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Edited by G. W. GOODAY, D. LLOYD and A. P. J. TRINCI

The Eukaryotic Microbial Cell

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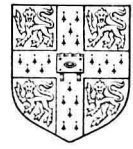

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EDITORS' PREFACE

This Symposium aims at reflecting the excitement of current advances in the cell biology of the eukaryotic microbes – the algae, protozoa, filamentous fungi and yeasts. As shown by previous Symposia in this series, these organisms have always been of great interest to microbiologists, as they play central roles in many important activities, such as primary productivity, pathogenesis, and nutrient recycling.

In recent years, however, the tremendous range of structure and function shown within this group of microbes has attracted the attention of a wider audience of biologists, biochemists and biophysicists, who have enthusiastically employed these organisms as models for similar or identical activities occurring in 'higher organisms'. The validity and success of their roles as models do not concern us here, but as microbiologists we can welcome the extra attention that these eukaryotic protists have consequently received, and we can especially welcome those 'higher biologists' who clearly have become captivated by the lives of their microbial models.

This Symposium forms a natural partner of that for 1978, 'Relations between Structure and Function in the Prokaryotic Cell'. Taken together, these two symposia show us the great wealth of knowledge provided by the microbes.

We hope that this volume will point to the future, showing the reader systems which promise rich dividends. We are aware, however, of the many other organisms that have yet to be investigated, and we encourage any uncommitted young microbiologists, or scientists looking for new horizons, to observe the algae, fungi and protozoa; they will very soon become captivated and find fruitful new topics on which to work.

Finally, we thank the authors for their timely and valuable contributions, and the many people in the Society for General Microbiology and Cambridge University Press who have made this Symposium possible.

G. W. GOODAY
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FROM PROKARYOTE TO EUKARYOTE: GAINS AND LOSSES

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INTRODUCTION

Ten years ago, the Society held a symposium on 'Organisation and Control in Prokaryotic and Eukaryotic Cells'. In the opening contribution Stanier (1970) stressed the profound differences between the two cell types and emphasised those structural features lacking in prokaryotes but common to all eukaryotes. Subsequent research has confirmed the validity of Stanier's views. It is unnecessary here to provide a detailed description of such features; instead I shall consider how they have opened evolutionary possibilities, improved performance and led to eukaryotic dominance in some activities and habitats. However, a major reorganisation, such as occurred in the origin of the eukaryotic cell must involve losses as well as gains, and the ways in which eukaryotes are less effective than prokaryotes will also be considered.

PROKARYOTE CAPABILITIES AND LIMITATIONS

Before considering the capabilities and limitations of eukaryotes it seems worthwhile to examine briefly those of prokaryotes. Perhaps the most striking conclusion is that prokaryotes can maintain a biosphere without any assistance from eukaryotes. They can utilise solar energy, either under anaerobic conditions (purple and green photosynthetic bacteria) or by oxygenic photosynthesis (cyanobacteria = blue-green algae). Carbon dioxide can be reduced to organic compounds and a wide range of organic compounds can be oxidised to carbon dioxide. Molecular nitrogen can be fixed and can be returned again to the atmosphere (denitrification). Ammonia can be oxidised to nitrate and nitrate reduced to ammonia. Inorganic sulphur compounds can be both oxidised and reduced. It is clear that the metabolic activities of prokaryotes do not result in any essential element being converted irrevocably to a particular oxidation state – there are other prokaryotes that can carry out further reactions. The metabolic capabilities of present

day prokaryotes are hence sufficient to maintain all the natural cycles of essential elements. It is certain that at one time, prior to the origin of eukaryotes, that they did so, first in an anaerobic and later in a predominantly aerobic environment. They could probably do so again, if eukaryotes were destroyed.

The metabolic capabilities of prokaryotes are very great. Energy can be obtained not only by photosynthesis but by the oxidation of hydrogen, reduced inorganic compounds and methane. Almost any naturally occurring and a great many new synthetic organic compounds can be degraded. Glucose can be metabolised by a variety of routes, and under anaerobic conditions a range of end products can result. The biosynthetic capabilities of prokaryotes are also extensive. There are few areas of bio-organic chemistry, synthetic or degradative, that have not been explored by prokaryotes.

Many prokaryotes have very high growth rates (generation times of 20 min or less), and can thus rapidly exploit newly available resources. On the other hand, bacterial endospores may persist for decades in a dormant state awaiting favourable conditions for growth. Moreover, some bacteria can adjust their metabolism from a state appropriate for 'famine' to that suitable for participation in a 'feast' with great rapidity (Koch, 1971). The metabolic versatility and genetic plasticity of bacteria permit them to respond effectively to new opportunities and hazards, such as novel substrates or antimicrobial agents.

It would seem that at the biochemical level the capabilities of prokaryotes are those of life itself; limitations appear only when morphological features – size and structural complexity – are considered. Prokaryotic cells are small compared with those of eukaryotes, volumes of one or a few cubic micrometres being typical. Those prokaryotes with larger cells are often very difficult to cultivate, through lacking adaptive flexibility and ability to accommodate to minor environmental changes (Stanier, Adelberg & Ingraham, 1977) suggesting that an upper size limit is being approached. A limited capacity for cellular interaction would appear to restrict the capacity for constructing true colonies with functional differentiation or multicellular organisms with co-ordinated cellular activities. The limited achievements of existing prokaryotes (especially actinomycetes, cyanobacteria and myxobacteria) in this direction have been discussed elsewhere (Carlile, 1979). However, any prokaryotes which specialised in activities that eukaryotes now perform outstandingly well probably became extinct after the origin of eukaryotes. Conclusions about prokaryote limitations are hence necessarily tentative.

THE ORIGIN OF EUKARYOTES

Speculation on the origin of eukaryotes is now a flourishing activity – see, for example, Margulis (1970) and Cavalier-Smith (1975) for the lucid presentation of differing viewpoints. Curiosity about origins in general and family trees in particular is an irrepressible human feature, but is it scientific and is it useful? Sneath (1974) contemplates the 'wrecks of broken theories' but concludes that by accumulating molecular detail and applying methods developed from numerical taxonomy, gradual progress towards a scientific phylogeny is possible. Stanier (1970), on the other hand, regards evolutionary speculation as an activity peripheral to science which is harmless provided that the microbiologist does not become an addict.

Phylogeny can be fully scientific in a group of organisms with a good fossil record. Under these circumstances an hypothesis can be demolished by a new discovery; philosophers stress that for a viewpoint to be scientific it must be capable of disproof. But the prospect of a scientific phylogeny of micro-organisms based on the fossil record is remote. The most hopeful alternative approach would seem to be the numerical treatment of the molecular features of existing forms as discussed by Sneath (1974); such a treatment yields an objective assessment of similarity together with a conclusion as to the most probable route by which such similarity arose. Such data have been assembled for the evolution of a few widespread molecules such as cytochrome. It remains uncertain, however, as to the extent to which such painstaking studies will illuminate major evolutionary steps. A new development, perhaps in a hitherto obscure group of organisms, might lead to a succession of rapid changes, not fully conforming to the usual tempo of molecular evolution. Meanwhile biologists will continue to speculate on the basis of non-quantitative data.

Such speculation may well be of value: evolution has undoubtedly occurred, natural selection takes place, and on these premises it is reasonable for a biologist to speculate on what might have happened. A fascinating phylogenetic theory, such as that of the symbiotic origin of the chloroplast and the mitochondrion, stimulates worthwhile investigations and serves a mnemonic role, making memorable a range of hitherto unconnected facts. However, evolutionary speculation, as Stanier (1970) concludes, is perhaps best regarded as a metascience, not itself strictly scientific but deeply influencing the activities of scientists.

I will not attempt here to give a full account of how the various eukaryote organelles may have evolved. Instead some of the steps which

could have led to the origin of eukaryotes will be discussed, with an emphasis on how some developments could open the way for others.

The ancestor of the eukaryotes

Eukaryotes are usually regarded as having arisen from prokaryote ancestors *c.* 1–2 $\times$ 10^9 years ago. Some authors (e.g. Darnell, 1978), noting certain biochemical features of the present day prokaryotes and eukaryotes, have seen major difficulties in deriving the latter from the former and propose instead that both are derived from some earlier form of life. While it is reasonable to accept that the ancestor of the eukaryotes may have differed greatly from any present day prokaryote, nevertheless it would have resembled the prokaryotes in lacking the elaborate nuclear and cytoplasmic organisation of eukaryotes. It hence seems better to accept the conventional view that eukaryotes arose from prokaryotes rather than to designate as a new major group organisms whose features must remain hypothetical.

The prokaryotic occurrence of essential eukaryotic constituents

There are some lipids and proteins which are of striking importance in eukaryotic cellular organisation but are often regarded as absent from prokaryotes. They, or similar substances, do however occur in at least some present day prokaryotes. They may hence have been present in the ancestor of the eukaryotes and available to assume new roles as evolution occurred.

Sterols and polyunsaturated fatty acids are normal components of most eukaryotes, being an essential part of the flexible and fusible eukaryotic cell membranes. They are often regarded as being absent or at very low concentrations in prokaryotes but there are exceptions, especially in organisms with extensive membrane invaginations. *Methylococcus capsulatus*, for example, synthesises sterols in amounts similar to those present in eukaryote cells (Bird *et al.*, 1971) and cyanobacteria contain both sterols and polyunsaturated fatty acids (Ragan & Chapman, 1978). Mycoplasmas have large amounts of sterols in their membranes, but obtain these from their hosts. There is at least one group of eukaryotes which neither synthesises nor requires sterols for vegetative development. The Pythiaceae (Pythium and Phytophthora) cannot synthesise sterols and their vegetative hyphae can grow indefinitely in the absence of sterols (Elliot, 1977). Sterols are however needed in this group for asexual and sexual sporulation.

Microfilaments composed of actin and microtubules composed of tubulin have a vital role in cell structure (the cytoskeleton), motility and

nuclear division in eukaryotes. Cavalier-Smith (1978*a*) observed that a filament is optimal for resisting stretch, and a tube for resisting bending or compression. He proposed that these structures originally had complementary cytoskeletal functions, and that a role in motility in association with myosin (microfilaments) and dynein (microtubules) came later. Various types of fibrils have been observed in the protoplasmic cylinder of spirochaetes (Holt, 1978) and proteins with some actin-like features (see however Rodwell, Rodwell & Archer, 1979) have been demonstrated in mycoplasmas (Niemark, 1977; Searcy, Stein & Green, 1978). In *Escherichia coli*, Minkoff & Damadian (1976) found an actin-like protein which they suggest is able, through contraction, to regulate cell volume, water content and ion uptake. Both spirochaetes (Holt, 1978) and mycoplasmas (Razin, 1978) are able to undergo flexing movements. Microtubules have been observed in some large spirochaetes and a gliding bacterium (Margulis, To & Chase, 1978); there is some evidence that these are composed of a tubulin-like protein.

Histones, an essential component of the nucleosome, have been demonstrated in many eukaryotic micro-organisms (Horgen & Silver, 1978; Morris; this volume). Histone-like proteins have recently been demonstrated in several prokaryotes (see Seavey *et al.*, 1978 and references in Horgen & Silver, 1978).

The evolution of cell envelope and cytoplasmic organisation

Peptidoglycans do not occur in the walls of eukaryotic cells. Hence it is reasonable to postulate as ancestral to the eukaryotes a prokaryote-like organism that lacked such cell walls. Such organisms may once have been common. Cell walls might well be of little value in large volumes of water (in which desiccation or exposure to osmotic fluctuations is unlikely) in a world in which predators did not yet exist. Further, since cell wall synthesis is expensive in energy, carbon and nitrogen, it could well be advantageous not to possess them. Organisms lacking cell walls may have arisen from bacteria with walls; mutants lacking peptidoglycans (L-forms) are widespread in bacteria. On the other hand it is possible that both eukaryotes and bacteria with walls arose from wall-less organisms, and it has been suggested that mycoplasmas are the modern descendants of such organisms (Morowitz & Wallace, 1973). Whether or not this is true, the increasing volume of information available about mycoplasmas (Razin, 1978) is of interest in relation to the problems faced by wall-less prokaryotes.

A wall-less prokaryote will be vulnerable to rapid changes in environmental osmotic pressure, being liable, as are bacterial protoplasts, to

shrinkage if the medium becomes hypertonic and bursting through sudden influx of water if it becomes hypotonic. Most modern mycoplasmas escape these problems by living in a uniform environment inside plants and animals, an option not open to the ancestors of eukaryotes. Large bodies of water may remain osmotically uniform for long periods, but smaller volumes may fluctuate rapidly in osmotic pressure. Gradual adaptation to changed ambient osmotic pressure could be achieved by taking up or excreting salts – osmotic pressure adjustment by excretion of Cl^+ and K^+ has been demonstrated in an alga (Nuccitelli & Jaffe, 1976) – or by synthesising or breaking down soluble organic compounds. Some volume change whilst adaptation is occurring could be tolerated provided that the plasma membrane is flexible. Large cells are likely to be more tolerant to an osmotic change since they will have a smaller surface to volume ratio than small cells and, given the same membrane permeability to water, a lower rate of influx per unit volume. If cells, in adapting to changed osmotic pressure, excreted salts into membrane invaginations and vesicles, then water would follow by osmosis. Given flexible and fusible membranes, a swelling water-filled vesicle on coming into contact with the cell surface might fuse with it and discharge its contents. Some such origin for water expulsion vesicles (contractile vacuoles) is a possibility. Thus the development in wall-less cells of a capability for coping with environmental osmotic changes may have been a factor in the evolution of a tough, flexible and fusible plasma membrane, exocytosis, a more dilute and hence less viscous cytoplasm, and larger size.

The origin of the eukaryote nucleus

The key event in the origin of eukaryotes is, by definition, the origin of the eukaryon, the true nucleus. Copious information is now appearing on both the molecular biology (Horgen & Silver, 1978; Morris, this volume) and ultrastructure (Kubai, 1978; Dodge & Vickerman, this volume) of the nuclei of eukaryotic micro-organisms, and this will not be repeated here. It is however, worth indicating how the origin of the eukaryote nucleus could have been yet another fruitful response to the problems of a wall-less prokaryote.

Nucleoid segregation following chromosome replication in prokaryotes involves the separation of chromosome attachment sites on the plasma membrane. Cavalier-Smith (1975) suggests that with the evolution of a more fluid plasma membrane the process would become inefficient and envisages the development of a microtubule mechanism for pushing the two chromosome attachment sites apart. Once such a

system was established, endocytosis of the attachment sites could occur with the invaginated membrane becoming the nuclear envelope. Cell fusion, feasible with the plastic cell envelope of an amoeboid organism, could lead to a fully diploid condition, and nuclear division in the absence of chromosome replication a return to the haploid condition. Cavalier-Smith (1974) has also discussed how endonuclease action could convert the circular prokaryotic chromosome into several linear chromosomes and how other features of eukaryotic nuclear organisation could have originated (Cavalier-Smith, 1975, 1978*a*).

The origin of phagocytosis, predation and endosymbiosis

Discussion has so far centred on coping with the disadvantages of a wall-less condition, rather than any advantage which might lead to a primitive eukaryote succeeding in competition with prokaryotes and leaving diverse descendants. The key advantage as appreciated by Stanier (1970), must surely have been the possibility of endocytosis and its exploitation in phagocytosis, predation and the origin of endosymbiosis.

Many bacteria produce extracellular enzymes which enable macromolecules to be broken down into small molecules that can be assimilated. Attack on much larger objects is also possible, as with the bacteriolytic and cellulolytic myxobacteria. The more intimate the contact between 'predator' and 'prey' (whether organic detritus or other bacteria) the more efficient and economical will be the utilisation of the predator's extracellular enzymes. A wall-less organism with a flexible membrane could be at an advantage, and it can be envisaged that intimate contact could evolve into partial invagination and finally into phagocytosis. The advantages of this form of nutrition would clearly be immense: the capture, in an environment often depleted of nutrients by small rapidly growing organisms, of all the required types of nutrient in a concentrated form. It is this capacity for phagocytosis that is most likely to have accounted for the initial success of eukaryotes in a prokaryotic world. Some organisms captured by a predator, however, might resist digestion and survive. These might be excreted or persist in the cell to become, if their metabolism harmed the host, the first intracellular parasites, and if it benefited the hosts, the first mutualistic endosymbionts, or perhaps each in turn. This can happen swiftly; Jeon & Jeon (1976) found that an accidental and harmful bacterial infection of a strain of *Amoeba proteus* had become an endosymbiont essential for the survival of the amoeba within five years – less than 1000 generations.

The Symbiotic Theory of the origin of eukaryotic organelles

Mitochondria are of almost universal occurrence in eukaryotes, and show a remarkable uniformity in the components of their electron-transfer paths, in contrast to the diversity shown in aerobic prokaryotes. This suggests that they were acquired very early in the evolution of eukaryotes, and being already highly effective, subsequently were little modified. Whatley, John & Whatley (1979) point out that the mitochondrial electron transfer path closely resembles that of *Paracoccus denitrificans*. They also draw attention to the amoeba *Pelomyxa palustris* which has many primitive features and which lacks mitochondria: perhaps they were never acquired or possibly they have been lost. *P. palustris* does, however, contain two types of endosymbiotic bacteria, one of which in its physical features and relationship with the membrane systems of its host suggests how mitochondria could have evolved from endosymbiotic bacteria. The view that mitochondria evolved from endosymbiotic aerobic bacteria (Margulis, 1970; Whatley *et al.*, 1979) very early in eukaryote evolution is now a popular one, although sceptics remain (Raff & Mahler, 1975; Cavalier-Smith, 1975). Such a primitive eukaryote would probably already have been able to tolerate oxygen, and perhaps to obtain energy by oxidation, through the possession of oxidative enzymes such as occur in peroxisomes and other eukaryote microbodies (Müller, 1975) and in some mycoplasmas (Searcy *et al.*, 1978).

A good case can be made for the origin of the chloroplasts of eukaryotes from endosymbionts having oxygenic photosynthesis. The various major groups of photosynthetic eukaryotes, however, differ from each other in the structure and pigmentation of their chloroplasts, hence it seems likely that each group independently acquired chloroplasts by the capture of a different type of photosynthetic organism. Stanier (1974) has considered in detail the resemblance between cyanobacteria and the chloroplasts of red algae (Rhodophyta); the origin of the chloroplasts of other groups has been discussed by Margulis (1970) and Whatley *et al.* (1979).

A symbiotic origin has also been postulated for other eukaryotic organelles including the hydrogen-evolving organelle (hydrogenosome) (Müller, this volume) of anaerobic ciliates (Whatley *et al.*, 1979) and eukaryotic flagella (Margulis, Chase & To, 1979) – but see Cavalier-Smith (1978*b*) for criticism of this suggestion. Whatever the validity of each specific proposal, the eukaryotic cell has undoubtedly exercised frequently the capacity to acquire, benefit from and become wholly dependent upon endosymbionts (e.g. Buchner, 1965).

SIZE, GROWTH RATES AND NATURAL SELECTION

Size, protoplasmic streaming and growth rate

The size of a spherical prokaryote is limited by problems of uptake, diffusion and excretion. Diffusion, efficient for a very small cell, becomes less so with increasing linear dimensions, and as size increases, surface to volume ratio decreases, bringing about problems of transport across the cell membrane (Koch, 1971). The surface to volume ratio can be increased by departing from the spherical form, but this will increase the maximum internal distance introducing problems of metabolic co-ordination.

Eukaryotic cells have a less viscous cytoplasm than prokaryotes and protoplasmic streaming is widespread (e.g. Allen, R. D. & Allen, N. S., 1978; Allen, N. S. & Allen, R. D., 1978). One of the factors determining streaming velocity will be the size of the channel in which it occurs; other factors being equal, the rate of flow in a cylindrical tube varies as the square of the radius of the tube (Hagen–Poiseuille Law). Hence flows in small cells may well be imperceptible but in large cells, where resistance to flow is less, it can be spectacular, reaching 1 mm s^{-1} in myxomycete plasmodia. It is of course in large cells that rapid protoplasmic streaming is needed to supplement diffusion, and the large sizes attainable by eukaryotic cells as compared with prokaryotes may be attributable to protoplasmic streaming. Nevertheless, protoplasmic streaming cannot wholly overcome the consequences of greater linear distances and lower surface to volume ratios in large cells, and hence eukaryotes tend to have lower metabolic rates per unit mass than do prokaryotes. Schmidt-Nielsen plotted the metabolic rate and body mass of a wide range of unicellular and other organisms and found in a double logarithmic plot a slope of 0.75 showing that metabolic rates do not increase proportionately to size (see Wilkie, 1977). The decrease in metabolic rate per unit mass in large organisms must set an upper limit on their growth rates.

The way in which size affects reproductive rates was illustrated for a range of micro-organisms, animals and plants by Bonner (1974) who showed in a double logarithmic plot an approximately linear relationship between body length and generation time. Under ideal conditions many prokaryotes can double their population several times per hour, and generation times of under ten minutes occur, e.g. for *Benekea natriegens* (Eagon 1962). The shortest generation times reported for eukaryotes are about one hour: Griffin, Timberlake & Cheney (1974) found 57 minutes for the water mould *Achlya bisexualis*, Trinci (1972)

66 minutes for the yeast-like fungus *Geotrichum candidum* and Fulton (1977) 1.7 hours for the amoebo-flagellate *Naegleria gruberi*. The most rapidly growing phototrophs have rather longer generation times (see van Baalen, 1974). A reasonable summary would be that under ideal conditions fast-growing prokaryotes can divide several times per hour, fast-growing eukaryotes several times per day.

Eukaryotes can, however, achieve far higher localised growth rates than prokaryotes. A hypha, for example, can increase in length far more rapidly than can a bacterial cell; the hyphae of *Neurospora crassa* can grow at 100 μm min^{-1} and the sporangiophores of *Phycomyces blakesleeanus* at 60 μm min^{-1}. This is because materials are transported by protoplasmic streaming to the hyphal apex where extension occurs from a growth zone which may extend for several millimetres behind the apex (Trinci, 1978*a*). An extreme form of such polarised growth can be seen in fungus colonies under conditions of very low nutrient concentration: the colony margin continues to advance but hyphae at the centre of the colony are emptied of protoplasm. The polarised growth of eukaryotic micro-organisms has some of the expected attributes of growth (biosynthesis, especially of new wall material) but also some of the attributes of motility, i.e. some protoplasm, and in extreme cases, all viable material, is moved from its site of synthesis. The effect has something in common with the movement of an amoeba or a myxomycete plasmodium: in one instance empty hyphal walls are left behind, in the other slime from the glycocalyx, and in both protoplasmic streaming is involved.

r-selection and K-selection

The concepts of *r*-selection and *K*-selection were introduced by Mac Arthur & Wilson (1967) in relation to island biogeography and have since been found fruitful in other areas of animal ecology (e.g. Pianka, 1970; Southwood, 1977) but with a few exceptions (e.g. Cavalier-Smith, 1978*b*) have received little attention from microbiologists. *r*-selection (*r* represents the intrinsic rate of increase) will be experienced in its most intense form by new arrivals in an uncolonised environment; the most successful will be those that multiply fastest. *K*-selection (*K* represents the carrying capacity of the environment) operates in crowded conditions where resources are scarce, and attributes other than a high growth rate are important; for example, the efficient use of resources, an ability to use resources unavailable to other organisms and effectiveness in attack and defense with respect to competitors. Any species will be exposed to both *r*- and *K*-selection, and depending on