Strange fungi with even stranger insides

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Since most mycologists work on ascomycetes or basidiomycetes it is easy to forget chytridiomycetes when thinking about fungi, let alone anaerobic chytridiomycetes. So it was hardly surprising that more than one hundred years ago scientists did not recognise the motile spores in a rumen sample as being fungi. Since it was general knowledge that the rumen was infested with bacteria and ciliates the flagellated cells seen by Liebetanz and Braune (1913; 1910) were considered to be flagellates (see Fig 1). About 50 years later there are some careful remarks in the literature about this Callimastix species by Vavra and Joyon (1966) but they do not explicitly mention that it might be a fungus. It took until the seventies before Colin Orpin finally dared to suggest that those strange anaerobic flagellates that live in the rumen might actually be fungi (Munn et al., 1981; Orpin, 1975; 1977). That scientific dogmas are enormous barriers is obvious from the fact that even the great rumen microbiologist Robert Hungate did not believe that fungi could be anaerobic. The late Rudolf Prins told me that in the sixties, when he and Hungate discovered ‘fluffy’ colonies in anoxic tubes, they always threw them away because oxygen must have seeped in!

Careful examinations by Heath (1983; 1988b) and Barr (1980; 1988) morphologically linked the anaerobic chytrids to the fungi. Modern phylogenetic analyses have confirmed these findings and reveal the
chytrid fungi to be the earliest fungal branch (Bowman et al., 1992; Doré and Stahl, 1991; Li and Heath, 1992; Van der Auwera and De Wachter, 1996).

The narrow ecological niche that these chytrids occupy is the rumen and hindgut of large herbivorous mammals (Trinci et al., 1994). There they assist in the initial breakdown of plant material, as do fungi in most other ecosystems (Heath, 1988a). The interesting thing is that they can do this without any oxygen! Most eukaryotes need oxygen; it is needed to generate large amounts of energy in the mitochondria, the biochemical powerhouses of the cell. When human cells run out of oxygen they start fermenting and make lactate to produce energy, which is obvious from the cramp in the legs after one cannot run any further. So, how do anaerobic fungi cope with the energy-demand under oxygen-free conditions? Interestingly enough, they do not have mitochondria but do have other organelles that produce energy. These organelles are called hydrogenosomes because they make molecular hydrogen. Originally these strange organelles were thought to be novel ‘inventions’ to cope with anaerobic conditions (Cavalier-Smith, 1987), but now it has become clear that hydrogenosomes are most likely to be specialised or derived mitochondria (Embley et al., 1997). Hydrogenosomes are not unique to anaerobic fungi, and can be found in a wide variety of anaerobic eukaryotes. Actually, they were first discovered in parasitic trichomonads by Miklós Müller (1973). Most hydrogenosome work has been done on Trichomonas vaginalis, the causal agent of a sexually transmitted disease that infects 200 million people annually. Typical mitochondrial features like the electron transport chain, cristae, and more importantly, a genome, are missing from fungal hydrogenosomes. Hydrogenosomes do contain unusual enzymes like hydrogenase and pyruvate: ferredoxin oxidoreductase that replaces the ‘normal’ mitochondrial pyruvate dehydrogenase. Notwithstanding these peculiar differences, there are sufficient similarities to support the hypothesis that the two organelles share common ancestors. Properties that fungal hydrogenosomes share with mitochondria

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**Fig 2** Generalised pathway of aerobic carbohydrate degradation in eukaryotes compared to that of the anaerobic fungus Neocallimastix frontalis (Marvin-Sikkema et al., 1993). Aerobic degradation is indicated by blue arrows and the Neocallimastix anaerobic route by red arrows. AcCoA, acetyl-Coa; CITR, citrate; FUM, fumarate; H2ASE, hydrogenase; ISOCITR, isocitrate; MAL, malate; 2OG, 2-oxoglutarate; OXAC, oxaloacetate; PEP, phosphoenolpyruvate; PFO, pyruvate: ferredoxin oxidoreductase; PDH, pyruvate dehydrogenase; PYR, pyruvate; red.eq., reducing equivalents; SUCC, succinate; SUCC-CoA, succinyl-CoA. Adapted from van Hellemond et al. (1995).
include the existence of a transmembrane pH gradient and an alkaline lumen. Free Ca\textsuperscript{2+} pools and calcium phosphate precipitates have also been detected in fungal hydrogenosomes suggesting that, like mitochondria, they accumulate this intracellular messenger (Biagini et al., 1997). Both organelles have a double membrane and use the same import pathway for proteins (see van der Giezen et al., 2002 and references therein). The major function of mitochondria, the conversion of pyruvate to acetyl-CoA (see Fig 2) and ATP production also take place in the hydrogenosomes. Whether other metabolic processes like amino acid metabolism and beta-oxidation also take place in hydrogenosomes is not known at present.

The most important message anaerobic fungi have for us is that it shows there are even more amazing things than the few model organisms which the general textbooks focus on. The fact that anaerobic fungi 'invented' hydrogen-producing mitochondria in order to survive anaerobic conditions demonstrates that cellular organelles which were considered to be defining features of eukaryotes are more plastic than we imagined.

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