The Origin of Plant and Animal Cells: The serial symbiosis view of the origin of higher cells suggests that the customary division of living things into two kingdoms should be reconsidered
Author(s): Lynn Margulis
Source: *American Scientist*, Vol. 59, No. 2 (March—April 1971), pp. 230-235
Published by: Sigma Xi, The Scientific Research Society
Stable URL: http://www.jstor.org/stable/27829542
Accessed: 26-04-2016 12:41 UTC

Lynn Margulis

The Origin of Plant and Animal Cells

The serial symbiosis view of the origin of higher cells suggests that the customary division of living things into two kingdoms should be reconsidered

Both primitive peoples and modern men divide the living world into two vast groups, plants and animals. This dichotomous view is not only consistent with intuition but, until recently, has been quite universally accepted by biologists. Animals, in general, are motile heterotrophs (other-nourished) and plants are immotile autotrophs (self-nourished). Certain organisms such as fungi and bacteria seem to be dependent plants, that is, they neither contain chlorophyll nor make their own organic food compounds; yet they do not have the characteristics of animals. By default, botanists have traditionally claimed them and placed them within the Thallophytes, or lower plants. Although many modifications and criticisms of this dichotomous view of life have been advanced at various times by botanists and systematists, it was not until recently that the entire concept underlying the kingdom level of taxonomy has come under severe fire (*1*).

Dr. Lynn Margulis, associate professor of biology, Boston University, received her bachelor's degree from the University of Chicago, the M.A. in zoology from the University of Wisconsin, and the Ph.D. in genetics from the University of California' Berkeley. Prior to her appointment at Boston University, she worked for several years developing science curricula for U.S. and African schools and training Peace Corps biology teachers for Latin America. Her continuing work on the symbiotic theory of the origin of eukaryotic cells was first published in the Journal of Theoretical Biology *(14:225). Recently the Yale University Press brought out her monograph,* Origin of Eukaryotic Cells, *which expands on her controversial theory. In 1967, Dr. Margulis received the Shell Award, the Boston University faculty publication merit award. Her present research is focused on a study of the metabolism of basal body and cilia regeneration in Stentor as it relates to her theory. The author makes grateful acknowledgment to T. N. Margulis, E. S. Barghoorn, G. E. Hutchinson, and V. Tartar for their aid, and to NASA and the National Science Foundation for support. Address: Department of Biology, Boston University, Boston, MA 02215.*

In general, scientists have believed that the only evolutionary mechanism for producing new populations of organisms is the progressive differentiation of descendants via mutations of many kinds and their natural selection. The evolutionary sequence usually envisioned for lower organisms is as follows: primitive heterotrophic bacteria led to photosynthetic bacteria and eventually to photosynthetic algae. A primitive phytoflagellate alga (sometimes called the "uralga") is considered to be the common ancestor to higher green plants on the one hand and, by loss of photosynthetic capabilities, the ancestor to fungi and animals on the other. This classical view of the phylogeny of animals and green plants is shown in Figure 1.

The alternative "serial symbiosis" point of view, while not denying the paramount importance of these processes, adds another relevant evolutionary mechanism: the acquisition of intracellular organelles by symbiosis and the subsequent joint evolution of the symbiotic partners as a unique entity (Fig. 1, right side). The unsuspicious reader should be warned that the progressive differentiation idea is still very widely accepted and that the alternative view—that the eukaryote cell arose by a series of symbioses—described in this article still represents a minority opinion, only very recently even discussed in "polite biological society" (*2*).

The symbiotic theory is actually based on several ideas that have a long classical tradition. The concept that cellular organelles, such as the chloroplasts in algae and green plants and the mitochondria of plants and animals, originated as endosymbionts has been present in the classical cytological literature since the discovery of these organelles (*3*, *4*). The notions of genetic autonomy of such organelles derive mainly from observations of the growth and division of the organelles inside the cytoplasm. While the sizes, staining properties, and correlation of the presence of the organelles with certain inherited traits always reinforced these views, critics of the endosymbiont origin idea have been correct in their assertion that the concept of the independent origin of organelles, although attractive, has been untestable. Now that biologists have developed a clearer picture of the actual workings of a minimal self-replicating system—the prokaryote cell (consisting basically of DNA, messenger RNA coded off that DNA, protein synthesis on ribosomes coded by messenger RNA surrounded by lipoprotein membrane containing an energy source and so forth)—the concept of a cell can be applied to the workings of an organelle within a cell.

In comparing the classical and symbiotic views (Fig. 1), it is clear that there is much agreement and overlap between them. Both the classical view and the symbiotic view agree that bacteria are primitive and that photosynthetic bacteria are ancestral to photosynthetic blue-green algae. They also agree that green algae are ancestral to higher green plants. The area of disagreement lies in the relationship between the admittedly primitive prokaryotic blue-green algae and the eukaryotic green algae and protozoans, that is, in the middle section of Figure 1. Whereas the classical view holds that blue-green algae evolved into photosynthetic phytoflagellates that later lost autotrophy to evolve animals and fungi, the symbiotic view insists that the blue-green algae were ancestral only to the plastid of eukaryotic algae.

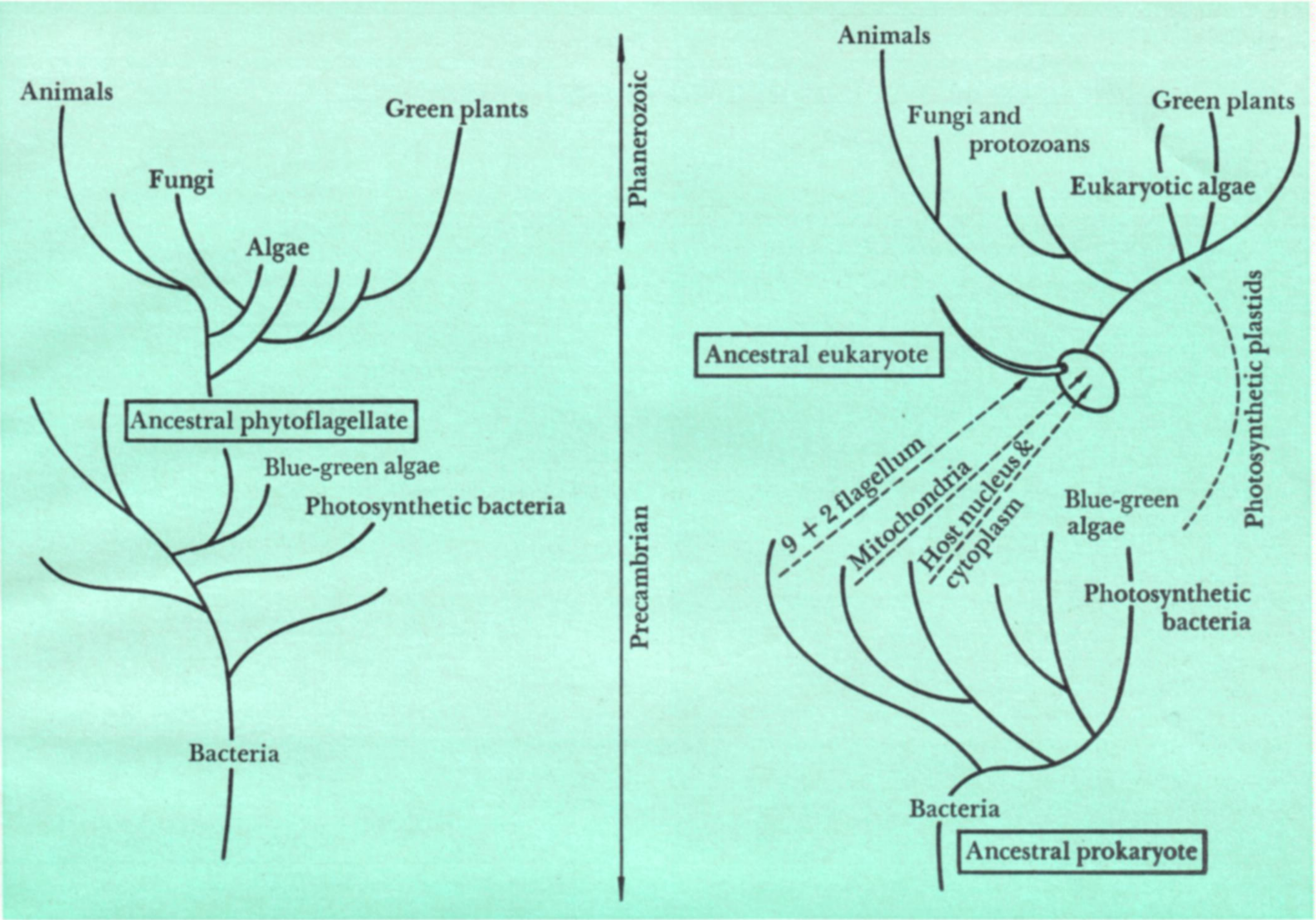


Figure 1. Comparison between the classical (*left*) and symbiotic (*right*) views of the evolution of plant and animal cells.

The cell symbiosis theory holds that a primitive amoeboflagellate, a heterotrophic cell, is ancestral to all eukaryotes: fungi, animals, nucleated algae, and higher plants. Some descendants of the amoeboflagellate became photosynthetic when they acquired intracellular blue-green algae-like symbionts. The photosynthetic symbiont was retained, selection acted on the entire complex, and with time the symbiont eventually differentiated into the membrane-bound photosynthetic plastid of algae and plants. Thus according to this view, asking What photosynthetic organism is the ancestor of the green algae? is quite analogous to asking What plant is ancestral to the lichen? Just as lichens have two immediate ancestors, a photosynthetic algal ancestor and a heterotrophic fungal ancestor (*5*), the serial symbiotic argument claims that all nucleated plants have at least two immediate ancestors, a photosynthetic ancestor to the plastid and a heterotrophic ancestor to the rest of the cell. The theory has really even been developed much further (*6*), claiming that the ancestral heterotroph itself formed as a product of intracellular symbiosis. That is, protozoans, fungi, animals, nucleated algae, and green plants had common heterotrophic ancestors—mitochondria-containing amoeboflagellates. These ancestral amoeboflagellates were cells in which mitosis and eventually meiosis evolved. Before the sequence of steps suggested for the origin of the eukaryote cell is described, some explanation is in order of the recently available evidence that makes such views defensible.

First, there is the fundamental recognition of the enormous difference in cell structure between the prokaryotes and the eukaryotes. Table 1, which summarizes some of these differences, is based on a large accumulation of twentieth-century cytological and microbiological work culminating in the recognition of this great evolutionary discontinuity in cell type first made by C. B. van Niel, R. Y. Stanier, and their colleagues (*7*). Unlike the distinction between animals and plants which becomes more and more blurred as one studies the flagellate algae and protozoans, the distinction between eukaryote and prokaryote cells has become progressively sharper and more valid with new microbiological investigation. Any given population of microbes may unequivocally be assigned to one or the other of these non-overlapping groups. The phylogeny and the symbiotic theory presented here is entirely dependent on the prior recognition of the eukaryote-prokaryote dichotomy of cell type.

Furthermore, the symbiotic theory rests upon recent discoveries concerning the metabolic capabilities of three types of eukaryotic organelles: mitochondria, photosynthetic plastids, and flagellar basal bodies. At least the first two of these are known definitely to contain their own nucleic acids and basic components of the protein synthesizing system that characterizes free-living prokaryotic cells. Although, no doubt, they have been modified by perhaps a billion years' association with nucleated cytoplasm, the case that mitochondria and plastids fulfill criteria for organelles originating inside cells as symbionts (Table 2) can be argued now on the basis of enor-

Table 1

Major Differences between Prokaryotes and Eukaryotes

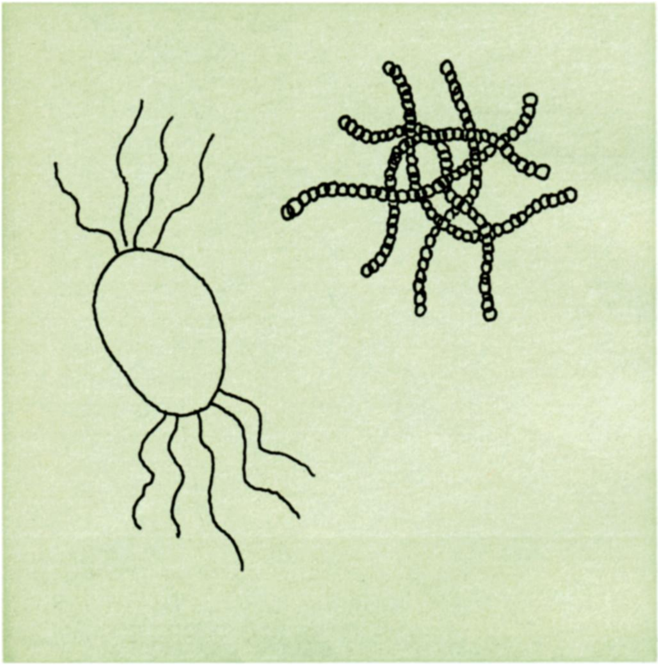
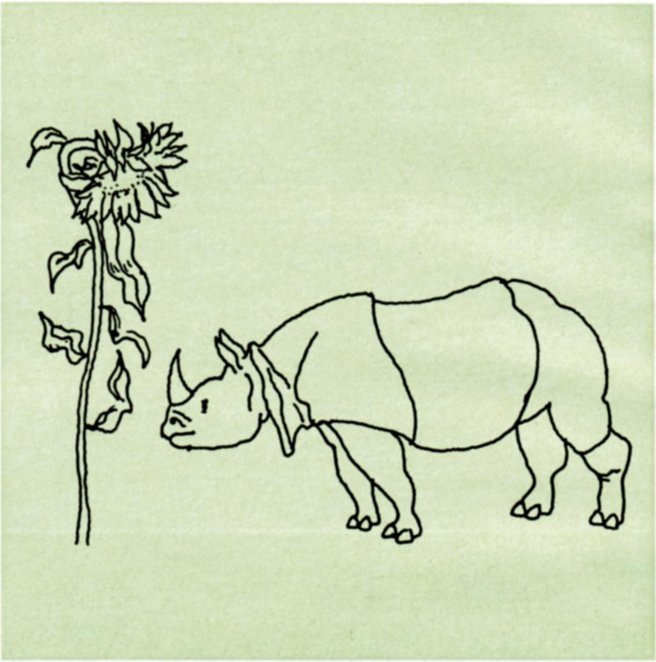
Prokaryotes	Eukaryotes
	
Mostly small cells (1–10 μ); all microbes; the most morphologically complex are filamentous or mycelial with fruiting bodies	Mostly large cells (10–10^2 μ); some are microbes, most are large organisms; the most morphologically complex are the vertebrates and the flowering plants
Nucleoid, not membrane-bound	Membrane-bounded nucleus
Cell division direct, mostly by "binary fission," chromatin body which contains DNA and polyamines; does not stain with the Feulgen technique. No centrioles or mitotic spindle	Cell division by classical mitosis; many chromosomes containing DNA, RNA, and proteins; stains bright red with Feulgen technique; centrioles, mitotic spindle present
Sexual systems absent in most forms; when present, unidirectional transfer of genetic material from donor to host	Sexual systems present in most forms; participation of both partners (male and female) in meiotic production of gametes
Multicellular organisms never develop from diploid zygotes, show no tissue differentiation	Multicellular organisms develop from diploid zygotes, show extensive tissue differentiation
Includes strict anaerobes (killed by O_2), and facultatively anaerobic, microaerophyllic, and aerobic forms	All forms aerobic (need O_2 to live; exceptions clearly secondary modifications)
Enormous variations in the metabolic patterns of the group as a whole; mitochondria absent; enzymes for oxidation of organic molecules bound to cell membrane, i.e. not "packeted"	Same metabolic patterns of oxidation within the group (i.e. Embden-Meyerhof glucose metabolism, Krebs cycle oxidations, molecular oxygen combines with hydrogens from foodstuffs, catalyzed by cytochromes, water produced); enzymes for oxidation of 3-carbon organic acids within "packeted" membrane-bounded sac; mitochondria present
Simple bacterial flagella, if flagellated	Complex "(9+2)" flagella or cilia, if flagellated or ciliated
If photosynthetic, enzymes for photosynthesis bound to cell membrane (chromatophores); not "packeted" in chloroplasts; anaerobic and aerobic photosynthesis—sulfur deposition and O_2 elimination	If photosynthetic, enzymes for photosynthesis "packeted" in membrane-bounded chloroplasts; O_2 eliminating photosynthesis.

Table 2. Criteria for organelles originating as endosymbionts

1. Symbiont originally had its own DNA, messenger RNA complimentary to that DNA, a source of ATP and other nucleotides, a functioning protein synthesizing system on ribosomes, and cell membrane synthesizing system. With progressive evolution of the symbiosis, intracellular symbiont may lose from none to all its independent synthetic capabilities except ability to replicate its own DNA. The symbiont may dedifferentiate down to the level of DNA.

2. If an organelle has been acquired symbiotically it will be retained only if there exists some mechanism insuring that at each cell division each daughter receives at least one copy of the symbiont genome.

3. If an organelle was acquired by symbiosis there should be no species that contain intermediate intracellular stages of that organelle.

4. If the symbiont is lost, all metabolic characteristics coded for on the symbiont genome must be lost together. Once lost the symbiont can only be regained by reingestion.

5. Since any intracellular symbiont must have its own genes, a correlation can be made between the genetic traits conferred on the host by the symbiont and the morphological presence of the symbiont (*3*). (For example "cytoplasmic" or "uniparental" inheritance.)

6. If an organelle originated as a free-living cell, it is possible that naturally occurring counterparts may still be found among extant organisms. Even if precise co-descendants can not be found, the organelle must have genetic and physiological characteristics known to be consistent with those generally present in terrestrial cells. (Possibilities of organelles and free-living counterparts might be: chloroplasts—blue-green algae, mitochondria—gram negative Krebs cycle containing rod shaped eubacteria, flagella—spirochaetes, and so forth.)

mous quantities of data from many different fields and many different organisms (*6*). The case for the basal body (the same entity recognized as the centriole in mitotic cell division) and its product the eukaryote cilium originating symbiotically is much less closed. Evidence has recently been presented that these highly characteristic eukaryotic organelles have DNA and RNA (*6*, *8*). Even more recent evidence for nucleic acids in basal bodies is negative, but this may not preclude symbiont origin (*9*).

The other profound contribution to new concepts of cellular evolution has come from an entirely different and hitherto unrelated field, Precambrian paleontology. Even this juxtaposition of words may seem unfamiliar to those who believe that the vast stretches of Precambrian time are unfossiliferous. Now this belief must be reconsidered in view of the recent demonstrations by E. S. Barghoorn and his colleagues J. W. Schopf and P. E. Cloud, Jr. that the Precambrian is full of fossils (Table 3) (*10–15*). Although some remains, such as algal stromatolites, are several feet across (Figure 2), the morphologically recognizable fossils of the era are mainly microbial; the algae that are primarily responsible for the initial deposition of the sediments are measured in microns. Be-

Table 3. Summary of evidence for Precambrian fossils

× 10^9 *years*	*Location and sediment*	*Type of fossil*	*Investigators*
3.0–3.3	South Africa Fig tree	Bacteria, blue-green algae	Barghoorn and Schopf (*9*)
2.7–2.0	North America Great Slave Lake, Canada	Algal stromatolites	Hoffman (*10*)
2.1–1.9	North America Gunflint	Blue-green algae, bacteria, green algae?	Cloud (*12*), Barghoorn and Tyler (*11*)
1.0–0.8	Australia Bitter Springs	Blue-green algae, green algae	Schopf (*13*)
0.7–present	Worldwide	Metazoans Beginning of continuous fossil record	Cloud (*14*)

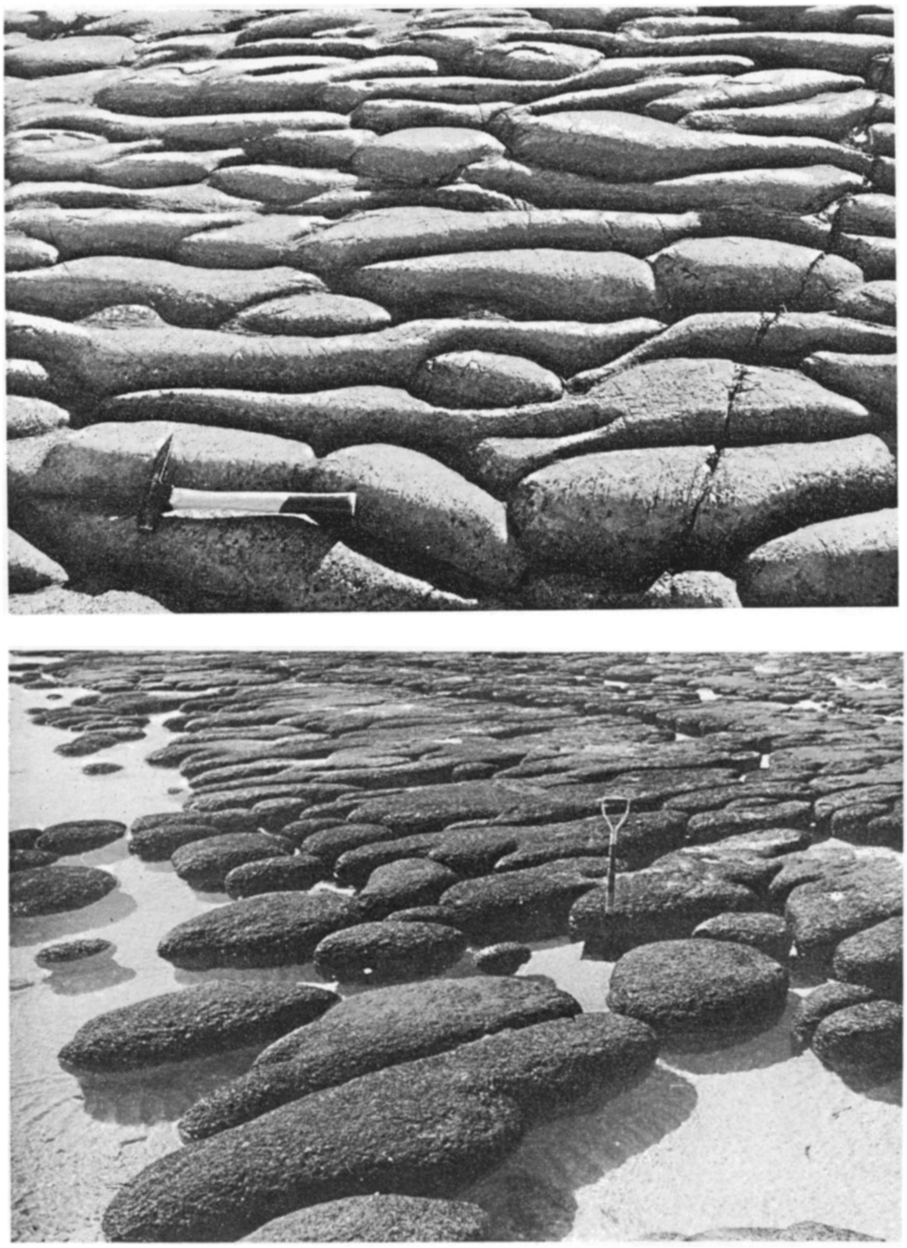


Figure 2. *Above:* Rocks between 1.8 and 2.5 billion years old from the Great Slave Lake area in the Northwest Territory of Canada. These are called "stromatolites" and were formed in the intertidal environment by blue-green algae. *Below:* Such stromatolites are being formed today, for example, in Shark Bay, Western Australia. Photographs courtesy of Dr. Paul Hoffman, Geological Survey of Canada, from his unpublished work. See (*6*) pp. 137–41, and (*11*).

sides the impressive finds of intact Precambrian microbes, organic chemists have determined that ancient rocks contain "chemical fossils" (*15*), which are organic materials corresponding to geological derivatives of common biotic molecules. These are found in even the oldest sediments.

Taken together, I believe all this evidence can be summarized most usefully in terms of the concepts of the symbiotic theory diagrammed on the right side of Figure 1. The Precambrian can be thought of as the "Age of Prokaryotes," the time during which the atmosphere changed from reducing or neutral to oxidizing as a result of blue-green algal photosynthetic activity. The Phanerozoic, on the other hand, is the well-known "Age of Eukaryotes." During this time, the aerobic metabolism and elegant genetic systems of these "higher cells" led to the eventual dominance of the most complex eukaryotes, the metazoans, and the green plants. These ideas have a significant effect upon the choice of classification system at the level of the highest taxa (Table 4).

Summary of the serial symbiosis view

This journal is not the place in which to elaborate on the recently published (*6*) serial symbiosis view. Rather, it can only be stated in simplified terms so that interested readers can consult the references and evaluate it for themselves. Essentially, the symbiotic view can be outlined as follows: all living organisms have a common ancestry; all were ultimately derived from a prokaryote heterotrophic bacteria-like cell that contained the present genetic code and the present protein synthesizing system (*17*). By mutation and selection the primitive heterotroph gave rise to many metabolically diverse populations of prokaryote organisms; among these were microbes capable of synthesizing porphyrins and isoprenoid derivatives, microbes able to fix atmospheric carbon dioxide and atmospheric nitrogen, microbes capable of reducing sulphur, and so forth. In early Precambrian times all of these microbes were anaerobic.

Eventually, from a population of microbes capable of fixing CO_2 and synthesizing porphyrins, there arose a class of bacteria that could utilize visible radiation from the sun to produce the key biological intermediate in energy transactions, adenosine triphosphate (ATP). Atoms from hydrogen gas, hydrogen sulfide, or from small organic compounds were used to reduce CO_2 to form the specific organic compounds requisite for cellular reproduction. These bacteria were ancestral to the present anaerobic photosynthesizers. Mutations occurred in this population of organisms that eventually led to the use of H_2O as hydrogen donor in CO_2 reduction. Such microbes eliminated unused oxygen from water into the atmosphere as a waste product. These photosynthetic microbes were the first green-plant photosynthesizers—ancestors to our present blue-green algae—and, according to the view presented here, ancestors to the photosynthetic plastids of nucleated algae and higher plants.

The elimination of highly reactive oxygen gas into the atmosphere led to a crisis among prokaryotes—a crisis that has left an indelible mark on the metabolism of these cells. They either had to adjust to the increasing presence of oxygen in the atmosphere by evolving metabolic mechanisms to cope with it or they had to find some anaerobic niche. Even a superficial perusal of prokaryotes will convince anyone that many different responses to oxygen—from obligate anaerobiosis to obligate aerobiosis—exist in the group as a whole. Thus, it was only during or after the transition to the oxidizing atmosphere that any eukaryote cell arose.

Table 4. Comparison of largest taxa derived from alternative views of the origin of plant and animal cells

Classical view		Serial symbiosis view	
Two kingdoms	Major members	Five kingdoms (*1*)	Major members
Plantae	Bacteria Fungi Algae Green plants	Monera (prokaryotes)	Bacteria Blue-green algae
Animalia	Protozoans Metazoans	Protista (lower eukaryotes)	Protozoans Nucleate algae
		Fungi	Mushrooms, molds, yeasts
		Plantae	Green plants (bryophytes, tracheophytes)
		Animalia	Metazoans

According to this theory, the ancestor to all eukaryotes became an aerobe when a large anaerobic heterotrophic microbe capable of catabolizing glucose to pyruvate established an intracellular symbiosis with a smaller aerobic bacterium. The aerobic endosymbiont metabolized 3-carbon organic compounds completely to CO_2 and water via the Krebs cycle oxidations. The increasing presence of atmospheric oxygen selected for the symbiotic complex eventually gave rise to all mitochondria-containing cells. This primitive mitochondria-containing heterotroph, now an amoeboid, acquired a further population of symbionts, motile organisms that stuck to the surface of the amoeboid much as spirochaetes are known to stick to the surfaces of certain protozoans. As in the modern case of *Myxotricha* (a hypermastigote flagellate found in the guts of termites and containing cortical spirochaetes responsible for the movement of their host), these motile symbionts were initially selected because they conferred motility on their amoeboid host, thus helping it to procure food more efficiently. By hypothesis, the motile symbionts were themselves ancestral to what later evolved into flagella, cilia, and all the other "9 + 2" homologues so universally characteristic of eukaryotes and so lacking in any prokaryote. In fact, again by far-out but testable hypotheses, the motile symbionts eventually differentiated into the "achromatic apparatus" of mitosis, that is the spindle, centrioles, and other nonchromatin portions of the mitotic figure.

This differentiation must have taken millions of years and, by hypothesis, produced along the way the many and fascinating variations upon the mitotic theme found in protozoans, certain fungi, nucleated algae, and other lower eukaryotes. Once mitosis and meiosis were perfected, the advanced tissue differentiation which is based upon the Mendelian genetic foundation and which is characteristic of higher plants and animals could evolve and eventually take over the earth, producing myriads of large organisms. In essential outline then, this is the serial symbiotic theory of the origin of eukaryotic cells. Even if eventually proved invalid, it provides a unified framework upon which to evaluate both the rapid influx of data from Precambrian sediments and from research on the genetics and biochemistry of eukaryote organelles (*18*).

References

1. R. H. Whittaker. 1969. New concepts of kingdoms of organisms. *Science* 163:150–59.
2. "More recently Wallin (1922) has maintained that chondriosomes [mitochondria] may be regarded as symbiotic bacteria whose associations with other cytoplasmic components may have arisen in the earliest stages of evolution... to many, no doubt, such speculations may appear too fantastic for present mention in polite biological society; nevertheless, it is in the range of possibility that they may some day call for more serious consideration." E. B. Wilson. 1925. *The Cell in Development and Heredity*. New York: Macmillan.
3. D. B. Roodyn and D. Wilkie. 1968. *The Biogenesis of Mitochondria*. London: Methuen and Co., Ltd.
4. J. T. O. Kirk and R. A. E. Tilney-Bassett. 1967. *The Plastids*. London and New York: W. H. Freeman.
5. V. Ahmadjian. 1963. The fungi of lichens. *Scientific American* 208:122–32.
6. L. Margulis. 1970. *Origin of Eukaryotic Cells*. New Haven: Yale University Press.
7. R. Y. Stanier, E. Adelberg, and M. Douderoff. 1970. *The Microbial World*. 3rd ed. Englewood Cliffs, N.J.: Prentice Hall, Inc.
8. J. Randall and C. Disbrey. 1965. Evidence for DNA at basal body sites in *Tetrahymena pyriformis*. *Proc. Roy. Soc.* Series B., 162:473–91.
9. L. Margulis. 1971. Cytoplasmic Genes: Our Precambrian Legacy, in *Stadler Symposia*, Vols. 1 & 2. G. P. Redei, ed. Columbia, Mo.: Univ. of Missouri Press.
10. E. S. Barghoorn and J. W. Schopf. 1967. Alga-like fossils from the Early Precambrian of South Africa. *Science* 156: 508–12.
11. P. Hoffman. 1968. See A. L. McAlester. *The History of Life*. Englewood Cliffs, N.J.: Prentice-Hall, p. 14. See also (*6*).
12. E. S. Barghoorn and S. A. Tyler. 1965. Microorganisms from the Gunflint Chert. *Science* 147:563–77.
13. P. E. Cloud, Jr. 1965. Significance of the Gunflint (Precambrian) microflora. *Science* 148:27–35.
14. J. W. Schopf. 1969. Microorganisms from the Late Precambrian of South Australia. *J. Paleontology* 43:111–18.
15. P. E. Cloud, Jr. 1968. Pre-Metazoan evolution and the origins of the Metazoa. In *Evolution and Environment*, E. T. Drake, ed. New Haven and London: Yale University Press, pp. 1–72.
16. G. Eglinton and M. Calvin. 1967. Chemical fossils. *Scientific American* 216: 32–43.
17. J. D. Watson. 1970. *Molecular Biology of the Gene*. New York: Benjamin Publishers.
18. S. S. Cohen. 1970. Are/Were Mitochondria and Chloroplasts Microorganisms? *American Scientist* 58:281–89.