review article

The origin of nuclei and of eukaryotic cells

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A new theory not involving symbiosis is proposed for the origin of eukaryotic cells. It explains how the evolution of phagocytosis by a wall-free blue-green alga would have created selection pressures leading directly to the formation of all characteristic eukaryote organelles and cell properties including mitosis, meiosis and sex.

THE problem of the evolutionary origin of eukaryotes has been a major one in biology ever since the fundamental distinction between prokaryotic and eukaryotic cells[1-3] became clear. It is generally accepted that eukaryotes evolved from prokaryotes, but how this happened is unknown[4-5]. Certain similarities between mitochondria and bacteria and between plastids and blue-green algae have led to the recent revival[6-8] of old theories[7-11] suggesting that these eukaryote organelles are derived from intracellular symbiotic prokaryotes and also to the suggestion[7,12,13] that microtubules, centrioles and flagella are similarly derived. This "serial endosymbiosis theory of the origin of eukaryotes", which supposes that eukaryotes evolved as a result of the symbiosis of from three to six[7,14-16] genetically different prokaryotes, has received more support[2-19] than the alternative theory that they evolved from a single prokaryote species by intracellular differentiation[20-22].

My strongest criticism of the symbiosis theory is that it fails to explain how the eukaryote condition itself (that is, the nucleus) evolved[24]. Most proponents of the symbiosis theory[5-19] do not seriously discuss the origin of the nucleus, but assume it to have evolved gradually from a prokaryote nucleoid.

Eukaryote nuclei differ in at least three fundamental ways from prokaryote nucleoids. They are surrounded by a double-membraned envelope bearing characteristic pores; they contain several non-identical chromosomes which are linear and not circular; segregation occurs by mitosis which always involves spindle microtubules. Here I show how these differences could have arisen and argue that the same selective forces would also have led to the formation of mitochondria, plastids and other characteristic eukaryote organelles and properties.

Like Stanier[5] I consider the evolution of endocytosis (phagocytosis and pinocytosis) to be of key importance in eukaryote evolution. But this is not because it enabled them to harbour endosymbionts. (I believe endosymbiosis to be one of many secondary and almost inevitable consequences of phagocytosis, but not the cause of the eukaryote condition.) It is because phagocytosis provided not only the selective pressure but also the physical mechanism (membrane budding and fusion) for cell compartmentation by intracellular membranes. Cell compartmentation explains not only the origins of mitochondria, plastids and nuclei, but also their characteristic properties more simply than does the symbiosis theory.

I assume that the ancestor of all eukaryotes was a single-celled, facultatively phototrophic, blue-green alga, unable to fix nitrogen but possessing oxygen-evolving photosynthesis and oxygen-using respiration based on cytochromes and other electron transport molecules borne on intracellular thylakoid membranes (Fig. 1*a*). The first step leading to eukaryotes must have been the loss of the cell wall by such an alga living in a shallow bacteria- and detritus-rich benthic environment (Fig. 1*b*). Cell wall degrading enzymes like those abundantly secreted by soil myxobacteria[3] may initially have produced a blue-green algal "L-form" which subsequently became a stable L-form. Whatever the mechanism, wall loss was essential for phagocytosis and explains the complete absence of peptidoglycan cell walls in eukaryotes.

Many blue-green algae (in contrast to bacteria, whose minute size would make the evolution of phagocytosis difficult) have cells as large as those of unicellular eukaryote algae[3,25], so size would be no barrier to the acquisition of phagocytosis—they would already be large enough to engulf bacteria. A strong selective force would favour any blue-green algal L-form able to develop phagocytosis and so become a "pre-alga". A phagocytic pre-alga could photosynthesise by day or during the Arctic summer, and phagocytose by night or during the Arctic winter (or in any dark environment). This versatility would give it a clear advantage over other blue-green algae (mostly obligate phototrophs) as well as over bacteria since it would seldom lack food.

Evolution of phagocytosis

I suggest that there is a fundamental similarity between the mechanism of plasma membrane budding to form a phagosome and the mechanism of eukaryote cell cleavage during cytokinesis. Both involve invagination, breakage and resealing of membranes. Clearly they differ in the timing and location of these processes. But I think these reflect differences in control rather than in the basic mechanism, and that the blue-green alga evolved cleavage first and endocytosis evolved subsequently from it.

Phagocytosis, like division, reduces the surface area of the plasma membrane but, unlike division, creates separate intracellular phagosome membranes. Extensive endocytosis is therefore not possible unless the phagosome membrane can refuse with the plasma membrane after absorption of its contents. Thus phagocytosis could not evolve in the absence of this reverse process (exocytosis—frequently the basis of secretion in eukaryotes). Since, in growing (but not in non-growing) cells, limited exocytosis is possible in the absence of endocytosis, exocytosis probably evolved before endocytosis (either as a mechanism of membrane growth additional to the insertion of individual molecules into an existing membrane, or more probably for secretion of extracellular digestive enzymes). Any blue-green alga possessing both cleavage and exocytosis would be preadapted for the evolution of phagocytosis. Figure 1 shows a possible evolutionary sequence.

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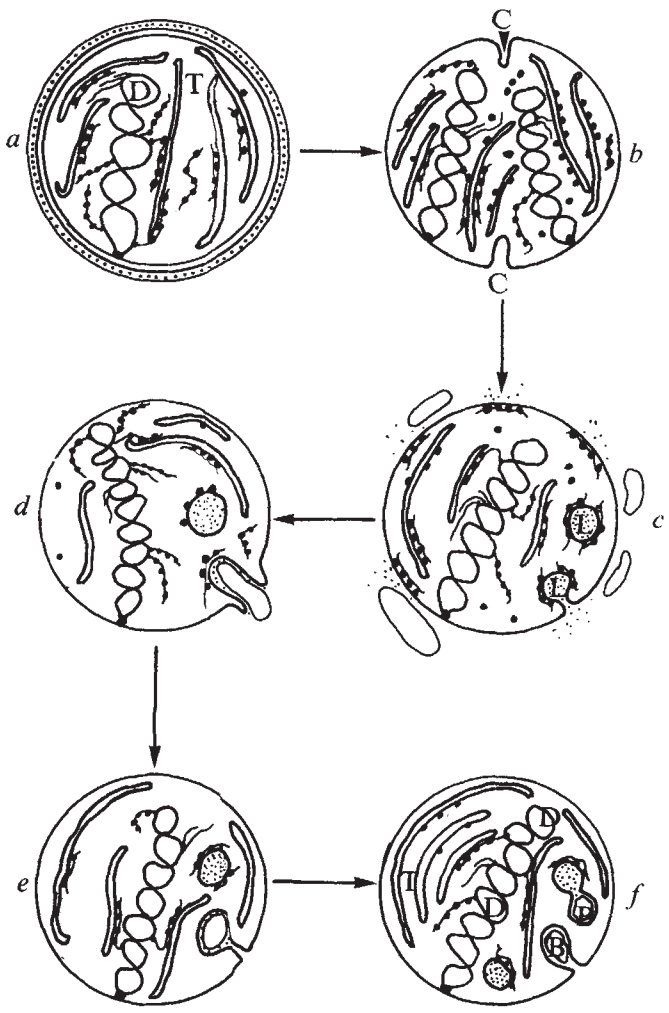


Fig. 1 The evolution of phagocytosis. A blue-green alga loses its cell wall (*a*) and evolves an acto-myosin dependent cell cleavage mechanism (*b*). The resulting L-form develops extracellular digestion (*c*) by direct secretion of digestive enzymes across the plasma membrane and/or by exocytosis by protolysosomes (L) derived from thylakoids specialising in the intracellular storage of digestive enzymes. Efficiency is increased by partially (*d*) or completely (*e*) surrounding the prey before liberating the enzymes. Finally in the fully phagocytic "pre-alga" only the plasma membrane engulfs the bacterium (B) and the protolysosome fuses with the resulting phagosome. DNA (D), with its attached polysomes, and most thylakoids (T) remain unchanged.

I suggest that not only exocytosis, endocytosis and cleavage but all cases of controlled membrane budding and fusion in eukaryotes (for example, budding of smoth vesicles from rough endoplasmic reticulum or Golgi apparatus, or the fusion of transmitter vesicles with presynaptic membranes) have a common basic mechanism, which I call cytosis. Since much of eukaryote cell evolution can be understood in terms of a diversification in the uses of and increased control over the timing and positioning of cytosis it is a pity that so little is known of its mechanism. Conceivably membranes containing polyunsaturated fatty acids (found in blue-green algae and in eukaryotes but not in bacteria[3]) were a prerequisite. Although phospholipid membranes have a natural tendency to bud and fuse I suggest that cytosis also universally involves a calcium-activated contractile actin–myosin-like microfilament system[26]. The simplest explanation for the universality of actomyosin in eukaryotes[2] is that it was the essential molecular innovation which made the origin and evolution of eukaryotes possible, and that it originated when our blue-green algal ancestor lost its cell wall and the prokaryote type of cell division by localised growth of a semi-rigid membrane was superseded by actin–myosin mediated cleavage by furrowing, that is by cytosis.

Subsequently, modifications led to exocytosis and then phagocytosis. Then selection for greater phagocytic efficiency would occur. Cells would be selected for greater size and for the ability to phagocytose over their whole surface. The actomyosin system would diversify independently to produce amoeboid movement—greatly increasing predation efficiency—and cytoplasmic streaming and organelle movement—speeding up contact between phagosomes and protolysosomes.

Origin of the spindle

Such a highly mobile cell surface would interfere with chromosome segregation (dependent in prokaryotes on attachment to a stable semi-rigid membrane[2]). Endocytosis of the chromosome attachment site would be especially serious, so there would be strong selection for a new rigid non-membrane segregation mechanism—the microtubule. Initially microtubules joined the two membrane attachment sites (Fig. 2*a*) and pushed them apart as they grew (like pole-to-pole spindle microtubules, the only universal components of modern spindles[24,29]; or like the reverse of sex pilus retraction (microtubules and sex pili are both tubular and interact with chromosome attachment sites—are they related or just functionally similar?)). This ensured that one chromosome ended up on each side of the cleavage furrow (a mechanism to ensure that cleavage was at the equator was also essential).

Efficient segregation by microtubules ended the selective advantage of chromosome attachment to the plasma membrane; the attachment site would soon be endocytosed and thereafter remain inside the cell as a protonuclear envelope (Fig. 2*b*), making the entire cell surface available for phagocytosis. The origin of mitosis was not a consequence, as commonly supposed, of the greater size or greater number of eukaryote chromosomes but was instead the essential prerequisite for these changes.

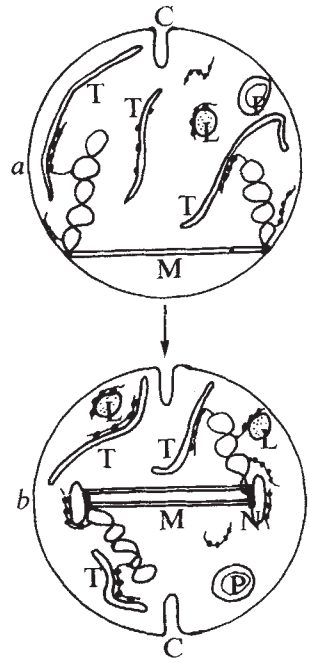


Fig. 2 The evolution of spindle microtubules (M) in the amoeboid pre-alga, as a device to push the two circular daughter chromosomes (here shown twisted into supercoils) apart to opposite poles of the cell to ensure that one is present in each daughter cell produced by the cleavage furrow (C). Initially chromosomes were attached to the cell membrane (*a*) but later (*b*) the attachment sites were endocytosed to become protonuclear envelope, N. Phagosomes (P), protolysosomes (L) and thylakoids (T) are also shown.

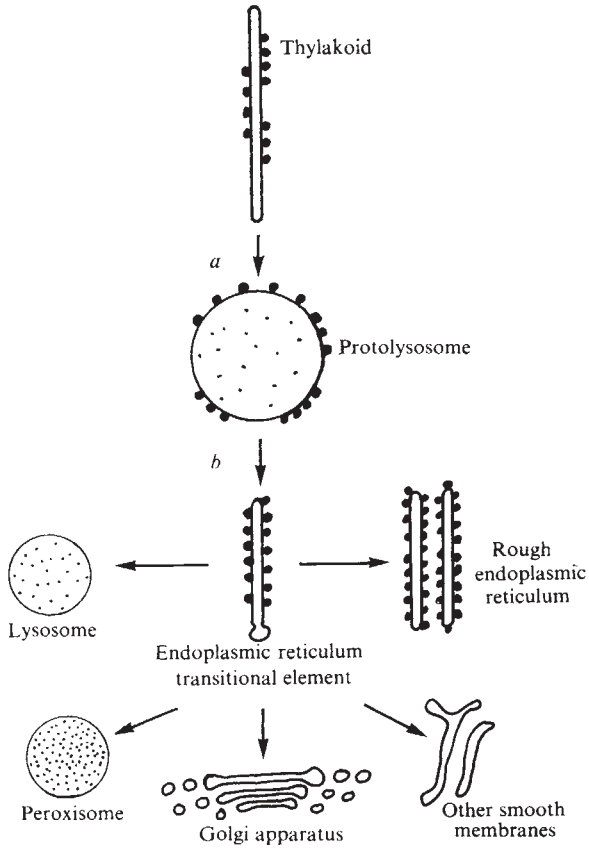


Fig. 3 Diversification of the (ribosome-covered) protolysosome (*a*) (originally derived from a ribosome-bearing thylakoid). The evolution of membrane budding by cytosis allowed differentiation and specialisation between the "rough" ribosome-bearing membranes and their various smooth-membraned products (*b*).

Cytosis and origin of sex

Cytosis also provided the mechanism for cell fusion, which must have evolved in a wall-free cell, and initially was probably poorly controlled and more frequent than today. Its initial selective advantage would be greatest in times of starvation (starvation still triggers sexual differentiation in many algae and fungi) when fused cells would have twice the internal food supply of unfused competitors. I suggest that it originated in this way in the amoeboid pre-alga before even the development of the nuclear envelope; many properties of eukaryote chromosomes are best explained by the simultaneous evolution of mitosis and meiosis.

With only one circular chromosome per cell meiosis was unnecessary; the primitive mitosis described above would ensure segregation. Recombination was easy in the absence of a nuclear envelope. Assuming reciprocal and random recombination (as in the *rec* system of *Escherichia coli*), an even number of crossovers would produce two recombined daughters but an odd number would produce double length circular DNA. This increase in genome size and redundancy would immediately provide raw material for rapid evolution of new functions and create multiple replicon origins. The random release of spare copies of genes from stabilising selection pressure would break up operons. But an indefinite increase in DNA would be disadvantageous (and double-sized DNA molecules would often be broken during segregation because of their two membrane–microtubule attachment sites), and so selected against—most simply by the chromosomes becoming linear by the mechanism I previously suggested[30]. With linear chromosomes odd as well as even numbers of crossovers will give normal reciprocal recombinants thus terminating the explosive burst of new genome creation.

Selection for increased recombination efficiency would lead to chromosome pairing mediated by a synaptinemal complex. Efficient pairing would remove the necessity for having all the DNA in one molecule (previously necessary to prevent aneuploidy). Indeed, positive selection for chromosome fragmentation by the mechanism previously suggested[30] is likely because this will give increased recombination by independent assortment of non-homologous chromosomes. Thus the most distinctive features of eukaryote chromosomes, mitosis, meiosis and sex probably all evolved in a very short space of time, during the earliest stages of eukaryote evolution as a direct consequence of the evolution of cytosis. Chloroplast fusion[31] was probably a late development.

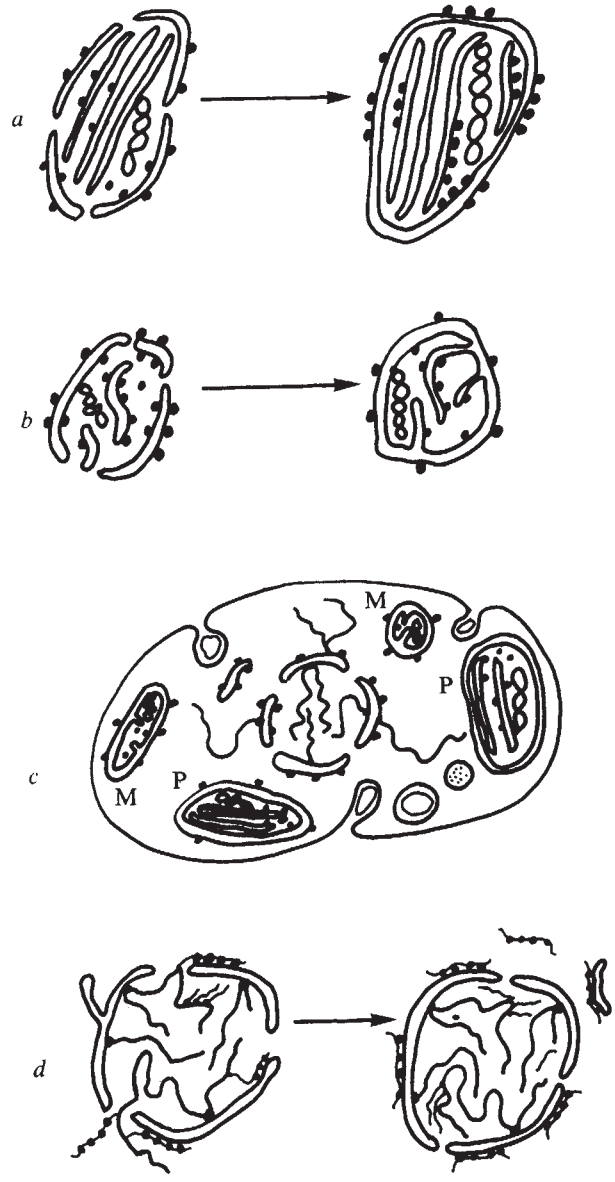
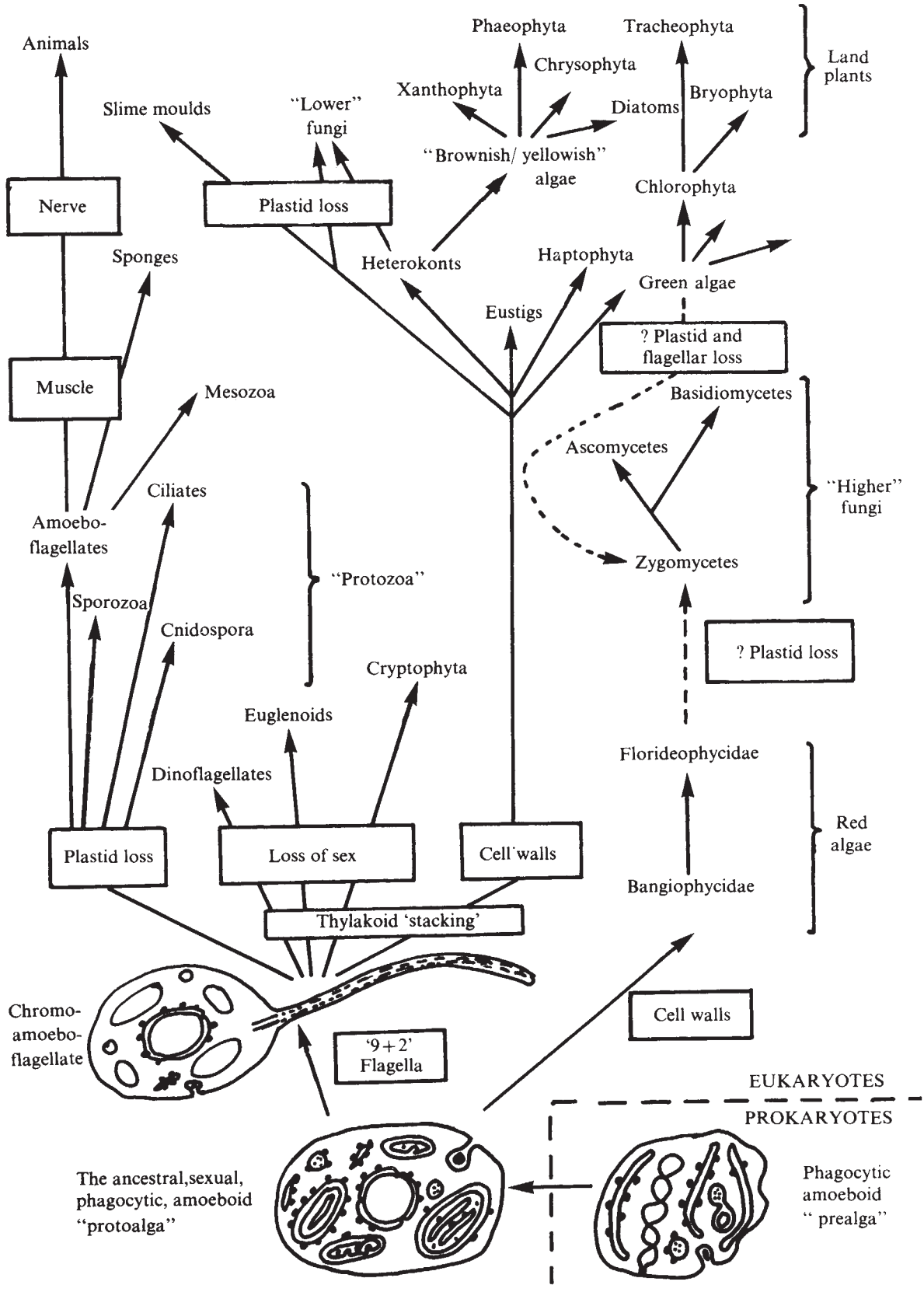


Fig. 4 The evolution of plastids, mitochondria and nuclei by fusion of DNA-associated thylakoids or endoplasmic reticulum cisternae. *a*, Plastids resulted from association of photosynthetic and plasmid-associated thylakoids to form a compartment containing DNA, ribosomes and Calvin cycle enzymes. *b*, Mitochondria resulted from fusion of plasmid-associated respiratory thylakoids to form a compartment containing Krebs cycle and fatty acid metabolising enzymes. *c*, Cell at intermediate stage with three distinct compartments: mitochondria (M), plastids (P) and nucleocytoplasm, whose protonuclear envelope (N) with six linear chromosomes will eventually fuse (*d*) to form a nuclear envelope separating the cytoplasm with protein synthesising enzymes from the nucleus with DNA and RNA synthesising and processing enzymes.

Cell compartmentation and organelle origins

Increase in cell size and in diversity of cell components in response to the selection pressures described above would dilute each component and lower the efficiency of reactions. This could be prevented only by vastly increasing the amounts made and the total concentration of materials or by dividing the cell into compartments each specialising in different functions. Cells adopting the latter course would have a tremendous selective advantage. The evolution of cytosis not only provides the selective pressure but also the mechanism

Fig. 5 A possible pattern of eukaryote diversification following the formation of the first true eukaryote (red algal-like) "proto-alga".



for compartmentation.

The early ribosome-covered protolysosomes (Fig. 1) were already separate compartments (because of the need to secrete, and protect the cell from, their hydrolases) and could very simply have differentiated into rough and smooth endoplasmic reticulum, lysosomes, peroxisomes and Golgi apparatus as shown in Fig. 3; they and the original thylakoids could have formed the plastid, mitochondrial and nuclear envelopes by fusion as shown in Fig. 4.

Initially ribosomes, DNA, RNA and nucleic acid polymerases were divided into 3 compartments, Fig. 4*c*. The nucleoid in the cytoplasmic compartment was segregated by microtubules and its DNA became linear and fragmented as suggested above. Chloroplast and mitochondrial plasmids were present always in large enough numbers per cell not to require a special segregation mechanism, and so (generally) remained circular because with multiple copies the selection pressure for linearity was much less. In both plastids and mitochondria, DNA, messenger RNA and ribosomes are in the same compartment (as in bacteria) so would be expected to retain many prokaryotic properties. By contrast nuclear DNA and RNA became segregated from cytoplasmic RNA and ribosomes (Fig. 4*d*) so ribosomes could no longer start translating messenger while it was still being made and new mechanisms were required for the transport of messenger and nascent ribosomal subunits across the nuclear envelope. (Nuclear pores allowing free passage of small and medium sized molecules, but not larger ones and macromolecular complexes[32], probably arose in response to the need to regulate nucleocytoplasmic exchange.) Nucleocytoplasmic separation would have imposed new selective forces on DNA and RNA. Though it is premature to speculate on their nature I predict that they will go far to explain other differences between nucleocytoplasmic genetic systems on the one hand and prokaryote/mitochondrial/plastid ones on the other.

The origin of the unique features of cytoplasmic ribosomes and of nucleoli probably dates from the time when the pre-alga became completely compartmented to form the first true eukaryote—the proto-alga (Fig. 5). I suggest that originally the pre-algal plasmids and nucleoid had identical ribosomal DNA present in multiple tandem copies (many copies were needed because of the large cell size), and that this identity was maintained by recombination involving a ribosomal DNA episome (replicating as a rolling circle[33]). But, after complete compartmentation, DNA and ribosomes could no longer cross the membranes (but proteins could be secreted directly across them by membrane-bound ribosomes[34]), so plasmid and nuclear ribosomal DNA then evolved independently. This predicts that gene amplification and rolling circle replication of nucleolar DNA will be found universally in eukaryotes. The existence of a distinct nucleolus is connected with the need to transport both ribosomal and messenger RNA across the envelope.

Nucleocytoplasmic separation, the breakup of operon-like gene clusters and the production of large amounts of redundant DNA as suggested above, were probably enough to lead to completely novel systems of gene regulation in eukaryotes[36] which would subsequently make possible the evolution of highly differentiated multicellular organisms. In future research it will be important to determine, by careful comparison of primitive unicellular eukaryotes and differentiated multicellular ones, which features (for example, giant heterogeneous nuclear RNA[35], repetitious DNA[36], palindromes[37]) are universal features of eukaryote genetic systems and which are specifically associated with complex multicellular differentiation.

Comparison with symbiosis theories

My model is superior to symbiosis theories in three main ways. First, it explains how eukaryote nuclei evolved. In doing so it provides a plausible selective advantage for the evolution of all major features of eukaryote nuclear structure and genetic systems (except the presence of histones). According to my theory the absence of sex in an entire major eukaryote group, for example euglenoids[38], is the result of secondary loss and not a primitive feature. The absence of histones in dinoflagellates[39] might also be a secondary feature perhaps resulting from the loss of sex. If so the primary function of histones could have been efficient packing of DNA to facilitate meiotic pairing and segregation.

Second, it gives plausible reasons for the differences between nucleocytoplasmic and prokaryote/plastid/mitochondrial genetic systems. This the symbiotic theories do not do; they ignore the fact that both kinds of genetic systems must have evolved from prokaryote systems, and so resemblances are not at all surprising[21]. The real problem is why the nucleus is different, which symbiosis does not explain.

Third, it is far simpler than any symbiotic theory. These postulate two to five separate symbiotic events[16]. Though the symbiotic origin of mitochondria and chloroplasts is a possibility (and one compatible with the origin of nuclei by the mechanism proposed here), the resemblances between them and prokaryotes are to be expected on either theory. The symbiotic origin of flagella and the mitotic apparatus[7,12], is untenable for many reasons[8,24]. The idea that the complexities of sex and meiosis evolved independently 27 times (Fig. 2–6 of ref. 7) in much the same way is incredible.

Eukaryote diversification

I regard the absence of flagella in red algae (possibly also in higher fungi if they evolved from them by plastid loss[40]) as primary[20,21,24]; they are probably the most primitive living eukaryotes. Though some amoebae without flagella could have evolved from primitive red algae by plastid loss, most eukaryotes must be derived from a red algal line which evolved 9+2 flagella from aggregates of microtubules. The selective advantage is obvious: they could colonise a completely empty niche as the first marine phytoplankton (or if, unlike today[25], there were then blue-green algae in the open sea, become their first predators) through their new ability to stay in suspension and migrate to the level most suitable for photosynthesis and (or) predation. By loss of phycobilins and the development of other pigments a great variety of brownish and green phytoflagellates were formed[39,41,42]. These were the ancestors of all plants and, by plastid loss, of non-photosynthetic protists and animals (Fig. 5). The generality of the circadian clock in eukaryotes (and possible absence in bacteria) is easiest to understand if it evolved in a photosynthetic common ancestor to maximise photosynthesis by day and division by night. Complex polysaccharide–protein cell walls or surface coats, often secreted by the Golgi apparatus, evolved in many lines. Adhesion between such extracellular layers led to multicellularity, in many separate lines[43,44].

Comparative studies clearly indicate that centrioles are derived from basal bodies[45] and probably became secondarily associated (perhaps on several independent occasions) with the spindle poles, and are not essential for mitosis[24,46]. Chromosome-to-pole spindle microtubules probably evolved long after the origin of mitosis, but only in some eukaryote groups[24]. Microtubules have also independently evolved into many other organelles of motility, such as axostyles[47], axopods[48], suctorian tentacles[49] and haptonemata[39] as well as numerous structural elements as in the cortex of protist cells[39,50], the phycoplast[51] or neurotubules[52].

My view that the origin of all eukaryotic organelles and genetic systems can be traced back to two fundamental innovations, (1) cytosis involving actomyosin and (2) microtubules, has many implications (too numerous to discuss properly here) which can be tested by observations on living organisms. Unfortunately evidence from the fossil record[42,53] will be very hard to come by because the ancestral eukaryotes had no cell walls and because the changes postulated could have occurred very rapidly indeed, possibly in a very restricted locality.

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Palaeolithic remains at the Hadar in the Afar region

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Studies of Plio–Pleistocene deposits along the Awash River in the Hadar region of Ethiopia have revealed for the first time several Palaeolithic sites. In addition to a large number of artefacts which provide evidence of early to late Stone Age industries the deposits have also yielded a rich vertebrate fauna including what may be the earliest hominid remains yet discovered.

NEAR the confluence of the rivers Awash and Hadar, about 60 km ESE of Bati, the latter river has cut deeply into the gravel covered surface of the floor of the Ethiopian Rift (see Fig. 1) and has exposed 105 m of fluviatile, lacustrine and tuffacious sediments of Plio–Pleistocene age.

The flat surface of the rift floor consists of an extensive boulder gravel, 3–6 m thick, which lies unconformably on the Upper Pliocene and Lower Pleistocene sediments of the Hadar Series. This gravel extends from the foot of the Ethiopian Rift escarpment in the west, thinning slowly to beyond the Awash River in the east[1]. It seems to have been deposited as a series of large confluent fans derived from the escarpment, which form an extensive behada or peripediment. It is not cemented and consists of well rounded to subrounded boulders and pebbles 30–40 cm in size, set in a matrix of sandy, calcareous silt. The pebbles are neither sorted nor oriented into any stream direction. The gravel is probably of Middle Pleistocene age, as indicated by Early Stone Age (ESA) implements found *in situ*; no fauna has yet been found.

Beneath the boulder gravel the Hadar has exposed a 105-m section of the Hadar sediments—Upper Pliocene and Lower Pleistocene fossiliferous beds of sandstones, sands and clays, and occasional tuffs. A very rich vertebrate fauna indicates a relative age of more than 3 Myr for these beds[2].

Fossils of *Australopithecus*, at least 3 Myr old[3], were found for the first time during the survey of the Lower Hadar sediments by members of the 1973 International Afar Expedition. These included three fragments of femur and one fragment of tibia from a small hominid and a piece of cranium (mastoid) from a more robust *Australopithecus*.

In the Hadar area the terraces of the Awash River are not very pronounced. The Awash meanders in a flood plain about 1 km wide. In the inner parts of the meanders the silty and fine-sandy, modern alluvial plain is covered by a thick riverine forest comprising various species of acacia and tamarisk. The height of the plain is not more than 2 m above low water level.

A terrace 3–5 m high runs along the inner meanders beyond the riverine forest. It is covered by a thin, bouldery gravel within a sandy matrix. The same terrace also stretches along the Denen Dora tributary further west. There, a broad terrace covered by large boulders and pebbles extends between the Denen Dora and the Sidi Hakoma tributary, rising to 4 m above the bed of the Denen Dora.

Any pre-existing higher terraces of the Awash and the Hadar have been destroyed by erosion. Significantly, many—though not all—of the Badland Hills, 25–90 m in height along the Awash, have a covering of loose, well-rounded boulders in a sandy–silty matrix lying unconformably on earlier Hadar deposits.

All the boulders which cover the river terraces and erosional surfaces in the Hadar area have been derived from the erosion of the Middle Pleistocene boulder gravel. The pebbles of this