EMERGENCE OF MEMBRANE BIOENERGETICS AND ITS COUPLING TO REDOX AND PHOTOSYNTHETIC ENZYMES. Armen Y. Mulkidjanian[1,2,3] Daria V. Dibrova[3] and Michael Y. Galperin[4], [1]School of Physics, Osnabrueck University, 49069, Osnabrueck, Germany (amulkid@uos.de); [2]School of Bioengineering and Bioinformatics, and [3]A.N. Belozersky Institute of Physico-Chemical Biology, Lomonosov Moscow State University, Moscow 119992, Russia; [4]National Center for Biotechnology Information, National Library of Medicine, National Institutes of Health, Bethesda, Maryland 20894, USA.

Energy converting systems of modern organisms are sophisticated, fine tuned networks of membrane-embedded protein complexes that use external energy sources such as light, nutrients or redox gradients to generate ion disequilibria across ion-tight membranes. The ion gradients formed can discharge through rotary membrane ATP synthases, allowing synthesis of ATP from ADP and inorganic phosphate. In prokaryotes, bioenergetic cycles exist in two versions, with either protons or sodium ions being translocated though the ATP synthase. A combination of comparative structural and phylogenomic analyses has suggested the evolutionarily primacy of the sodium-dependent bioenergetics [1,2].

The emergence of modern energy-converting networks probably was not a one-time event. Rather, it should have been a evolutionary process gradually involving new members. We believe that membrane bioenergetics may have developed from an ancient system of cellular Na^+/K^+ homeostasis [1-4]. Indeed, the cell cytoplasm of archaea, bacteria and eukaryotes contains substantially more potassium than sodium, and the prevalence of potassium ions is specifically required for many key cellular processes [3,4]. This distinct ionic composition and requirements have been attributed to the emergence of the first cells in K^+-rich habitats [3,5]. Specifically, since the $[K^+]/[Na^+]$ ratio is greater than unity at vapor-dominated zones of inland geothermal systems, we argued that the first cells could have emerged in the pools and puddles at the periphery of primordial anoxic geothermal fields, where the elementary composition of the condensed vapor would resemble the internal milieu of modern cells [3].

Marine and freshwater environments generally show a $[K^+]/[Na^+] < 1.0$. Therefore, to invade such environments, while maintaining the cytoplasmic $[K^+]/[Na^+] > 1.0$, primordial cells needed means to extrude sodium ions. The foray of primordial cells into new, Na^+-rich habitats was the likely driving force behind the evolution of diverse sodium export pumps. While initially the Na^+-exporting enzymes could have been driven by cleavage of chemical bonds, the set of such enzymes may have been gradually complemented by redox-, light- and osmotically-driven Na^+ pumps [4].

In the proposed scenario, the first chlorophyll-containing photochemical reaction centers could initially provide redox equivalents for cellular metabolic chains as well as for redox-driven sodium export pumps. The first cytochrome *bc* complexes may have evolved from membrane-anchored dehydrogenases within photosynthetic membranes [6].

At high external sodium levels and in concert with the gradual tightening of the lipid membranes that allowed maintaining of increasingly high values of the membrane potential, an ATP-driven rotary Na^+ export pump, still functioning in some prokaryotes [7-9], could change the direction of rotation and become a Na^+-driven ATP synthase [1,2,10]. The resulting interplay between several, initially independent sodium export pumps and the consumers of Na^+ gradient would have yielded the Na^+-dependent membrane bioenergetics.

The transition to modern-type proton driven bioenergetics required sophisticated proton-tight membranes and seemed to happen separately in bacteria and archaea [1,2]. Only after the emergence of oxygen-evolving photochemical reaction centers, the advantages of proton-dependent bioenergetics could be fully exploit owing to the emergence of high-potential terminal oxidases, which pump protons, but not sodium ions [11]. After the oxygenation of the atmosphere, the proton-dependent bioenergetics could spread over the tree of life.

References

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