Sequenced Mitochondrial Genomes of Bryophytes

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Abstract: The determination of complete DNA sequence of mitochondrial genome of liverwort, *Marchantia polymorpha,* opens the way to study the structure and organization of mitochondrial genomes of bryophytes. Since then several studies to sequence mitochondrial genomes of various plant groups have been made. Consequently 71 mitochondrial genomes (as on September 28, 2012) of Viridiplantae are available in organelle genome resources database at National Center for Biotechnology Information. Among these mitochondrial genomes the lineage sampling of bryophytes are poorly represented with only three liverworts, two mosses and two hornworts. The present review deals with features of sequenced mitochondrial genomes of bryophytes.

Introduction

Mitochondria are cytoplasmic organelles which plays a pivotal role in cellular metabolism. These organelles fulfill the majority of cellular energy demands and considered to originate through endosymbiotic process. The ancestor of mitochondria are thought to be related to a proteobacteria (Gray et al. 1999, Fitzpatrick et al. 2006). Therefore mitochondria perform several physiological and biochemical functions related to their bacterial ancestors. During evolution a massive loss/transfer of mitochondrial genes to the host genome occurs consequently mitochondria harbors a very small fraction of the endosymbiont's genome. Moreover they are highly diversified in different phyla of photosynthetic organisms (Knoop 2004). The small mitochondrial genome contains the genes for the ribosomal and transfer RNA which help in protein synthesis for mitochondrial respiratory chain. However, hundreds of nuclear encoded proteins, synthesized on cytoplasmic ribosomes and transported to mitochondrion, are also needed to replicate, transcribe, and maintain the mitochondrial genome and to assemble the translation machinery needed to express its proteins (Gray et al. 2001, Timmis et al. 2004). In comparison to other eukaryotes large and complex mitochondrial genomes are present in plants.

Bryophytes represent the early stage of land plant evolution (Mishler and Churchill 1984; Qiu 2008). Since the determination of complete DNA sequence of mitochondrial genome of *Marchantia polymorpha* (Oda et al. 1992) few studies to deduce gene organization of mitochondrial genomes of bryophytes have been conducted. In addition nucleotide sequences of mitochondrial genomes of algae, pteridophytes, gymnosperms and angiosperms are also available. These sequenced mitochondrial genomes represent a sparse taxonomic diversity of land plants (71 as on September 28, 2012). Among them only a small fraction (7 out of 71) belongs to bryophytes http://www.ncbi.nlm.nih.gov/genomes/GenomesGroup.cgi?taxid=33090&opt=organelle). In comparison to sequenced chloroplast genomes of land plants very few mitochondrial genomes of plants have been sequenced (NCBI Organelle Genome Resources). However at present the number of sequenced mitochondrial genomes of bryophytes outnumber the sequenced chloroplast genomes of bryophytes (Shanker 2012). The information of sequenced mitochondrial genomes of bryophytes is given in Table 1. This review presents features of these mitochondrial genomes.

Mitochondrial Genomes of Liverworts

Marchantia polymorpha

The complete sequence of the liverwort, *Marchantia polymorpha*, mitochondrial DNA was determined using electron microscopy and restriction endonuclease mapping. The mitochondrial genome of *M. polymorpha* was found to be a single circular molecule which consists of about 186609 base pairs (bp). Several genes including genes for three species of ribosomal RNA, transfer RNA and 30 open reading frames (ORFs) for functionally known proteins were detected. Apart from this 29 ORFs were predicted as possible genes considering the G+C content in first, second and third letters of codons. Moreover three ORFs were found to show similarity with ORFs of unknown function in the mitochondrial genomes of other organisms. A total of 32 introns belonging to either group I or group II intron were detected in the coding regions of 17 genes. The RNA editing was found to be absent in mitochondrial genome of *M. Polymorpha* (Oda et al. 1992).

Table 1. Information of sequenced mitochondrial genomes of bryophytes.

S. No.	Organism Name	*Accession No.	Genome Size (bp)	Reference
	Liverworts			
1.	*Marchantia polymorpha*	NC_001660	186609	Oda et al. 1992
2.	*Pleurozia purpurea*	NC_013444	168526	Wang et al. 2009
3.	*Treubia lacunosa*	NC_016122	151983	Liu et al. 2011
	Mosses			
4.	*Physcomitrella patens*	NC_007945	105340	Terasawa et al. 2007
5.	*Anomodon rugelii*	NC_016121	104239	Liu et al. 2011
	Hornworts			
6.	*Megaceros aenigmaticus*	NC_012651	184908	Li et al. 2009
7.	*Phaeoceros laevis*	NC_013765	209482	Xue et al. 2010

*Complete genome sequence at NCBI will be accessed using accession number.

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Pleurozia purpurea

Mitochondrial genome sequence of *Pleurozia purpurea* contains 168526 bp. A total of 43 protein coding genes, 3 rRNA genes, 25 tRNA genes, and 31 group I or II introns were detected in mitochondrial genome of *P. purpurea*. It lacks two genes (trnRucg and trnTggu) and one intron (rrn18i1065gII) found in mitochondrial genome of *M. polymorpha*. The gene orders in the mitochondrial genomes of *P. purpurea* and *M. polymorpha* were found to be identical with highly similar sequences in exons, introns, and intergenic spacers. Comparative analysis of mitochondrial genome of *P. purpurea* with mitochondrial genome of *M. polymorpha* shows that the mitochondrial genome evolution in liverworts is extremely conservative (Wang et al. 2009).

Treubia lacunosa

The mitochondrial genome sequence of *Treubia lacunosa* consists of 151983 bp with AT contents of 56.6%. It contains protein coding genes for respiration and protein synthesis, rRNA and tRNA genes. In the mitochondrial genome of *T. lacunosa* the proportions of the various types of sequences with respect to total genome size found to be 53% genes, 26% exons, 27% introns and 47% intergenic spacers (Liu et al. 2011). The gene order in *T. lacunosa* mitochondrial genome found to be similar with those of *Marchantia polymorpha* and *Pleurozia purpurea* mitochondrial genomes. The analysis of mitochondrial genome sequence of *T. lacunosa* showed that it does not contain any functional mitochondrial genes involved in cytochrome c biogenesis. These genes were found to be either pseudogenized (ccmB and ccmFC) or lost (ccmC and ccmFN). The hornworts, *Megaceros aenigmaticus* and *Phaeoceros laevis*, were also known to have no functional mitochondrial gene for cytochrome c biogenesis (Li et al. 2009, Xue et al. 2010). The nad7 gene known to be a pseudogene in other liverworts (Groth-Malonek et al. 2007) was found as a functional gene in *Treubia*. In other liverworts the functional copy of this nad7 pseudogene was supposed to reside in the nuclear genome (Kobayashi et al. 1997). In comparison to *Haplomitrium*, known to have higher level of RNA editing at least in nad1 and nad7 (Dombrovska and Qiu 2004, Groth-Malonek et al. 2007), the *Treubia* mitochondrial genome showed low level of RNA editing (Liu et al. 2011).

Mitochondrial Genomes of Mosses

Physcomitrella patens

The complete nucleotide sequence of mitochondrial DNA of *Physcomitrella patens* consists of 105340 bp and contains 3 rRNAs, 24 tRNAs and 42 protein encoding genes. The mitochondrial genome sequence of *P. patens* lacks 5 tRNA genes, supposed to be encoded by the nuclear genome. A total of 27 introns were identified within 16 genes. Out of these introns 9 of the intron positions found to be common with angiosperms and 4 with *Marchantia*. The overall mitochondrial genome structure of *P. patens* was found to be similar with that of *Chara vulgaris* and *Marchantia polymorpha*. The inversions and translocations can be easily identified between these genomes. However the mitochondrial genome sequence of *P. patens* lacks significant synteny with angiosperm and chlorophyte mitochondrial genomes (Terasawa et al. 2007).

Anomodon rugelii

The mitochondrial genome of *Anomodon rugelii* contains 104239 bp with AT contents of 58.8%. It contains protein coding genes for respiration and protein synthesis, rRNA and tRNA genes. In the mitochondrial genome of *A. rugelii* the proportions of the various types of sequence with respect to total genome size found to be 70% genes, 39% exons, 31% introns and 30% intergenic spacers. The order of genes identified in mitochondrial genome of *A. rugelii* were identical with *Physcomitrella patens* mitochondrial genome. All cisspliced group I or group II introns detected were similar with previously sequenced mitochondrial genome of moss. Very low levels of RNA editing was found in mitochondrial genome of *A.* r*ugelii* (Liu et al. 2011) which parallels the situation in the mitochondrial genome of *Physcomitrella patens* where only 11 editing events occur in the mitochondrial genome (Rudinger et al. 2009).

Mitochondrial Genomes of Hornworts

Megaceros aenigmaticus

The completely sequenced mitochondrial genome of *Megaceros aenigmaticus* consist of 184908 bp, with 17 tRNA genes, 3 rRNA genes and 32 protein coding genes. A total of 30 group II introns were also detected in mitochondrial genome of *M. aenigmaticus*. The gene order of many genes in mitochondrial genome of *M. aenigmaticus* were similar with a liverwort, a moss, several green and red algae, and also with an early branching eukaryote, *Reclinomonas americana*, which contains most ancestral form of mitochondrial DNA. Considering gene order 8 inversions and translocations were found between mitochondrial DNA of *M. aenigmaticus* and *Physcomitrella patens* (a moss). In comparison to green alga mitochondrial genome the *M. aenigmaticus* mitochondrial DNA have increased genome size, RNA editing, intron gains and gene losses. These derived features were thought to be gained by mitochondrial genomes of hornworts during the origin and early evolution of land plants (Li et al. 2009).

Phaeoceros laevis

Among bryophytes, the mitochondrial genome of *Phaeoceros laevis* is known to be the largest mitochondrial genome sequenced. It consists of 209482 bp with 3 rRNA genes, 21 tRNA genes, 30 protein codind genes along with 34 cis-spliced group II introns disrupting 16 protein genes. A total of 11 pseudogenes were found in the mitochondrial genome of *P. laevis* out of which 9 pseudogenes were common with mitochondrial genome of *Megaceros aenigmaticus*, a distant relative of *P. laevis*. Considering the genome structure and organization the mitochondrial genomes of *P. laevis* and *Megaceros aenigmaticus* differ by seven genes, four introns and four inversions and translocations. A comparative sequence analysis to detect the level of conservation in mitochondrial genome evolution within hornworts showed 80 to 95% identity in exons, introns and intergenic spacers between these genomes. Overall the mitochondrial genome evolution in hornworts found to be less conservative in comparison to liverworts (Xue et al. 2010).

These sequenced mitochondrial genomes indicate that during the origin of land plants there is an significant increase in the genome size of mitochondrial genomes. However the genome size remains relatively constant in bryophytes. No foreign DNA of chloroplast or nuclear origin was detected in any of these mitochondrial genomes. Despite the improtance of bryophytes in evolution of plants on land, their mitochondrial genomes are poorly represented in biological database at NCBI with only three liverworts, two mosses and two hornworts have completely sequenced, annotated mitochondrial genomes. Considering the significance of bryophytes more sequences will be required to get new insight on evolution of plants on land.

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