

# Travel Light: Reductive Genome Evolution in Free-Living Eukaryotes

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## Editorial

Genome reduction is a common phenomenon in intracellular endosymbionts, parasites and pathogens. Because of substantial gene and functional loss, genome reduction precipitates reliance on the host for nutrition and energy supplies [1]. In contrast, free-living organisms undergoing genome reduction need to maintain independent lifestyles and to sustain the ability to respond to diverse external stimuli and changing environments. Therefore, genome reduction in free-living organisms is expected to be more complex and tuned to a variable environment. The past few years have witnessed the emergence of eukaryotic genome data associated with genome reduction as a result of the tremendous advance in DNA sequencing techniques and bioinformatics. Although the study of genome reduction in free-living eukaryotes is still in its infancy, the novel instances of genome reduction that have been found offer new paradigms that challenge current dogma and expand our understanding of eukaryotic genome evolution in general.

## Genome Reduction Drives Biological Complexity and Diversity

The sequencing of red algal genomes (such as *Porphyridium purpureum* [2] and *Chondrus crispus* [3]) revealed a modest gene inventory (5,000-1,000 genes) for this phylum (Rhodophyta) when compared to its sister lineage Viridiplantae (green algae and land plants) such as *Chlamydomonas reinhardtii* (121Mb with 15,143 genes [4]) and *Klebsormidium flaccidum* (117Mb with 16,215 genes [5]). This has primarily resulted from an ancient phase of genome reduction that occurred in the common ancestor of all extant red algal taxa since its divergence from Viridiplantae [6]. This episode of genome reduction led to the loss in red algae of one quarter of the anciently derived algal core genes and loss of the flagellum and functional pathways such as macro-autophagy [6]. Additional rounds of genome reduction occurred in extremophilic red algae (*Galdieria* and *Cyanidioschyzon*) that have simple, coccoid morphologies and are restricted to volcanic hot-spring areas [7]. In contrast, one ancient lineage of red algae managed to conquer mesophilic environments and diversified into a large group of taxa that have stunning taxonomic diversity, a global distribution, diverse morphologies, complex multicellularity, and sophisticated life cycles.

The mechanisms that drove mesophilic red algal diversification and complexity are largely unclear. It is likely that Horizontal Gene Transfer (HGT) played a role in ameliorating the effects of genome reduction via the regain of once lost functions. One such example represents the nickel-dependent urease pathway that was lost in the common ancestor of extremophilic red algae and was later re-acquired in *Galdieria phlegrea* via HGT from bacteria [7]. Another mechanism likely involves convergent evolution. Red algae are the only known algal taxa that have completely lost the macro-autophagy pathway that normally has indispensable functions [6,8]. Given the antiquity of red algae, it is likely that toolkits of independent origins evolved in this lineage to fulfill the functions analogous to macro-autophagy. Indeed, red algae possess 30% to 50% lineage-specific novel genes that have no detectable homologs in other phyla. With its history of genome reduction and subsequent diversification, red algae demonstrate the remarkable flexibility and tremendous potential of eukaryotic genomes in supporting biological complexity and diversity.

## Genome Reduction Creates Ecologically Successful and Economically Useful Lineages

The recent genome sequencing of *Bathycoccus prasinos* (15Mb with 7,847 genes [9]) adds to the list of Prasinophyceae genomes which includes the picoeukaryotes such as *Ostreococcus lucimarinus* (13Mb with 7,805 genes [10]) and *Micromonas* sp. RCC299 (21Mb with 10,286 genes [11]) that are well-known for their highly reduced genomes. These Prasinophyceae species represent important members of picophytoplankton that have a cosmopolitan marine distribution and are particularly prominent in primary production and food webs in oligotrophic open ocean environments. Interestingly, some other phytoplankton lineages including the centric diatom *Thalassiosira pseudonana* (32.4 Mb with 11,776 genes [12]) and the pennate diatom *Phaeodactylum tricorutum* (27.4 Mb with 10,402 genes [13]) do not contain significantly more genes. It is tempting to speculate a history of genome reduction for diatoms, although a rigorous test of this

idea requires genome data from additional diatom and related non-diatom stramenophyte lineages.

Genome reduction in the green alga *Picochlorum* SENEW3 occurred in the Trebouxiophyceae lineage and is associated with adaptation to highly fluctuating environments with respect to salinity and light [14]. In addition to stress tolerance, *Picochlorum* possesses other features that are desirable for nutrition and biofuel production such as high lipid content and a rapid growth rate. Interestingly, other candidates for biofuel production also display reduced genome size and gene inventory including the stramenophyte *Nannochloropsis gaditana* (29Mb with 8,892 genes [15]) and the haptophyte *Chrysochromulina tobin* (59Mb with 16,777 genes [16]). The former is closely related to its gene-rich sister lineage, the brown algae (214Mb with 16,256 genes [17]), whereas the latter is associated with the coccolithophore forming *Emiliania huxleyi* (142Mb with 30,569 genes [18]). Genome reduction appears therefore to represent a common trait associated with fast-growing algae that are suited for biofuel production. Discovering novel unicellular algal taxa with small genomes will likely provide additional candidates for the production of biofuel and other commercially valuable products.

### Genome Contraction in Land Plants and Animals

Among plants, the model species *Arabidopsis thaliana* was targeted for whole genome sequencing primarily because of its small genome size (135Mb with 27,025 genes). Sequencing of another *Arabidopsis* species, *A. lyrata* (207Mb with 32,670 genes [19]) showed that about one-half of the original genome content was likely lost in *A. thaliana* in the past 10 million years [19]. Rapid genome reduction in *A. thaliana* resulted primarily from numerous small deletions in non-coding DNA and transposons [19]. More extreme cases of non-coding DNA loss in plants are represented by the carnivorous bladderworts *Utricularia gibba* (82Mb with 28,500 genes [20]) and *Genlisea aurea* (44Mb with 17,755 genes [21]). These two species belong to the family Lentibulariaceae that underwent genome reduction independently. Remarkably, *U. gibba* shed almost its entire repeat DNA in the process of multiple rounds of whole genome duplications [20]. As a consequence, it possesses a gene number typical of plants with minimal amounts of non-coding DNA [20]. These results suggest significant impact of genome reduction on plant genome evolution that is otherwise considered to be dominated by expansion via genome duplication and the proliferation of repetitive elements.

Genome contraction primarily through massive deletion of non-genic DNA (not coding sequences) appears to be a feature that is shared with small animal genomes. With a 99-Mb genome, the Antarctic midge *Belgica antarctica* shows drastic reduction in total genome size, repetitive elements, and intron lengths when compared to other sister dipteran species [22]. Yet, it possesses 13,517 genes that are comparable to other dipteran lineages [22]. A similar situation occurs in the long-known small genomes in puffer fishes such as *Tetraodon nigroviridis* (342Mb with 27,918 genes). Although genome contraction in *B. antarctica* was related to cold adaptation [22], a phylogeny-based analysis of genome size data from more chironomid species suggested that the reduced *B. antarctica* genome may reflect an ancestral trait that is common to the Orthocladinae subfamily [23].

### Conclusion

The multiple instances of genome reduction that have recently been described in free-living eukaryotes are reshaping our understanding of this important yet poorly understood force in genome evolution. It is clear that genome reduction is widespread in the eukaryotic tree of life and is partially responsible for the large variation in gene inventory and genome size among eukaryotes. In particular, aquatic algal species (non-plant, photosynthetic organisms) seem to be strongly associated with genome reduction rather than genome duplication that dominate in plants and animals. More importantly, genome reduction represents a distinct force that drives eukaryotic biodiversity and organismal complexity, and often results in ecologically successful lineages, some of which are models for molecular biological study and applied uses. With the accumulation of genomic data from taxonomically diverse eukaryotes, comprehensive analyses that put individual genomes into a broad evolutionary context will enable us to understand the distribution, impact, causation, mechanisms, and consequences of genome reduction in free-living eukaryotes.

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