# Research Reviews

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Biology is a broad and rapidly changing discipline. The manuscripts submitted to *The American Biology Teacher* do not always cover the full breadth of biology, nor do they usually approach the frontiers of biological knowledge. Attempts by the *ABT* editors to solicit diverse and timely articles are often unsuccessful; practicing biologists are very busy people. As the new editor of Research Reviews, I plan to review articles on biology and biology education that introduce or summarize major new ideas. If I do this correctly, reading Research Reviews will cause you to revise your teaching materials and methods and inform your students about parts of their textbooks that are outdated. A primary benefit of this approach will be that teachers and students alike will be constantly reminded of the dynamic nature of biology.

I invite you to submit reviews of articles you feel are important and to suggest articles and topics for inclusion in future columns.

## How Many ATPs per Glucose Molecule?

**Beavis, A.D. & Lehninger, A.L. (1986). The upper and lower limits of the mechanistic stoichiometry of mitochondrial oxidative phosphorylation. *European Journal of Biochemistry, 158,* 315-322.**

If a eucaryotic cell is provided with a molecule of glucose, how many ATP molecules will it be able to assemble under aerobic conditions? Like many of my fellow biology teachers, I have been guilty of implying to my students that there is an answer to this question, a nice round number like 36 or 38. However, with the general acceptance of Peter Mitchell's chemiosmotic hypothesis, biologists began to realize that we do not know how many ATP's might be produced. Further, the number is probably much less than 36, not an integer and highly dependent on conditions in the cell.

Figure 1 summarizes our present understanding of how mitochondria use energy present in reduced NAD (or FAD) to assemble ATP molecules. In step one, a pair of electrons from reduced NAD flows through the electron transport system in the inner mitochondrial membrane. The electrons lose energy in the process; oxygen is the recipient of these now low-energy electrons. The energy lost by the electrons is used to pump protons (hydrogen ions) into the outer compartment of the mitochondrion at three different sites in the electron transport system. The number of protons pumped per pair of electrons was initially assumed to be six (two at each site). Beavis and Lehninger provide evidence that eleven protons (four at the first two sites and three at the third site) are brought across the membrane by a pair of electrons from reduced NAD. Lower energy electrons from reduced FAD do not transport protons at site one, and thus would only move seven protons to the outer compartment.

At step two, the energy stored as a proton gradient is used to assemble ATP molecules from inorganic phosphate (Pi) and ADP. The protons flow back to the inner compartment, attracted by both chemical and electrical gradients. The exact way energy released by proton flow is used to make ATP is not known. The site of proton flow is referred to as an F0/F1 complex, and is composed of about a dozen polypeptide subunits. Beavis and Lehninger's data suggest that the passage of four protons releases enough energy to assemble one ATP. This would mean that a mitochondrion could make 2.75 ATPs for each reduced NAD and 1.75 ATPs for each reduced FAD. If we insist on counting ATPs per glucose, we must reduce our total by three based on the above values. But the proton gradient is used for other things besides making ATP.

Step three represents a transmembrane protein, phosphate translocase. It uses some of the proton gradient for active transport of inorganic phosphate into the inner mitochondrial compartment. The movement of some other metabolites into the inner compartment is also powered by the proton gradient. We must therefore reduce our estimates of ATP production even more.

At step four, the proton gradient (more positive charges in the outer compartment) is used to power the

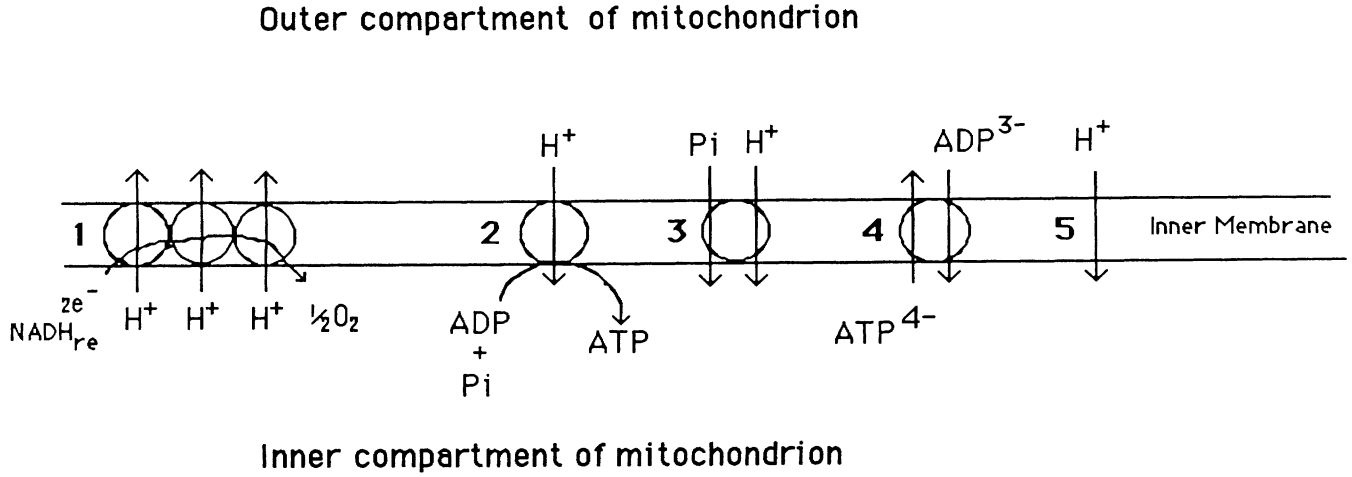


Figure 1. Current model of oxidative phosphorylation

exchange of ATP for ADP so that ATP will be available in the cytoplasm of the cell. Another transmembrane protein, ATP-ADP translocase, is responsible for this exchange.

Step five represents the tendency for protons to simply leak back into the inner compartment. This movement is difficult to quantify, but it is significant.

When we consider the mechanism by which mitochondria make ATP and the evidence provided by Beavis and Lehninger, it is clearly impossible to calculate the exact amount of ATP a typical cell can make from the energy in a glucose molecule. Instead, our discussions of mitochondrial (and chloroplast) function should stress what we know about the process of ATP production, thus providing a good opportunity to illustrate the imprecise, changing nature of biological science.

## Meiotic Precision

**Dawson, D.S., Murray, A.W. & Szostak, J.W. (1986). An alternative pathway for meiotic chromosome segregation in yeast.** ***Science, 234,*** **713-717.**

It is a common biological strategy for organisms to use multiple, independent backup systems to ensure that critical events happen correctly. A good example is the multiple controls over blood glucose levels. Dawson, Murray and Szostak provide evidence for a backup system that increases the probability of correct chromosome segregation in meiosis.

There is evidence that, in addition to generating variation, crossing over is necessary for chromosome segregation in meiosis. Mutations in *Drosophila* and yeast that reduce the number of crossover events also increase the amount of nondisjunction. Observable crossovers (chiasmata) keep homologous pairs together until positioned on the metaphase plate, and are probably part of the mechanism that causes centromeres of homologs to be attached to spindle fibers from opposite poles.

Dawson, et al. used artificial chromosomes to demonstrate that chromosomes will segregate in the absence of crossing over. The artificial chromosomes were constructed from bacteriophage lambda DNA plus the centromere and a few genes from a yeast chromosome. These chromosomes could be made to be either homologous or nonhomologous. They were much smaller than normal chromosomes, and crossing over rarely occurred in them. Their presence in the products of meiosis could be detected by genetic markers. Tests showed the artificial chromosomes were distributed into gametes in a manner consistent with a homology-independent segregation system. Such a system makes it ten times more likely that homologous chromosomes will segregate properly in meiosis even if they do not cross over. A mechanism for the system is not known.

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