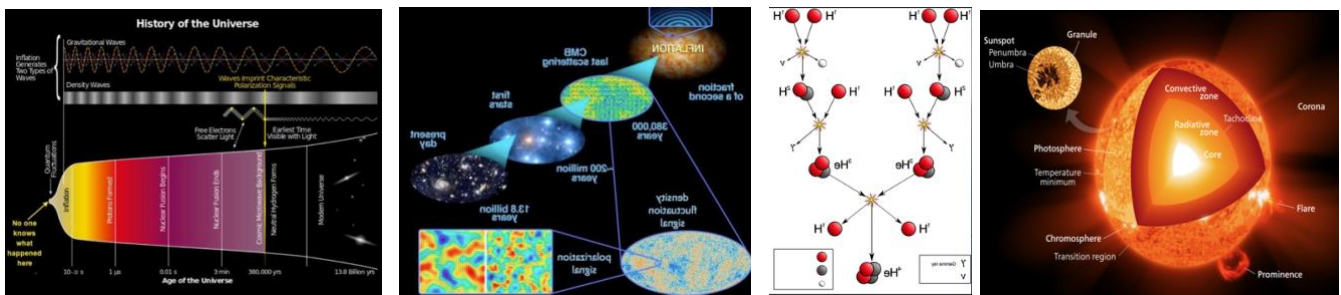


proton

Just after the beginning, **protons** became one of the basic particles of matter. Later, as they crowded together, collisions between protons created energy, released as *photons*. Only then did light fill the early universe.



When life arose on Earth, protons again became the basis of energy production, this time fueling cellular metabolism. The central unit of life is the **cell**, whose outer boundary is limited by a **membrane**. Inside the cell membrane is alive. Outside is the non-living world. Early on, managing the flow of protons across membranes became the source of energy, ultimately recycling ADP to form **ATP**, the currency of energy in living systems.

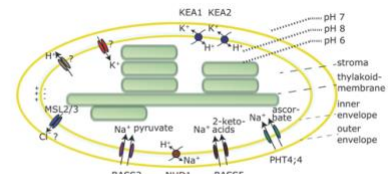
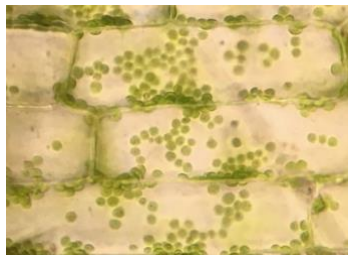
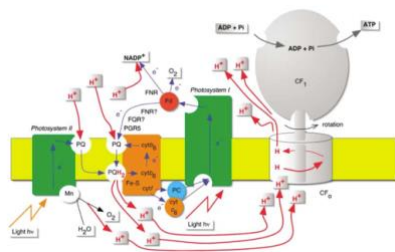
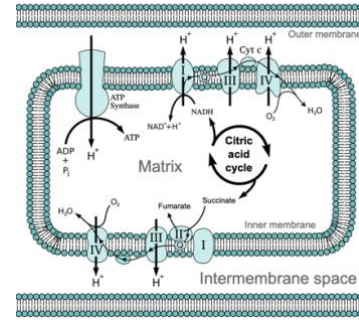
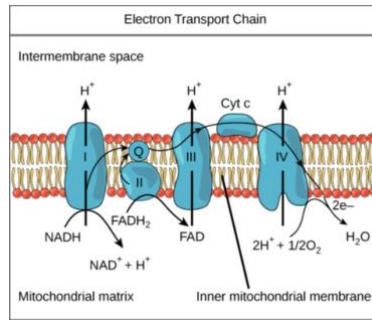
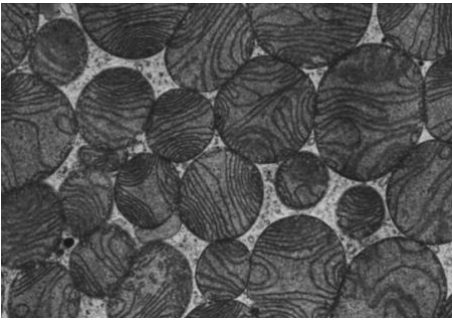
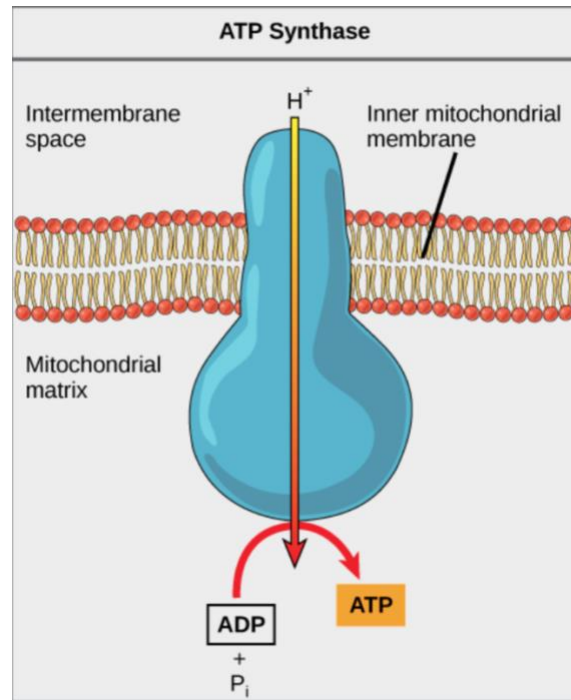
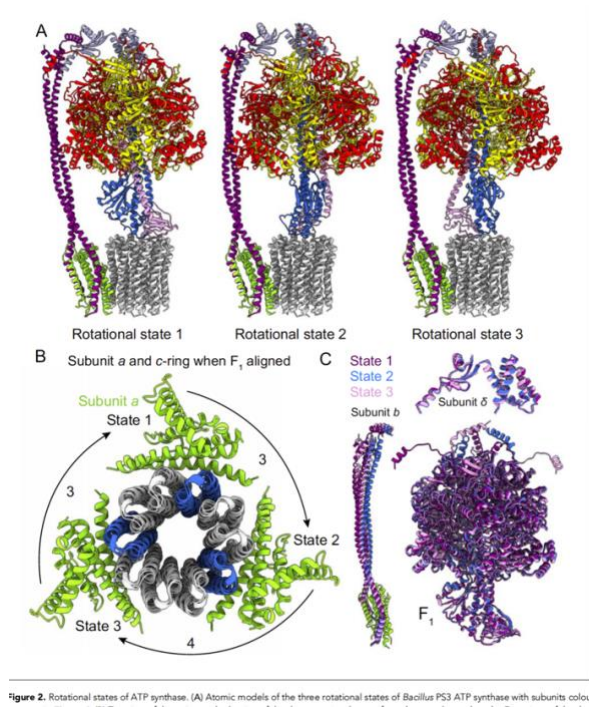


FIGURE 2 | Selected transporters in the chloroplast envelope membrane. Transporter activities are shown for chloroplasts in the light. The nature of

In **archaea** and **bacteria**, the outer membrane alone is available to serve as a barrier to form a proton gradient. Fueled by chemical reactions in an elaborate **electron transport system imbedded in the membrane**, protons (H^+), accumulate outside the cell. Then, moving down a proton gradient through a pore in the center of **ATP synthase**, they deliver torque, spinning the molecular machine. In addition, certain bacteria developed the ability to use *photons* of light as an energy source to drive the electron transport chain, splitting water, ejecting protons (H^+), and releasing oxygen (O_2) to the outside world.



Once oxygen had accumulated in the environment, another membrane became available to provide separation for a proton gradient: the inner membrane of **mitochondria**, which inhabited eukaryotic cells. In other cells, internalized photosynthetic bacteria gave the ability to use photons to drive a proton gradient across the membranes of **chloroplasts**.



Protons thus provide energy not only for stars, but also for living cells.