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Reconciling an archaeal origin of eukaryotes with engulfment: a biologically plausible update of the Eocyte hypothesis

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Abstract

An archaeal origin of eukaryotes is often equated with the engulfment of the bacterial ancestor of mitochondria by an archaeon. Such an event is problematic in that it is not supported by archaeal cell biology. We show that placing phylogenetic results within a stem-and-crown framework eliminates such incompatibilities, and that an archaeal origin for eukaryotes (as suggested from recent phylogenies) can be uncontroversially reconciled with phagocytosis as the mechanism for engulfment of the mitochondrial ancestor. This is significant because it eliminates a perceived problem with eukaryote origins: that an archaeal origin of eukaryotes (as under the Eocyte hypothesis) cannot be reconciled with existing cell biological mechanisms through which bacteria may take up residence inside eukaryote cells.

Keywords: Stem group; Crown group; Eocyte hypothesis; Phagocytosis; Eukaryotes; Archaea

1. Introduction

A range of models for the origin of the eukaryote cell have been proposed on phylogenetic, genomic and cell biological grounds (reviewed in Embley and Martin, 2006; Martin et al., 2001; Poole and Penny, 2007b; Gribaldo et al., 2010). There is a general agreement that the ancestor of mitochondria[1] was an α-proteobacterium, contributing many (though probably not all—(Esser et al., 2004, 2007; Lester et al., 2006)) genes of bacterial origin to the eukaryote nuclear genetic complement. It is likewise beyond doubt that the mitochondrion was one of many features present in the Last Eukaryotic Common Ancestor (LECA) from which modern eukaryote diversity has derived. This also appears to be the case for key parts of the machinery for phagocytosis—cell engulfment (Yutin et al., 2009). As summarised in Table 1, the emerging consensus from a range of studies is that the LECA was essentially a fully-fledged eukaryote cell.

Broad agreement on the timing and specific evolutionary origin of mitochondria stands in stark contrast to disagreement concerning the nature of the other partner in this endosymbiosis: the host. Two main views have been expounded in the literature. One is that the host was an archaeon, the other that the host was a protoeukaryote capable of cell engulfment (discussed in Embley and Martin, 2006; Martin et al., 2001; Poole and Penny, 2007b). These seemingly opposing views have been the source of extensive recent debate on two levels: one phylogenetic, one cell biological (Davidov and Jurkevitch, 2007, 2009; Poole and Penny, 2007a,b,c, Hartman and Fedorov, 2002; Kurland et al., 2006; Martin and Koonin, 2006; Lopez-Garcia and Moreira, 2006; Gribaldo et al., 2010).

Phylogenetically, eukaryotes and archaea might each be monophyletic, as suggested by the bacterial rooting of the tree of life (Gogarten et al., 1989; Iwabe et al., 1989; Woese et al., 1990), meaning that eukaryotes and archaea are sister groups

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[1] Mitochondria and related organelles—mitosomes and hydrogenosomes—all derive from a common ancestor (reviewed in van der Giezen and Tovar, 2005). For brevity, we will refer to mitochondria throughout, but references we make to the mitochondrial ancestor will assume that we are talking about the ancestor of all three, irrespective of important differences in their metabolic repertoire.

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Table 1
Features of contemporary eukaryote cells proposed to be present in the Last Eukaryotic Common Ancestor (LECA).

Feature	References
Mitochondrion	Embley and Martin, 2006; van der Giezen and Tovar, 2005
Phagocytosis	Cavalier-Smith, 2002b; Jékely, 2003, 2007a; Yutin et al., 2009
Nucleus and nuclear pore complex	Bapteste et al., 2005; Devos et al., 2004, Devos et al., 2006; Mans et al., 2004; Neumann et al., 2010
Endomembrane system	Dacks et al., 2003; Dacks and Field, 2007; Field and Dacks, 2009; Jékely, 2003, 2007a; Neumann et al., 2010
Mitosis and meiosis	Cavalier-Smith, 2002a; Ramesh et al., 2005; Egel and Penny, 2008
Introns and spliceosomal apparatus	Collins and Penny, 2005; Jeffares et al., 2006; Roy and Gilbert, 2005, 2006; Roy and Irimia, 2009
Linear chromosomes and telomerase	Nakamura and Cech, 1998
RNA processing	Collins et al., 2009; Gardner et al., 2010
Peroxisome	Gabaldon et al., 2006; Gabaldon, 2010
Cytokinesis	Eme et al., 2009

that diverged from some common ancestor (Poole and Penny, 2007b; Pace, 2006; Cavalier-Smith, 2002b; Woese et al., 1990—Fig. 1A). Alternatively eukaryotes may have evolved directly from within archaea (Fig. 1B) (Cox et al., 2008; Embley and Martin, 2006; Martin and Müller, 1998; Rivera and Lake, 1992, 2004). Numerous authors have reported evidence for one or the other general topology, with little sign of an emerging consensus (Gribaldo et al., 2010).

Phylogenetics is central to our understanding of the origin of the eukaryote cell because trees can distinguish between the two tree topologies given in Fig. 1 (Panels A and B). However, the two trees in Fig. 1 have been taken to imply very different (and incompatible) series of cell biological events for the endosymbiotic origin of the mitochondrion and the origin of eukaryotes. The tree in Panel A is equated with the hypothesis that the modern eukaryote cell evolved via a protoeukaryotic host (PEH) cell engulfing an ancient α-proteobacterium (Panel C) (Cavalier-Smith, 2002b, 2009; Poole and Penny, 2007a,b). In contrast, the tree in Panel B has been interpreted to mean that the host (the cell that did the engulfing) must have been an archaeon (Panel D) (Martin and Koonin, 2006; Martin and Müller, 1998). The model in Panel C has the advantage that it relies on cell biological processes known to be in action in the present (i.e. phagocytosis or subversion of phagocytic machinery as a mechanism for host infiltration), whereas the latter (Panel D) currently lacks cell biological evidence because no archaea are known to be capable of phagocytosis, and no archaea have been documented to harbour any bacterial endosymbionts (Poole and Penny, 2007a,b).

The primary point of this paper is to show that the tree topologies (Panels A and B) and the cell biological processes for endosymbiosis (Panels C and D) are not logically connected, despite a historical association between the models in Panels A and C, and between Panels B and D. To illustrate this, we will make the assumption that recent phylogenetic analyses reporting support for the Eocyte tree topology ((Lake, 1988; Rivera and Lake, 1992) — schematically represented in Panel B) (Cox et al., 2008; Foster et al., 2009) correctly recover the evolutionary relationship between archaea and eukaryotes. These analyses place eukaryotes as sister to the crenarchaeota, and, if subsequently corroborated, the implication is that eukaryotes have evolved directly from archaea. We show that, under an archaeal origin of eukaryotes, no special unknown cell biological mechanisms of the type illustrated in Panel D (Embley and Martin, 2006; Martin and Müller, 1998; Davidov and Jurkevitch, 2009) are required to understand the origins of the eukaryote cell.

2. Ancestors, missing links, stems and crowns

In assuming that the Eocyte tree is correct, the biological problem that we face is as follows. All sequences used to investigate the deep phylogeny of eukaryotes and archaea necessarily come from extant organisms. The evidence for a complex eukaryote at the base of the eukaryote tree (LECA) (Koonin, 2010; Poole, 2010) (Table 1) is resultant from the observation that no intermediate forms are preserved among extant eukaryote lineages (Poole and Penny, 2007b).

In debate over human origins, Sarich (1973) famously remarked, ‘the biochemist knows his molecules have ancestors, while the palaeontologist can only hope that his fossils left descendants’. The problem for those seeking to reconstruct eukaryote evolution is the exact opposite. Comparative molecular and cell biology has painted a surprisingly sharp picture of LECA as a modern eukaryote cell (Table 1), but evolution has left no trace of the intermediate stages. Even tantalising fossils such as the 3.2 billion year old Acritarchs recently reported by Javaux et al. (2010) are difficult to interpret within this framework. While the suspicion that these are stem group eukaryotes has been voiced (Buick, 2010), the issue of whether they are or not is nevertheless unlikely to shed light on the questions raised by the reconstruction of LECA because detailed cell ultrastructure is not discernible in these fossils. It is moreover not possible to relate this find to the timing of the origin of archaea, as there is no firm evidence for the timing of their origin in the fossil record (Brocks et al., 2003).

That eukaryotes possess a multitude of large multiprotein complexes and internal structures that lack counterparts in both archaea and bacteria means eukaryogenesis cannot be understood by reference to cellular features of extant bacteria and archaea, because obvious precursor structures from which those traits could be derived are absent. Are we then restricted to speculation regarding the steps in eukaryogenesis?

The answer is a resounding no. The apparent controversy is perhaps a casualty of only being able to examine the diversity of extant eukaryotes. All extant eukaryote lineages are by