



Society for Experimental Biology Annual Main Meeting 28th June – 1st July 2009, Glasgow, UK

C3 – EVOLUTION OF THE EUKARYOTIC CELL

C3.1

09:10 Tuesday 30th June 2009

Eating before sex: Predation and the origins of eukaryotic cell structure and genetic systems

Tom Cavalier-Smith (University of Oxford)

Abstract to follow.

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C3.2

09:55 Tuesday 30th June 2009 (SEB Cell Section President's Medallist Lecture 2009)

The role of horizontal gene transfer in the evolution of trophic mechanisms across the eukaryotes

Tom Richards (University of Exeter), Darren M. Soanes (School of Biosciences University of Exeter), Peter G. Foster (The Natural History Museum), Guy Leonard (Centre for Eukaryotic Evolutionary Microbiology University of Exeter), Nicholas J. Talbot (School of Biosciences University of Exeter)

Horizontal gene transfer (HGT) describes the transmission of genetic material between distinct evolutionary lineages. Large-scale HGT was a significant process in the endosymbiotic origin of the mitochondrial and chloroplast organelles and was important in the foundation and diversification of the eukaryotes. Reports of HGT between eukaryotes are far less frequent and the significance of this process is poorly understood. Analysis of protozoan and algal genomes suggests HGT may have been driven by phagotrophic lifestyles and that this has been an important factor in the spread of plastid organelles and phototrophy. This work strongly suggests that ecological associations between donor and recipient lineages are also a pre-requisite for HGT, suggesting that plants and fungi, which share numerous habitats, may have also shared genetic information. We tested this hypothesis by carrying out phylogenomic analysis of plant and fungal genomes. This demonstrated a pattern of infrequent gene transfer between these

two non-phagotrophic eukaryotic 'kingdoms', transmitting several distinct metabolic traits. However, the minimal pattern of HGT implies that the absence of phagotrophy is not a barrier to transmission, but may impede the frequency of transfer. To further investigate HGT in non-phagotrophic eukaryotes we analysed the genomes of three oomycete osmotrophic plant pathogens. Our analyses of the oomycetes show a number of fungal derived HGTs. The putative function of these transferred genes suggests that these acquisitions were important in the evolutionary history of the oomycetes, which has encompassed a radical change in lifestyle, from ancestral phagotrophic algae to filamentous osmotrophic pathogens.

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C3.3

10:55 Tuesday 30th June 2009

Eukaryotic life without mitochondria?

Mark Van der Giezen (University of Exeter)

Mitochondria are a universal feature of all extant eukaryotes. The notion that several groups of present-day eukaryotes do not contain this important organelle has been shown to be incorrect. However, the scientific effort at debunking that notion has resulted in a wealth of data from otherwise little-studied anaerobic protists and has caused a serious rethinking of the origin of eukaryotes as a whole. Over the last 5–10 years, it has become apparent that the organelle known as the mitochondrion is a much more fluid entity than generally believed. Various versions of mitochondria have been discovered that perform the kind of biochemistry normally associated with anaerobic bacteria. However, this should come as no surprise as the general image of 'normal' mitochondria only represents mammalian mitochondria, and then only from a certain cell type. Why would an organelle such as the mitochondrion be the same in all eukaryotes while other cellular structures show such great evolutionary malleability? The establishment of the mitochondrion has been one of the most important evolutionary events that shaped life on our planet. When we consider

the total repertoire of metabolic capacity of the extended mitochondrial family, it hardly seems conceivable that an obligate aerobe such as *Rickettsia* is the closest extant relative of the bacterium that gave rise to mitochondria. Our emerging knowledge of mitochondrial diversity points to more likely candidates from among the facultative anaerobic alpha-proteobacteria and that realisation will change the way we think this key endosymbiosis became established in the first place.

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11:30 Tuesday 30th June 2009

When is a cell not a cell? The evolution of cell death as a developmental strategy

Hilary J. Rogers (Cardiff University)

Cell death is a central process in plant and animal development, concerning both individual cells in an organ and, in plants, the final stages in the death of whole organ such as a leaf or petal. The death of a limited number of cells during organ development may be considered as a common strategy. For example selected cell death occurs in the formation of the egg cell from four meiotic products both in mammals and in most higher plants. In contrast, senescence of whole organs and their replacement by new organs of the same type is perhaps a specific adaptation of plants to cope with changing environmental conditions. A distinct feature of plant senescence is also the reversibility of the process before final stages of cell death are initiated. At a cellular level, some cytological features of cell death are conserved across plant and animal kingdoms. However, in plants some of the major regulators appear to be divergent in sequence and compartmentalisation, although there is some functional conservation. The importance of cell death in development has been recognised over the last 20 years, even if the processes involved are still to be fully resolved in any organism.

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Eukaryotic glyoxalases: Their evolutionary origins and role in cell homeostasis

J. Andrew, C. Smith (University of Oxford), Renee B.Y. Lee (University of Oxford)

All biological cells produce methylglyoxal, a toxic 2-oxoaldehyde that causes covalent modification of nucleic acids and proteins to form advanced glycation end products. Quantitatively, the main source of methylglyoxal in cells is central carbohydrate metabolism, in which it is formed as a byproduct of the triose phosphate isomerase reaction in glycolysis and gluconeogenesis. As such, pathways for the detoxification of methylglyoxal must have been an important feature of the earliest cells. The most widespread detoxification pathway is the glyoxalase system, consisting of the metalloenzymes glyoxalase I and glyoxalase II; together these convert methylglyoxal to D-lactate with the aid of a thiol cofactor (usually glutathione). Glyoxalase I is of particular interest phylogenetically because two different forms of the enzyme are known: a zinc-dependent form found in most eukaryotes, including animals, fungi and apicomplexans, and a nickel-dependent form widespread in

bacteria that was also recently discovered in trypanosomatids. Because the enzyme has been relatively little studied in plants, we investigated the glyoxalase I gene family in *Arabidopsis thaliana*, which appears to possess three distinct genes encoding glyoxalase I. All three genes were shown to encode functional glyoxalase I proteins on the basis of complementation tests and assays of the recombinant proteins. Localization of YFP-fusion proteins also indicated that the three isoforms are targeted to different subcellular compartments. The implications of these results will be considered in relation to the evolutionary origins of eukaryotic cells, with their functionally distinct intracellular compartments, and to the use of different metal ions as cofactors in biology.

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14:00 Tuesday 30th June 2009

The evolution of eukaryotic genomes

Chris A. Cullis (Case Western Reserve University Cleveland)

The analysis of eukaryotic genomes has revealed them to be dramatically dynamic. However, it is clear that the tolerance of genomic variation varies among organisms. Humans show phenotypic effects resulting from segmental duplications whereas plants can have complete genomes added with little phenotypic effect. The accumulation of the molecular data has steadily shifted the perception of the genome from that of a static repository of the genetic material and a fixed characteristic of a species to a fluid characteristic that can vary within and between species. As complete genomes from different individuals within a species are sequenced the extent and distribution of variation identified, a clearer picture of the rate at which this variation occurs has emerged. Thus the extensive genomic variation between maize inbreds involves genic regions, pseudogenes as well as the extensively documented transposon explosions. However, most conclusions have been drawn from static comparisons of genomes and not identifying the specific events as they are occurring. In flax, restructuring of the genome can be followed as it happens in particular varieties. The data has identified new processes of genome evolution, regions that are particularly susceptible to modification and sheds new light on the evolution of crop genomes.

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Eukaryotic genome sizes: Implications for DNA replication and the cell cycle

Dennis Francis (Cardiff University), John A. Bryant (University of Exeter)

There is a wide range of genome sizes amongst eukaryotes. Generally, genome size is related to the complexity of the organism; the human genome is nearly 100 times larger than the genome of budding yeast. However, that loose relationship breaks down in groups such as *Amphibia* and flowering plants in which DNA amounts vary hugely between species. Within flowering plants for example, genome sizes vary over three orders of magnitude. Leaving aside the mechanisms that have led to this, such variation has significant implications for DNA replication. A predicted positive effect of

genome size on S-phase is confounded by ploidy level particularly within an allopolyploid series. This also raises further doubts about consensus sequences defining replication origins. Indeed ploidy level may not have a completely predictable effect on cell cycle times in eukaryotes. In an analysis of 110 published cell cycle times in plant species exhibiting a 290-fold variation in genome size, the widest range of cell cycle times was in perennials regardless of ploidy level. We shall develop a model that centres on the licensing of initiation points of DNA replication that maybe a component of the positive effect of genome size on the duration of the mitotic cell cycle in eukaryotes.

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Evolution of DNA replication mechanisms: A review of evidence from the Archaea

John A. Bryant (University of Exeter)

The initiator and replicator model for DNA replication was first developed for prokaryotes; the initiator is a DNA sequence from which replication is initiated, i.e. the replication origin, and the replicator is a complex of proteins. This model can, with some modification be applied to eukaryotes. In the latter, chromatin is organised for replication as multiple replicons, each with its own origin (which is not necessarily a specific sequence). The proteins that are involved in replication are organised as series of complexes, each with a role at a particular stage, from recognition of origins through to synthesis of the daughter strands. These complexes are also involved in the licensing mechanisms which, except in specific developmental situations, permit replication of DNA only once per cell cycle. It is clear then, that the initiator–replicator system in eukaryotes is much more complex than in prokaryotes. Current evidence strongly suggests that eukaryotes have evolved from archaeobacteria (more specifically that eukaryotes share a common ancestor with extant archaeobacteria – the eocyte hypothesis). Amongst extant archaeobacteria, there is evidence for the evolution of the eukaryotic DNA replication system, both in terms of the organisation of chromatin and in terms of the proteins involved. This evidence will be reviewed.

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16:20 Tuesday 30th June 2009

Heterokont protein kinases: Novel families, stress adaptation and the acquisition of multicellularity

John H. Bothwell (Marine Biological Association)

The eukaryotic heterokont lineage forms an evolutionary clade of similar size and complexity to animals or green plants. This clade contains members as diverse as the brown seaweeds which

dominate temperate sublittoral zones, the unicellular diatoms which can affect oceanic biogeochemistry and the oömycetes which include many commercially important plant pathogens. Heterokonts diverged from green plants, red algae and the opisthokonts (animals and fungi) during the crown radiation of the eukaryotes more than 1200 million years ago and have evolved independently ever since. A number of heterokont genomes have been sequenced over the past few years and I compare the protein kinase complements of five of these heterokonts: the brown seaweed, *Ectocarpus siliculosus*, the diatoms *Thalassiosira pseudonana* and *Phaeodactylum tricornutum* and the oömycetes *Phytophthora ramorum* and *P. sojae*. Protein kinases are molecular switches which co-ordinate cellular processes and which can make up 1–2% of the total gene number in many organisms. Analysis of protein kinase complements can, therefore, shed light on genome evolution and regulation. My comparative analysis of heterokont kinomes reveals the existence of novel, heterokont-specific protein kinase families and sheds light on the independent evolution of complex multicellularity by the heterokont lineage.

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Overview: Possibilities gained and lost by being a eukaryote

John A. Raven (University of Dundee at SCRI)

The differences between cells of Eukarya and those of Archaea and Bacteria provide many opportunities but also a number of constraints. The lecture compares aspects of cell structure and function among the three cell types to give two insights into evolution at the cell level. One is the possible natural selection fitness enhancement traits that are involved in the evolution of the universal features of the ancestral eukaryotic cell. There are parallels in Bacteria of the endomembrane system in compartmenting substrates and enzymes. One such compartment is in anammox bacteria, separating the reaction intermediate hydrazine from the rest of metabolism, another is the vacuoles of vertically migrating sulphur-oxidising bacteria, transporting the oxidant nitrate down to the reductant sulfide. The other aspect is the subsequent evolution of unicellular Eukarya and the niches that they fill that are not accessible to Archaea and Bacteria, e.g. phagotrophic nutrition. By contrast, many niches cannot be filled by cells of Eukarya, at least without (not genetically integrated) symbioses providing chemolithotrophy, diazotrophy or methanogenesis. Primary producers in the plankton are an example of oxygen-producing phototrophs represented by both Bacteria (Cyanobacteria) and Eukarya (the polyphyletic algae). There is some overlap of size for unicellular Cyanobacteria (the smallest with a diameter of 0.5 µm) and unicellular algae, with the latter attaining effective spherical diameters of up to 0.5 mm. The ecological implications of this size range is explored with respect to (for example) specific growth rate.

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