

ORIGINAL PAPER

Evolution of the Chloroplast Genome in Photosynthetic Euglenoids: A Comparison of *Eutreptia viridis* and *Euglena gracilis* (Euglenophyta)

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The chloroplast genome of *Eutreptia viridis* Perty, a basal taxon in the photosynthetic euglenoid lineage, was sequenced and compared with that of *Euglena gracilis* Ehrenberg, a crown species. Several common gene clusters were identified and gene order, conservation, and sequence similarity was assessed through comparisons with *Euglena gracilis*. Significant gene rearrangements were present between *Eutreptia viridis* and *Euglena gracilis* chloroplast genomes. In addition, major expansion has occurred in the *Euglena gracilis* chloroplast accounting for its larger size. However, the key chloroplast genes are present and differ only in the absence of *psaM* and *roaA* in *Eutreptia viridis*, and *psal* in *Euglena gracilis*, suggesting a high level of gene conservation within the euglenoid lineage. Further comparisons with the plastid genomes of closely related green algal taxa have provided additional support for the hypothesis that a *Pyramimonas*-like alga was the euglenoid chloroplast donor via secondary endosymbiosis.

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Key words: *Eutreptia viridis*; chloroplast; Euglenophyta; *Euglena gracilis*; genome.

Introduction

The euglenoids represent a diverse, ancient eukaryotic lineage. Huber-Pestalozzi (1955) describes over 800 species belonging to about 40 genera, of which about two thirds are non-photosynthetic. Molecular phylogenies place euglenoids near the base of the eukaryotic tree of life (Adl et al. 2005; Cavalier-Smith 1998; Lane and Archibald 2008; Moreira et al. 2007; Parfrey et al. 2010; Simpson and Roger 2004) with the phagotrophic forms positioned basal to the photosynthetic genera. This study will focus on the

photosynthetic euglenoids and specifically on the acquisition and evolution of the chloroplast.

Euglenoids are believed to have gained the ability to photosynthesize through the acquisition of a chloroplast via secondary endosymbiosis of a green alga. This hypothesis originally was based on the existence of closely related non-photosynthetic phagotrophic euglenoids and the presence of three membranes surrounding the resulting chloroplast rather than the two membranes typical of green algae and higher plants (Gibbs 1978, 1981). In recent years the sequencing of chloroplast genomes has been used to infer deep evolutionary relationships among photosynthetic lineages (Burger et al. 2007; Nock et al. 2011; Parks et al. 2009; Qiu et al. 2006). This is due in part

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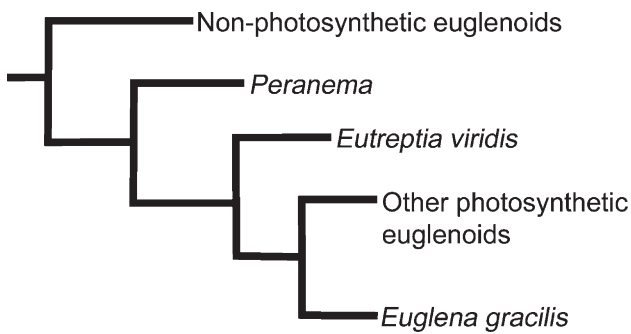


Figure 1. Diagrammatic representation of the current state of euglenoid phylogeny adapted from Marin et al. 2003. *Peranema* is a non-photosynthetic phagotrophic euglenoid found basal to the photosynthetic euglenoids including *Eutreptia viridis* and *Euglena gracilis*.

to the small size and comparative simplicity of these genomes relative to their nuclear counterparts and to the ability to analyze multigene datasets without delving into the more complex eukaryotic nuclear genome. Sequencing of the chloroplast genome is also facilitated by the typically high chloroplast genome copy number present within cells relative to the nuclear genome and the ability to use multiplexed, massively parallel sequencing (Parks et al. 2009). At last count a total of 229 chloroplasts have been sequenced to completion, most of which are representative or economically important land plant species (Benson et al. 2011). Few are algal species and most of these are green algae with meager representation of other algal lineages. Within the photosynthetic euglenoids, the only chloroplast genome that has been sequenced is from *Euglena gracilis* (Hallick et al. 1993).

Euglena gracilis is the model organism for photosynthetic euglenoids due to its ease in culturing and the ability to achieve high cell densities. However, *Euglena gracilis* is not a typical representative photosynthetic euglenoid due to the diversity within the lineage, and it is not closely related to the phagotrophic forms believed to have been the host for the endosymbiont. The diversity of the euglenoid lineage warrants further exploration into their chloroplast evolution, which could elucidate understanding of this key basal eukaryotic lineage.

To date, all inferences regarding the chloroplast donor taxon have relied on the chloroplast sequence of *Euglena gracilis*. Based on established phylogenetic assessment of the photosynthetic euglenoids, *Euglena gracilis* is consistently a crown species of the lineage (Fig. 1; Linton et al. 2010; Marin et al. 2003; Triemer et al. 2006).

Although euglenoids are thought to have obtained their chloroplast from a green alga, the chloroplast of *Euglena gracilis* shows some significant changes. Most notably, the *Euglena gracilis* chloroplast genome is not divided into large and small single copy regions separated by inverted repeats containing the rRNA genes (as well as a few other genes). Not only does *Euglena gracilis* lack the inverted repeats, but the ribosomal operon is organized in at least three and a half tandemly arranged copies (5S/23S/16S:5S/23S/16S:5S/23S/16S:16S, Hallick et al. 1993). The *Euglena gracilis* gene content appears consistent with other sequenced green algal chloroplast genomes, but the arrangement is not (Turmel et al. 2009). This raises several questions with regard to chloroplast evolution within the photosynthetic euglenoids. Is the chloroplast genome of *Euglena gracilis* representative of all photosynthetic euglenoids? Will the chloroplast genome of more basal taxa look more like that of green algae? What changes have occurred during the evolution of the chloroplast in the euglenoid lineage?

To address these questions the chloroplast genome of *Eutreptia viridis* was sequenced. *Eutreptia viridis* is the type species of the genus *Eutreptia* which consistently falls basal to photosynthetic euglenoids in phylogenetic assessments of both nuclear and chloroplast ribosomal genes as well as nuclear encoded protein coding genes (Fig. 1; Linton et al. 2010; Marin et al. 2003; Triemer et al. 2006). A diagrammatic representation of euglenoid phylogeny based on analysis by Marin et al. in 2003 demonstrates the position of *Eutreptia viridis* relative to *Euglena gracilis* and the non-photosynthetic euglenoids (Fig. 1). Furthermore, *Eutreptia viridis* differs morphologically from *Euglena gracilis* by the presence of two emergent flagella versus one. This is notable in that the closest extant phagotrophic euglenoids such as *Peranema* also have two emergent flagella. This study will assess and compare gene content, arrangement, size, and sequence similarity between these two photosynthetic euglenoids.

Results and Discussion

The *Eutreptia viridis* chloroplast genome was assembled from reads obtained by sequencing total genomic DNA using Roche 454 sequencing and de novo assembly. Because the ribosomal genes form a tandem array rather than inverted repeats as in the green algae, it was difficult to determine the exact number of ribosomal operons and the 3'

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