to be a close ally of the Erythrotrichiaceae (as Erythropeltidaceae; Zuccarello et al., 2000) and not the immediate ancestor to the florideophyte algae or the earliest red algal lineage. Consistent with the molecular results, *Rhodochaete* shares many of the diagnostic features that ally the three families of the Compsopogonales sensu lato (discussed later). Nonetheless, Zuccarello et al. (2000) considered that *Rhodochaete* warranted recognition at the ordinal level, as did the Erythrotrichiaceae in their system, leaving the Compsopogonales sensu stricto with only the two freshwater families.

The studies discussed generally had low representation for the Porphyridiales sensu lato (i.e., including Cyanidiales), the order containing the many unicellular and pseudofilamentous members of the Rhodophyta. Oliveira and Bhattacharya (2000) filled the gap and provided the most comprehensive bangiophyte trees published to that date. Their study used the plastid SSU and, consistent with earlier reports, resolved the Bangiophyceae as paraphyletic in positioning the Florideophyceae as sister to the Bangiales. They resolved three distinct lineages of a polyphyletic Porphyridiales sensu lato: one weakly allied to the Compsopogonales; a second sister to that assemblage; and the third equivalent to the Cyanidiales as recognized by some workers (e.g., Ott and Seckbach, 1994). Müller et al. (2001) provided a nuclear SSU rDNA phylogenetic hypothesis the following year, containing even more taxa, but essentially inferring the same relationships as the earlier plastid-based investigation. The studies of Oliveira and Bhattacharya (2000) and Müller et al. (2001) are unquestionably the most substantial in contributing to our understanding of relationships among the lineages of the Bangiophyceae. In an effort to understand better the evolution of secondary plastids, Yoon et al. (2002a, b) combined from two to five plastid genes and provided further insights into red algal phylogeny. Their results echoed many aspects of the earlier studies, viz., an early divergence for the Cyanidiales, an association for the Bangiales and Florideophyceae, and a strongly resolved Compsopogonales/Erythropeltidales/Rhodochaetales clade. Yoon et al. reported that the divergence of the Cyanidiales from the remaining red algae predates the origin of the entire kingdom Chromista sensu lato, an event they estimated at ca. 1.3 billion years ago. Yoon et al. also resolved an association between the Bangiales/Florideophyceae and the Compsopogonales and its allies (Fig. 2), albeit with no support. We find some satisfaction in such an association because a single origin for complex multicellularity and pit plugs (unique to, and almost always associated with, complex multicellular development in red algae) would characterize a common ancestor to this lineage. Only through

further investigation will the validity of this interesting association be evaluated.

For the Florideophyceae, ordinal-level investigations by Saunders and Kraft (1994, 1996) provided the first molecular advances on the initial studies of Freshwater et al. (1994) and Ragan et al. (1994). Saunders and Bailey (1997) published a comprehensive ordinal representation for the Florideophyceae in which four lineages were clearly identified (Fig. 2), defined, in part, by pit-plug ultrastructure. Saunders and Kraft (1997) imparted some degree of informal recognition for these groups as lineages 1 through 4. Following these works, a series of papers used SSU, *rbcL*, or a combination of these genes, as well as anatomical observations, to recognize a number of new orders in the Florideophyceae: Balbianiales (Sheath and Müller, 1999); Balliales (Choi et al., 2000); Colaconematales (Harper and Saunders, 2002); Thoreales (Müller et al., 2002); a resurrected Nemastomatales (Saunders and Kraft, 2002); and the Pihelliales (Huisman et al., 2003). In addition, Harper and Saunders (2001) used the large-subunit rDNA to assess ordinal relationships among the Florideophyceae, and Saunders et al. (2004) have completed a comprehensive SSU investigation of lineage 4.

Although a number of unresolved issues remain in red algal taxonomy (discussed later), a phylogenetic consensus at and above the ordinal level is starting to emerge (Fig. 2).

VEGETATIVE, REPRODUCTIVE AND ULTRASTRUCTURAL DIVERSITY

Being an ancient lineage, the red algae have undergone a broad range of modifications in cellular organization. Even the spectrum of morphological possibilities, from unicellular forms . . . to complex . . . parenchymatous thalli, fails to convey the degree of cellular diversity (Pueschel, 1990, p. 8).

The morphological and ultrastructural diversity of the red algae is as striking as their genetic variation revealed in the molecular studies. Even a cursory survey of the chapters in *Biology of the Red Algae* by Cole and Sheath (1990) provides ample evidence. Pueschel (1990) noted that among the red algae, there are at least three patterns of Golgi association, three methods by which cells achieve multinuclearity in development, and several methods of establishing intercellular connections through cellular fusions and pit-plug formation. Scott and Broadwater (1990) described five distinct patterns of mitosis, differing in details of microtubule number and mode and location of formation, number and disposition of gaps in the nuclear envelope, shape and size of the nuclear-associated organelles, and the mode of cytokinesis. Coomans and Hommersand (1990) described three patterns of cytokinesis, whereas Hommersand and Fredericq (1990) recognized three distinct patterns by which the various reproductive structures are formed in red algae, these clearly associated with different evolutionary lineages. The following section outlines the key anatomical features and the fluctuating taxonomic systems dependent on them for each of the lineages observed in the molecular analyses (Fig. 2).

Cyanidiales—Taxa in this lineage consistently resolve as sister to the rest of the red algae (Fig. 2). Chapman et al. (1968) concluded that these algae were not only distinct at the family level, but that they warranted a distinct order, Cyanidiales (first proposed in Christensen, 1962), based on their biliprotein composition. Chapman (1974) reversed his earlier

decision, retaining the lineage at the family level within the Porphyridiales. Garbary et al. (1980) reevaluated bangiophyte taxonomy and considered that *Cyanidium* and its allies were best included in the Phragmonemataceae, Porphyridiales, largely owing to an absence of pyrenoids and the presence of endospores. In contrast, Merola et al. (1981) treated these algae as distinct at the class level, Cyanidiophyceae, which was part of a larger thesis to consider *Cyanidium* and its allies as a "phylogenetic bridge" between the prokaryotic cyanobacteria and the eukaryotic red algae. However, the key supporting character, plastids bounded by a single membrane (Merola et al., 1981), was later shown to be erroneous. Gabrielson et al. (1985) advocated that the new class be rejected because it lacked defining synapomorphies and continued to include these taxa in the Porphyridiales. Seckbach (1987) continued the trend of taxonomic elevation for the Cyanidiales and proposed phylum status, Prerhodophyta, for this unusual lineage of eukaryotes. Seckbach et al. (1992, p. 100) subsequently reversed the earlier elevation and recognized this lineage as a distinct subclass of the Bangiophyceae. Seckbach and Ott (1994, p. 141) reconsidered the attributes of the cyanidiophytes and, despite generally referring to them as a class throughout their publication, concluded that the system of Chapman (1974; family of the Porphyridiales) was best supported from the available evidence, whereas Ott and Seckbach (1994, p. 149) in the same volume supported ordinal status within the Bangiophycidae. Seckbach (1999) revived the class-level designation, and researchers working directly with these organisms have generally accepted this system (e.g., Muravenko et al., 2001). Other red algal systematists have tended to retain the group as an order, Cyanidiales, of the Bangiophyceae (e.g., Müller et al., 2001).

Although the main argument of Gabrielson et al. (1985) for rejecting the Cyanidiophyceae, viz., the absence of a defining synapomorphy, may be considered valid by some phycologists, this does not change the reality of the molecular data, which consistently place them as sister to the remaining Rhodophyta. Further, Gross et al. (2001) have uncovered levels of SSU divergence among strains of cyanidiophytes equivalent to ordinal and lineage level divergence among florideophytes (Fig. 2). In support of the molecular data, *Cyanidium* and its allies have a Golgi-ER association, as is common in other eukaryotes, but rare among red algae; thick proteinaceous cell walls; endospores; heterotrophic capacity; and the ability, perhaps unique among eukaryotes, to live in extreme acidophilic/thermophilic environments (cf. Chapman, 1974; Gross et al., 2001). Muravenko et al. (2001) further provided evidence that the cyanidiophytes have the smallest known genomes of any phototrophic eukaryotes. Many putative synapomorphies have been listed here, but more importantly the unique attributes of these organisms provide a sense that the Cyanidiales are as distinct from other red algae as are phyla in the plant and animal kingdoms relative to one another.

Porphyridiales—Even with removal of the anomalous Cyanidiaceae from Porphyridiales, molecular analyses generally have indicated that this order is paraphyletic (Oliveira and Bhattacharya, 2000; Müller et al., 2001), although Yoon et al. (2002a, b) provided the first results consistent with monophyly for this order. Regardless, it is clear from all of the previous studies that there are three distinct and highly divergent lineages in this order as currently circumscribed. The nomenclatural history surrounding this lineage has been convoluted and com-

plex (cf. Dixon, 1973; Silva, 1996), and for the most part, the three lineages identified in the molecular trees are at odds with all previous taxonomic proposals. Generic concepts and species complements have changed markedly through the various schemes (Garbary et al., 1980, Table 1), resulting in a bewildering variety of taxonomic systems in the literature for these algae. Garbary et al. (1980) provided a major step forward in removing an earlier emphasis on unicells vs. pseudofilaments (e.g., Dixon, 1973; Chapman, 1974), but their proposed taxonomic groupings are strongly at odds with the subsequent molecular data (Fig. 2). It is timely to reconsider these organisms in light of the molecular trees (cf. Müller et al., 2001).

Porphyridiales 1, represented in the molecular trees to date by *Dixoniella*, *Glaucosphaera*, and *Rhodella*, are primarily a lineage of unicellular taxa (Müller et al., 2001), which have contrasting states for many of the characters traditionally considered to be taxonomically useful (Fig. 2). *Dixoniella* and *Glaucosphaera* have their Golgi associated with the nucleus and an encircling thylakoid in the plastid, whereas *Rhodella* has a Golgi-ER association and lacks an encircling thylakoid (Scott et al., 1992). *Rhodella* is more similar to *Dixoniella* in having a stellate plastid with a central pyrenoid, whereas *Glaucosphaera* has a parietal reticulate plastid lacking a pyrenoid (Broadwater and Scott, 1994). In addition to the molecular data, structural data may prove this lineage distinct from the other two porphyridial groups in the types of Golgi association.

In Porphyridiales 2 (Müller et al., 2001), the unicellular genus *Rhodorus* is sister to a host of pseudofilamentous genera (and allies, e.g., unicell *Chrootheca* and pseudofilament *Chroodactylon*; Lewin and Robertson, 1971). Members of this group are similarly variable in plastid morphology and pyrenoid disposition, as well as the presence or absence of an encircling thylakoid (Fig. 2). The last feature is absent from the unicellular *Rhodorus* (Broadwater and Scott, 1994), supporting other plastid differences and molecular data in recognizing this genus as distinct within Porphyridiales 2. Members of this group are, where known, characterized by a Golgi-ER/mitochondrial association, a feature shared with Porphyridiales 3 (Broadwater and Scott, 1994) and the Bangiales and Florideophyceae (Pueschel, 1990).

Porphyridiales 3 include, thus far, the unicells *Flintiella* and *Porphyridium*. Again, these two genera are distinct in features of plastid morphology and possibly pyrenoid disposition (Broadwater and Scott, 1994), but alike in lacking the peripheral encircling thylakoid. The presence of a peripheral thylakoid is generally considered primitive rather than derived (Pueschel and Magne, 1987), a hypothesis consistent with the distribution of this feature on the molecular trees (Fig. 2), and thus the absence of this attribute may ultimately prove a synapomorphy for this lineage.

We can conclude that the emphasis on plastid morphology and pyrenoid occurrence at familial and ordinal taxonomic levels among red algae (e.g., Garbary et al., 1980) is not justified, although these features may prove useful for taxonomy within the major lineages of the Porphyridiales. Similarly, these two features failed to resolve higher-level taxa within the florideophyte order Acrochaetiales sensu lato, but were nonetheless useful in distinguishing among closely related genera (Harper and Saunders, 2002).

Compsopogonales, Erythropeltidales, and Rhodochaetales—Garbary et al. (1980) united the families Boldiaceae,

Compsopogonaceae, and Erythrotrichiaceae (as Erythropeltidaceae) together in the Compsopogonales (as Erythropeltidales; cf. Wynne, 1986) based on a similar pattern of monosporangial production. Monosporangia are produced from an undifferentiated vegetative cell following the formation of an oblique curved wall, which divides the cell into two, the smaller differentiating as a sporangium. A Golgi-ER association, encircling thylakoids in the plastid, and a thylakoid-free central region of the plastid further define this lineage (cf. Rintoul et al., 1999), as well as the order Rhodochaetales. Silva (1996) argued that the members of the Compsopogonaceae are more complex than those of the Erythrotrichiaceae and that the latter should form the basis of an emended Erythropeltidales. This proposal is supported by recent molecular analyses (e.g., Zuccarello et al., 2000; Müller et al., 2001), a freshwater vs. marine habitat, and aspects of the plastid ultrastructure and nuclear-associated organelle structure (Scott and Broadwater, 1989), which also serve to unite the Boldiaceae and Compsopogonaceae at the ordinal level, to the exclusion of the Erythrotrichiaceae. In addition to the features noted, the Rhodochaetales possess pit plugs without caps or membranes similar to those in the Compsopogonaceae (Pueschel and Magne, 1987). Nonetheless, the Rhodochaetales have generally been treated as a separate order owing to their apical rather than diffuse growth (Gabrielson et al., 1985). In phylogenetic studies by Zuccarello et al. (2000), the Rhodochaetales were a close sister to the Erythropeltidales, with this combined lineage only a relatively distant sister to the Compsopogonales, which includes two freshwater families, Boldiaceae and Compsopogonaceae (Fig. 2).

Rhodochaete parvula Thuret is an alga that has been considered as a likely sister to the Florideophyceae (cf. Gabrielson and Garbary, 1986) owing to branched uniseriate filaments with apical growth, naked pit-plugs (i.e., no caps or membranes; Pueschel and Magne, 1987), intercalary reproductive structures (Magne, 1960), and a putatively triphasic life history (Guiry, 1987) that incorporates a “proto-carposporophyte” generation consisting of two cells, one of which forms a carposporangium that releases a single carpospore. However, this evolutionary hypothesis is more likely an artifact of *Rhodochaete* similarities to the Acrochaetales, an order of Florideophyceae long, albeit incorrectly (Saunders and Bailey, 1997), considered the ancestral lineage of florideophytes. Indeed, the interpretation of a triphasic life history for *Rhodochaete* (cf. Gabrielson and Garbary, 1986; Guiry, 1987) is probably more an overinterpretation based on the assumption of a close alliance to the Florideophyceae than an accurate interpretation of the postfertilization events.

Bangiales—This bangiophyte order is the most closely allied to the Florideophyceae (Fig. 2) in all recent molecular systematic analyses (e.g., Müller et al., 2001). This relationship is supported by the Golgi-ER/mitochondrion association and similarities between the *Conchocelis* (diploid stage in sexual cycles) phase of the Bangiales and the florideophytes (Cole and Conway, 1975). The *Conchocelis* phase has an encircling peripheral thylakoid in the plastid, apical growth, and pit plugs with a single cap layer (cf. Cole and Conway, 1975; Gabrielson et al., 1985), whereas the bangialean gametophyte is parenchymatous and unique (exceptions discussed later) among red algae in producing carposporangia and spermatangia in distinct packages via a series of successive divisions (cf. Hommersand and Fredericq, 1990). Although these gametophytic

attributes are generally regarded as ancestral, they are more probably derived character states for this order.

Florideophyceae—Red algal species in the class Florideophyceae have been subjected to nearly a century of taxonomic thought dominated by unwavering emphasis on female reproductive anatomy and postfertilization development. In turn, this taxonomic framework has shaped the way that taxonomists view all aspects of red algal evolution; e.g., life history patterns, reproductive structures, and vegetative anatomy, with regards to ancestral vs. derived character states. Recent ultrastructural and molecular investigations have challenged the foundation of the dominant assumptions on which red algal classification is constructed, directing the taxonomic structure for these organisms down a new and often unexpected path.

Over a century ago, Schmitz (1892) started red algal systematics along a new course by placing emphasis on aspects of the female reproductive system and postfertilization development. In retrospect, it is a testament to Schmitz's intuition and appreciation of red algal species that he took this path, although the sheer wonder of red algal life histories alone could justify such an approach. In red algae, there are no motile stages in the life history, and this, in turn, manifests itself in an unusual complement of reproductive structures (Fig. 3). The full dynamics of this life history were realized through the cytological work of Yamanouchi (1906) while investigating the genus *Polysiphonia*. In short, male gametophytes produce spermatia that are released into the water column to contact passively trichogynes (long receptive extensions of the oogonia, termed carpogonia) that extend beyond the surface of the female gametophyte (Fig. 3). The male nucleus makes its way down the central channel of the trichogyne to fuse with the haploid nucleus of the carpogonium, the fusion product of which develops on the female gametophyte into a diploid generation termed the carposporophyte. In some species, the carposporophyte can develop directly from the carpogonium, but it is common for the fertilized carpogonium to transfer the diploid nucleus (directly or indirectly) to a “vegetative” cell of the thallus, termed an auxiliary cell, from which carposporophyte development initiates. The carposporophyte remains dependent on the female gametophyte and produces a number of carposporangia, each of which releases a diploid carpospore (Fig. 3). This nonflagellate spore attaches to suitable substrate and initiates vegetative development to yield the sporophyte generation. The florideophycean sporophyte is called a tetrasporophyte because meiosis characteristically results in sporangia with four spores; these in turn release to develop into the gametophyte generation (Fig. 3). We would argue that this is truly the most elaborate sexual life history among the macrophytic algae.

Schmitz was not alone in changing the tide of red algal taxonomy; his work was accepted and embellished by key players in red algal systematics, notably Oltmanns (1904–1905) and Kylin (1932, 1956). Kylin, in particular, codified red algal taxonomy based on his interpretation of comparative red algal morphology. Kylin's scheme recognized the Acrochaetiaceae with their sessile carpogonia as basal to other members of the Nemaliales, which produce distinct carpogonia-bearing branches, but for which carposporophytes still developed directly from the fertilized carpogonium. In more “advanced” systems, the fertilization nucleus is transferred to a remote (nonprocarpy) or nearby (procarpy) auxiliary cell from which the carposporophyte develops. Kylin (1956) further dis-

“Typical” Florideophyte Life Cycle

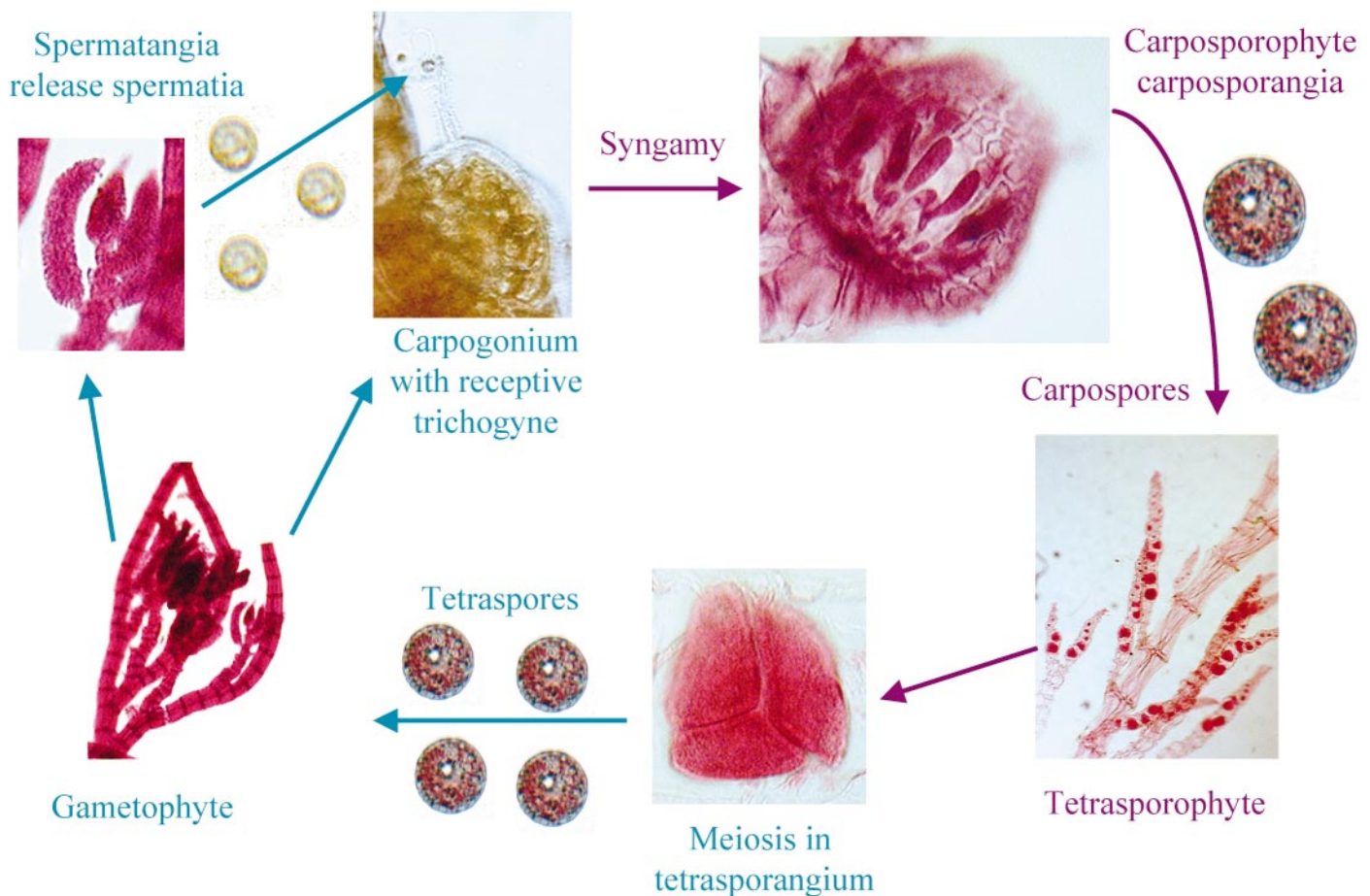


Fig. 3. A generic look at the “typical,” albeit remarkable, florideophyte life history. Blue and purple text and arrows represent haploid and diploid stages, respectively. Consult text for a description of the structures.

tinguished between the case in which the auxiliary cell is present before or in the absence of fertilization vs. production only following fertilization (Fig. 4), a condition he considered the peak in red algal evolution. Fritsch (1945) and Feldmann (1952) also had much influence in establishing the *Acrochaetaceae* as ancestral among the *Florideophyceae*.

The first break with the Schmitz/Kylin system came with the establishment of the *Bonnemaisioniales* (cf. Feldmann, 1952) based on life history studies that established that members of the *Naccariaceae* and *Bonnemaisioniaceae* possessed heteromorphic life histories in which a conspicuous gametophyte was followed by a microscopic filamentous or crustose tetrasporophyte (cf. West and Hommersand, 1981), in contrast to the isomorphic life history found in *Polysiphonia* and most red algae. Subsequent life history studies of a variety of red algae grown in culture demonstrated that many unrelated red algal species had heteromorphic life histories (cf. West and Hommersand, 1981). For this and other reasons, Dixon (1973) downgraded the significance of life history in classification of red algae and subsumed the *Bonnemaisioniales* and the *Gelidiales* under an emended order *Nemaliales*. Guiry (1978) ini-

tiated a controversial split with the existing paradigm by erecting the *Palmariales* for certain members of the *Rhodymeniales* based on aspects of tetrasporangial development rather than female reproductive anatomy and postfertilization development (unknown for these species at that time). Pueschel and Cole (1982) dramatically challenged the traditional classification on the basis of pit plug ultrastructure and provided support for some earlier contentious ordinal proposals including the *Bonnemaisioniales*, *Corallinales* (formally proposed later by Silva and Johansen, 1986), *Gelidiales*, and *Palmariales*, as well as for the new orders *Batrachospermales* and *Hildenbrandiales*. Hommersand and Fredericq (1988) later formally reinstated the *Gelidiales* following detailed anatomical investigations, whereas Fredericq and Hommersand (1989) proposed the *Gracilariales* on the basis that the carposporophyte developed directly from a carpogonial fusion cell rather than an auxiliary cell as had previously been thought. In the same year, Maggs and Pueschel (1989) established the *Ahnfeltiales* based on the presence of naked pit plugs that lacked caps and membranes and a carposporophyte that developed outwardly directly from the terminal fertilized carpogonium. Molecular data were com-

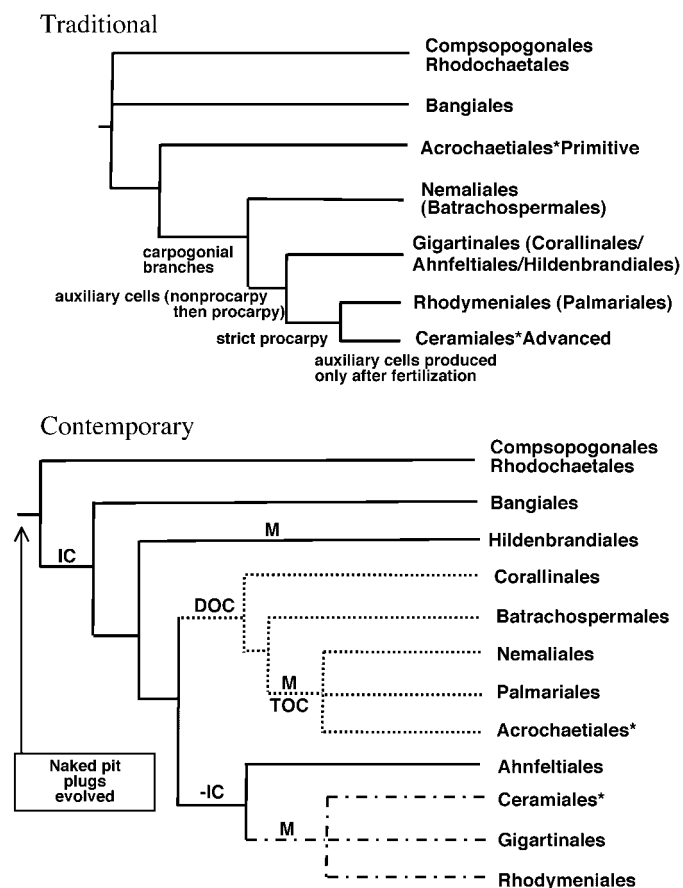


Fig. 4. Schematic representation of red algal evolution from traditional (Kyllin, 1956) and contemporary (Pueschel, 1994; Saunders and Bailey, 1997) perspectives. Dotted and dash/dot lines lead to extant members of lineages 2 and 4, respectively (cf. Fig. 2). IC = gain (– indicates loss of this same feature) of single (inner in later taxa) cap layers; M = gain of cap membranes; DOC and TOC represent gain of domed and thin (plate) outer cap layers in lineage 2; * highlight the putatively primitive Acrochaetiales and advanced Ceramiales.

combined with anatomical studies by Saunders and Kraft (1994) to propose the Plocamiales and later, the Halymeniales (Saunders and Kraft, 1996). Subsequent investigations have contributed to the recognition of six additional orders (discussed earlier).

On the phylogenetic front, Pueschel (1994) presented a detailed hypothesis in which naked pit plugs (lacking covering membranes and caps at their cytoplasmic faces) were regarded as ancestral and all taxa with two cap layers were derived from a common ancestor. Pueschel argued for the latter taxa that the domed outer cap was ancestral to the thin outer plate (Fig. 4) and that the presence of cap membranes was a derived state. Molecular studies using SSU (Saunders and Bailey, 1997) have confirmed Pueschel's hypothesis and clarified relationships among the many other florideophyte orders for which plug features fail to provide a distinguishing character (cf. Fig. 2). A significant result has been the recognition that the Acrochaetiales are a recently derived order and that the Ceramiales are not the pinnacle of red algal evolution (Fig. 4). Saunders and Kraft (1997) designated the four major florideophyte groupings resolved in the previous study as lineages 1 through 4 and defined them on the basis of pit plug attributes

(Figs. 2 and 4). Harper and Saunders (2004) and Saunders et al. (2004) provided detailed reviews of the orders, and component families of the four florideophyte lineages (summarized in Fig. 2). We consider that the time for formal taxonomic recognition of these lineages is overdue. Prior to taxonomic designation for these ordinal assemblages, however, it is necessary to consider red algal supraordinal taxonomy.

PREVIOUS TAXONOMIC PROPOSALS

Once a system of classification becomes widely adopted, it takes on many of the attributes of a creed. Not only does it constitute the framework about which the botanist does his thinking but it rapidly becomes a substitute for it . . . To function properly, all systems must be kept in a fluid and flexible state (Arnold, 1948, pp. 3–4).

Dixon (1973) provided a summary of red algal supraordinal taxonomy until that time. By the early 1900s, red algal systematists had generally settled on a single class, Rhodophyceae, with the two subclasses Bangiophycidae and Florideophycidae. Dixon (1973) discussed a trend during the 1900s to raise the status of all major algal groups and treat them as phyla, in this case the Rhodophyta, with the two major groups now recognized at the class level. Dixon considered the issue of whether the two major divisions should be recognized at the subclass or class level and concluded, based largely on differences in vegetative development (intercalary vs. apical), that two classes were justified. Gabrielson et al. (1985) subsequently argued that the Bangiophycidae are paraphyletic and lack a distinguishing synapomorphy and therefore only a single class, Rhodophyceae, with two subclasses is warranted. This argument clearly lacks validity—the Bangiophycidae are equally paraphyletic and wanting of a unifying synapomorphy regardless of taxonomic rank. Clearly, all of the information must be considered in trying to frame a contemporary system of taxonomy for red algae, not only the monophyly of constituent lineages, but also the antiquity and diversity of these same lineages.

Magne (1989) has provided the only substantive “bottom-up” attempt at reforming supraordinal classification among the red algae. He specifically challenged the lack of monophyletic groupings and proposed three subclasses: Archaeorhodophycidae for those red algae lacking sporangia (in essence the Porphyridiales sensu lato); Metarhodophycidae for those orders in which members converted only a portion of the parent cell to a sporangium (Compsopogonales, Erythropeltidales, Rhodochaetales); and the Eurhodophycidae for those taxa that he considered to have true sporangia (complete protoplasm converted to sporangia) including the Bangiales and Florideophyceae. Although Magne's system comes closer to recognizing monophyletic lineages (Archaeorhodophycidae are the exception), the recognition of these major units at the subclass level fails to acknowledge the substantial diversity within and between the various lineages. Nonetheless, Magne's contribution is significant in recognizing the need for more than two upper-level groups, in acknowledging a relationship between the Bangiales and Florideophyceae and opening the door for new proposals on red algal supraordinal taxonomy. Silva (1996, p. 912) rejected Magne's proposals, noting that “despite significant differences, there is sufficient common ground among the Archaeorhodophycidae, Metarhodophycidae, and Bangiales to warrant the traditional recognition of the Bangiophycidae . . . at least for pedagogical purposes.” Although we

are sympathetic with this point, the weight of evidence dictates that the previous taxonomic entities are not closely allied and thus the taxonomic system currently in place needs revision.

Ironically, at the highest levels of eukaryote taxonomy ("top-down approach") the significance and antiquity of the red algae is recognized, and the group is granted, along with the Glaucophyta, kingdom or subkingdom status in some systems (e.g., Cavalier-Smith, 1981, 1998). In his 1998 summary, Cavalier-Smith included infrakingdom rankings for the Glaucophyta and Rhodophyta in his subkingdom Biliphyta, which was considered as probably a paraphyletic assemblage. Cavalier-Smith (1998) further considered that the Bangiophyceae were so diverse that two classes were warranted: Bangiophyceae sensu stricto for the Bangiales and Rhodochaetales, which have pit connections; and Rhodellophyceae for the Porphyridiales, Cyanidiales, and Compsopogonales, which he considered lacked pit plugs. Unfortunately for this system, the Compsopogonales have members with pit plugs, and neither of his two groupings was monophyletic based on analyses of any of the available anatomical or molecular evidence (Fig. 2). At the same time, Cavalier-Smith established the subphylum Rhodellophytina for his new class and united his Bangiophyceae sensu stricto with the Florideophyceae as a new subphylum Macrorhodophytina. Again, neither of these groupings is monophyletic, and the status of the Erythropeltidales was left equivocal. Doweld (2001) established the kingdom Rhodymeniobiota including the subkingdoms Cryptomonadobiotina, Glaucobiotina, and Rhodymeniobiotina. This kingdom is not monophyletic, but the recognition of distinct subkingdoms for the glaucophytes and rhodophytes, although they should be included within the kingdom Plantae, represents an improvement to Cavalier-Smith's (1998) system. A further advancement in Doweld's classification is recognition of a distinct phylum for cyanidiophytes (Cyanidiophyta) relative to the remaining rhodophytes.

Within the Florideophyceae themselves, the biggest revisionist attempt was provided by Chadeaud (1960). In this work, we find an attempt at supraordinal taxonomy in the Florideophyceae in which he recognized the Eo-floridées (Acrochaetales, Eu-Nemaliales), Meso-floridées (remaining Nemaliales, Gigartinales, Rhodymeniales, etc.), and the Meta-floridées (Bonnemaisionales, Ceramiales). We now know that this perspective of the "primitive" Acrochaetales leading to the "advanced" Ceramiales is erroneous, so that Chadeaud's system is not natural (Fig. 4).

A CONTEMPORARY TAXONOMIC PERSPECTIVE

Our understanding of the phylogeny of red algae, and hence their classification, is presently in a period of major upheaval unprecedented since the end of the nineteenth century . . . revisions are potentially as far-reaching as those that occurred in the Chlorophyta in the 1970s and early 1980s (Garbary and Gabrielson, 1990, p. 478).

It is obvious from the previous discussion that red algae are an old and diverse lineage of organisms at all levels (morphology to molecules). Any revisionist attempt at red algal classification must incorporate this richness, as well as strive to recognize monophyletic groupings. Much work has been completed over the past decade, particularly for the Florideophyceae and more recently for the Bangiophyceae, to resolve monophyletic lineages, but there has been general (exceptions noted previously) hesitation to implement taxonomic changes

at the supraordinal level. Here we merge the recently acquired phylogenetic knowledge with the fossil and molecular evidence on the antiquity of the red algal lineages to provide a new and comprehensive system of classification. In so doing, we have attempted to use available, particularly typified, names as discussed in the International Code of Botanical Nomenclature (hereafter ICBN; Greuter et al., 2000).

Kingdom Plantae

Subkingdom Rhodoplantae G.W. Saunders et Hommersand subregnum nov.

Plantae sine flagellis omnino; materia photosynthetica in cytoplasmate condita; lamellae chloroplasti non-aggregati; pigmenta accessoria (incl. "phycoerythrin" et "phycocyanin") in corporibus in pagina lamellae chloroplasti dictis "phycobilisome."

Eukaryotic organisms lacking flagella in all life history stages; photosynthetic reserve stored in the cytoplasm; plastids with non-aggregated thylakoids; accessory pigments including phycoerythrin and phycocyanin in phycobilisomes on the thylakoid surfaces.

Comments—Although we concur with Cavalier-Smith (1998) that the red algae deserve subkingdom status within kingdom Plantae, we agree with Doweld (2001) that they should not be included in the same subkingdom as Glaucophyta. We restrict subkingdom Biliphyta Cavalier-Smith (1998; originally proposed as a kingdom, Cavalier-Smith, 1981) to the Glaucophyta and establish a separate subkingdom for red algae in the kingdom Plantae. In our opinion, the descriptive (i.e., nontypified) name Rhodoplantae is the best choice for the red algae because Thuret (1855) was first to unite the bangiophycean and florideophycean algae together into a taxonomic construct for which he used the name Rhodophyceae Ruprecht (cf. Ragan and Gutell, 1995). We thus reject the typified name Rhodymeniobiotina Doweld, as is permitted under the ICBN (Art. 11.9).

Phylum 1: Cyanidiophyta Moehn ex Doweld 2001

Unicellular red algae inhabiting extreme environments; Golgi associated with endoplasmic reticulum, cell walls thick and proteinaceous; production of endospores; heterotrophic capacity.

Class Cyanidiophyceae Merola et al., 1981

Characters as for phylum.

Order Cyanidiales T. Christensen 1962

Comments—It is clear that the Bangiophyceae are paraphyletic to the Florideophyceae (Freshwater et al., 1994; Ragan et al., 1994; Saunders and Kraft, 1997) and that the Cyanidiales are more evolutionarily divergent from the remaining red algae as are phyla and classes of organisms in other kingdoms relative to one another (discussed earlier). We consider that this lineage warrants distinction at the level of phylum, which was advocated also by Doweld (2001). Seckbach (1987) established the phylum Prerhodophyta for this lineage, which has unfortunate evolutionary connotations. To the best of our knowledge, this name has not been validly published because Seckbach (1987) failed to provide a Latin diagnosis and we were unable to identify subsequent validation in the literature. Further, it is a descriptive name, and its use is thus not required

under the ICBN. Doweld (2001) has provided a typified designation to this lineage at the phylum level, which we accept here. At the current time, only the single order, Cyanidiales T. Christensen, and family, Cyanidiaceae Geitler, are recognized in this phylum. Considering the substantial genetic diversity among the isolates studied thus far (Gross et al., 2001; Pinto et al., 2003), future taxonomic divisions within this group are likely.

Phylum 2: Rhodophyta Wettstein 1901

Comments—This name has long been associated with red algae at the phylum level. The application of a typified name, Rhodymeniophyta, by Doweld (2001) is a superfluous act that will only add unnecessary confusion to the taxonomic literature. We thus retain the original descriptive name.

Subphylum 1: Rhodellophytina Cavalier-Smith 1998

Unicellular or pseudofilamentous red algae with variable plastid morphologies and organellar associations; sexual reproduction unknown.

Class Rhodellophyceae Cavalier-Smith 1998

Characters as for subphylum.

Order 1 “Porphyridiales 1” (in Fig. 2; including *Rhodella*, on which the class and subphylum are based)

Order 2 Stylonematales K. Drew 1956 (Porphyridiales 2 in Fig. 2, includes Stylonemataceae K. Drew)

Order 3 Porphyridiales Kylin ex Skuja 1939 (Porphyridiales 3 in Fig. 2, includes Porphyridiaceae Skuja)

Comments—Although we would prefer a taxonomic elevation of the Archaeorhodophycidae Magne (1989; his group was largely monophyletic, and use of this taxon would be consistent with proposals for other subphyla discussed later), we use a restricted (remove Cyanidiales and Compsopogonales) concept of Cavalier-Smith’s (1998) subphylum Rhodellophytina, which is presumably based on *Rhodella*, i.e., a typified name, and can be unambiguously assigned to this group. We similarly emend his class Rhodellophyceae. Cavalier-Smith’s taxa are problematic in that they are not based on a “legitimate name of an included family based on a generic name” (ICBN Art. 16.1) and are not, as we understand the code, automatically typified. This presumably could be remedied when necessary taxonomic proposals are applied to Porphyridiales 1 (Fig. 2), which include *Rhodella* and currently lack familial or ordinal level classification. We have refrained from presenting formal taxonomic proposals for Porphyridiales 1 pending inclusion of *Phragmonema*, type of the family Phragmonemataceae, in overall phylogenetic analyses among porphyridialean algae. Classification for this subphylum is thus an interim recommendation to reduce unnecessary taxonomic congestion in the literature. This class is likely paraphyletic and, as was the case for the Cyanidiophyceae, will need considerable taxonomic restructuring in light of the exceptional levels of divergence noted among and within the three component lineages. Silva (1996) provides an excellent summary of the nomenclature pertaining to this group, particularly with regards to the ordinal designations.

Subphylum 2: Metarhodophytina G.W. Saunders et Hommersand subphylum nov.

Metarhodophycidae Magne *Cryptogamie Algologie* 10: 112 (1989).

The characters of subphylum Metarhodophytina are consistent with the subclass Metarhodophycidae Magne (1989); the former is validated by citation of the latter taxon. The characters are essentially as outlined next for the single class included in this lineage.

Class Compsopogonophyceae G.W. Saunders et Hommersand classis nov.

Rhodophyta cum monosporangiis et spermatangiis separatis ex cellulis usitatis per parietes curvatos; corpus dictus “Golgi” cum reticulo endoplasmatico consociatus; lamella cingens in chloroplasto adest; historia vitae (ubi cognita) generationibus duobus.

Red algae with monosporangia and spermatangia usually cut out by curved walls from ordinary vegetative cells; Golgi-ER association; encircling thylakoids in the plastid; life history biphasic if known.

Order 1 Compsopogonales Skuja 1939: 34. (includes Boldiaceae Herndon and Compsopogonaceae Schmitz)

Order 2 Erythropeltidales Garbary et al. 1980 (includes Erythrotrichiaceae G.M. Smith [cf. Silva, 1996])

Order 3 Rhodochaetales Bessey 1907 (includes Rhodochaetaeaceae Schmitz)

Comments—The new subphylum is an elevation in rank of Magne’s (1989) Metarhodophycidae. Although it could be argued that the Erythropeltidales be subsumed into the Rhodochaetales, the two orders are distinct in a number of regards (Zuccarello et al., 2000) and are as divergent at the molecular level as are some of the florideophyte orders relative to one another. We thus continue to recognize these orders as distinct. There is considerable confusion regarding the authorities to many of the taxa in this subphylum, and particularly the Erythropeltidales; the reader is directed to Silva (1996) in this regard. A recent study by Nelson et al. (2003) indicated that at least some of the taxa now included in this lineage have lost the diagnostic pattern of sporangial and spermatangial development and converged on the mode of division more typical of the Bangiales. This is an interesting discovery, one that requires considerably greater investigation by red algal systematists, but not one that would alter the overall taxonomic hierarchy presented here.

Subphylum 3: Eurhodophytina G.W. Saunders et Hommersand subphylum nov.

Eurhodophycidae Magne *Cryptogamie Algologie* 10: 112 (1989).

The characters of subphylum Eurhodophytina are consistent with the subclass Eurhodophycidae Magne (1989); the former is validated by citation of the latter taxon. General characteristics include: Golgi in an endoplasmic reticulum/mitochondrial association; life histories where known biphasic or triphasic; pit plugs present in at least one stage of sexual life histories.

Comments—Macrorhodophytina Cavalier-Smith (1998) was a subphylum erected to contain all of the Eurhodophytina as defined here, as well as the Rhodochaetales. As circumscribed, it is too broad to be applied to any of our groups, and because it is a descriptive, rather than typified name, it cannot be un-

ambiguously allied to a specific group of taxa. Use of priority is not mandatory for taxa above the rank of family (ICBN Art. 11.9) and is only recommended (ICBN Art. 16B) for typified taxa (i.e., descriptive taxa are not included), and thus we reject Macrorhodophytina here in favor of an elevated status for Magne's Eurhodophycidae, which was a monophyletic grouping and is thus unambiguously assignable to this lineage. We consider that the two distinct lineages in this subphylum should be recognized at the class level.

Class 1: Bangiophyceae A. Wettstein 1901

Life history biphasic, heteromorphic, gametophyte macroscopic, initially uniseriate, becoming pluriseriate or foliose by diffuse growth; carposporangia and spermatangia produced in packets by successive perpendicular divisions; sporophyte filamentous, with pit plugs, a single cap layer present but lacking membranes; typically forming concho-spores in fertile cell rows.
Order Bangiales Nägeli 1847

Comments—Although monophyly of Bangiales is beyond dispute (cf. Müller et al., 2001), the component genera are not natural entities (cf. Müller et al., 2003; and references therein) and are characterized by SSU divergence levels among species that dwarf some ordinal level distances among florideophytes (Oliveira et al., 1995). A considerable amount of taxonomic work is required in this group, which will undoubtedly lead to the recognition of many more genera and families (currently a single family, Bangiaceae) among these morphologically conservative species.

Class 2: Florideophyceae Cronquist 1960

Growth by means of apical cells and lateral initials forming branched filaments in which the cells are linked throughout by pit connections; life history fundamentally triphasic consisting of gametophytic, carposporophytic, and tetrasporophytic phases; reproductive cells (monosporangia, spermatangia, carposporangia, tetrasporangia) generally terminal or lateral on the filaments; carpogonia terminal or lateral, bearing an apical extension, the trichogyne, to which the spermatangia attach; carposporophyte developing directly from the carpogonium or its derivative.

Comments—Doweld (2001) introduced the typified name Rhodymeniophyceae for this class. Although some may argue that it would be better to use a typified name for this taxonomic entity (i.e., move away from descriptive names, cf. Silva, 1996), the Florideophyceae trace back to the Floridées Lamouroux (1813)—the first time red algae were grouped together as a distinct lineage. It has also been applied for over a century to an unambiguous taxonomic construct. We thus reject Rhodymeniophyceae as an unnecessary name that will only add confusion to the taxonomic literature. The included subclasses (discussed next) constitute the traditional Florideophyceae and are derived from the four lineages of Saunders and Kraft (1997).

Subclass 1: Hildenbrandiophycidae G.W. Saunders et Hommersand subclassis nov.

Hildenbrandiales Pueschel et K.M. Cole *American Journal of Botany* 69: 718 (1982).

The characters of subclass Hildenbrandiophycidae are con-

sistent with the order Hildenbrandiales Pueschel and Cole (1982); the former is validated by citation of the latter taxon. Diagnostic features include: red algae that are crustose and smooth to tubercular or with erect branches; composed of a basal layer of laterally adhering branched filaments and laterally adhering simple or branched erect filaments; tetrasporangia zonately or irregularly divided, apomeiotic, borne in ostiolate conceptacles; sexual reproduction unknown; pit plugs with a single cap layer and membrane.
Order Hildenbrandiales Pueschel et K.M. Cole 1982: 718.

Comments—Hildenbrandiales have not changed in familial composition since granted ordinal designation (cf. Pueschel and Cole, 1982).

Subclass 2: Nemaliophycidae Christensen 1978

Pit plugs characterized by two cap layers.
Order Nemaliales Schmitz in Engler 1892
Other orders listed in Fig. 2 (lineage 2)

Comments—Nemaliophycidae have been the subject of a recent taxonomic review (as lineage 2), and the reader is directed to Harper and Saunders (2002) for an updated perspective of the included orders and their constituent families (summarized in Fig. 2).

Subclass 3: Ahnfeltiophycidae G.W. Saunders et Hommersand subclassis nov.

Carpogonia terminalia sessiliaque; carposporophytum extrorsum exoriens; obturamenta intercellularia nuda, opercula et membrans carens.

Carpogonia terminal and sessile; carposporophyte developing outward; pit plugs naked, lacking caps and membranes.

Order 1 Ahnfeltiales Maggs et Pueschel 1989: 349.
Order 2 Pihelliales Huisman et al. 2003

Comments—Huisman et al. (2003) have recently established the order Pihelliales and should be consulted along with Maggs and Pueschel (1989) for a discussion of diagnostic features, as well as family-level taxonomy.

Subclass 4: Rhodymeniophycidae G.W. Saunders et Hommersand subclassis nov.

Rhodophyta cum historis vitae generaliter generationibus tribus; carposporophytum ex carpogonio vel cellula fusioni statim exoriens, vel cellula auxiliari indirecte exoriens; obturamenta intercellularia cum membranis solum (Gelidiales cum operculo intrinseco unico).

Red algae with sexual life histories generally triphasic; carposporophyte developing directly from the carpogonium or carpogonial fusion cell, or indirectly from an auxiliary cell that has received the postfertilization diploid nucleus; pit plugs with membranes only (single inner cap in Gelidiales).
Order Rhodymeniales Schmitz in Engler 1892: 19.
Other orders listed in Fig. 2 (lineage 4).

Comments—Saunders et al. (2004) have recently completed for Rhodymeniophycidae (as lineage 4) a comprehensive molecular systematic survey, which includes a listing of orders with their recognized families (summarized in Fig. 2).

CONCLUSION

It has been more than twenty years since Pueschel and Cole (1982) introduced ultrastructural criteria to ordinal-level definitions for red algae and a decade since the pioneering molecular studies of Freshwater et al. (1994), Ragan et al. (1994), and Saunders and Kraft (1994) provided new insights into red algal phylogeny. These new and powerful ultrastructural and molecular techniques have, in combination with critical anatomical investigations, resulted in profound changes to red algal taxonomy at and below the ordinal level. At the same time, these methods have also provided insights into the antiquity and diversity of the red algal lineages, the major ones of which are themselves more divergent than entire classes and phyla in other lineages and are remarkably consistent with inferences from the fossil record as to the age of the various red algal lineages. Despite all of the evidence to the contrary, however, mainstream red algal systematists seemed locked into a system in which, at best, only two classes were recognized—one of these fully acknowledged as paraphyletic. However, outside the realm of mainstream algal systematics, in the cyanidiophyte literature (e.g., Seckbach, 1987) as well as taxonomic investigations at the kingdom level (e.g., Cavalier-Smith, 1998), there was recognition that the system of classification used for the red algae was deflated and in need of revision.

Change is what we have provided here. We do not consider that we have settled once and for all the conundrums of red algal taxonomy. We fully acknowledge that at least one of our groups, Rhodellophytina, is not monophyletic and that major revisions are required within the Cyanidiophyceae and Bangiophyceae to better reflect the levels of diversity in these lineages. We hope to have removed a long-standing obstruction to change at the supraordinal level among red algae while moving red algal classification closer to a natural system.

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