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Evolution of the mitochondrial ribosomal proteome

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1. Background

It is now fairly well accepted that all present-day eukaryotes derive from an ancestor (Last Eukaryotic Common Ancestor : LECA) that already harboured the α -proteobacterial endosymbiont that gave rise to the mitochondrion.

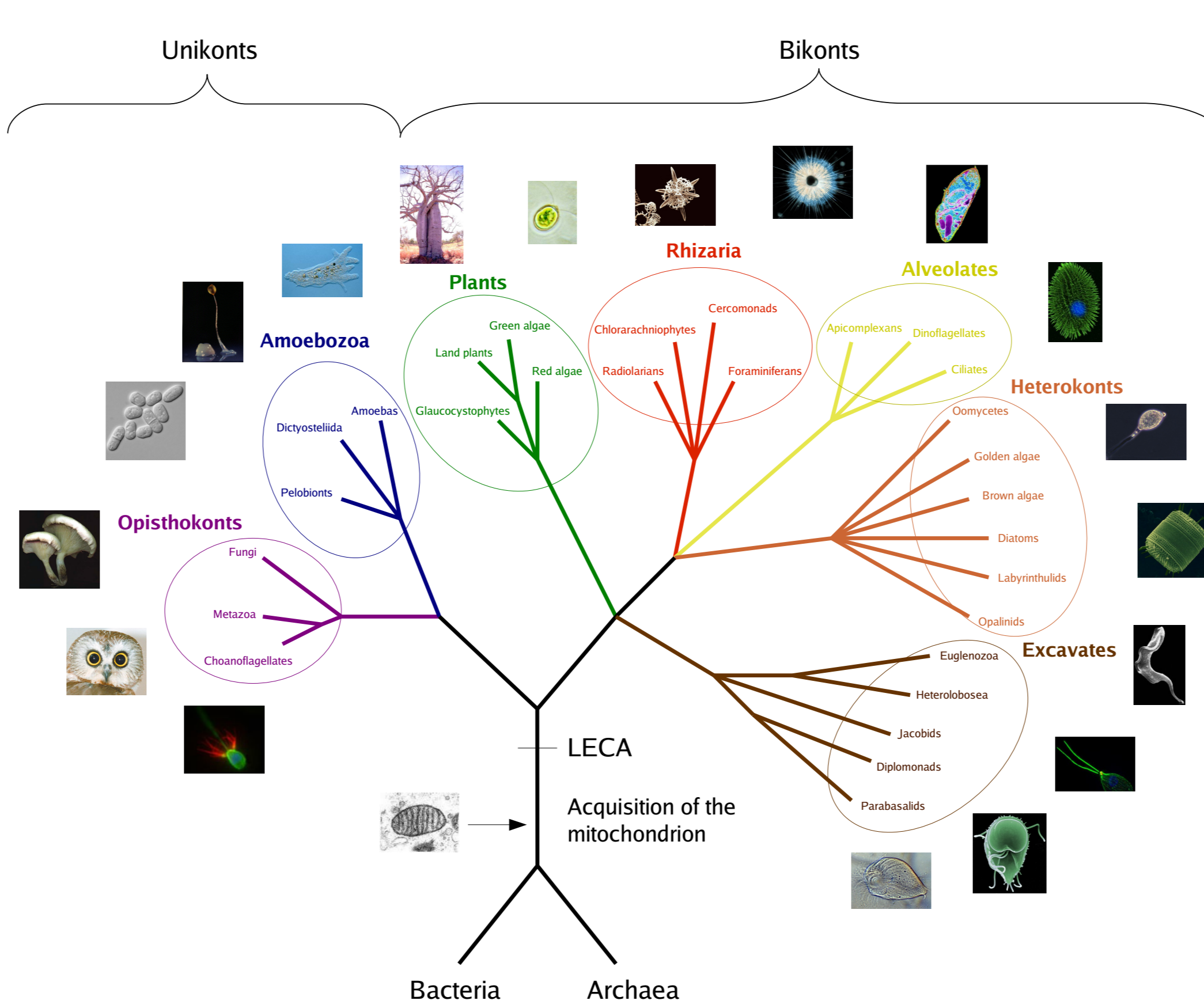
The explosive increase of genomic data from eukaryotes, especially protists, coupled to the improvement of molecular phylogeny tools and approaches such as multigene analyses suggests a rapid divergence of eukaryotic lineages into a number of major supergroups [1]. Based on the distribution of two shared derived characters it has been proposed that the first divergence in the evolution of present-day eukaryotes may have separated an ancestrally uniciliate lineage that led to Opisthokonts and Amoebozoa (Unikonts) on one side from an ancestrally biciliate lineage that led to all other supergroups (Bikonts).

4. Phylogenomic approaches

The last ten years have witnessed an explosive increase of genomic data from representatives of the three domains of life. This allows the application of phylogenomics approaches to understand the evolution of different cellular systems. These approaches consist in investigating the distribution of the homologs of the components of a particular cellular system over the species tree and to analyse their phylogeny.

Starting from experimentally characterized proteins, a recent analysis investigated the evolution of mitochondrial ribosomes by exploring the distribution and phylogeny of their components over 18 eukaryotic genomes [6]. We have extended this analysis by building recursive HMM models to search exhaustively for MRPs homologs over a wider sample of 38 eukaryotic genomes, including a whole new supergroup (Heterokonts). Since MRPs are often very small and divergent proteins, our larger sampling allowed us to detect a number of previously unreported homologs.

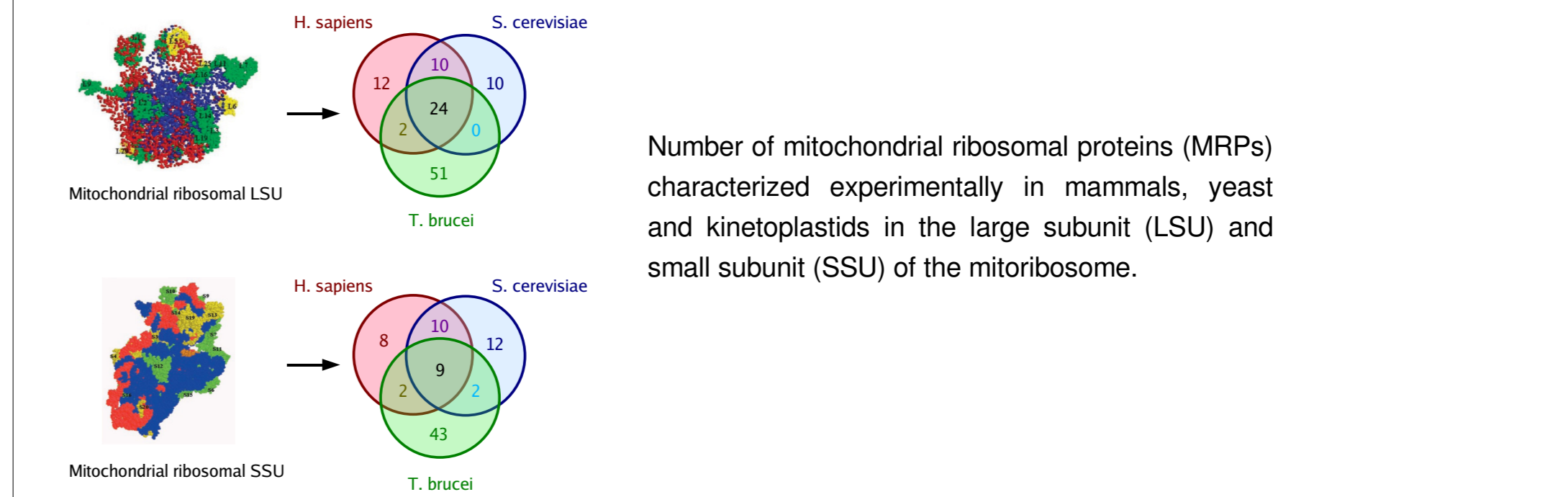
2. Phylogeny of eukaryotes



3. Proteomic characterizations

On the way to become an organelle, the α -proteobacterial endosymbiont reduced drastically its genome, part being lost and part being relocated to the host genome. It is known that mitochondrial ribosomes experienced a very dynamic evolutionary history, having notably reduced their RNA components and acquired eukaryotic-specific proteins.

Currently, proteomic characterizations of mitochondrial ribosomal proteins (MRPs) are available only from representatives of mammals [2] & [3], yeast [4] and kinetoplastids [5] which represent only two eukaryotic supergroups. However, these characterizations have already highlighted a high number of lineage-specific innovations. For example, 94 proteins are characteristic of the mitochondrial ribosomes of kinetoplastids, the majority of them having no homologs in any other eukaryotic lineage.



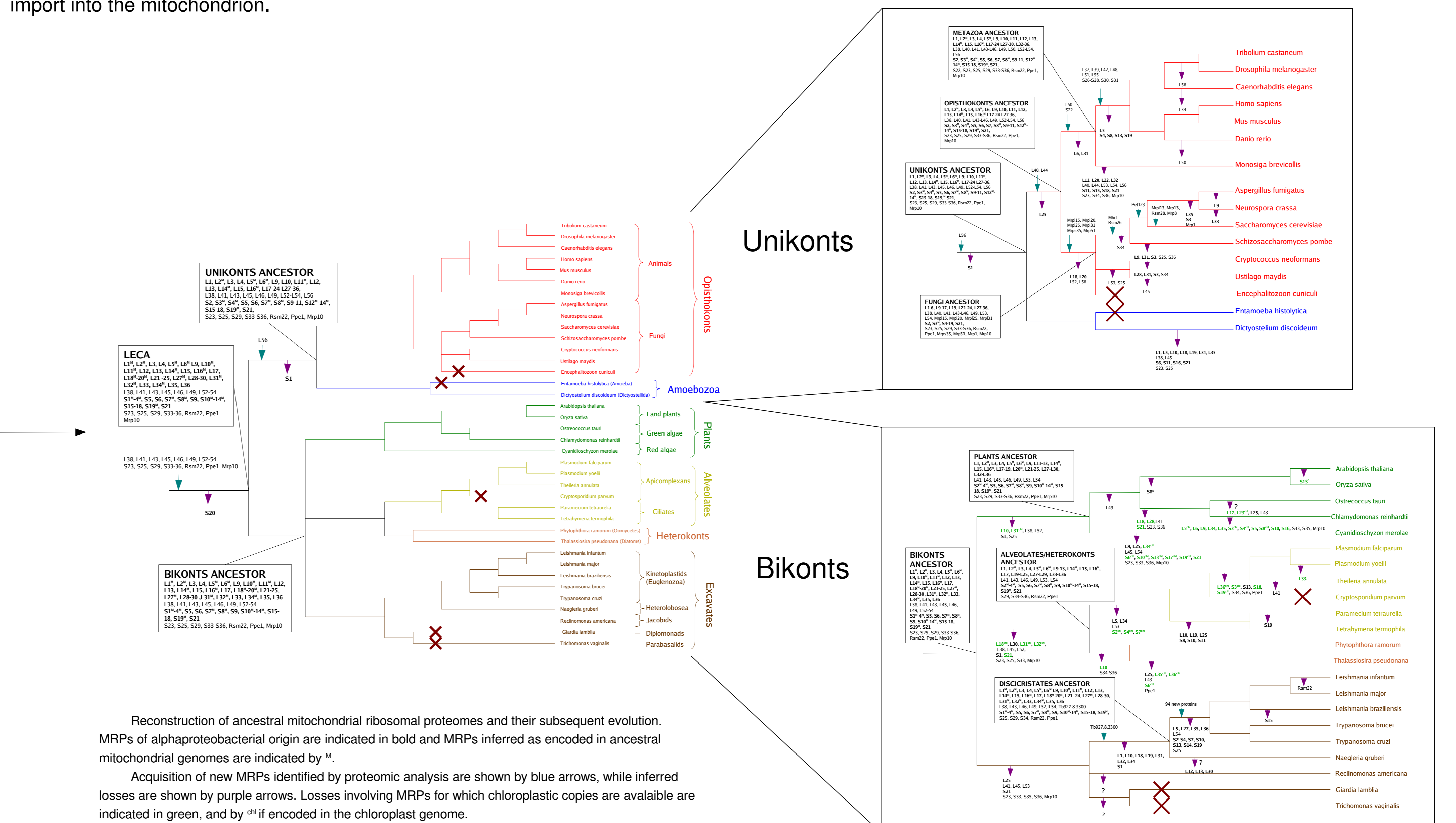
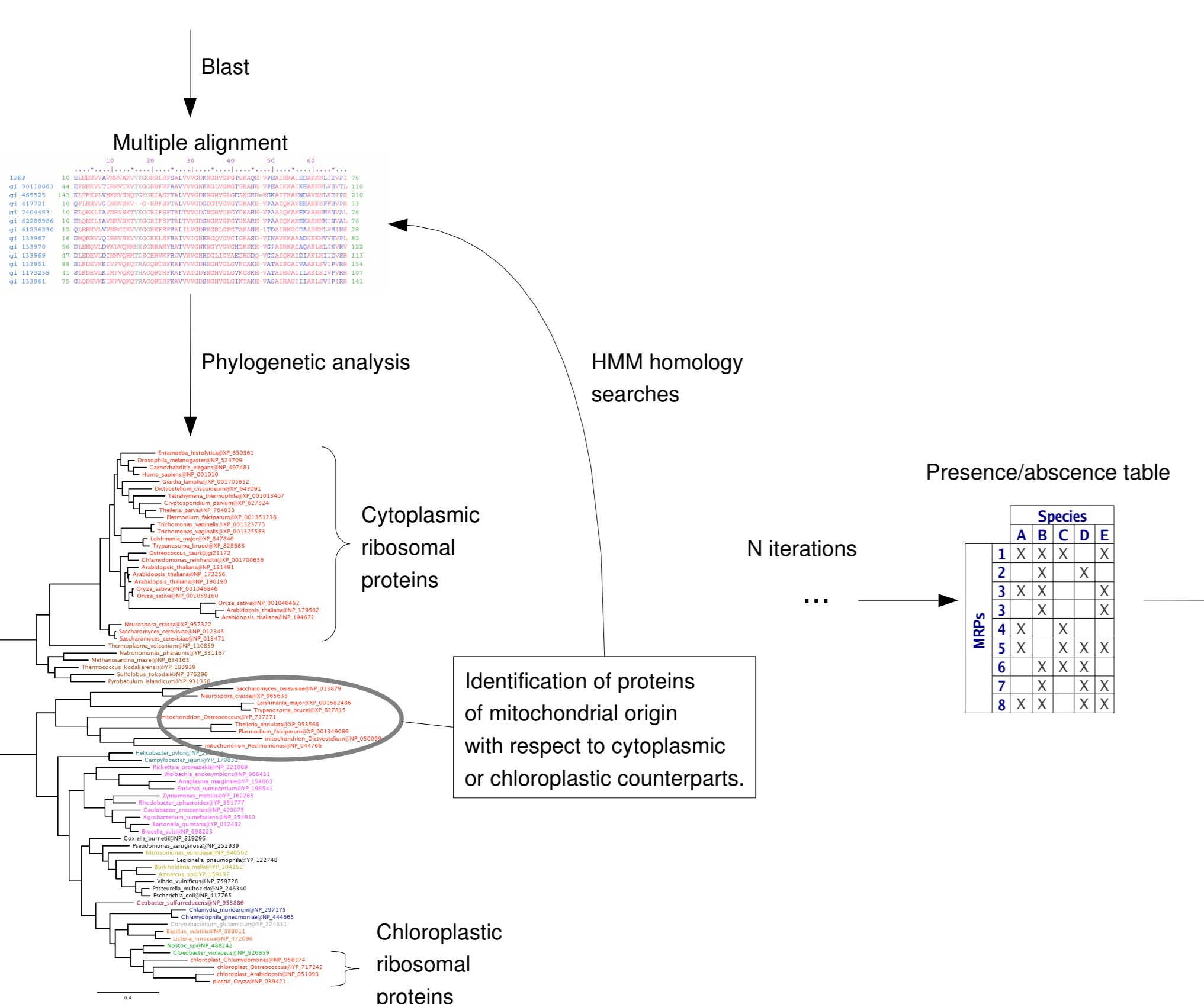
5. Reconstruction of ancestral mitochondrial ribosomal proteomes

We infer that the ancestral mitochondrial ribosome of the LECA contained already 72 proteins, with only one loss (S20) but 19 innovations with respect to the α -proteobacterial ancestor. That means that a long time probably elapsed between the acquisition of the mitochondrion and the radiation of eukaryotes.

Subsequent evolution of the mitochondrial ribosomal proteome was then very dynamic and different in the various lineages. In some phyla we predict such a large amount of MRP losses that the ribosome would hardly be viable. It is thus likely that these losses are compensated by novel acquisitions, although this can only be verified by proteomic characterization of mitoribosomes from representatives of these lineages. This is the case of kinetoplastids where the evolution of mitochondrial ribosomes appear to have been dramatic, involving acceleration of evolutionary rates and a high number of losses which proteomic characterization indicates to have been replaced by novel MRP acquisitions, to obtain a very protein rich mitoribosome with 133 MRP, of which 94 are unique innovations of the kinetoplastid lineage.

In photosynthetic organisms some MRP losses may be compensated by chloroplastic copies, this implying for some of them export from the chloroplast and import into the mitochondrion.

For each MRP characterized experimentally (α -proteobacteria, mammals, yeast, kinetoplastids)



6. Timing of transfer of MRPs of α -proteobacterial origin to the nuclear genome

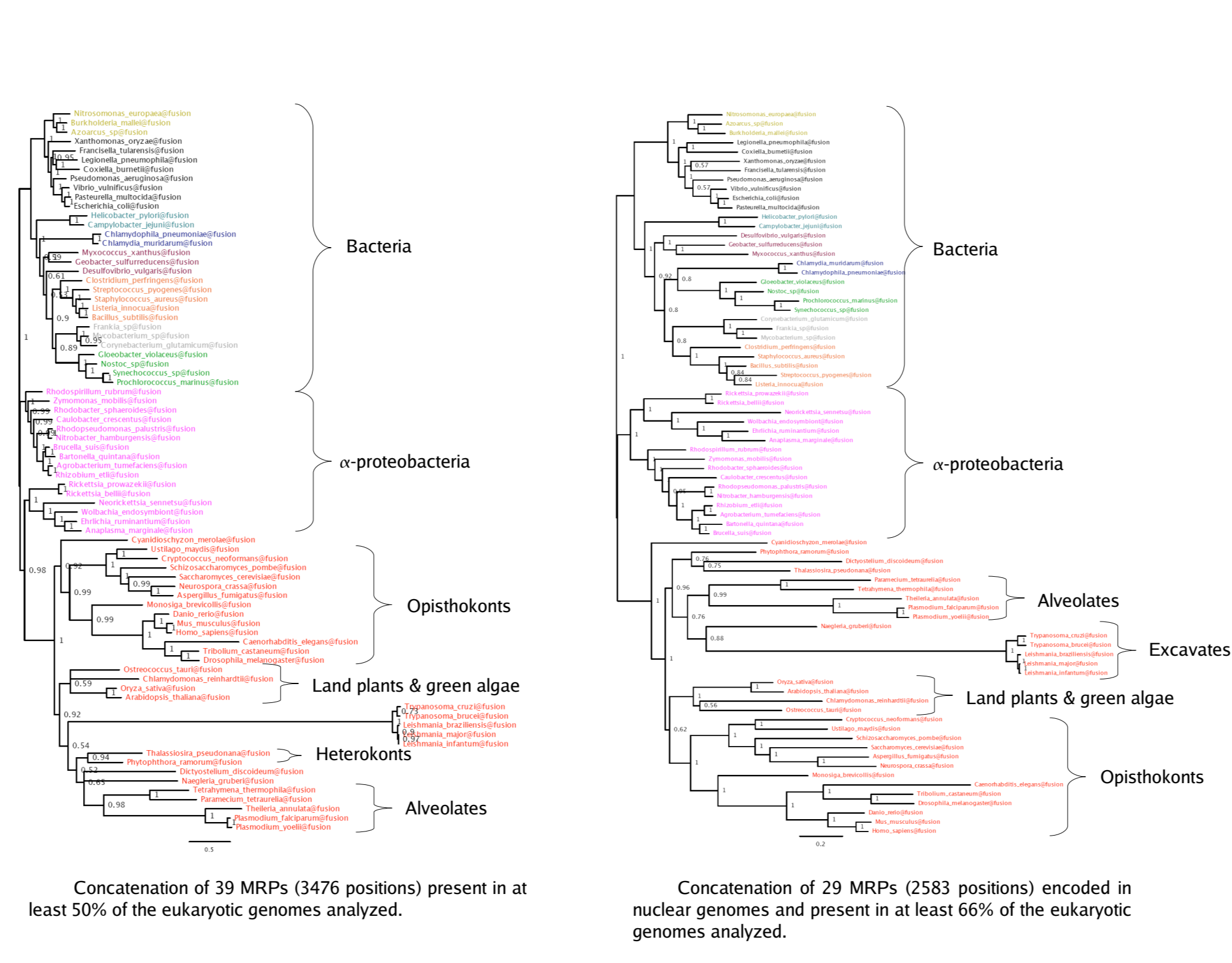
Most MRPs are today encoded in the nuclear genome, but their number varies between phyla : for example no MRPs are encoded in mitochondrial genomes of animals and fungi, while the mitochondrial genome of the excavata *Reclinomonas americana* still encodes 27 MRPs genes.

We infer that 26 MRPs were transferred to the host nucleus before the radiation of the different eucaryotic supergroups. Interestingly, 14 of these (in red) are also missing from the genome of the aphid bacterial symbiont *Carsonella ruddii*, which appear to be on the way of becoming an organelle [7], and has lost 21 ribosomal proteins (empty cases). This may indicate a repeated tendency of these MRPs as being the first to be relocated to the nucleus during regression of a symbiont to organelle. Interestingly *C. ruddii* has also lost the MRP S20.

LSU	α -proteobacteria	<i>C. ruddii</i>
L1	X	X
L2	X	X
L3	X	X
L4	X	X
L5	X	X
L6	X	X
L7/L12	X	X
L9	X	X
L10	X	X
L11	X	X
L13	X	X
L14	X	X
L15	X	X
L16	X	X
L17	X	X
L18	X	X
L19	X	X
L20	X	X
L21	X	X
L22	X	X
L23	X	X
L24	X	X
L25	X	X
L26	X	X
L27	X	X
L28	X	X
L29	X	X
L30	X	X
L31	X	X
L32	X	X
L33	X	X
L34	X	X
L35	X	X
L36	X	X
S1	X	X
S2	X	X
S3	X	X
S4	X	X
S5	X	X
S6	X	X
S7	X	X
S8	X	X
S9	X	X
S10	X	X
S11	X	X
S12	X	X
S13	X	X
S14	X	X
S15	X	X
S16	X	X
S17	X	X
S18	X	X
S19	X	X
S20	X	X
S21	X	X
S22	X	X

7. Concatenations

We tried to use different datasets of MRPs to reconstruct the eukaryotic phylogeny. Although the trees are not completely resolved a number of supergroups are recovered.



8. Conclusions

The mitoribosome of the LECA was already a very complex structure, very different from its α -proteobacterial ancestor, notably including already 19 novel MRPs. This indicates that the acquisition of the mitochondrion probably does not coincide with the radiation of eukaryotes, contrary to what often assumed.

The mitochondrial ribosomes appear to have undergone a very dynamic history with respect to cytoplasmic ribosomes, having notably experienced differential losses that appear to be still ongoing. Importantly, the available current proteomic data -albeit still limited- indicates that there is no evolutionary gradual trend towards protein-rich mitochondrial ribosomes, but that many novel components have been independently added in different eukaryotic lineages. The integration of phylogenomics and proteomics approaches will reveal essential in the future to dissect the evolution of cellular systems.

9. References

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