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Review

The intriguing realm of protein biogenesis: Facing the green co-translational protein maturation networks

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ABSTRACT

The ribosome is the cell's protein-making factory, a huge protein-RNA complex, that is essential to life. Determining the high-resolution structures of the stable "core" of this factory was among the major breakthroughs of the past decades, and was awarded the Nobel Prize in 2009. Now that the mysteries of the ribosome appear to be more traceable, detailed understanding of the mechanisms that regulate protein synthesis includes not only the well-known steps of initiation, elongation, and termination but also the less comprehended features of the co-translational events associated with the maturation of the nascent chains. The ribosome is a platform for co-translational events affecting the nascent polypeptide, including protein modifications, folding, targeting to various cellular compartments for integration into membrane or translocation, and proteolysis. These events are orchestrated by ribosome-associated protein biogenesis factors (RPBs), a group of a dozen or more factors that act as the "welcoming committee" for the nascent chain as it emerges from the ribosome. In plants these factors have evolved to fit the specificity of different cellular compartments: cytoplasm, mitochondria and chloroplast. This review focuses on the current state of knowledge of these factors and their interaction around the exit tunnel of dedicated ribosomes. Particular attention has been accorded to the plant system, highlighting the similarities and differences with other organisms.

1. Introduction

1.1. The complexity and importance of a functional cellular proteome

The workings of ribosomes have been of great interest to scientist since this huge machine was first discovered in the 1950s. The second Noble Prize awarded for ribosome research was for discovering the high-resolution structures of the prokaryotic complexes, the first largest functional complex ever studied. The 3D structure of plastid and mitochondrial ribosomes was also revealed and beginning in 2010, several major studies have reported medium to high-resolution structures of the eukaryotic cytosolic ribosome, from lower eukaryotes (protists, yeast) to higher ones (insects, mammals, plants), completing the full picture (Fig. 1A and B). At the same time, the impressive advances made in cryo-electron microscopy, X-ray crystallography, and single-molecule fluorescence resonance energy transfer (FRET) have largely contributed to allowing an initial view of the basic structural dynamics mechanism of protein synthesis, particularly with regards to the steps of initiation, elongation, and termination. Many of these mechanisms are highly conserved in prokaryotes and eukaryotes including plants, suggesting similarity in the basal mechanism of translation. However, emerging studies revealed that protein composition or/and rRNA of ribosomes could be varied at different stages of the organism life cycle or in response to biotic or abiotic stresses, resulting in distinct ribosomal populations (see for review [1,2]). In an attempt to compensate for their sessile nature, plants have developed several unique features to deal with changes in their environment, and these features also related to mitochondria and chloroplast, highly specialized organelles with dedicated translational apparatus.

Recent findings have emphasized the importance of non-ribosomal proteins. These are ribosome-associated protein biogenesis factors (RPBs, [3]) that permanently or transiently associate with the ribosome (Supplemental Table 1) and act as soon as a nascent polypeptide reaches the exit from the ribosomal tunnel. RPBs are involved in co-translational events, which include protein modifications, folding, targeting to various membranes or cellular compartments, and proteolysis. A group of a dozen or more RPBs plays the part of the welcoming committee for the nascent chain as it emerges from the ribosome. Although we do not yet have a complete picture of how all RPBs work on the ribosome and dialog with it, several pioneer breakthroughs have appeared recently, with new proposed models. The occurrence of comparable docking sites at the tunnel-exit extremity and of the large majority of RPBs suggests conservation in the fundamental features governing the co-translational events associated with the

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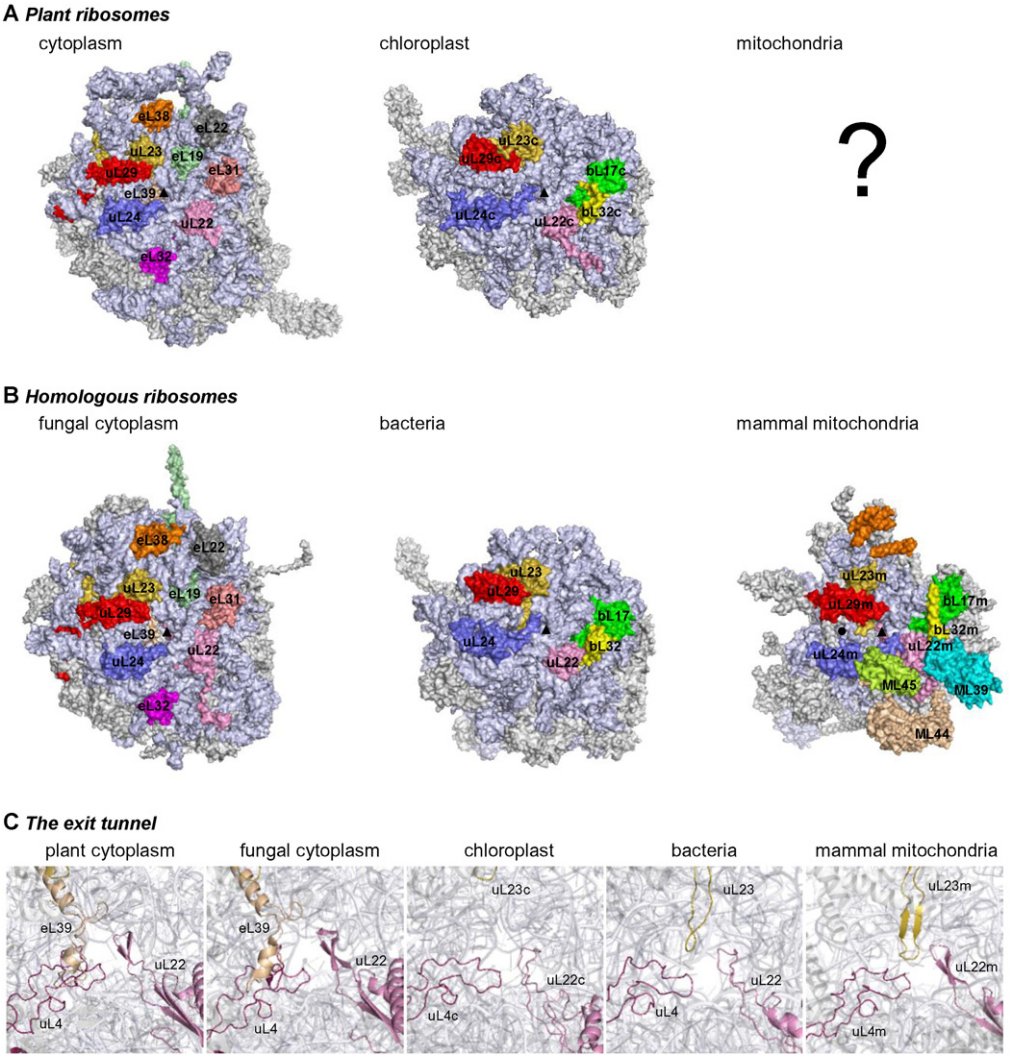

Fig. 1. Structures of plant ribosomes and their homologs in eukaryotes and bacteria. The structure of each type of ribosome at near-atomic resolution. The archetype of each large subunit, with ribosomal tunnel-exit extremity (marked by a black triangle) at the center of the picture, is shown. Ribosomal proteins surrounding the tunnel-exit extremity are colored, using the same color if proteins are conserved among different ribosomes. (A) Structures of plant cytoplasmic and chloroplastic ribosomes have been solved by cryo-electron microscopy (adapted from [23,246]), while the plant mitochondrial ribosome structure still remains unsolved. (B) Cytoplasmic and chloroplastic plant ribosomes are homologous to eukaryotic cytoplasmic and bacterial ribosomes, respectively. From left to right the structures of fungal cytoplasm ribosome, bacteria ribosome and mammal mitoribosome are shown (adapted from [14,24,247]). The conventional polypeptide-exit site (PES) is marked by a black triangle and the mitochondrial specific polypeptide-accessible site (PAS) is shown with a black circle. (C) A zoom on the ribosomal tunnel-exit extremity highlights ribosomal proteins which, associated with rRNA, constitute the exit tunnel wall, with uL4 and uL22 as common proteins, eL39 specific of cytoplasmic ribosomes and uL23 in chloroplastic, bacterial and mammalian mitochondrial ribosome.

maturation of the nascent chain, even in plants. The present review summarizes this field, searching for the similarities and the differences between the plant system and other organisms. We will begin the review by describing the current structural knowledge of the tunnel-exit extremity of various ribosomes. Next, we will assess current knowledge pertaining to all RPBs, with emphasis on plants and their specific systems.

2. Ribosome and its tunnel-exit ligand-binding platform

2.1. Three types of plant ribosomes — origin and cellular compartment

In plants, translation occurs in three distinct cellular compartments – cytoplasm, chloroplast, and mitochondria –. Consequently, plants possess three types of ribosomes, whose basic organization is similar to that of prokaryote and eukaryote counterpart, in that they are comprised of ribosomal RNAs and proteins in the large and small subunits.

In eukaryotes the nuclear encoded proteins are synthesized on the 80S cytosolic ribosomes, which differ from the 70S prokaryotic type primarily by their larger size and higher number of proteins (Supplemental Table 2). Recently, a common nomenclature has been adopted for most ribosomal proteins to unambiguously identify them and overcome the confusion caused by the past assignment of identical names to unrelated ribosomal proteins from different species [4,5]. We propose to use this innovative naming system also for plant ribosomal proteins as described in Supplemental Table 3 to facilitate the comparison with other organisms.

Each 80S ribosome is comprised of a large 60S subunit containing three RNA species (5S, 5.8S, 23S-like rRNA) and up to 47 different ribosomal proteins (r-proteins), and a small 40S subunit containing a single 18S rRNA and up to 33 different r-proteins (Supplemental Table 2, Fig. 2, and Movie 1 which presents the cytoplasmic 80S ribosome of *Triticum aestivum*). Characterization of cytosolic ribosomes of various eukaryotic sources have revealed that the 79 r-protein families present in plant ribosomes are equivalent to those found in yeast and mammals [6].

Chloroplastic and mito-ribosomal proteins are encoded by both organelle and nuclear genomes and the sets of proteins encoded by these different genomes vary between plant species [7].