CHLOROPLAST RIBOSOME STRUCTURE

Translating photosynthesis

Chloroplasts contain their own genomes and genetic systems. Their ribosomes synthesize conserved core proteins in photosynthesis. A complete chloroplast ribosome structure now reveals features convergent with those of ribosomes in mitochondria.

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Chloroplast, mitochondrial and bacterial ribosomes have a sedimentation coefficient of 70S, while 80S is the value for ribosomes of archaea and the eukaryotic cytosol. Sequence similarity between chloroplast and bacterial ribosomal RNAs[1] is early and persuasive evidence in favour of the endosymbiotic origin of chloroplasts[2]. Protein and RNA structural features are now seen in a model based on cryo-electron microscopy of the complete spinach chloroplast ribosome at 3.0 Å resolution[3]. The model allows comparison with the mitochondrial ribosome[4] and reveals detailed differences between ribosomes of chloroplasts and bacteria. One of these is an extended, 30 Å channel in the exit tunnel for the nascent chloroplast polypeptide. Other differences are unique component polypeptides whose interactions form the bridge between the large and small chloroplast ribosomal subunits.

Reporting in *Nature Plants*, Boerema et al.[3] describe this model. In addition to the protein and RNA structure, their description shows two regulatory factors that are clearly resolved within the complete ribosome structure. One of these is the remarkable ribosome-recycling factor (RRF) that allows release of the ribosome from translation,

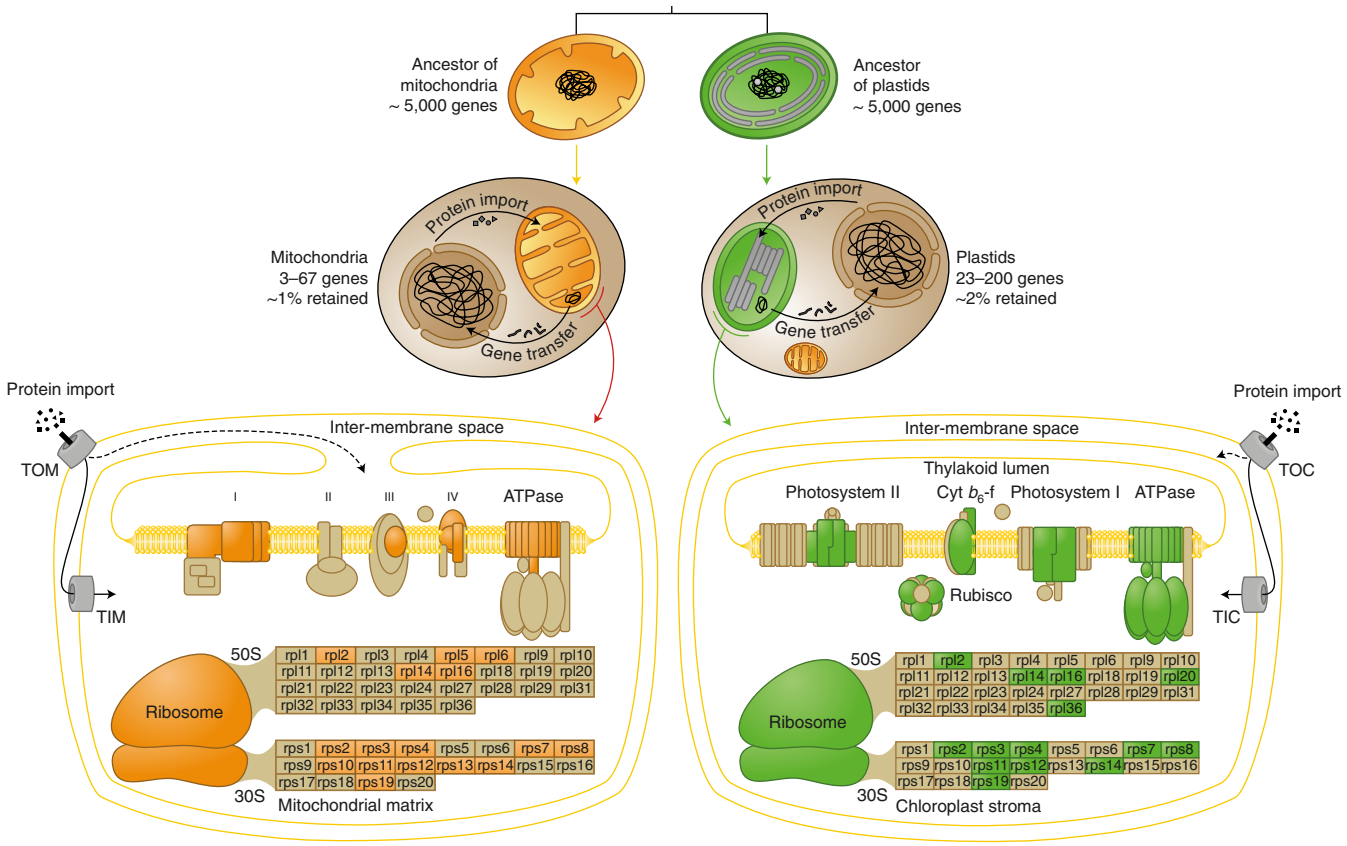

Fig. 1 | Convergent evolution of gene content for proteins made in chloroplasts and mitochondria. The ancestors of chloroplasts and mitochondria were prokaryotes with genomes encoding around 5,000 genes. Following endosymbiosis, genes were transferred from each organelle to the host's nuclear genome, and the corresponding gene products were imported back to the organelles as precursor proteins. An ancestral genome size of around five thousand genes decreased to 3–67 genes in mitochondria and 23–200 genes in chloroplasts. The colour coding within compartments in the lower part of the figure illustrates the convergent evolution of genes retained in the two bioenergetic organelles: genes for components of oxidative phosphorylation, photosynthesis, and proteins of 50S and 30S ribosomal subunits. Organelle-encoded genes are coloured brown for mitochondria and green for plastids. TIM/TOM, protein translocator of the inner/outer mitochondrial membrane; TIC/TOC, protein translocator of the inner/outer chloroplast membrane; Cyt, cytochrome. Figure reproduced from[11].

ready for subsequent polypeptide synthesis. RRF is a protein subunit that accurately mimics the structure of transfer RNA (ref. [5]). The second regulatory factor is a small protein hibernation factor that switches off protein synthesis by dimerizing ribosomes when small ribosomal subunits bind together.

Given their endosymbiont origin, why should chloroplast ribosomes differ in structural detail from those of bacteria? Boerema et al.[3] suggest that pigment incorporation into light harvesting proteins is a special requirement so that "chlororibosomal activity is spatiotemporally coupled to the synthesis and incorporation of functionally essential co-factors in a light regulated manner"[3]. While this must be true for the photosynthetic reaction centre and electron transfer complexes, major light-harvesting chlorophyll proteins are encoded in the cell nucleus, synthesized on cytosolic ribosomes and imported into chloroplasts as protein precursors that never need to see a chloroplast ribosome. Boerema et al. suggest that chloroplast-specific regulatory mechanisms are involved. These are likely to be connected with the function of protein products in photosynthesis — regulation by light and by the redox state of electron carriers are clear possibilities. Another consideration is the unusual composition of the subset of cellular proteins that are encoded in chloroplast DNA and therefore synthesized on chloroplast ribosomes[6]. These are mostly intrinsic to the chloroplast thylakoid membrane. The chloroplast ribosome may thus be particularly well adapted to co-translational insertion and assembly of membrane-intrinsic proteins with their different arrays of co-factors[7]. Precise redox photosynthetic control of chloroplast gene transcription adjusts the ratio of photosystems I and II (ref. [8]), and parallel regulation of photosynthesis by protein post-translational modification explains many aspects of plant adaptation to environmental change. It is reasonable to expect tight control of translation, the crucial intermediate stage of chloroplast gene expression.

In mature leaves, the entire chloroplast genetic system appears to drive synthesis of just one protein, the D1 protein of the reaction centre of photosystem II and product of the chloroplast *psbA* gene. Behind synthesis of this single gene product stands a host of other structural and regulatory components. Each of these components is also the result, directly or indirectly, of nuclear gene expression and protein synthesis on 80S cytosolic ribosomes. The explanation of this strange specialization for D1 synthesis is that the protein is very short-lived, turning over in the order of 20 minutes or so after breakdown that is an unavoidable consequence of reaction centre photochemistry[9]. Rapid and regulated re-synthesis of D1 is vital, and may be sufficient to justify an expensive and elaborate system for its biogenesis de novo. Co-translational assembly of complete D1 must accompany its precise insertion into a functional and complete photosystem II as the missing half of a symmetrical heterodimer. Perhaps the 30 Å extended channel of the exit tunnel of chloroplast ribosomes is there to allow such coordination.

In contrast to the dedicated and especially rapid synthesis of D1, at least 46 chloroplast proteins, among them 37 membrane proteins[7], are made at earlier stages of higher plant leaf and chloroplast development, and there are many more in algae. These proteins include the apoproteins of electron transport as well as ATP synthesis components; a subset of proteins of the chloroplast ribosome itself; and the large subunit of the enzyme Rubisco, "the most abundant protein in the world"[10]. Chloroplast protein is mostly Rubisco. If the chloroplast ribosome is specially adapted to synthesis of its unusual set of protein products, then great versatility is required. In contrast to D1, Rubisco is long-lived and extrinsic to the thylakoid membrane.

Evolutionary convergence of the gene content of chloroplasts and mitochondria (Fig. 1) might be explained partly by the majority of their gene products being predominantly hydrophobic and membrane intrinsic, while convergence of their soluble, ribosomal proteins could be connected instead with the order in which they must be synthesized during ribosome assembly[11]. Redox control of gene expression has been proposed to account for the persistence of genomes and genetic systems in bioenergetic organelles, and for the fact that they resemble those of their bacterial ancestors more than they do those of the eukaryotic cell nucleus and cytosol[12]. For chloroplasts the focus from this viewpoint has been on the bacterial nature of the transcriptional machinery[8]. Chloroplast ribosome structure may now provide a framework to identify and understand regulatory requirements placed on chloroplast translation, and thus help to explain why chloroplasts contain ribosomes at all. ❐

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Competing interests

The author declares no competing interest.