



The mitochondrial proteome of the moss *Physcomitrella patens*



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ABSTRACT

Extant basal land plants are routinely used to trace plant evolution and to track strategies for high abiotic stress resistance. Whereas the structure of mitochondrial genomes and RNA editing are already well studied, mitochondrial proteome research is restricted to a few data sets. While the mitochondrial proteome of the model moss *Physcomitrella patens* is covered to an estimated 15–25% by proteomic evidence to date, the available data have already provided insights into the evolution of metabolic compartmentation, dual targeting and mitochondrial heterogeneity. This review summarizes the current knowledge about the mitochondrial proteome of *P. patens*, and gives a perspective on its use as a mitochondrial model system. Its amenability to gene editing, metabolic labelling as well as fluorescence microscopy provides a unique platform to study open questions in mitochondrial biology, such as regulation of protein stability, responses to stress and connectivity to other organelles. Future challenges will include improving the proteomic resources for *P. patens*, and to link protein inventories and modifications as well as evolutionary differences to the functional level.

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1. Introduction

1.1. Similar, yet different

About 500–450 million years ago plants began to colonize the land masses of Earth (Kenrick and Crane, 1997; Lang et al., 2010) and evolved to organisms so diverse as to include large towering trees and small ground-covering mosses, shaping our current ecosystems. Common for all land plants are selective pressures such as temperature fluctuations, the availability of water and nutrients, the levels of oxygen and CO₂, as well as sunlight. In addition, plant survival strategies include the need to balance emerging stresses such as e.g. drought, flooding or high UV irradiation.

Many open questions remain, both fundamental and applied, regarding the dynamic organization of plant metabolism. Main interests are the organelles governing plant energy metabolism and many

Abbreviations: ABA, abscisic acid; ATE, arginyl-tRNA protein transferase; COX, cytochrome *c* oxidase; DIGE, differential in gel electrophoresis; MS/MS, tandem mass spectrometry; OAS-TL, *O*-acetylserine (thiol) lyase; PCA, principal component analysis; PINK, PTEN-induced putative kinase 1; ROS, reactive oxygen species; RuBisCO, ribulose-1,5-bisphosphate carboxylase/oxygenase; SDS PAGE, sodium dodecylsulfate polyacrylamide gel electrophoresis; TEM, transmission electron microscopy; TOM, translocase of the outer mitochondrial membrane.

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biosynthetic pathways, namely chloroplasts and mitochondria. During normal conditions as well as abiotic stresses, these electron transport chain-containing compartments are crucial partners in maintaining plant ROS balance, vitality and growth (Mittler, 2002; Møller, 2001; Schwarzländer and Finkemeier, 2013). To date, plant mitochondria are less well investigated than their chloroplast partners and merit attention to unravel their exact roles and organization in plants.

As representative species from several early-diverging land plant lineages are available as model organisms, they represent a valuable resource to study mitochondria for several reasons. First, they provide a necessary reference point to reconstruct land plant evolution. Second, their study can unravel the mechanisms of alternative metabolic organization and plant survival strategies facing stresses. Third, they can offer technical advantages, such as amenability to microscopy techniques (Furt et al., 2012; Mueller et al., 2014; Wu and Bezanilla, 2014) and the ease of precise genome engineering via a high rate of homologous recombination, such as in the model moss *Physcomitrella patens* (Reski, 1998).

Interestingly, comparative studies regarding mitochondrial genomes have already revealed that they have undergone extreme changes during land plant evolution. There is a trend for increasing size and complexity paired with the gain of RNA-editing sites and introns (Li et al., 2009; O'Toole et al., 2008; Rüdinger et al., 2012). DNA transmission, maintenance and transcription as well as RNA processing have been modulated considerably.

On the other hand, mitochondrial proteomic data regarding model organisms outside angiosperms such as the green alga *Chlamydomonas*

reinhardtii (Atteia et al., 2009) and non-vascular land plants are still scarce. This review summarizes the available proteome information for the model moss *Physcomitrella patens* and gives a perspective on future interests in moss mitochondrial biology.

1.2. A moss view on mitochondria

Mosses are basal land plants with a wide distribution in different habitats. Their different survival mechanisms are partly still enigmatic compared to vascular plants. Most tissues of *Physcomitrella patens* are single cell layers or filaments, which are poikilohydric (i.e. equilibrate with the humidity of the environment), yet this moss is more resistant to several abiotic stresses such as salt stress and dehydration than most vascular plants (Mishler and Oliver, 2009; Oliver et al., 2005). Thus, *P. patens* can recover from a water loss of up to 75–92% of its fresh weight (Cui et al., 2012; Frank et al., 2005), a dehydration tolerance that can be further increased by treatment with the plant stress hormone ABA (Khandelwal et al., 2010; Koster et al., 2010). Under these adverse conditions, the protection of membrane integrity and the limitation and repair of damage caused by reactive oxygen species (ROS) are likely among the main issues in mitochondria (Koster et al., 2010; Møller, 2001; Schwarzländer and Finkemeier, 2013), similar to the situation in mature seeds (Wang et al., 2015).

Notably, it is already known that some aspects of moss mitochondrial biology, such as morphology and movement are differing from known patterns: moss mitochondrial form is very variable and ranges from elongated network-like morphology to small round structures (Fig. 1A, B), whereas movement is an order of magnitude slower than in the model flowering plant *A. thaliana* (Furt et al., 2012; Mueller and Reski, 2015).

2. Land plant organelles in the evolutionary spotlight

2.1. Resources: prediction and comparative genomics platforms

The *Physcomitrella patens* genome has been available since 2008 (Rensing et al., 2008) with the genome annotation V1.6 (Zimmer et al., 2013) encompassing 32,275 protein-coding genomic loci while annotation is continuously being improved (V3.3, www.cosmos.org,

Lang et al., 2016). The *P. patens* gene models have been readily integrated into comparative genomics platforms such as PLAZA, Phytozome, KEGG and OrthoMCL (Chen et al., 2006; Goodstein et al., 2012; Kanehisa et al., 2014; Van Bel et al., 2012) which allow for the convenient search of homologous genes between many plant species with high-throughput genomics data.

In order to automatically allocate predicted moss proteins and thereby metabolic functions to subcellular compartments (Zimmer et al., 2013), annotation can be either transferred from protein models of other previously annotated organisms, and/or subcellular localization assigned by prediction algorithms (Emanuelsson et al., 2007; Mitschke et al., 2009; Hooper et al., 2014). Both approaches suffer from some pitfalls, as sequence similarity is no guarantee for similar function or localization, and thus transfer of e.g. GO terms between species may even mask evolutionary changes in eukaryotic metabolic compartmentation. Moreover, prediction algorithms can only be as good as their training sets and often do not provide congruent results (Heazlewood et al., 2004; Hooper et al., 2014). Thus, the increasing amount of annotations inferred by electronic annotation (labelled IEA) needs to be balanced by experimental datasets in order to improve gene annotation and conduct sensible cross-species comparative analyses.

Currently, the predicted mitochondrial proteome of *P. patens* consists of the 42 proteins encoded by the mitochondrial genome (Terasawa et al., 2006), and proteins encoded by 1947 (6%) of the 32,275 protein-coding genomic loci either predicted by *pred2goa* (Zimmer et al., 2013) or based on manual annotation (cosmos.org, Nightly-build downloaded 20160303). *Pred2goa* combines the predictions of several computational localization prediction algorithms to decide on a consensus for the predictions.

By comparison, protein isoforms encoded by 2549 of 27,206 protein-coding genomic loci (TAIR 10) are annotated to localize to mitochondria in *Arabidopsis* (see also Rao et al. in this issue) according to SUBAcon (SUBAIII 20160307, Tanz et al., 2013) representing approximately 9.4% of all nuclear-encoded protein models. The SUBAcon algorithm (Hooper et al., 2014) integrates both experimental data (GFP localizations and MS/MS identifications) and localization predictions to derive subcellular localization of proteins, which are still mostly lacking for *P. patens*.

However, initial MS/MS datasets are available for *P. patens* including analyses integrating different environmental conditions and

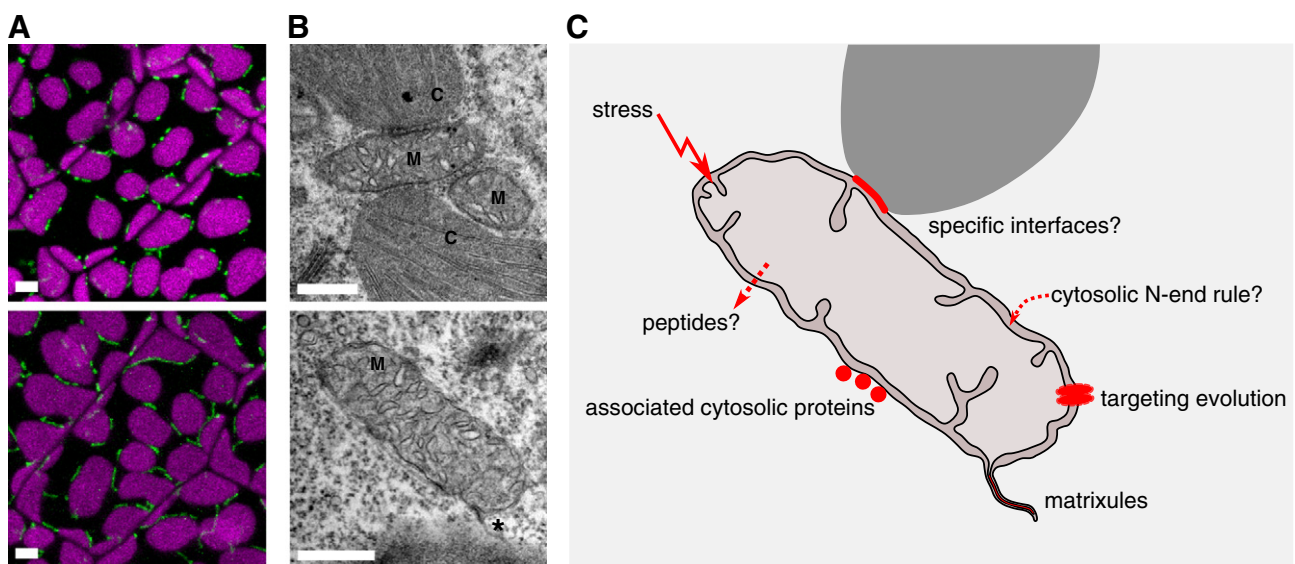


Fig. 1. Moss mitochondria: Morphology and current research topics. (A) Maximum intensity projections of *P. patens* mitochondria labelled with mtmEOS (green) (Mueller and Reski, 2015) and chlorophyll autofluorescence (magenta): moss mitochondria can exhibit small and round morphologies (top) or long elongated structures (bottom). Scale bars 5 μ m. (B) TEM images of *P. patens* mitochondria (prepared as described in Schuessle et al. (2016)). Proximity between different subcellular compartments (top, C chloroplast, M mitochondrion) and tubular mitochondrial extensions (matrixules, *bottom) can be observed, but the functional significance is unclear. Scale bar 0.5 μ m. (C) Schematic representation of current research topics in mitochondrial biology with an emphasis on moss as model system.

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