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## PERSPECTIVES ON THE ORIGIN OF MITOCHONDRIA

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Received 8 September 1984; Revised 18 January 1985

### Abstract

*The two main theories of the evolutionary origin of the mitochondria are examined. Evidence that is frequently cited to support each theory is presented to determine how well it supports each. It is concluded that most of the evidence can be fit into either scheme, and that even the best data constitute only circumstantial evidence in favor of any evolutionary origin of mitochondria.*

### Introduction

In all schemes of the evolutionary advancement of life there is a point where a relatively simple cell must be converted into the more complex cells of which all higher organisms are composed. There are two general theories as to how this division occurred (Figure 1). The autogenous theory claims the cellular organelles arose through a gradual process of compartmentalization of genes and enzymes present in the ancestor. The endosymbiont theory claims the organelles evolved separately from the main part of what is now the eukaryotic cell and became associated with

it by being engulfed and then forming a symbiotic relationship.

The debate between the proponents of these theories has been long and sometimes acrimonious with each in turn claiming solid proof of its validity. Consequently many students of origins may find this aspect of the debate between evolutionists confusing and could benefit from a short review outlining the pro and con of these two views. We will limit our discussion to the mitochondrion principally because the authors are more interested in animal cell biology than plant. Some researchers feel the phylogenetic relationship between the plastid and its endosymbiotic ancestor has been established much more firmly than for mitochondria. Those interested in studying this aspect of origins should obtain the review by Gray and Doolittle<sup>1</sup> or the article by Rao et al.<sup>2</sup>

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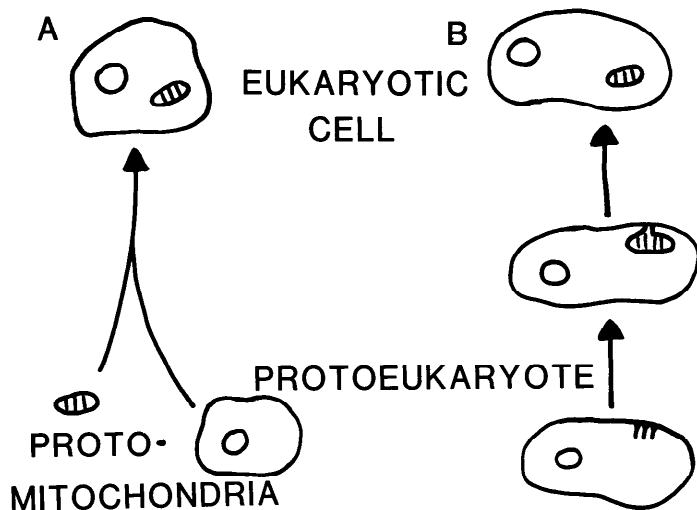


Figure 1. General comparison of the endosymbiotic (A) and autogenous (B) theories. In 'A' an anaerobic protoeukaryotic cell engulfs an aerobic bacterium and develops a symbiotic relationship with it. The endosymbiotic theory maintains that all other cellular organelles arose in a similar fashion. In 'B' the mitochondrion gradually develops as the respiratory enzymes and some DNA are partitioned into a separate compartment.

#### Physiology and Morphology

To some the endosymbiotic theory might seem implausible as a possible mechanism. However, it is well known that such close symbiotic relationships do occur. For example, lichen is composed of two distinct organisms which can, with great difficulty, be grown separately from each other. Only when together do they form a structure we recognize as lichen. Lynn Margulis,<sup>3</sup> possibly one of the strongest supporters of the endosymbiont theory, lists 13 examples of known endosymbiosis of which some can be separated and then shown to reestablish the symbiotic relationship. While this does not constitute proof the eukaryotic cells have arisen by endosymbiosis it does prevent us from initially discarding the theory as unworkable.

The similarity in morphology between mitochondria and some bacteria led early workers to speculate on their possible relationship. Both mitochondria and some bacteria have dimensions of about one micron. However, the highly convoluted inner membrane of mitochondria (Figure 2) does not at all resemble the structure of the inner membrane of bacteria. The membrane lipids of mitochondria and bacteria have also been compared to show their close relation. The prokaryotes (bacteria) have no sterol and only saturated and monounsaturated fatty acids in their membrane, while mitochondria, like the remainder of the eukaryotic cell, do contain cholesterol and polyunsaturated fatty acids in addition to saturated fatty acids. Also, the phospholipid composition differs between prokaryotes and eukaryotes.<sup>4</sup> As an exception the mycoplasma are the only prokaryotes which contain both cholesterol and polyunsaturated fatty acids in their membrane and lack cell walls. While this at first might seem to make the mycoplasma good candidates for the ancestors of mitochondria, a different bacterium, *Paracoccus denitrificans*, has been found which has many more similarities to mitochondria. Typical phospholipid compositions of mitochondria, *Escherichia coli*

and *Paracoccus denitrificans* are compared in Table I. Only the composition of the inner membrane of the mitochondria is reported here as it is generally assumed that if mitochondria did come into existence by endosymbiosis the outer membrane would arise from the phagocytic vacuole. Such a situation can be seen in the development of symbiosis of a bacterium and the amoeba *Pelomyxa palustris*. It is evident from Table I that while mitochondria do have lower levels of phosphatidylcholine than the plasma membrane of eukaryotes (which contain about 80 percent) and that there are similarities between *P. denitrificans* and mitochondrial composition there are also great differences. In particular the content of phosphatidylglycerol is much higher in *P. denitrificans* than either of the other membranes shown. Consequently, while *P. denitrificans* has a phospholipid composition which is closer to that of mitochondria than other bacteria this is no more than circumstantial evidence of a relationship. Table II shows the comparative amounts of saturated, unsaturated and cyclopropane fatty acids esterified to the phospholipids of these membranes. It is pointed out that the amounts of saturated and unsaturated fatty acids in *P. denitrificans* are similar to that of mitochondria. However, the types of fatty acid within each class are quite different. The bacteria (including *P. denitrificans*) have only monounsaturated fatty acids and their longest fatty acids (saturated or unsaturated) are only 18 carbons long. Mitochondria have fatty acids up to 20 or 22 carbons long and they are rich in polyunsaturated fatty acids. Thus it can be said that the similarities in fatty acid composition may be fortuitous and cannot be used accurately to show a relationship.

A consideration of the synthesis of lipids for mitochondria shows that any comparison of compositional data is useless no matter how closely they might converge. All of the lipids used in the synthesis of mitochondrial membranes (sterols, fatty acids and phospholipids) are produced in the endoplasmic reticulum of the "host" cell. The completed phospholipids are

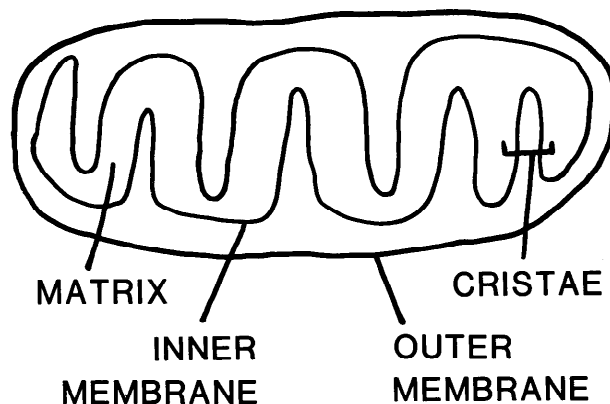


Figure 2. The mitochondria are sometimes called the power house of the eukaryotic cell as they produce the cell's ATP from nutrients and oxygen. The final stages of this oxidative process occur on the cristae which are folds of the inner membrane. These greatly increase the surface area available. Most of the other enzymes involved in respiration are located in the matrix which is similar to the cellular cytoplasm. The mitochondrial DNA is also located in the matrix and is generally circular like that of the bacteria. The outer membrane is similar in composition to the endoplasmic reticulum of the 'host' cell and some even feel it is contiguous with it.

**TABLE I**  
Comparative Phospholipid Composition of Rat Liver Mitochondria Inner Membrane, *Escherichia coli* and *Paracoccus denitrificans*<sup>5, 6</sup>

Lipid	Percent Present		
	<i>E. coli</i>	<i>P. denitrificans</i>	Mitochondria
phosphatidylethanolamine	80	6	28
phosphatidylserine	0	0	Trace
phosphatidylcholine	0	31	45
phosphatidylglycerol	10	52	2
phosphatidylinositol	0	0	4
cardiolipin	10	3	22
cholesterol*	(0)	(0)	(3)

\*Percent of total membrane lipid.

then transported into the mitochondria by phospholipid transfer proteins. If the mitochondrion is in fact the descendant of a bacterium it has totally lost the ability to synthesize lipids. As a consequence it makes no difference what the lipid composition of the mitochondrial ancestor is since as soon as it must import its lipids it will take on the compositional characteristics of the host. This might make the autogenous theory seem more attractive as it could be argued to be simpler in that it does not require the loss of a pre-existing ability. In both cases the phospholipid transfer proteins must be fully evolved before the new organelle can function. The timing of this might be slightly less critical for the endosymbiont theory as there is the potential for both the import and synthesis of phospholipid while the import apparatus must be totally functional before the developing organelle of the autogenous theory is fully enclosed. However, such advantages are likely to be slight and open to debate.

**TABLE II**  
Comparative Fatty Acid Composition of Rat Liver Mitochondria, *Escherichia coli* and *Paracoccus denitrificans*<sup>7</sup>

Lipid	Percent Present		
	<i>E. coli</i>	<i>P. denitrificans</i>	Mitochondria
saturated	39	21	34
unsaturated	48	78	63
Cyclopropane	10	—	—

### Respiration

Ostensibly the development of the mitochondrion was favored evolutionarily as it supposedly provided the host cell with the greater energy yields possible with oxidative compared to anaerobic respiration. If this is the case some predictions can be made concerning both the host and premitochondrial cells. The host cell would have to have only a fermentative mode of respiration in order for there to be a selective advantage in the acquisition of protomitochondria and the mitochondrial ancestor must have had fully developed oxidative respiration. It is generally assumed that such

an organism would have arisen from a purple photosynthetic bacterium which had lost the ability to photosynthesize while retaining its respiratory chain (Figure 3).<sup>8</sup> The strength of the selection of *Paracoccus denitrificans* as being related to the mitochondrial ancestor is based primarily on its respiratory apparatus as listed in Table III. While many bacteria possess some features of oxidative respiration which are the same or similar to mitochondria, only *P. denitrificans* has as extensive a list of correlations. Further, *P. denitrificans* does not seem to lack any major feature of the mitochondrial respiratory chain.<sup>10</sup> Relatively few bacteria have ubiquinone-10 as their sole quinone, while most mitochondria possess only ubiquinone-10. The bacterium *P. denitrificans* requires 1000 times more rotenone than mitochondria to inhibit NADH oxidation, but most bacteria are not affected by rotenone at all. The enzyme transhydrogenase is involved in the transfer of protons across the inner mitochondrial membrane utilizing the adenine dinucleotides NADP<sup>+</sup> and NAD<sup>+</sup>. It is also coupled to oxidative phosphorylation and similarities have been found in the amount of ATP used by mitochondrial and *P. denitrificans* enzymes. Since it is coupled to oxidative phosphorylation the number of protons (H<sup>+</sup>) moved per oxygen atom can be experimentally determined. Mitochondria have a H<sup>+</sup>/O ratio of six while the bacterium's ratio is eight. This difference is generally attributed to constraints in the experimental design. The bacteria do possess some dehydrogenases not possessed by mitochondria which allow them a wider variation in substances on which to grow. The loss of these dehydrogenases (such as formate dehydrogenase) would not be prevented and might be favored evolutionarily since the substances encountered within the host cell would be expected to be less varied. Of greater importance is the need for the protomitochondrion to acquire an ATP carrier. Normally ATP would be generated in the interior of the cell as it is to be utilized in that cell's metabolism. The mitochondrion, however, is producing ATP for the host cell and must export it to achieve this purpose. The purpose of the adenine nucleotide carrier is to do just that and any endosymbiotic or autogenic protomitochondrion would be useless without it.

From this discussion it is evident that if the mitochondrion did develop from an endosymbiont then this bacterium is a very good candidate for its closest living relative. The critics of this idea generally do not quibble with the selection of *P. denitrificans* but rather point out that the prediction of an anaerobic cytoplasm of the host cell may not be fulfilled.<sup>11, 12</sup> That this is the case is evident from several perspectives. The synthesis of sterols and unsaturated fatty acids, which are mandatory for the growth of eukaryotic cells, is an aerobic process. Even the fermentative eukaryotes such as yeast require a supply of sterol and unsaturated fatty acid to grow anaerobically over extended periods. The synthesis of these lipids takes place on the endoplasmic reticulum which is an integral part of the eukaryotic cell. Since bacteria synthesize no sterol and produce unsaturated fatty acids by an anaerobic pathway it cannot be claimed that the enzymes for lipid synthesis were transferred from the protomitochondrion to the cytoplasm as they are not at all similar.

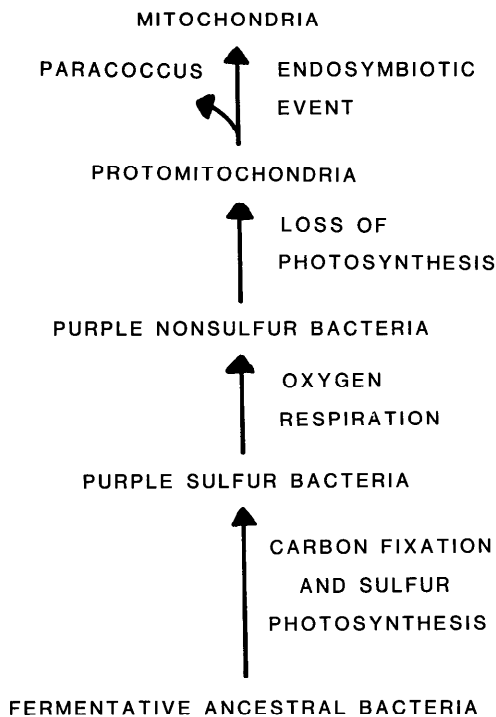


Figure 3. A possible phylogenetic tree of the evolution of the mitochondrion by endosymbiosis.

While aerobic cells require oxygen for their existence they must also be protected from its toxic effects. Aerobic cells therefore possess the enzymes superoxide dismutase and catalase. These enzymes convert the superoxide radical ( $O_2^-$ ) to hydrogen peroxide and then water. Without this form of protection this oxygen radical, which is a byproduct of cellular metabolism, would react with the lipids, proteins and nucleic acids of the cell resulting in their destruction or inactivation. These enzymes are located in the cytoplasm which may indicate the protoeukaryote was aerobic.<sup>13</sup> Alternately these enzymes might have been transferred from the incorporated aerobic bacterium into the cytoplasm of the host. As there is no real evidence as to which of these is so, either theory can conjecture without limit. It should also be pointed out that most of the enzymes and cofactors of oxidative respiration can be found in the nuclear membrane,<sup>14</sup> and eukaryotes have an electron transport system on the endoplasmic reticulum similar to that in the mitochondria, which is important in the oxygen-coupled synthesis of a variety of compounds.<sup>15</sup> This all goes to suggest that the cytoplasm either was never anaerobic or it evolved into an aerobic cell in synchrony with the development of the mitochondrion.

**DNA**

The presence of DNA in mitochondria is probably an expected feature if this organelle arose symbiotically, in which case it would be the remains of the bacterial genome of the protomitochondrion. If so, the present mitochondrial genome should show much in common with the prokaryotes. If on the other hand it is a plasmid which was included in a developing compartment as claimed by the autogeneous theory it might be expected to show similarity to the nuclear

genome from which it was presumably derived (Figure 1). Thus these two theories provide us with some predictions we may use in their evaluation.

Bacterial genomes exist as closed circles of double stranded DNA, while eukaryotic DNA is organized into linear chromosomes of double stranded DNA which is wound onto a support protein called histones. Mitochondrial DNA lacks histones and is generally circular like bacterial DNA. However, linear mitochondrial DNA is also found, principally, in the protozoa and a few fungi.<sup>16</sup> The size of the mitochondrial genome is much smaller than the smallest bacterial genome and is in the range of some viruses.<sup>17</sup> Since only 10 percent of the organelle's components are coded for by the mitochondrial genome this small size should not be too disturbing. There is immense variation in size of the mitochondrial genome with yeast being up to five times longer than human, and plant at least five times longer than yeast. In spite of these great differences in length mitochondrial genomes generally code for the same sets of products. These include two rRNA, and some of the proteins involved in the electron transport chain and ATP generation. The length differences are due to wide variations in the amount of inserted DNA with human mitochondrial DNA having almost none of these inserts while yeast mitochondrial DNA has many. In the nuclear genome of eukaryotic cells these intervening sequences are often found in the middle of genes creating a "split gene." Split genes are unknown in bacteria.<sup>18</sup> Thus there are similarities to both eukaryotic and prokaryotic genomes depending on which mitochondrion is being examined. Human mitochondria do not have split genes so resemble bacterial genomes while yeast mitochondria do have split genes and so resemble the nuclear genome. When split genes are transcribed the intervening portion must be removed before a viable message is formed and a protein or RNA can be syn-

**Table III**  
Comparison of *Paracoccus denitrificans* and Mitochondrial Oxidative Respiration<sup>a</sup>

Feature	<i>P. denitrificans</i>	Mitochondrion
Succinate Dehydrogenase	+ <sup>a</sup>	+
NAHD Dehydrogenase	+	+
Transhydrogenases and FeS proteins	+	+
Ubiquinone -10 sole quinone	+	+
Sensitive to low antimycin concentration	+	+
NADH oxidation inhibited by rotenone	(+) <sup>b</sup>	(+)
Succinate oxidation inhibited by carboxin	+	+
Oxidative phosphorylations H/O ratio 8 with NADPH	(+)	(+)
Respiration regulated by ADP levels	+	+
Formate dehydrogenase	+	- <sup>c</sup>
cytochrome o	+	-
Adenine nucleotide carrier	-	+

a. present; b. similar; c. lacking.

thesized. In eukaryotic cells this is accomplished by a splicing enzyme which cuts out the excess DNA and rejoins the ends of the valuable message. The inserted material of chromosomal genes does not carry any known information. However, it has been found that in yeast mitochondrial DNA the information needed to make the splicing enzyme is located in the inserted DNA which is to be removed.<sup>89</sup> Another way in which the mitochondrial genome has been found to be unique is that the information for the two rRNA subunits<sup>20</sup> on yeast mitochondrial DNA are so far apart that they must be made at different times.<sup>21</sup> In both nuclear and bacterial cells these subunits are made at the same time. In both bacteria and eukaryotes the transcription of each gene or cluster of genes on the genome is controlled by a special region of DNA located at that gene's leading edge which interacts with inhibitor or activating molecules. In human mitochondrial DNA there is only one such site for the entire genome, while yeast have many.<sup>22</sup>

The genetic code of mitochondrial DNA is known to be different from the "universal" code of the nucleus and bacteria. It has been suggested that this represents the more primitive genetic code of the early stages of cellular evolution. However, the point to notice in our discussion is that not only does the mitochondrial genetic code differ from the universal code but there are differences in code between the mitochondria of different organisms.<sup>23</sup>

We see then that the genome of the mitochondria exhibits such diversity that no conclusions can be drawn as to the validity of the two major evolutionary models of its origin. Indeed, the main impression one obtains is of the many instances in which the mitochondrial genome is unique. This impression remains even if we accept that much of the variation in size and genetic code is due to fairly recent evolutionary events such as random drift.

### Protein Synthesis

Protein synthesis begins with the transcription of the information on the DNA molecule onto a strand of mRNA (messenger RNA). This message is then read by the ribosomes which are composed of rRNA and ribosomal proteins. The ribosome attaches amino acids into a chain in the order specified on the mRNA, a process termed translation. The amino acids are brought to the ribosomes on tRNA (transfer RNA). While this sequence is essentially unchanged in pro- and eukaryotes the ribosomes and other molecules involved are distinctly different. One of the claims made in favor of the endosymbiotic theory was that protein synthesis in the mitochondrion was very similar to that in bacteria. Recent discoveries have shown that this may not be the case.

The transcription of the DNA information into mRNA form involves the enzyme RNA polymerase. The mitochondrial RNA polymerase, like all the enzymes required for mitochondrial DNA synthesis, is coded for in the nucleus. The polymerase of the nucleus and of bacteria is composed of several different subunits and is of high molecular weight. In contrast the mitochondrial polymerase is composed of a single subunit and is of lower molecular weight.<sup>24</sup>

The mRNA of bacteria and eukaryotes differs in the treatment of the 3' tail. In eukaryotic cells a series of

adenine molecules is added one at a time to the 3' end by a special enzyme after completion of its transcription from DNA. In bacteria this polyadenation of the 3' end does not always occur, while a polyadenine tail has been found on mitochondrial mRNA. However, the adenines added to mitochondrial mRNA seem to be added as groups rather than singly.<sup>25</sup>

The ribosome is a central structure in protein synthesis since it is here that amino acids carried on tRNA's are brought together in the order dictated by the mRNA and bonded into a polypeptide chain. The characterization of ribosomes is based on the amount of protein they contain, their base composition and their size. The first problem we encounter in investigating the mitochondrial ribosome is that there is so much variation between them that they show little evidence of a common ancestry.<sup>26, 27</sup> Secondly, it is now acknowledged that the mitochondrial ribosome is vastly different from both their bacterial and eukaryotic homologs. The characteristics of ribosomes are outlined in Table IV.

**Table IV**  
**Ribosomal Characteristics<sup>28-31</sup>**

	Mitochondria	Bacteria	Cytoplasm
<b>Size (Svedberg Units<sup>a</sup>)</b>			
Mature Ribosome	55S to 80S	70S	80S
Small Subunit	28S to 55S	30S	40S
Large Subunit	39S to 60S	50S	60S
<b>Percent Protein</b>			
Content	60+	40	40 to 50
<b>Number of Proteins</b>			
Small Subunit	30 to 44	21	33
Large Subunit	31 to 40	34	45

a. Svedberg units measure the size of a particle by the distance it moves in a centrifugal field.

Bacterial ribosomes contain about 60 percent RNA and 40 percent protein while eukaryotic ribosomes are about 50 percent RNA. Mitochondrial ribosomes are reported to often have over 60 percent protein with a great deal of variation between organisms. Likewise, while the number of proteins associated with the subunits of ribosomes of bacteria and eukaryotic cytoplasm is fairly constant, there is great variation in this respect for the mitochondrial ribosome.

There is also great variation of size in mitochondrial ribosomes while bacterial and eukaryotic ribosomes show constant values which differ from each other. Molecular weight determinations using gel electrophoresis also indicated that mitochondrial rRNA are not the same size as bacterial rRNA. If rRNA in the mitochondria were derived from the cytoplasm there should be a correlation between them but this is also found not to be so.

The base composition of mitochondrial rRNA would be expected to be similar to the eukaryotic rRNA if they are both derived from a common ancestor (auto-genous theory). Measurements reveal that while bacterial rRNA is fairly constant with a G+C of 50-55 percent,<sup>32</sup> eukaryotic and mitochondrial G+C contents are variable. There is a rather strong correlation between the base composition of mitochondrial rRNA,

cytoplasmic rRNA and the DNA of the nucleus, which some point to as evidence of a relationship between the mitochondrial and eukaryotic rRNA,<sup>33</sup> i.e. support for the autogenous theory.

The tRNAs of mitochondria are now known to be different from their counterparts in bacteria and the cytoplasm. There are examples of tRNA for certain amino acids resembling the homologous bacterial tRNA, but these are balanced by there also being examples of similarity to eukaryotic homologs. The first tRNA used in the synthesis of protein is termed the initiator and is chemically modified. The mitochondrial initiator is similar but not identical with the bacterial initiator.<sup>34</sup>

While the synthesis of protein in mitochondria was once thought to show a strong relationship to bacteria, more recent studies have shown that at every step mitochondrial protein synthesis is unique.

### Conclusions

#### Selection of an Evolutionary Model

There are three classifications of data discussed in this paper. First, is the evidence such as much of the physiological comparisons which are found to have no weight in either direction. Second, there are items which seem to strongly support one theory over the other. And third, there is that evidence which can support either theory depending on the weight one puts on that particular point and the assumptions one is willing to make. In fact, this third class often extends to include the second class as appropriate assumptions are made to shift its importance from one side of the argument to another. This third class is by far the largest group of data and so it is best to conclude that there is currently no clear cut evidence that shows either the autogenous or endosymbiotic theories to be correct.

#### Impact on Creationism

Many creationists will want to place this evidence concerning mitochondria in perspective regarding the evidence it supplies in favor of creation. The force with which creationism is supported by this evidence ranges from powerful to none depending on one's previous assumptions. The evidence does not demonstrate an undisputed evolutionary origin for mitochondria, which might be taken as support for creation. The evolutionist, on the other hand, will find that the uniqueness of mitochondria does not demand the rejection of evolution. Rather it demonstrates how little we really know about organellar biochemistry and provides no evidence in favor of creation. In the minds of objective workers possibly the most impressive thing about the data is how their support of creation or evolution depends on the assumptions one makes and therefore the weight applied to individual

points of information. These data provide no clear cut "proof" of either model of origins but only circumstantial evidence.

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### QUOTE

In another respect Augustine continued in the path of Greek philosophy while enriching it with elements of Christian revelation: knowledge was for him, as it was for Plato and Aristotle, a matter of "seeing" (*theoria*). He greatly widened and elaborated the derived notion of "inner vision," by means of which he overcame the argument of the skeptics about the unreliability of the senses.

Niemeyer, Gerhart. 1984. Augustine's political philosophy? in Morris, Lynne, editor. *The Christian vision: man in society*. The Hillsdale College Press, Hillsdale, MI, p. 56.