Biodata of **Juan M. Lopez-Bautista**, author of ***"Red Algal Genomics: A Synopsis"***

Dr. Juan M. Lopez-Bautista is currently an Associate Professor in the Department of Biological Sciences of The University of Alabama, Tuscaloosa, AL, USA, and algal curator for The University of Alabama Herbarium (UNA). He received his PhD from Louisiana State University, Baton Rouge, in 2000 (under the advisory of Dr. Russell L. Chapman). He spent 3 years as a postdoctoral researcher at The University of Louisiana at Lafayette with Dr. Suzanne Fredericq. Dr. Lopez-Bautista's research interests include algal biodiversity, molecular systematics and evolution of red seaweeds and tropical subaerial algae.

E-mail: **jlopez@ua.edu**

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RED ALGAL GENOMICS: A SYNOPSIS

JUAN M. LOPEZ-BAUTISTA
Department of Biological Sciences, The University of Alabama, Tuscaloosa, AL, 35487, USA

1. Introduction

The red algae (or Rhodophyta) are an ancient and diversified group of photoautotrophic organisms. A 1,200-million-year-old fossil has been assigned to *Bangiomorpha pubescens*, a *Bangia*-like fossil suggesting sexual differentiation (Butterfield, 2000). Most rhodophytes inhabit marine environments (98%), but many well-known taxa are from freshwater habitats and acidic hot springs. Red algae have also been reported from tropical rainforests as members of the subaerial community (Gurgel and Lopez-Bautista, 2007). Their sizes range from unicellular microscopic forms to macroalgal species that are several feet in length. In aquatic environments, they are found as members of the planktonic and benthonic communities. Rhodophytan life cycles are highly contrasting. They include simple life cycles characterized by binary cell division and complex triphasic, haplo-diplobiontic life cycles, with one haploid (gametophytic) and two diploid (tetrasporophytic and carposporophytic) generations. The latter life cycle can be either isomorphic or heteromorphic. This is dependent on whether or not gametophytes and tetrasporophytes are morphologically similar or dissimilar, respectively. Rhodophyta share many biochemical and ultrastructural features with other algal groups. However, they are often characterized by a unique set of features such as the absolute lack of flagella and centrioles, presence of phycobilisomes and unstacked thylakoids in the chloroplast, absence of parenchyma, and presence of pit-connections between cells. Rhodophyta are characteristically red in color, but other shades of green, brown, and purple are common. Photosynthetic pigments include chlorophyll *a*, which is accompanied by accessory pigments or phycobiliproteins. These phycobiliproteins are responsible for the alga's red coloration. They include water-soluble pigments such as phycoerythrin (red), phycocyanin (blue), and allophycocyanin (blue-greenish) (Grossman et al., 1993). These red and blue pigments are associated into phycobilisomes, a light-harvesting complex, on the surface of thylakoids. In this report, a summary is presented of genomic studies targeting this algal group, the Rhodophyta, with suggestions for future research in phylogenomics.

Red algae systematics is an exciting and dynamic field, because of recent advancement in molecular biology, computational technology, and phylogenetics. New classification systems and new taxa descriptions are frequent in recent systematic literature. The two most recent current systems of classification were

proposed by Saunders and Hommersand (2004) and Yoon et al, (2006). These systems recognize the red algae as one of the earliest divergent groups in the Plant Kingdom, the monophyly of Florideophyceae, a redefined Bangiophyceae *sensu stricto*, and the sister position of Cyanidiales to the rest of the red algae. Both systems recognize the class level of the latter group, as Cyanidiophyceae, a level previously revived by Seckbach (1999). This intriguing group of ancient red algae is found inhabiting acidic hot springs.

During the last 15 years, rhodophytan systematics has made significant progress due to the advent of molecular-based analyses (Gurgel and Lopez-Bautista, 2007). The two most commonly used genes are the chloroplast-encoded *rbc*L large subunit of the ribulose 1,5-bisphosphate carboxlase/oxygenase enzyme and the nuclear-encoded ribosomal cistron encoding 18S, ITS1, 5.8S, ITS2, and the 28S rDNA regions (Freshwater et al., 1994; Harper and Saunders, 2001; Hommersand et al., 2006). The latest systematic account by Yoon et al. (2006), using the *psa*A (PSI P700 chl *a* apoprotein A1) and *rbc*L coding regions resulted in the recognition of seven major lineages in Rhodophyta. These authors proposed Rhodophyta to be classified in two new subphyla, the Cyanidiophytina with a single class Cyanidiophyceae and the Rhodophytina, which include six classes: Bangiophyceae, Compspogonophyceae, Florideophyceae, Porphyridiophyceae, Rhodellophyceae, and Stylonematophyceae. Recently, a new order, Rufusiales, has been inferred as a potential sister group to Stylonematophyceae (Zuccarello et al., 2008). A member of this order, *Rufusia pilicola*, is found in a rather unusual habitat, sloth fur.

Representatives of red algae are used as an economic resource for humans. Diverse industries based on red seaweeds account several billions of dollars per year. Most of these industries are related to human consumption in the form of aquaculture and phycocolloid production (Gurgel and Lopez-Bautista, 2007). Red seaweeds are used as food. This is well represented by the processed food nori (*Porphyra* spp.) and many other red algae. The phycocolloid industry harvest many different kinds of red seaweeds for their highly valuable gels. These seaweeds include carrageenophytes (*Chondrus crispus* and other Gigartinaleans) and agarophytes (i.e., species of *Gracilaria* and *Gelidium*). From a negative point of view, some red algae have been deemed as invasive species. Recently, reports of direct or indirect human introductions of nonindigenous red algae have accumulated; these reports include areas of Australia, Brazil, Europe, and USA. Negative effects from these invasive species include losses in native biodiversity, detrimental effects to the fishing industry, and a loss of recreational activities (Ruiz et al., 2000; Ribera-Siguan, 2003).

The importance of red algae is undeniable. From the biological point of view, they are amid the most ancient eukaryotic photobionts on our planet. A plethora of molecular phylogenies have accumulated in the last decade. This has resulted in a modern rhodophytan classification system that reflects evolutionary relationships. With the advancement of new molecular biology techniques, the development of faster computer systems, and increasingly more affordable DNA

sequencing, the analysis of complete red algal genomes has become a tangible and desirable goal (Weber et al., 2007).

2. Nuclear Genomes of Red Algae

In a series of recent publications (Matsuzaki et al., 2004; Misumi et al., 2005; Nozaki et al., 2007), a 100%-complete nuclear genome sequence for the rhodophytan *Cyanidioschyzon merolae* was elucidated. This is the first published complete nuclear genome known for a red alga. More information on *C. merolae* Genome Project can be found at http://merolae.biol.s.u-tokyo.ac.jp/. The nuclear genome of *C. merolae* consists of 16,546,747 bp and 4,775 protein-coding genes were identified (Nozaki et al., 2007). Matsuzaki et al., 2004; Misumi et al., 2005; and Nozaki et al., 2007 have highlighted some notorious and interesting features for this microscopic rhodophyte, which lives in extreme environments. All histones genes in *C. merolae* are located on a single chromosome forming the most compact gene cluster ever reported. Telomeres termini in *C. merolae* are unique in having telomere repeats of AATGGGGGG at all chromosomal ends. Most plants have telomere repeats of TTTAGGG. Transposable elements, 26 class I elements (retrotransposons) and 8 class II elements (transposons), only account for 0.7% of the *C. merolae* genome. This is an extremely low value when compared with other genomes. Only three copies of the rRNA gene units and a low number of genes with introns (0.5%) were found in *C. merolae*. These set of characteristics have prompted these authors (Nozaki et al., 2007) to emphasize that the nuclear genome of *C. merolae* is not only unique but also "constitutes the simplest set of genomic features found in any nonsymbiotic eukaryote yet studied." These attributes are an example of a reductive evolution in a very small eukaryote organism. Furthermore, these features were considered plesiomorphic (ancestral) characters of the nuclear genome. As an alternative explanation, Nozaki et al. (2007) interpreted these genomic features as adaptations to the extreme environments.

Another ongoing project of a Cyanidiophyceae, *Galdieria sulphuraria*, has become available for comparison (Weber et al., 2004, 2007; Barbier et al., 2005). The *G. sulphuraria* genome project can be accessed at http://genomics.msu.edu/galdieria. Information on nuclear genome size for species of *Galdieria* have been reported between 10 and 17 Mbp (Barbier et al., 2005) and thus in the range with *C. merolae*. Although found in similar thermoacidophilic habitats, *C. merolae* and *G. sulphuraria* have various differences. While *C. merolae* is an aquatic obligate photoautotroph, reproducing by binary fission, and lacking a rigid cell wall, *G. sulphuraria* is a metabolically flexible (photoautotroph, heterotroph, and mixotroph), can live endolithically, reproducing by endospores, and contains a rigid cell wall (Oesterhelt et al., 2008; Barbier et al., 2005). Based on a comparative analyses between the *C. merolae* and >70% of the genome of *G. sulphuraria*, Barbier et al. (2005) concluded that over 30% of *G. sulphuraria* sequences have no similarity with genes from *C. merolae.* Furthermore, the same study estimated

that *G. sulphuraria* contain more introns, membrane transporters, and enzymes for carbohydrate metabolism than *C. merolae.* Some of these gene features are most likely attributed to the presence of a rigid cell wall and mixotrophic abilities demonstrated by *G. sulphuraria* (Oesterhelt et al., 2008; Barbier et al., 2005).

3. Chloroplast Genomes of Red Algae

The number of studies on chloroplast genome sequences for red algae includes more taxa than that for nuclear genomes. This fact maybe, partially, due to the smaller size of the chloroplast genome, which results in faster sequencing time and reduced fees. It could also be due to the wealth of valuable phylogenetic information revealed by the structure of the chloroplast genome. In green algae and land plants, for example, recent analyses of the architecture of the chloroplast genome (Pombert et al., 2005; Turmel et al., 2006; Pombert et al., 2006; Turmel et al., 2007) have challenged our previous understanding of evolution in Viridiplantae. In these remarkable studies, phylogenetic analyses of several genes as well as gene and intron content, gene order, and insertion/deletion of coding regions have uncovered the green algal ancestry of land plants. In Rhodophyta, studies on the architecture of the chloroplast genome have been reported in three of the seven classes (Table 1), which include two Cyanidiophyceae *C. merolae* (Ohta et al., 2003) and *Cyanidium caldarium* (Glöckner et al., 2000), one Bangiophyceae *Porphyra purpurea* (Reith and Munholland, 1993, 1995), and the Florideophyceae *Gracilaria tenuistipitata* var. *liui* (Hagopian et al., 2004).

In photosynthetic eukaryotes, chloroplast genome sizes range from 35 to 200 kb (Hagopian et al., 2004). Chloroplast genome features from rhodophytans are given in Table 1. These red algal chloroplast genomes are in the higher size range but show similar amounts of bp among them from 150 to 191 kb. Other rhodophytan plastid genomes also fall into the same range such as *Porphyra yezoensis* 185 kb (Shivji, 1991), *Griffithsia pacifica* 178 kb (Li and Cattolico, 1987), *C. crispus* 173 kb, and *Antithamnion* sp. 180 kb (Simpson and Stern, 2002). Surprisingly, rhodophytans lack introns. In contrast, the green lineage is known

Table 1. Chloroplast genome characteristics of red algae.

	Class: Cyanidiophyceae		**Class: Bangiophyceae**	**Class: Florideophyceae**
	C. merolae	***C. caldarium***	***P. purpurea***	***G. tenuistipitata***
Length (bp)	149,987	164,921	191,028	183,883
Genes	243	232	251	238
G + C (%)	37.6	32.7	33	29.1
rRNA operons	1	1	2	1
Introns	None	None	None	None
Reference	Ohta et al. (2003)	Glöckner et al. (2000)	Reith and Munholland (1995)	Hagopian et al. (2004)

to have many chloroplast introns. Reith and Munholland (1993) argued that the absence of introns might represent an ancestral character trait, since a similar situation is found in eubacteria. In terms of number of chloroplast rRNA operons, most red algae contain only one copy (including also *G. pacifica* [Shivji et al., 1992] and *C. crispus* [Leblanc et al., 1995a, b]); *P. purpurea* is the lone exception with a reported rRNA operon duplication (Reith and Munholland, 1995). Because of the sister relationship between the Bangiophyceae (*Porphyra*) and the Florideophyceans (*Gracilaria, Griffithsia,* and *Chondrus*) Hagopian et al. (2004) suggested that *Porphyra's* rDNA direct repeat was a condition that was lost secondarily in Florideophyceae.

Red algal chloroplasts have roughly the same number of genes. The range of genes in red algae fluctuates between 232 and 251. However, when the number of genes in the rhodophytan chloroplast genomes is compared with those from the green algae, a far greater distance is evident. Green algae and land plants have been shown to have only between 110 and 118 genes in the chloroplast (Hagopian et al., 2004). In this regard, we can consider the chloroplast genome of red plastids as having twice the number of genes than green plastids. Most of the genes found in the green lineages are related to photosynthesis and gene expressions. In contrast, most of the genes found in the red algal lineage are related to ribosomal proteins and photosynthesis components (Ohta et al., 2003). Chloroplast genomes of red algae have been shown to contain the most ancient repertoire of genes among the photosynthetic eukaryotes (Hagopian et al., 2004). This genome condensation is particularly remarkable in the Cyanidiophyceae, *C. merolae,* with up to 40% of its protein genes overlapped (Ohta et al., 2003), and in both, *C. merolae* and *C. caldarium,* where the median intergenic distance is shorter (14 and 60 bp, respectively) than other red algae (i.e., *P. purpurea* with 100 bp; Ohta et al., 2003). Chloroplast genomes from Cyanidiophyceae, *C. caldarium* and *C. merolae*, share a significant number of genes (Ohta et al., 2003). Many notable features of the red algal chloroplast genome can be interpreted as a result of their extremophilic characteristics (thermoacidophilic habitats). In these habitats, similar evolutionary selection pressures may help to maintain similar chloroplast genes (Glöckner et al., 2000).

Plastid genome evolution has been an exciting field since the publication of Mereschkowsky's hypothesis (1905) that explained for the first time that plastids evolved from endosymbiotic cyanobacteria (Raven and Allen, 2003). From this initial primary endosymbiotic event, three lineages evolved – Glaucocystophyta, Chlorophyta, and Rhodophyta. The origin of plastids from a single primary endosymbiosis that involved, a eukaryote and a cyanobacterium has been a common understanding (Keeling, 2004). However, recent investigations on the freshwater amoeba *Paulinella chromatophora* with a second and more recent primary endosymbiosis are challenging this concept (Rodriguez-Ezpeleta and Philippe, 2006). The green algae or Chlorophyta, one of the primary plastid lineages, in turn became the source for plastids via a secondary endosymbiosis event. This secondary green lineage includes the Euglenophyta and the Chlororachniophyta.

The plastids of red algae or Rhodophyta, a primary plastid lineage, through secondary endosymbiosis generated a diverse group of algal groups. This secondary red lineage includes the Cryptophyta, Heterokontophyta, Haptophyta, and probably some Dinoflagellates (Dinophyta) (Delwiche, 1999). One remarkable difference between these plastids and the free-living cyanobacteria is the reduction in both genome size and gene content, in the plastid genome. For example, plastid genomes encode for about 5–10% of proteins when compared with free-living cyanobacteria (Ravi et al., 2008). Genome size of the cyanobacterium *Synechocystis* PCC 6803 contains 3,573,470 bp and ca. 3,168 genes (Kaneko et al., 1996) while in red algae the genome size range is between 150 and 191 kb with a gene content fluctuating between 232 and 251 (Table 1). The reduction of the plastid genome size has been explained by implicating three mechanisms – loss of plastid genes lacking selective advantage, substitution of plastid genes by pre-existent nuclear genes, and transfer of plastid genes to the nuclear genome (Delwiche, 1999).

4. Mitochondrial Genomes of Red Algae

Studies on complete mitochondrial genomes of red algae are not as numerous as chloroplast genomes. In green algae, mitochondrial genomes have been analyzed for evolutionary relationships (Nedelcu et al., 2000; Pombert et al., 2006). In these chlorophytan lineages, two different mitochondrial genome types have been described – a reduced-derived and an ancestral type (Nedelcu et al., 2000). In other studies, comparative analyses of mitochondrial genomes are challenging their higher rank relationships among green algal lineages (Pombert et al., 2006). In red algae, complete analyses of the architecture of the mitochondrial genome have been reported (Table 2) for three (out of seven) classes of rhodophyta: the Cyanidiophycean *C. merolae* (Ohta et al., 1998), the Bangiophycean *P. purpurea* (Burger et al., 1999), and the Florideophycean *C. crispus* (Leblanc et al., 1995b).

In general, mitochondrial genome sizes fall into two extremes (Leblanc et al., 1995b). There are small mitochondrial genomes, which are usually found in animals. These genomes range between 14 and 42 kb, they are uniform in architecture, and are extremely compact. In contrast, green plant mitochondrial genomes are larger, more complex, and range in size from 200 to 2,400 kb (Leblanc et al., 1997).

Table 2. Mitochondrial genome characteristics of red algae.

	Class: Cyanidiophyceae	**Class: Bangiophyceae**	**Class: Florideophyceae**
	C. merolae	***P. purpurea***	***C. crispus***
Length (bp)	32,211	36,753	25,836
Genes	34	57	51
G + C (%)	27.2	33.5	27.9
Reference	Ohta et al. (1998)	Burger et al. (1999)	Leblanc et al. (1995b)

In Rhodophyta, mitochondrial genomes are small with a range in size from 25.8 to 36.7 kb. Further reports indicate a similar range in *Gracilariopsis lemaneiformis (40 kb), G. pacifica (25–28 kb), and C. caldarium* (33 kb) (Leblanc et al., 1997). Rhodophytan mitochondrial genomes are considerably smaller than green plants. However, rhodophytans have a genomic size in a similar range to the green algae (15.8–55.3 kb) (Nedelcu et al., 2000). Although Turmel et al. (2007) discovered in *Chlorokybus atmophyticus*, an early divergent clade of the charophycean lineage, an unexpectedly large (201,763 bp) mitochondrial genome. Analyses on *C. merolae*'s mitochondrial genome highlighted the similarities between its mitochondrial genome and those from animals and plants (Ohta et al., 1998). Compactness of genome in *C. merolae*, absence of introns, the encoding for only 34 proteins, presence of short intergenic spacers, and a high coding density explain in part the reduced size of *C. merolae* mitochondrial genome (Ohta et al., 1998). Small compact genomes are also reported for *P. purpurea* (Burger et al., 1999). Only 9% of its genome is without detectable coding content. Similarly, *C. crispus* (Leblanc et al., 1995b) includes a high coding density with only 4.8% of noncoding regions reported. Only one group II intron has been reported for *C. crispus* (Leblanc et al., 1995b). Two group II introns interrupt the LSU rRNA coding region for *P. purpurea* (Burger et al., 1999). According to Burger et al. (1999), mitochondrial genomes from *P. purpurea* and *C. crispus* are almost identical in gene content and order. Although the universal genetic code is used in mitochondrial genomes of land plants and some chlorophytes and heterokontophytes, there are a multitude of examples that deviate from the universal code (Leblanc et al., 1997). One example is the modification of the termination code UGA to tryptophan. This is the case for *C. crispus* (Leblanc et al., 1995b). However, this modification is absent in *C. merolae* or in *C. caldarium* (Ohta et al., 1998). These data seem to indicate that the stop UGA codon was the ancestral character state in Rhodophyta. Therefore, the UGA tryptophan codon represents an autoapomorphy for the *C. crispus* lineage (Ohta et al., 1998; Leblanc et al., 1995b).

There is a consensus in the scientific community that mitochondria have evolved through an endosymbiotic process (analogous to plastid evolution). This process involved a unicellular phagotrophic eukaryote engulfing prokaryotic organisms that eventually became (through endosymbiosis) the eukaryotic organelles. This view of a nucleus-bearing amitochondriate cell as the original eukaryote host cell has been debated. An alternate scenario that involves a prokaryotic host cell has been proposed (Embley and Martin, 2006). The endosymbiotic origin of the mitochondria can be traced back to eubacterial lineages, in particular to α-proteobacteria (Leblanc et al., 1997; Ohta et al., 1998). Although monophyletic in origin, the mitochondrial genome exhibits a wide diversity in gene size, order, and content in extant taxa. Approximately half of the mitochondrial gene set was lost in rhodophytes after the divergence from a common ancestor shared with chlorophytes (Burger et al., 1999). An evolutionary explanation for the rhodophytan genome compactness is that red algae lost genes at faster rates than green algae (Ohta et al., 1998). Mitochondrial genome diversity

is exemplified by the two extremes where one mitochondrial genome is larger and the other is smaller (Leblanc et al., 1997). The addition of newly sequenced mitochondrial genomes may help one to explain the aforementioned extreme size range. According to Leblanc et al. (1997), "paralogous evolution resulting from similar evolutionary constraints and strategies" are yet to be discovered.

5. Conclusions

The Rhodophyta are an ancient group of eukaryotes with over 6,000 species and can be found in most regions in the planet. They are considered the sister group to green algae and land plants. Over the last 15 years, there has been an increase in available sequence data for the analysis of red algal genomes. Perhaps, owing to their obvious presence and economical importance, green plants have been the common sources for genomic research other than red algae (Reyes-Prieto et al., 2006). Recommendations for future algal genomic research have been proposed. However, there are several criteria that need to be met before an algal candidate is selected. Waaland et al. (2004) highlighted the absence of major efforts to complete nuclear genome sequence from a macroalga. The only completed nuclear genome in Rhodophyta is that of *C. merolae*, a microscopic alga (Nozaki et al., 2007). Among the criteria to select algal candidates for genomic sequencing, Waaland et al. (2004) and Grossman (2005) proposed: growth in a defined medium, defined sexual life cycle, economic importance, evolutionary interest, ecological importance, uninucleate cells, and established background of scientific information. Of course, the researchers must also be both knowledgeable and belonging to a well-organized community of scientists. The data presented in this synopsis point out that the rhodophytans already investigated fall under the criteria of highly significant taxa for the evolution and ecology of extremophiles (Cyanidiophyceae) as well as for their economic importance (*Porphyra* spp., *Gracilaria* spp., *Chondrus crispus*, and more recently *Gracilaria changii* (Teo et al., 2007)). With the recent emergence of phylogenomics, a new area of research is becoming increasingly important in red algal genomics (Eisen and Fraser, 2003). Phylogenomics is a new field where, as described by Reyes-Prieto et al. (2006), genomics (the study of the function and structure of genes and genomes) has intersected with molecular phylogenetics (the study of the hierarchical evolutionary relationships among organisms, their genes, and genomes). There are some caveats while working with genome-scale phylogenies (as pointed out by Rodriguez-Ezpeleta et al., 2007). However, the application of this new field to molecular systematics is highly promising. A recent study by Li et al. (2006) has outlined a phylogenomic pipeline and discovered a significant endosymbiotic gene transfer from red algal genes shared with chromalveolates (see Blackwell, 2009 for discussion of names) and suggesting a monophyletic origin for some of the taxa under study. It is clear that phylogenomic research will be an ever increasing field in algal systematics. Thus, there is a need, as suggested by Waaland et al. (2004)

and pointed out by Grossman (2005), to select candidates for genomic studies that are "positioned at important evolutionary branchpoints." Yoon et al. (2006) defined the major lineages of red algae as consisting of seven classes. Our current knowledge of complete genomes of rhodophyta is circumscribed to only one class for a nuclear genome (Cyanidiophyceae; Nozaki et al., 2007). Chloroplast and mitochondrial genomes are known only for three different red algal classes (Cyanidiophyceae, Bangiophyceae, and Florideophyceae). Overall, only one rhodophytan genome, *C. merolae,* has been completely sequenced (nuclear, chloroplast, and mitochondrial) and accounts for a total of 16,728,945 bp for its entire genome (Nozaki et al., 2007). Several classes in the rhodophytan system (Yoon et al., 2006) are still lacking information for phylogenomic comparison including the Compsopogonophyceae, the Porphyridiophyceae, and the Rhodellophyceae. This phylogenomic information may provide a clearer vision of the systematics of Rhodophyta to understand the evolutionary history of this ancient group of red algae.

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7. References

Barbier, G., Oesterhelt, C., Larson, M., Halgren, R., Wilkerson, C., Garavito, R. M., Benning, C. and Wever, A.P.M. (2005) Comparative genomics of two closely related unicellular thermo-acidophilic red algae, *Galdieria sulphuraria* and *Cyanidioschyzon merolae*, reveals the molecular basis of the metabolic flexibility of *Galdieria sulphuraria* and significant differences in carbohydrate metabolism of both algae. Plant Physiol. **137**: 460–474.

Blackwell, W. (2009) Chromista revisited: a dilemma of overlapping putative kingdoms, and the attempted application of the botanical code of nomenclature. Phytologia **91**(2) (in press).

Burger, G., Saint-Louis, D., Gray, M. and Lang, B.F. (1999) Complete sequence of the mitochondrial DNA of the red alga *Porphyra purpurea*: cyanobacterial introns and shared ancestry of red and green algae. Plant Cell **11**: 1675–1694.

Butterfield, N.J. (2000) *Bangiomorpha pubescens* n. gen., n. sp.: implications for the evolution of sex, multicellularity, and the Mesoproterozoic/Neoprotorezoic radiation of eukaryotes. Paleobiology **26**: 386–404.

Delwiche, C. (1999) Tracing the thread of plastid diversity through the tapestry of life. Am. Nat. **154**: S164–S177.

Eisen, J. and Fraser, C. (2003) Phylogenomics: intersection of evolution and genomics. *Science* **300**(5626): 1706–1707.

Embley, T.M. and Martin, W. (2006) Eukaryotic evolution, changes and challenges. Nature **440**: 623–630.

Freshwater, D.W., Fredericq, S., Butler, B., Hommersand, M.H. and Chase, M. (1994) A gene phylogeny of the red algae (Rhodophyta) based on plastid *rbc*L. Proc. Natl Acad. Sci. USA **91**: 7281–7285.

Glöckner, G., Rosenthal, A. and Valentin, K. (2000) The structure and gene repertoire of an ancient red algal plastid genome. J. Mol. Evol. **51**: 382–390.

Gurgel, C.F.D. and Lopez-Bautista, J. (2007) Red algae, In: *Encyclopedia of Life Sciences*. Wiley, Chichester, UK.

Grossman, A.R. (2005) Paths toward algal genomics. Plant Physiol. **137**: 410–417.

Grossman, A.R., Schaefer, M.R., Chiang, G.G. and Collier, J.L. (1993) The phycobilisome, a light-harvesting complex responsive to environmental conditions. Microbiol. Rev. **57**: 725–749.

Hagopian, J., Reis, M., Kitakima, J. Bhattacharya, D. and de Oliveira, M.C. (2004) Comparative analysis of the complete plastid genome sequence of the red alga *Gracilaria tenuistipitata* var. *liui* provides insights into the evolution of rhodoplasts and their relationship to other platids. J. Mol. Evol. **59**: 464–477.

Harper, J. and Saunders, G.W. (2001) Molecular systematics of the Florideophyceae (Rhodophyta) using nuclear large and small subunit rDNA sequence data. J. Phycol. **37**: 1073–1082.

Hommersand, M.H., Freshwater, W., Lopez-Bautista, J. and Fredericq, S. (2006) Proposal of the Euptiloteae Hommersand and Fredericq, Trib. Nov. and transfer of some southern hemisphere Ptiloteae to the Callithamnieae (Ceramiaceae, Rhodophyta). J. Phycol. **42**: 203–225.

Kaneko, T., Sato, S., Kotani, H., Tanaka, A., Asamizu, E., Nakamura, Y., Miyajima, N., Hirosawa, M., Sugiura, M., Sasamoto, S., Kimura, T., Hosouchi, T., Matsuno, A., Muraki, A., Nakazaki, N., Naruo, K, Okumura, S., Shimpo, S., Takeuchi, C., Wada, T., Watanabe, A., Yamada, M., Yasuda, M. and Tabata, S. (1996) Sequence analysis of the genome of the unicellular cyanobacterium *Synechocystis* sp. Strain PCC6803. II. Sequence determination of the entire genome and assignment of potential protein-coding regions. DNA Res. **3**: 109–136.

Keeling, P. (2004) Diversity and evolutionary history of plastids and their hosts. Am. J. Bot. **91**(10): 1481–1493.

Leblanc, C., Boyen C., and Goër, S.L. (1995a) Organization of the plastid genome from the rhodophyte *Chondrus cripus* (Gigartinales); sequence and phylogeny of the 16S rRNA gene. Eur. J. Phycol. **30**: 133–140.

Leblanc, C., Boyen, C., Richard, O., Bonnard, G., Grienenberger, J.-M. and Kloareg, B. (1995b) Complete sequence of the mitochondrial DNA of the rhodophyte *Chondrus crispus* (Gigartinales). Gene content and genome organization. J. Mol. Biol. **250**: 484–495.

Leblanc, C., Richard, O., Kloared, B., Viehmann, S., Zetsche, K. and Boyen, C. (1997) Origin and evolution of mitochondria: what have we learnt from red algae? Curr. Genet. **31**: 193–207.

Li, N. and Cattolico, R.A. (1987) Chloroplast genome characterization in the red alga *Griffithsia pacifica*. Mol. Gen. Genet. **209**: 343–351.

Li, S., Nosenko, T., Hacket, J. and Bhattacharya, D. (2006) Phylogenomic analysis identifies red algal genes of endosymbiotic origin in the Chromalveolates. Mol. Biol. Evol. **23**(3): 663–674.

Matsuzaki, M., Misumi, O., Shin-I, T., Maurama, S., Takahara, M., Miyagishima, S., Mori, T., Nishida, K., Yagisawa, F., Nishia, K., Yoshid, Y., Nishimura, Y., Nakao, S., Kobayashi, T., Momorama, Y., Higashiyama, T., Minoda, A., Sano, M., Nomoto, H., Oishi, K., Hayashi, H., Ohta, F., Nishizaka, S., Haga, S., Miura, S., Morishita, T., Kabeya, Y., Terasawa, K., Suzuki, Y., Ishii, Y., Asakawa, S., Takano, H., Ohta, N., Kuriwa, H., Tanaka, K., Shimizu, N., Sugano, S., Sato, N., Nozaki, H., Ogasawara, N., Kohara, Y. and Kuroiwa, T. (2004) Genome sequence of the ultrasmall unicellular red alga *Cyanidioschyzon merolae* 10D. Nature **428**: 653–657.

Mereschkowsky, C. (1905) Über nature und ursprung der Chromatophoren im Pflanzenreiche. Biol. Centralbl. **25**: 593–604. English translation from: Martin, W. and Kowallik, K. (1999) Annotated English translation of Mereschkowsky's 1905 paper *Über nature und ursprung der Chromatophoren im Pflanzenreiche*. Eur. J. Phycol. **34**: 287–295.

Misumi, O., Matsuzaki, M., Nozaki, H., Miyagishima, S., Mori, T., Nishida, K., Yagisawa, F., Yoshida, Y., Kuroiwa, H. and Kuroiwa, T. (2005) *Cyanidioschyzon merolae* genome. A tool for facilitating comparable studies on organelle biogenesis in photosynthetic eukaryotes. Plant Physiol. **137**: 567–585.

Nedelcu, A., Lee, R., Lemieux, C., Gray, M. and Burger, G. (2000) The complete mitochondrial DNA sequence of *Scenedesmus obliquus* reflects an intermediate stage in the evolution of the green algal mitochondrial genome. Genome Res. **10**: 819–831.

Nozaki, H., Takano, H., Misumi, O., Terasawa, K., Matsuzaki, M., Maruyama, S., Nishida, K., Yagisawa, F., Yoshida, Y., Fujiwara, Y., Takio, S., Tamra, K., Chung, S. J., Nakamura, S., Kuroiwa,

H., Tanaka, K., Sato, N. and Kuroiwa, T. (2007) A 100%-sequence reveals unusually simple genomic features in the hot-spring red alga *Cyanidioschyzon merolae*. BMC Biol. **5**: 28.

Oesterhelt, C., Vogelbein, S., Shrestha, R., Stanke, M. and Weber, A.P.M. (2008) The genome of the thermoacidophilic red microalga *Galdieria sulphuraria* encondes a small family of secreted class III peroxidases that might be involved in cell wall modification. Planta **227**: 353–362.

Ohta, N., Matsuzaki, M., Misumi, O., Miyagishima, S., Nozaki, H., Tanaka, K., Shin, I., Kohara, Y. and Kuroiwa, T. (2003) Complete sequence and analysis of the plastid genome of the unicellular red alga *Cyanidioschyzon merolae*. DNA Res. **10**: 67–77.

Ohta, N., Sato, N. and Kuroiwa, T. (1998) Structure and organization of the mitochondrial genome of the unicellular red alga *Cyanidioschyzon merolae* deduced from the complete nucleotide sequence. Nucleic Acids Res. **26**(22): 5190–5198.

Pombert, J.-F., Otis, C., Lemieux, C. and Turmel, M. (2005) The chloroplast genome sequence of the green alga *Pseudendoclonium akinetum* (Ulvophyceae) reveals unusual structural features and new insights into the branching order of chlorophyte lineages. Mol. Biol. Evol. **22**(9): 1903–1918.

Pombert, J.-F., Lemieux, C. and Turmel, M. (2006) The complete chloroplast DNA sequence of the green alga *Oltmannsiellopsis viridis* reveals a distinctive quadripartite architecture in the chloroplast genome of early diverging ulvophytes. BMC Biol. **4**: 3

Raven, J.A. and Allen, J.F. (2003) Genomics and chloroplast evolution: what did cyanobacteria do for plants? Genome Biol. **4**(3): 209.

Ravi, V., Khurana, J.P., Tyagi, A. and Khurana, P. (2008) An update on chloroplast genomes. Pl. Syst. Evol. **271**: 101–122.

Reith, M. and Munholland, J. (1993) A high-resolution gene map of the chloroplast genome of the red alga *Porphyra purpurea*. Plant Cell **5**: 465–475.

Reith, M. and Munholland, J. (1995) Complete nucleotide sequence of the *Porphyra purpurea* chloroplast genome. Plant Mol. Biol. Reporter **13**(4): 333–335.

Reyes-Prieto, A., Yoon, H.S. and Bhattacharya, D. (2006) Phylogenomics and its growing impact on algal phylogeny and evolution. Algae **21**(1): 1–10.

Ribera-Siguan, M.A. (2003) Pathways of biological invasions of marine plants, In: G.M. Ruiz and J.T. Carlton (eds.) *Invasive Species (Vectors and Management Strategies)*. Island Press, Washington, pp. 183–226.

Rodriguez-Ezpeleta, N. and Philippe, H. (2006) Plastid origin: replaying the tape. Curr. Biol. **16**(2): R53–R56.

Rodriguez-Ezpeleta, N., Brinkmann, H., Roure, B., Lartillot, N., Lang, B.F. and Philippe, H. (2007) Detecting and overcoming systematic errors in genome-scale phylogenies. Syst. Biol. **56**(3): 389–399.

Ruiz, G.M., Fofonoff, P.W., Carlton, J.T., Wonham, M.J. and Hines, A.H. (2000) Invasion of coastal marine communities in North America: apparent patterns, processes, and bias. Ann. Rev. Ecol. Syst. **31**: 481–531.

Saunders, G.W. and Hommersand, M.H. (2004) Assessing red algal supraordinal diversity and taxonomy in the context of contemporary systematic data. Am. J. Bot. **91**(10): 1494–1507.

Seckbach, J. (1999) The Cyanidiophyceae: hot spring acidophilic algae, In: J. Seckbach (ed.) *Enigmatic Microorganisms and Life in Extreme Environments.* Kluwer, Dordrecht, The Netherlands, pp. 427–435.

Shivji, M.S. (1991) Organization of the chloroplast genome in the red alga *Porphyra yezoensis*. Curr. Genet. **19**: 49–54.

Shivji, M.S., Lin, N. and Cattolico, R.A. (1992) Structure and organization of rhodophyte and chromophyte plastid genomes: implications for the ancestry of plastids. Mol. Gen. Genet. **232**: 65–73.

Simpson, C. and Stern, D.B. (2002) The treasure trove of algal chloroplast genomes. Surprises in architecture and gene content, and their functional implications. Plant Physiol. **129**: 957–966.

Teo, S.-S., Ho, C.-L., Teoh, S., Lee, W.-W., Tee, J.-M., Rahim, R.A. and Phang, S.-M. (2007) Analyses of expressed sequence tags from an agarophyte, *Gracilaria changii* (Gracilariales, Rhodophyta). Eur. J. Phycol. **42**(1): 41–46.

Turmel, M., Pombert, J.-F., Charlebois, P., Otis, C. and Lemieux, C. (2007) The green algal ancestry of land plants as revealed by the chloroplast genome. Int. J. Plant Sci. **168**(5): 679–689.

Turmel, M., Otis, C. and Lemieux, C. (2006) The chloroplat genome sequence of *Chara vulgaris* sheds new light into the closest green algal relatives of land plants. Mol. Biol. Evol. **23**(6): 1324–1338.

Waaland, J.R., Stiller, J. and Cheney, D.P. (2004) Macroalgal candidates for genomics. J. Phycol. **40**: 26–33.

Weber, A., Oesterhelt, C., Gross, W., Bräutigam, A., Imboden, L., Krassovskaya, I., Linka, N., Ruchina, J., Schneidereit, J., Voll, H., Voll, L., Zimmermeann, M., Jamai, A., Riekhof, W., Yu, B., Garavito, R. and Benning, C. (2004) EST-analysis of the thermo-acidophilic red microalga *Galdieria sulphuraria* reveals potential for lipid A biosynthesis and unveils the pathway of carbon export from rhodoplasts. Plant Mol. Biol. **55**(1): 17–32.

Weber, A., Barbier, G., Shrestha, R., Horst, R., Minoda, A. and Oesterhelt, C. (2007) A genomics approach to understanding the biology of thermo-acidophilic red algae, In: J. Seckbach (ed.) *Algae and Cyanobacteria in Extreme Environments*. Springer, Dordrecht, The Netherlands, pp. 505–518.

Yoon, H.S., Müller, K., Sheath, R. G., Ott, F.D. and Bhattacharya, D. (2006) Defining the major lineages of red algae (Rhodophyta). J. Phycol. **42**: 482–492.

Zuccarello, G., West, J. and Kikuchi, N. (2008) Phylogenetic relationships within the Stylonematales (Stylonematophyceae, Rhodophyta): biogeographic patterns do not apply to *Stylonema alsidii*. J. Phycol. **44**(2): 384–393.