

Eukaryogenesis: The Beginning of Life as We Know It

In essence...we have two rival schools of biology based upon evolutionary speculations: the classical or “traditional” biologists who believe that the eukaryotic cell is the end-result of a gradual but continuous evolution from the prokaryotic cell via the accumulation of mutational events, and the endosymbiotic proponents whose thesis is that the eukaryotic cell is the result of a sudden (or “revolutionary”) acquisition of whole prokaryotic cells, followed by the symbiotic evolution of guests and hosts.
(Fredrick 1981:x)

So began Jerome Frederick in his opening statement to the New York Academy of Sciences, chairperson of a conference held in January 1980 entitled “Origins and Evolution of Eukaryotic Intracellular Organelles”. In the time since Fredrick made these opening remarks about eukaryogenesis (the origin of the eukaryotic condition) evolutionary biologists have (for the most part) come down upon one side of this once contentious debate — the endosymbiotic. And yet, for the most part, endosymbiosis (and, for that matter, symbiosis in general) has remained in the shadows of mainstream (populist) biological thought (like Dawkins 1976, 1986; Gould 1977, 1989, 1996; and Wilson 1994). Eukaryogenesis (the evolution of the eukaryotic condition) is an event so crucial to life as we see it on earth today that it is held, by those who have assumed the responsibility of investigating it, as *the* crucial precursory event in the diversification of life on earth. From the advent of the eukaryotic condition sprung everything we commonly associate with life (and evolution) — things like multicellularity, sexuality and speciation (see Margulis and Sagan 1984, Paterson 1989) — including, of course, our own species. And yet, for all of its magnanimous evolutionary consequences there remains a stupendous silence within the populist literature about the eukaryogenic theory (syntrophogenesis) that has, over the past twenty years or so, gained such widespread acceptance. In this short essay I shall attempt to assess (critically) the alternative explanations of eukaryogenesis, commenting less upon the biochemical, cellular, molecular and microbial evidence (I realize that I do not possess the depth of knowledge nor the expertise to critique the work of people like Lynn Margulis who’ve dedicated their entire lives to investigating these phenomenon), and more upon how they have (or have not) gained acceptance within *biology*, as Rose (1997:19) understands it: “Biology — not the phenomena of life, but their scientific study — is itself historically constructed.”

The profound differences in cellular structure between prokaryotic (from the Greek ‘pro’ meaning ‘before’, and ‘karion’ meaning ‘nucleus’) and eukaryotic (from the Greek eu = true) cells have been known to biologists for well over a century (in fact, the first proponents for an endosymbiotic origin of eukaryotic intracellular organelles were two scientists, Altmann and Schimper, working in the 1880s — see Lang *et al.* 1999:352). It

is these differences (see Table 1) that have, since that time, begged evolutionary biologists to elicit an evolutionary explanation in order that evolution, the theory closest to the epistemological foundations of biology (again, the scientific body of knowledge, the discourse, not the living systems themselves), might work to maintain its position within biological discourse¹.

Table 1: The major differences between prokaryotic and eukaryotic cellular structure and function (see de Duve 1996; Knox *et al.* 1994; Kostianovsky 2000; Margulis 1970,1993)

| Prokaryotes | Eukaryotes |
|--|--|
| <ul style="list-style-type: none"> • Cells small (1-10µm across) • Nucleoid, not membrane bound • One set of genes (haploid), arranged into a circular chromosome • Cell division mainly via binary fission or budding • All are microbes: unicellular, colonial, filamentous and mycelial forms; no extensive tissue differentiation • No packaged membrane-bound enzyme sacs, no heritable organelles • Rigid, thick cell external cell wall • Some have simple flagella • No phagocytosis, pinocytosis or cyclosis • Include anaerobes (killed by oxygen), microaerobic and aerobic forms | <ul style="list-style-type: none"> • Cells large (10-100µm across) • Nucleus bound by a double membrane • Two sets of genes (i.e., diploid, except gametes), chromosomes in strands • Cell division via mitosis • Some microbes, mostly large organisms: unicellular, colonial, mycelial and multi-cellular forms; extensive tissue differentiation in multicellular forms • Contain an endomembrane system including rough and smooth endoplasmic reticulum, the Golgi complex, lysosomes, secondary granules, peroxomes, microbodies, hydrogenosomes, chloplasts and mitochondria • Complex internal cytoskeleton • Except fungi, most have undulipodia: i.e. [9(2)+2] ‘flagella’ or cilia • Phagocytosis, pinocytosis, cyclosis present • All are aerobic (need oxygen to live), exceptions are secondary modifications |

¹ For a discussion of ‘science as discourse’ see Smocovitis (1996) Chapter 4, “The New Contextualism: Science as Discourse and Culture”, pp.73-94.

Microfossil, stromatolite and chemical fossil evidence suggest an origin for the prokaryotic cell of between 3 and 3.5 billion years ago and of the eukaryotic cell between 1 and 1.5 billion years ago (Margulis 1993:120-121, 156). Neither eukaryogenic explanation disagrees that the eukaryotic condition evolved from an ancestral prokaryote (a position supported by the universality of certain cellular components and metabolic pathways). Rather they differ in how they explain the transition from an ancestral prokaryote to a eukaryotic cell. In order that a theory maintain itself within the scientific discourse, it must be able to offer an explanation of the evidence at hand. Of course, as time goes by, the evidence at hand changes, and so the theory must either account for the new evidence or change its mode of explanation.

This is exactly what has happened with eukaryogenic explanations. It is traditional within the scientific literature to pit one theory against the other, each facing the other in mortal combat, one destined to oust the other (following the narrative structure of Western myth — see Landau 1991, Smocovitis 1996:87). However, what actually happens within scientific discourse is nothing like this. It is very rare (perhaps nonexistent) for one theory to completely replace (conquer) the other. What usually (perhaps always) happens is that new theories appropriate certain elements from old explanations, rearranging them into new discursive structures to produce new modes of explanation (or theoretical *synthesis*). This is the case for eukaryogenic explanations. The endosymbiotic theory never ousted the traditional viewpoint, rather it retained certain aspects of its explanation, discarded some and invented others as it was (and continues to be) reformulated. The reformulation has, in fact, never ended and, so long as new evidence continues to be sought and found, never will.

According to Smocovitis (1996:196) it was Borghoorn and Tyler whom introduced cellular evolution into the continuum when Precambrian (i.e. older than 600 million years) microfossils were ‘discovered’ in 1954, using a new imaging technology, electron microscopy. In light of this evidence the origin and evolution of cellular structure began to be investigated in earnest. The initial explanations pertaining to eukaryogenesis were formulated in terms of the current evolutionary rhetoric: organisms evolve by the accumulation of mutational change and their natural selection (Kostianovsky 2000:63). According to this theory, all of the differences between prokaryotic and eukaryotic cells could be accounted for in terms of the accumulation of single step mutational changes within an ancestral protoeukaryotic cell. As the evidence mounted it became clear this theory was not adequate to explain the differences between prokaryotes and eukaryotes. How could the similarities between mitochondrial division and prokaryotic division be accounted for? Why was it that certain organelles contained genetic material? And why was that genetic material haploid and circular?

The similarities between the prokaryotic cell and certain of the eukaryotic intracellular organelles (namely the mitochondria and chloroplasts) had been known since the end of the 19th century, however it was not until the late 1960s that the endosymbiotic theory, originally formulated by Mereschkowsky earlier that century to account for the origin of plastids (Kostianovsky 2000:65), was once again launched by Margulis using modern biochemical, genetic, cytological, and paleontological information as evidence (Margulis

1970:5). According to Margulis's synthesis eukaryotes were borne from a stepwise symbiotic union of prokaryotic cells, where one prokaryote eventually engulfed another. The other cellular features we associate with eukaryotes evolved (according to this synthesis) during and after the symbiotic event (Roger 1999:S147). Her early synthesis outlined how eukaryotic cells came to possess many of their features (intracellular organelles, organelle genomes and the division of mitochondria and plastids, for example), but did little to elaborate upon how (mechanistically) one ancestral prokaryote could engulf another — an event that is rather central to the theory.

It was left to other early theorists like de Duve and Stanier, also working in the late 60s, to postulate the development of an early phagocytic protoeukaryote (a eukaryotic precursor capable of engulfing voluminous bodies) prior to endosymbiosis (Roger 1999:S147, see also de Duve 1996). This protoeukaryote, according to de Duve (who called it the *urkaryote* — see de Duve 1991:62) needed to develop certain eukaryotic features in order to phagocytose: the cytoskeleton and the endomembrane system. Having developed these features the urkaryote had the structural capability of ingesting prokaryotic cells that, later, became endosymbiotic bacterial organelles. Taylor dubbed this new synthesis the serial endosymbiosis theory (SET) (Lang *et al.* 1999:352) which was, in effect, a synthesis of Margulis's endosymbiosis, de Duve's urkaryote and the traditional formulation: natural selection (since each new characteristic had to have, after all, conferred to the organism some selective advantage in order that it spread throughout the population, no matter if that characteristic was the result of mutational change or of symbiosis).

In no way, then, did the SET synthesis oust the traditional approach, rather it built upon a foundation set by earlier thinkers, modifying certain aspects, discarding others. And of course the synthesis didn't stop there. There are still many issues left to resolve, and always more evidence to explain. In what order did these early evolutionary events occur (see Roger 1999)? Are the mitochondria and chloroplasts of monophyletic or polyphyletic origin (see Moreira *et al.* 2000, Palmer 2000, Penny and O'Kelly 1991)? Did the origin of the mitochondrion contribute to the origin of the nuclear genome (see Lang *et al.* 1999)? Are undulipodia of symbiotic origin (see Margulis 1993: Ch.9)?

One of the most interesting points about the development of eukaryogenic theory remains: Why, given the current widespread acceptance of SET, have the symbiotic aspects of evolution remained largely an ignored topic within mainstream evolutionary biology? Perhaps, I would suggest, it has something to do with the history of the discipline. Evolutionary relationships (phylogeny and cladistics) are traditionally expressed in terms of the "branching tree" model. Evolutionary biology traditionally explains evolution as 'branching' of this 'tree of life'. The model doesn't readily predispose itself to the idea that branches sometimes weave themselves back into one another, made particularly difficult if those branches are imagined to be on opposite sides of the tree. This is, of course a problem within biology (the discipline) not with life itself.

Evolutionary biology traditionally concerns itself with examining the differences between living organisms, how they arise, and how those differences confer selective advantages,

concentrating more upon competition and less upon exchange. In doing so the tendency is to paint the picture of an organism, alone in an inhospitable world, pitted against, never aided by, other organisms (again, a healthy articulation of the myth structure of Western culture, and how we imagine our own species to be placed in the world). It is ironic (yet historically consistent, given the nature of our society) that this should be the case since natural selection actually works to *minimize* intraspecific competition (which is exactly why, if two organisms occupy the same ecological niche, one of them will disappear from the community). Intense competitions, where they are seen, are always short-lived phenomena that, very soon, eliminate themselves. Of course, this is why symbioses are such successful adaptations: they work to minimize the competition between organisms. Symbioses are, typically, based upon *exchange*, and exchange (as every economist knows) is one sure way of *reducing* competition (which is why laws have to be passed limiting the exchange of information between competing companies).

Seen in this light, the endosymbiotic origin of eukaryotic organelles is simply another incredible evolutionary innovation conferring such a degree of evolutionary success to eukaryotes because it works to minimize the level of competition between the eukaryote and its endosymbiotic bacterial organelles by maximizing their level of exchange. The adaptation works (it seems) in much the same way that the next major evolutionary transition (see Szathmary and Smith 1995), multicellularity, works: to minimize intracellular competition between individual eukaryotic cells by maximizing the level of intracellular exchange.

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