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Similar Relative Mutation Rates in the Three Genetic Compartments of Mesostigma and Chlamydomonas

Jimeng Hua[a], **David Roy Smith**[a,b], **Tudor Borza**[a], and **Robert W. Lee**[a,1]

[a]Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4R2, Canada
[b]Current address: Canadian Institute for Advanced Research, Department of Botany, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

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Levels of nucleotide substitution at silent sites in organelle versus nuclear DNAs have been used to estimate relative mutation rates among these compartments and explain lineage-specific features of genome evolution. Synonymous substitution divergence values in animals suggest that the rate of mutation in the mitochondrial DNA is 10-50 times higher than that of the nuclear DNA, whereas overall data for most seed plants support relative mutation rates in mitochondrial, plastid, and nuclear DNAs of 1:3:10. Little is known about relative mutation rates in green algae, as substitution rate data is limited to only the mitochondrial and nuclear genomes of the chlorophyte *Chlamydomonas*. Here, we measure silent-site substitution rates in the plastid DNA of *Chlamydomonas* and the three genetic compartments of the streptophyte green alga *Mesostigma.* In contrast to the situation in animals and land plants, our results support similar relative mutation rates among the three genetic compartments of both *Chlamydomonas* and *Mesostigma*. These data are discussed in relation to published intra-species genetic diversity data for the three genetic compartments of *Chlamydomonas* and are ultimately used to address contemporary hypotheses on the organelle genome evolution. To guide future work, we describe evolutionary divergence data of all publically available *Mesostigma viride* strains and identify, for the first time, three distinct lineages of *Mesostigma*.
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Key words: *Chlamydomonas*; genome architecture; *Mesostigma*; mutation rate; silent substitution rate.

Introduction

Knowledge of mutation rate is essential for understanding biological evolution. Although difficult to estimate, insights into this fundamental parameter can be gained by measuring the rate of nucleotide substitution at silent sites (defined as noncoding sites and the synonymous positions of protein-coding DNA) between closely related species (Kimura 1983). Significant advances in our understanding of mutation and genome evolution have come from nucleotide substitution rate data, especially with respect to the evolution of nuclear versus organelle genomes (Graur and Li 2000; Lynch 2007).

Wolfe and colleagues (1987, 1989) reported that for angiosperms the silent-site substitution rates of genes in the mitochondrial DNA (mtDNA) were three-fold lower than those in the plastid DNA (ptDNA) and 12-times lower than those in the nuclear DNA (nucDNA) — more recent

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[1]Corresponding author; fax +1 902 494 3736
e-mail robert.lee@dal.ca (R.W. Lee).

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calculations using an expanded data set and the maximum likelihood (ML) method reveal an even greater relative synonymous substitution rate for the nuclear genome of angiosperms and an overall relative rate for seed plant mitochondrial, plastid, and nuclear genes of 1:3:10 (Drouin et al. 2008). This trend, although having some conspicuous exceptions (Mower et al. 2007 and references therein), is in sharp contrast to the situation for most animals where the silent-site substitution rate of the mtDNA is estimated to be 10-50 times that of the nucDNA (Brown et al. 1979, 1982; Lynch et al. 2006; Miyata et al. 1982). The disparity in relative rates between these two lineages appears to be a reflection of differing organelle DNA mutation rates, as both groups are believed to have similar nucDNA mutation rates (Lynch 2007; Lynch et al. 2006).

The above data have been used to help explain why land plants and animals have comparable nuclear genome architectures but organelle genomes with opposing levels of genomic complexity. Land plant mitochondrial genomes are capacious, intron- and repeat-dense, and undergo high levels of post-transcriptional editing (i.e., RNA editing), whereas animal mtDNA is compact, intron- and gene-poor, and with few exceptions is not post-transcriptionally edited (e.g., Janke and Pääbo 1993; Yokobori and Pääbo 1995). The structure of land plant plastid genomes, which generally have a moderate noncoding DNA content and experience minor levels of RNA editing, is intermediate to that of land plant and animal mtDNAs (Table 1). It is argued that the mutationally active mtDNA of animals makes for a less permissive environment for the accumulation of genomic embellishments than the mutationally quiescent land plant mtDNA. The argument being that escalations in genomic complexity, such as the addition of introns or regulatory sites for RNA editing, increase the mutational liability of the genome because they represent targets for potentially deleterious mutations, where the higher the mutation rate the greater the burden of the adornment (Lynch 2007). It is also suggested that high organelle DNA mutation rates promote the migration of organelle-DNA-encoded genes to the nuclear genome (e.g., Berg and Kurland 2000).

Green algae are an interesting case study for the evolution of genome architecture because they harbor a diverse array of genomic structures. Little is known, however, about either the absolute or relative silent-site substitution rates in this important group, which includes the Chlorophyta (a lineage containing most of the green algal diversification) and the algal members of its sister group, the Streptophyta (a lineage also containing the land plants) (Becker and Marin 2009).

In a broad sense, the organelle and nuclear genome architectures of both chlorophyte and streptophyte green algae are distinct from those of land plants and animals. Green algae tend to have relatively streamlined, intron-poor mitochondrial genomes, which are more compact than those of land plants but more complex than animal mtDNAs. Green algal plastid genomes are generally larger and more bloated than their mitochondrial counterparts, but for land plants the opposite is true. Moreover, there is no evidence of RNA editing in green algal organelle DNA (Lenz et al. 2010 and references therein). The nuclear genomes of green algae, with some exceptions, are smaller, have fewer genes, and less noncoding DNA than those of land plants and animals (Merchant et al. 2007; Prochnik et al. 2010; Worden et al. 2009).

To the best of our knowledge, the only studies to investigate micro-evolutionary rates in both the nuclear and organelle genomes of green algae (or any other algal group in the Plantae) are those of Popescu et al. (2006) and Popescu and Lee (2007), which compared the gene sequences of *Chlamydomonas reinhardtii* and *Chlamydomonas incerta* (model unicellular species belonging to the chlorophycean class of the Chlorophyta) and showed that the silent-site substitution rates of the mitochondrial and nuclear compartments are approximately the same. Here we build upon these works and analyze the silent-site substitution rate between the plastid compartments of *C. reinhardtii* and *C. incerta*, allowing for a complete picture of relative evolutionary rates in this lineage. *Mesostigma viride* is a model unicellular streptophyte green alga (Lemieux et al. 2007 and references therein; Marin and Melkonian 1999) and our preliminary analysis of published EST sequence data from two different *Mesostigma viride* strains indicate that these likely originate from deeply divergent populations or correspond to distinct biological species. Therefore, to broaden our understanding of evolutionary rates in green algae beyond *Chlamydomonas*, we analyzed the rates of silent-site substitution in the mitochondrial, plastid, and nuclear genomes between these two *Mesostigma* lineages and to guide future studies on genetic divergence in this taxon we compared homologous sequences from all publically available *Mesostigma viride* strains and prepared a phylogenetic tree of these sequences. Altogether, these data provide novel insights into the forces governing genome evolution in green algae and green plants as a whole.

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