The Plastid Genome of the Red Macroalga *Grateloupia taiwanensis* (Halymeniaceae)

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**Abstract**

The complete plastid genome sequence of the red macroalga *Grateloupia taiwanensis* S.-M. Lin & H.-Y. Liang (Halymeniaceae, Rhodophyta) is presented here. Comprising 191,270 bp, the circular DNA contains 233 protein-coding genes and 29 tRNA sequences. In addition, several genes previously unknown to red algal plastids are present in the genome of *G. taiwanensis*. The plastid genomes from *G. taiwanensis* and another florideophyte, *Gracilaria tenusiptipta* var. *liui*, are very similar in sequence and share significant synteny. In contrast, less synteny is shared between *G. taiwanensis* and the plastid genome representatives of Bangiophyceae and Cyanidiophyceae. Nevertheless, the gene content of all six red algal plastid genomes here studied is highly conserved, and a large core repertoire of plastid genes can be discerned in Rhodophyta.

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**Introduction**

The red algae (division Rhodophyta) comprise over 6,300 species [1] of mostly multicellular, marine, photosynthetic organisms. Along with Viridiplantae (green algae and higher plants) and Glauco phyta, Rhodophyta is one of the three lineages of eukaryotes originating from primary endosymbiosis of an ancient cyanobacterium, forming the supergroup Plantae *sensu lato*. The monophyly of Plantae *s.l* is well supported in several analyses [2][3][4]. Subsequent secondary endosymbioses have occurred, resulting in a great diversity of plastid-bearing eukaryotes throughout the tree of life. The chlorarachniophytes and euglenoids separately acquired green algal endosymbionts, whereas the numerous “brown” lineages (including haptophytes, cryptophytes, stramenopiles, and alveolates) acquired red algal endosymbionts. It remains unclear, however, at which point (or points) in evolutionary history the acquisition of those red algal plastids took place, and several hypotheses have been suggested to explain the pattern, which have been tested and supported to varying degrees [5]. However, it is clear that additional data collection and analysis are needed for both the hosts and endosymbionts in this partnership, that is, for brown algal lineages and the red algae from which their plastids originated.

Molecular phylogenetic analysis has divided the red algae into seven classes [6][7]. This phylogeny is given in Figure 1. Almost all red algal species — over 6,000 — belong to the class Florideophyceae, which is most closely related to the class Bangiophyceae (~150 species [1]). These two classes have been grouped in the subclass Rhodophyceae. The most anciently diverged of the classes, the Cyanidiophyceae, consists of very few species divided into three genera of extremophilic unicellular algae known to inhabit acidic hot springs. Five red algal plastid genomes have been published thus far, including representatives of these three classes: *Gracilaria tenusiptipta* var. *liui* Zhang & Xia (Florideophyceae); *Porphyra parasitica* (Roth) C.Agardh and *Pyropia yezoensis* (Ueda) M.S.Hwang & H.G.Choi (Bangiophyceae); and *Cyanidium caldarium* (Tilden) Geitler and *Cyanidoschyzon merolae* P.De Luca, R.Taddei & L.Varano strain 10D (Cyanidiophyceae). Because almost all known red algal diversity is found in the Florideophyceae, the plastid genome sequence of a single species (*G. tenusiptipta* var. *liui*) is clearly insufficient information to understand the whole spectrum of characteristics that are shared by florideophyccean plastids. A thorough understanding of present-day red algal plastids, with sufficient coverage across the red algal tree of life, can help demonstrate the characteristics of ancestral red algae and their plastids, which would have been the source of the secondary endosymbiotic plastids of the brown algal lineages.

The florideophyccean genus *Grateloupia* C. Agardh contains around 90 species [1] of benthic macroalgae that are distributed in warm temperate to tropical waters worldwide. Some species of *Grateloupia* are known invasive species. *Grateloupia taiwanensis* S.-M.Lin & H.-Y. Liang was first described in 2008 by Lin et al. [8] but it has since been recorded in the Gulf of Mexico [9]. The genus is currently being split into several genera based on combined molecular and morphological analysis [10], and it is possible that *G. taiwanensis* will be placed into a new genus.

*Grateloupia* belongs to the order Halymeniaceae, whereas *Gracilaria* *tenusiptipta* var. *liui* is in the order Gracilariales. Both orders are classified in the subclass Rhodomeniophycidae, but their phylogenetic relationships within the subclass are unresolved, due to consistent ambiguity in the phylogenetic position of Gracilariales [11][12][13]. Comparisons between the plastid genomes of *Gracilaria tenusiptipta* and *Grateloupia taiwanensis* will establish a
Figure 1. Phylogeny of Rhodophyta, adapted from Yoon et al. [6]. Numbers of species are from AlgaeBase [1].
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Figure 2. The *Grateloupia taiwanensis* plastid genome. Colors indicate different gene classifications, as listed in Table 2.
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Table 1. Characteristics of red algal plastid genomes analyzed in this study.

| General characteristics | Florideophyceae | Bangiophyceae | Cyanidiophyceae |
|-------------------------|----------------|--------------|----------------|
| Size (bp)               | 191,270        | 191,028      | 191,952        |
| G+C (%)                 | 30.6           | 33.0         | 33.1           |
| Intergenic space (%)    | 18.1           | 15.3         | 15.9           |
| Number of protein-coding genes | 234 | 207 | 193 |
| Unique gene annotations | 35             | 0            | 4              |
| Number of ribosomal proteins | 47  | 47 | 45 |

Start codon usage (%)

| ATG | GTG | TTG | others |
|-----|-----|-----|--------|
| 87.6| 6.0 | 6.4 | –      |
| 89.7| 2.0 | 7.8 | 0.5    |
| 91.8| 5.8 | 2.4 | 1.0    |
| 92.3| 5.3 | 1.4 | –      |
| 97.9| 2.1 | 1.0 | –      |
| 98.5| 1.0 | 0.5 | –      |

RNAs

| Number of tRNAs | Number of rRNA operons |
|-----------------|------------------------|
| 29              | 1                      |
| 29              | 2                      |
| 37              | 2                      |
| 38              | 2                      |
| 31              | 1                      |
| 30              | 1                      |

GenBank accession

| K894740 | AY673996 | PPU38804 | AP006715 | AB002583 | AF022186 |

Intergenic space is defined as any portion of the genome that does not bear a gene or RNA annotation.

The G. taiwanensis plastid genome was imported to Geneious (Geneious version 5.1.7; available from http://www.geneious.com/) and set to circular topology. Using the Geneious ORF Finder and the standard genetic code, the start codons ATG and GTG, and a minimum length of 90 bp, the genome contained 768 ORFs. Preliminary annotation was performed using DOGMA [16] with an e-value cutoff of 10^-20 for BLAST hits. After alignments for each gene, these were checked manually and the corresponding ORF in the genome sequence was annotated. The remaining ORFs were translated using the standard genetic code and submitted to phmmer (http://hmmer.janelia.org/), searching against the UniProtKB database (http://www.uniprot.org). After including the additional start codon TTG, any ORFs occurring outside any annotation were searched for functional domains using the InterProScan Geneious plugin version 1.0.5 [17]. Annotations for those ORFs with putative functional domains were included in the genome.

To determine tRNA sequences, the plastid genome was submitted to the tRNAscan-SE version 1.2.1 server [18][19]. The genome was searched with default settings using the “Mito/Chloroplast” model. To determine rRNA sequences, a set of known plastid tRNA sequences was extracted from the Gracilaria tenuistipitata var. liui genome and used as a query sequence to search the G. taiwanensis genome using BLAST. A search for tmRNA sequences was performed using BRUCE v1.0 [20]. The genome was visualized using GenomeVx [21] and edited using Adobe Illustrator CS2 (http://www.adobe.com/products/illustrator.html).

The five published red algal plastid genomes, with annotations, were downloaded from GenBank. Gene names were checked with the preferred name in UniProtKB and revised in order to make the most accurate comparisons between genomes. In situations where one gene had multiple names, if all were orthologous...
According to BLAST ($e \leq 10^{-10}$) against UniProtKB, the name used by the majority of species was used. Names of known and putative protein-coding genes (i.e., excluding tRNAs or rRNAs) were extracted from the genomes, and the sets were compared using VENNTURE [22]. Genes found to be missing from a certain species or group of species were checked using BLAST in order to ensure that this gene is not present. For structure and arrangement comparisons, the genomes were aligned using the

Table 2. List of genes in the *Grateloupia taiwanensis* plastid genome (233 total).

| Classification | Number | Genes |
|----------------|--------|-------|
| **Genetic systems** | | |
| Maintenance | 2 | dnaB, rne |
| RNA polymerase | 5 | rpoA, rpoB, rpoC1, rpoC2, rpoZ |
| Transcription factors | 4 | ntcA, ompR, rbcR, ycf29 |
| Translation | 4 | infB, infC, tsf, tufA |
| **Ribosomal proteins** | | |
| Large subunit | 28 | rpl1, rpl2, rpl3, rpl4, rpl5, rpl6, rpl9, rpl11, rpl12, rpl13, rpl14, rpl16, rpl18, rpl19, rpl20, rpl21, rpl22, rpl23, rpl24, rpl27, rpl28, rpl29, rpl31, rpl32 |
| Small subunit | 19 | rps1, rps2, rps3, rps4, rps5, rps6, rps7, rps8, rps9, rps10, rps11, rps12, rps13, rps14, rps16, rps17, rps18, rps19, rps20 |
| tRNA processing | 1 | tis |
| Protein quality control | 4 | clpC, dnaK, ftsH, groEL |
| **Photosystems** | | |
| Phycobilisomes | 12 | apcA, apcB, apcD, apcE, apcF, cpcA, cpcB, cpcC, nblA |
| Photosystem I | 13 | psaA, psaB, psaC, psaD, psaE, psaF, psaL, psaM, ycf3, ycf4 |
| Photosystem II | 19 | psbA, psbB, psbC, psbD, psbE, psbF, psbH, psbI, psbJ, psbK, psbL, psbN, psbT, psbV, psbX, psbY, psbZ, ycf12 |
| Cytochrome complex | 11 | ccs1, ccsA, petA, petB, petE, petD, petF, petG, petJ |
| Redox system | 7 | acsF, bas1, dsbD, fbr, grx, psbA, trxA, acsF |
| **ATP synthesis** | | |
| ATP synthase | 8 | atpA, atpB, atpD, atpE, atpF, atpG, atpH, atpI |
| **Metabolism** | | |
| Carbohydrates | 6 | cfxQ, odpA, odpB, pgmA, rbcL, rbcS, cfxQ, odpA |
| Lipids | 5 | accA, accB, accD, acpP, fabH, accA, accB, accD |
| Nucleotides | 2 | carA, upp |
| Amino acids | 8 | argB, gltB, lab, ilvH, syfB, syh, trpA, trpG |
| Cofactors | 4 | chll, moeB, preA, thiG, chll, moeB, preA, thiG |
| Transport | 9 | cemA, secA, secG, secY, ycf16, ycf24, ycf38, ycf43, ycf63 |
| **Unknown** | | |
| Conserved ORFs | 28 | ORF58, ORF65, ORF83, ORF621, ycf17, ycf19, ycf20, ycf21, ycf22, ycf26, ycf33, ycf34, ycf35, ycf36, ycf37, ycf39, ycf40, ycf45, ycf46, ycf52, ycf53, ycf54, ycf55, ycf56, ycf60, ycf65, ycf80, ycf82 |
| Unique ORFs | 34 | Gtai_orf01, Gtai_orf02, ..., Gtai_orf34 |

Genes in bold are shared among all red algal plastids (140 total). Genes underlined are shared among Eurhodophyta (21 total). Genes italicized are shared among Florideophyceae (5 total). Categories for classification follow Ohta et al. [30].

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Mauve Genome Alignment version 2.2.0 [23] Geneious plugin using the progressiveMauve algorithm [24] and default settings. To aid in visualization, we designated the beginning of the rbcL marker as position 1 in each genome.

**Results**

The *Grateloupiia taiwanensis* plastid genome

The 191,270 bp plastid genome (Figure 2) includes 233 ORFs identified as protein-coding genes, of which 35 are found only in *G. taiwanensis* and not in the other red algae examined in this study. Additionally, it contains 29 rRNA sequences, 3 tRNA sequences, and 1 tmRNA sequence (Table 1). The rRNA operon is not repeated. The tmRNA sequence appears to be homologous to the ssrA tmRNA of *Gracilaria tenuistipitata* var. *liui*. The GC-content of the *G. taiwanensis* plastid genome is 30.1%. The proportion of intergenic space in *G. taiwanensis* was 18.1%, which is comparable to the other Eurhodophytina and higher than the Cyanidiophyceae (Table 1). The sequence was deposited in GenBank (accession number KC894740).

**Gene content**

All of the plastid genomes considered in this study share a set of 140 protein-coding genes, and an additional 21 genes are shared
among the Euthrophyta (Table 2). Five additional genes are
shared only between G. taiwanensis and G. tenuistipitata var. liui. In
total, 167 of the protein-coding genes found in the plastid of G.
taiwanensis are shared with G. tenuistipitata var. liui. Of the 35
putative genes found only in G. taiwanensis, one is a gene for
Eutrophycan (grx). This gene is 104 aa in length and is most
similar to that of the cyanobacterium Arthrospira platensis (UniProt
blasts, match length 107 aa, 78.0% positives, e = 8.0 x 10^{-30}). The
remaining 34 genes are unique ORFs with functional domains
indicated by InterProScan (see Table S1 for annotations). G.
taiwanensis and G. tenuistipitata var. liui share the same 29 plastid
rRNA genes (Table 3). Porphyrna purpurea and Pyropia yezoensis contain
more tRNA genes than the others, with 37 and 38, respectively;
two tRNA genes – trn(GAT) and trn(TGC) – occur inside the
repeated rRNA operon. In terms of tRNA gene content, the
Florideophyceae and Cyanidiophyceae are more similar to each
other than to the Bangiophyceae.

Plastid genome rearrangements
Pairwise Mauve genome alignments for G. taiwanensis along with
each other five plastid genomes used in this study are given in
Figure 3. We calculated the double-cut-and-join (DCJ) genome
distance, indicative of the number of rearrangements that have
taken place between two genomes. The alignment of G. taiwanensis
and Gracilaria tenuistipitata var. liui shows a DCJ distance of 3; G.
taiwanensis and Porphyrna purpurea, 4; G. tenuistipitata and Pyropia
yezoensis, 8; G. taiwanensis and Cyanidioschyzon merolae, 20; G.
taiwanensis and Cyanidium caldarium, 21.

Discussion
The plastid genome of G. taiwanensis is similar to that of G.
tenuistipitata var. liui in terms of size, GC%, gene content, and
overall structure. However, there are several notable differences;
G. tenuistipitata contains 67 putative protein-coding genes not present
in G. tenuistipitata var. liui, including 32 previously named genes and
34 novel ORFs. When additional plastid genome sequences for
Florideophyceae become available, it is possible that many of these
novel ORFs will be found in other red algae.

The results of the current study are generally consistent with the
phylogeny of Rhodophyta proposed by Yoon et al. [7]. Unlike in
Porphyrna purpurea and Porphyrna yezoensis, in which the rRNA operon
is repeated directly, G. tenuistipitata has only one rRNA operon. This
is consistent with the hypothesis of Hagopian et al. [25] that the
repeated rRNA operon was lost separately in the Cyanidiophyceae
and the Florideophyceae. A similar pattern arose in the rRNA
genomes in Cyanidiophyceae and Florideophyceae. The reason for
this is unclear, but because it is commonly accepted that the
Cyanidiophyceae is the sister group to the rest of the red algae, we
suggest that this is an example of convergent gene loss.

As expected, our analyses show that pairs of plastid genomes of
red algae found in the same taxonomic class demonstrate the most
structural and functional similarity (Cyanophora/Cyanidium, Porphyra/Porphyra, and Grateloupia/Grateloupia), which decreases with-
the degree of relatedness. The presence of 140 “core” plastid genes
reflects high conservation in the plastids of red algae, compared to
green algal plastids, which show much more variability in genome
size, GC%, and other attributes [26]. Despite their similar sizes,
red algal plastid genomes contain many more genes than green
algal genomes, and the genes are packed tightly together with
much less intergenic sequence. Thus far, G. taiwanensis shows the
most intergenic sequence of any red algal plastid (18.1%), but this
case is relatively low compared to those of green algal plastids.

As more and more genomes are annotated and published,
comparative genomes of primary and secondary plastids will
provide new insights into the pattern and process of endosymbiosis,
especially in those lineages with red-derived plastids. The genes
shared among all red algal plastids are likely to be essential
for plastid function in Rhodophyta and offer a useful starting point
for future annotation of plastid genomes. Several previous studies
focused on red-derived plastids [27][28][29] have shown the
potential of plastid genome research in answering unresolved
questions in the history of these lineages. For these reasons, red
algal plastid genomes remain a highly interesting subject for
research. Forthcoming sequence data will advance our under-
standing of the evolution of the red algal plastid.

Supporting Information
Table S1 Novel ORFs found in the G. taiwanensis
plastid genome.

(DOCX)

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Author Contributions
Conceived and designed the experiments: MSD JLB. Performed the
experiments: MSD. Analyzed the data: MSD. Contributed reagents/
materials/analysis tools: MSD DB JLB. Wrote the paper: MSD.

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