Review

CellPress

Evolutionary mechanisms for establishing eukaryotic cellular complexity

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Through a comparative approach, evolutionary cell biology makes use of genomics, bioinformatics, and cell biology of non-model eukaryotes to provide new avenues for understanding basic cellular processes. This approach has led to proposed mechanisms underpinning the evolution of eukaryotic cellular organization including endosymbiotic and autogenous processes and neutral and adaptive processes. Together these mechanisms have contributed to the genesis and complexity of organelles, molecular machines, and genome architecture. We review these mechanisms and suggest that a greater appreciation of the diversity in eukaryotic form has led to a more complete understanding of the evolutionary connections between organelles and the unexpected routes by which this diversity has been reached.

Bringing together cell biology and evolutionary biology

The emergence of the eukaryotic state nearly 2 billion years ago transformed life on Earth. Efforts to unravel the evolutionary mechanisms that have shaped, and continue to shape, eukaryotic cells are beginning to address this monumental evolutionary shift. Understanding these mechanisms will help us to make conceptual connections between the cell biology of taxonomically diverse modern eukaryotes, porting knowledge derived in model systems to less studied organisms of agricultural (e.g., crops, plant pathogens), environmental (e.g., aquatic primary producers like haptophytes and diatoms), or medical (e.g., parasites such as *Plasmodium falciparum*, the causative agent of malaria) relevance. This broad comparative approach known as evolutionary cell biology (see Glossary) facilitates the generation of hypotheses that attempt to explain the cell biological functions shared among the full range of eukaryotes.

This approach has been applied successfully to many aspects of the eukaryotic cell (e.g., [1]). The combination of ultrastructure and molecular cell biology with genomic data from a sampling of organisms spanning the taxonomic breadth of eukaryotes [2,3] (Figure 1) has provided a wealth of knowledge regarding the evolution of eukaryotic cell biology and its diversity. From the perspective of a cell biologist, this wealth of data allows the integration of established evolutionary theory with the study of cellular mechanisms.

Glossary

Complexity: a measure of the number of components and interactions of one system relative to another equivalent system.
Endosymbiosis (primary): the process whereby a prokaryotic cell (endosymbiont) is incorporated into the cytoplasm of a eukaryotic cell (host), with a relationship being established via metabolic integration and EGT such that neither partner can survive on its own.
Endosymbiosis (secondary): the same process as primary endosymbiosis except that the endosymbiont is a eukaryotic cell possessing a primary plastid. The process can be extended to tertiary endosymbiosis (the endosymbiont is a cell possessing a secondary plastid) and serial secondary endosymbiosis (a lineage possessing one type of secondary plastid replaces its secondary plasmid with a secondary plastid of a different lineage).
Endosymbiotic gene transfer (EGT): a special case of horizontal gene transfer (see below), whereby the gene in question is acquired by the host lineage from the genome of the endosymbiont.
Evolutionary cell biology: an emerging discipline that incorporates comparative perspectives and techniques from cell biology, protistology, molecular evolution, and mathematical evolutionary theory to address questions of the origins and diversity of cells.
First eukaryotic common ancestor (FECA): the cell (or population of cells) belonging to the lineage that gave rise to the modern line of eukaryotes at the earliest point at which it possessed cell biological features distinct from those in prokaryote-like cells. Although this organism is deduced to have existed, a useful way to treat the FECA is as a theoretical reconstruction with the traits defining it as an exciting open research question.
Horizontal gene transfer: the acquisition of a gene by a genome from a source other than the immediate parental lineage.
Last eukaryotic common ancestor (LECA): the cell (or population of cells) belonging to the lineage that gave rise to the modern line of eukaryotes at the latest point at which the various descendent lineages diverged to leave the extant eukaryotic lineages. Again, this concept is most useful as a theoretical reconstruction or reference point to assess the antiquity of various cell biological features.
Monophyletic: a group is considered 'monophyletic' when it encompasses all descendants of a single ancestor.
Paraphyletic: a group is considered 'paraphyletic' when it encompasses some, but not all, descendants of a single ancestor.
Paralog: genes that are the result of a gene duplication process.
Selection: the process by which a factor (including the presence of another organism) presents a circumstance that results in the preferential death of some organisms in the environment over others.

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Keywords: constructive neutral evolution; endosymbiosis; evolutionary cell biology; organelle paralogy hypothesis; protocoatomer; transfer-window hypothesis.

0962-8924/$ – see front matter
 http://dx.doi.org/10.1016/j.tcb.2014.02.003

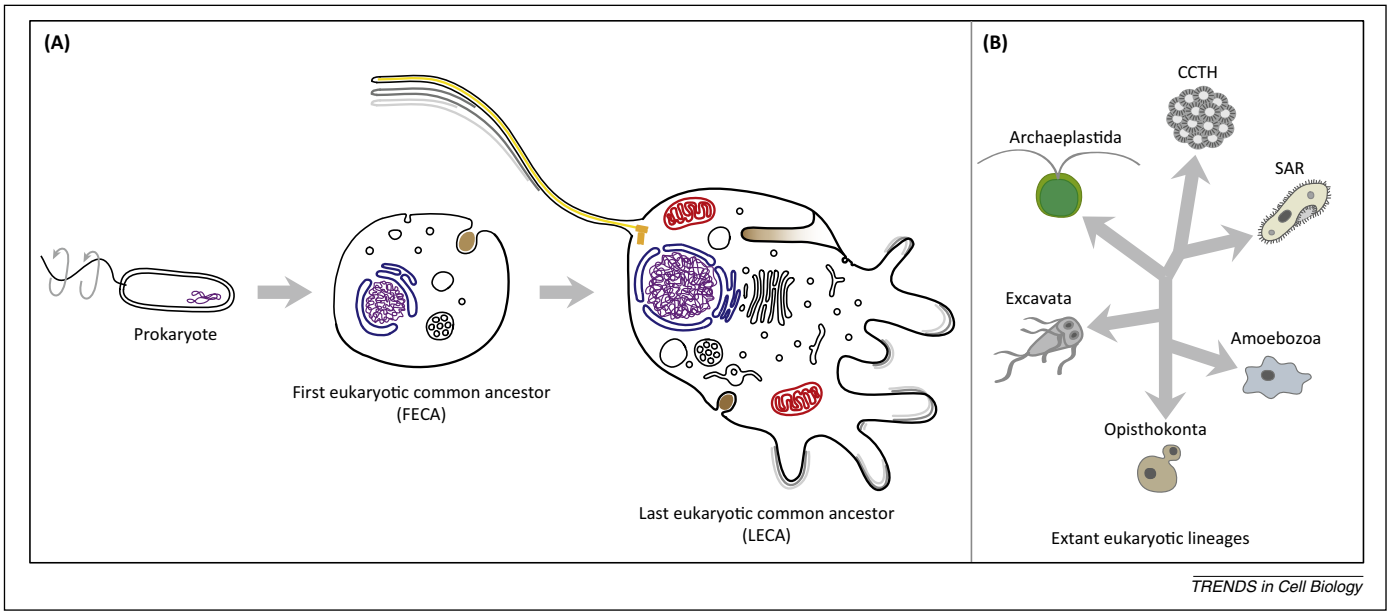

Figure 1. Retracing the emergence of modern eukaryotes. **(A)** The emergence of eukaryotes can be divided into at least three successive evolutionary stages: (i) transition from a prokaryote-like starting point to the first eukaryotic common ancestor (FECA); (ii) transition from the FECA to the last eukaryotic common ancestor (LECA); and (iii) evolution and divergence after the LECA to form the major lineages of eukaryotes as we know them today [2,11]. **(B)** After the LECA, six extant eukaryotic lineages (Box 1) have been characterized [11]. These are the Opisthokonta, Amoebozoa, Excavata, and Archaeplastida, the stramenopiles, alveolates and rhizarians (SAR), and the contentious grouping of cryptomonads, centrohelids, telonemids, and haptophytes (CCTH). Cartoon images of representative organisms from each supergroup are not to scale.

Significant progress has been made in revealing the mechanisms underpinning the emergence of complexity in the eukaryotic cell. The number and sophistication of internal compartments in eukaryotes distinguish them from prokaryotes and it is this sophistication that translates into vastly greater 'complexity' in eukaryotic cellular configuration, which is measured by the number of components in a system and the number of interactions between them [4,5] compared with another, equivalent system (e.g., cell versus cell). There is general agreement from both molecular phylogenetic analyses [6,7] and evidence from the fossil record ([8,9], but see [10]) that prokaryotes predated eukaryotes. This evidence suggests that eukaryotes must have arisen from a state resembling that of a prokaryote; that is, that the acquisition of organelles and complex cellular machines in eukaryotes must be explained from a cellular state lacking the extensive presence of these features. Evolution from less complexity (prokaryote state) to increased complexity of cellular architecture (eukaryote state) can be divided into at least three successive evolutionary stages (Figure 1). First, a transition from an organism lacking some or all internal membranes to an organism that possesses some cellular features that define it as eukaryotic [i.e., a first eukaryotic common ancestor (FECA)] must occur. Next, the organism must transition from the FECA to a last eukaryotic common ancestor (LECA). Finally, evolution and divergence after the LECA must occur to form the major lineages of extant eukaryotes [2,11].

Research on the prokaryote-to-eukaryote transition (e.g., [1]) has reconstructed a surprisingly sophisticated LECA possessing a well established actin/tubulin cytoskeleton, an elaborate endomembrane system, a nucleus, mitochondria, and machinery for processes such as intron splicing and meiosis (Figure 1). Furthermore, at least one additional major cellular innovation has influenced post-LECA increases in complexity: the acquisition of plastids. Therefore, an important question for evolutionary cell biology is what mechanisms drive increased cellular complexity at the level of molecular machines and the formation of organelles. Here we review the progress that has been made in addressing this question.

Mechanisms for organelle acquisition

Before 1974, the null hypothesis for the evolution of internal membrane-bound compartments (organelles) within the eukaryotic cell was an autogenous process; that is, eukaryotic cells are built in a stepwise manner from individual building blocks present in the pre-eukaryotic ancestor [12,13]. However, evidence demonstrating that both mitochondria and chloroplasts are of bacterial origin (endosymbiosis) [14,15] shifted the theoretical basis of the eukaryotic evolutionary field such that both endosymbiotic and autogenous explanations are now viable alternatives to entertain when addressing the origins of a eukaryotic organelle. Our scientific understanding of both mechanisms is maturing, with endosymbiosis being far better understood. Below, we discuss the current standing on the emergence of complexity of eukaryotic cells through endosymbiosis and autogenous processes.

Endosymbiosis

Endosymbiosis is the incorporation and residence of one organism, the endosymbiont, inside another, the host. Beyond the familiar examples of endosymbiosis (i.e., the chloroplast of plants and the nearly ubiquitous mitochondrion), a diverse array of organisms with organelles derived from additional endosymbiotic events also exists