Hydrogenosomes and Symbiosis

Johannes H.P. Hackstein, Nigel Yarlett

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Introduction

Hydrogenosomes are organelles approximately 1–2 μm in size that compartmentalize the terminal reactions of the anaerobic cellular energy metabolism. They were first described in the parabasilid flagellate, *Tritrichomonas foetus*, in a seminal publication by Lindmark and Müller (1973) as subcellular compartments that produce hydrogen and ATP. Since this time, hydrogenosomes or variations of them have been described in quite a number of rather different unicellular eukaryotes, which are adapted to microaerobic or anoxic environments (Roger 1999; Yarlett 2004). Several researchers considered these organelles as variations of mitochondria adapted to anaerobic environments (Biagini et al. 1997; Embley et al. 1997, 2003), but it is still a matter of debate whether or not these ancestral "mitochondria" had an aerobic metabolism using oxygen as a terminal electron acceptor – or whether these organelles functioned anaerobically, and, consequently, produced hydrogen like present-day hydrogenosomes (Tjaden et al. 2004).

The identification of rudimentary, mitochondrial-remnant organelles in organisms previously considered devoid of mitochondria (named "archaezoa" by Cavalier-Smith 1993) further complicated the considerations about the nature of the "universal" ancestor, since these mitochondrial-remnant organelles (named mitosomes or cryptons) do neither produce hydrogen nor ATP (Mai et al. 1999; Tovar et al. 1999, 2003; Yarlett 2004). Notably, some of these organisms, such as for example *Giardia* or *Entamoeba* can produce hydrogen with the aid of a cytoplasmic hydrogenase, while others, such as the Microsporidia, do not exhibit any hydrogenase activity, or do not possess hydrogenase genes, respectively (Katinka et al. 2001; Lloyd et al. 2002; Williams et al. 2002; Nixon et al. 2003). The relationship of these elusive organelles to each other,

J.H.P. Hackstein (e-mail: j.hackstein@science.ru.nl)
Department of Evolutionary Microbiology, Faculty of Science, Radboud University Nijmegen, Toernooiveld 1, NL 6525 ED Nijmegen, The Netherlands
Nigel Yarlett
Haskins Laboratories and Department of Chemistry and Physical Sciences, Pace University, New York, USA

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regardless whether hydrogen-producing or not, and to the mitochondrion has been examined by many researchers, and several theories have been put forward in an attempt to explain the origins of all of these organelles (Martin and Müller 1998; Hackstein et al. 1999, 2001; Dyall and Johnson 2000; Martin et al. 2001; Tielens et al. 2002; Embley et al. 2003; Dyall et al. 2004). However, since all mitochondrial-remnant organelles and all hydrogenosomes (except in two host taxa, i.e., *Nyctotherus/Metopus* and *Blastocystis,* see below) lack an organelle genome (Embley et al. 2003; Dyall et al. 2004), a straightforward analysis of their evolutionary history is seriously hampered. It is obvious that evidence derived from the ultrastructure of the organelles and/or from the phylogenetic analysis of a few nuclear-encoded organelle proteins is insufficient to solve all the problems concerning the complex evolutionary history of these very diverse organelles.

In this review we will discuss not only the available evidence concerning the phylogenetic analysis of hydrogenosomal/mitosomal proteins, but also the structure and function of the various hydrogenosomes, which clearly shows that not all hydrogenosomes are the same. Although the mitochondrial-remnant organelles, the mitosomes and the hydrogenosomes appeared to be evolutionarily related to mitochondria, there is persuading evidence that they evolved repeatedly and independently as adaptations to anoxic environments. In essence, hydrogenosomes are organelles that facilitate a compartmentalized energy metabolism in anoxic niches, whereas mitosomes or cryptons retained essential functions in iron-sulphur metabolism, but none related to the energy metabolism (Müller 1998; Vanacova et al. 2003; Bakatselou et al. 2003; Henze and Martin 2003; Balk and Lill 2004). These morphologically and physiologically extremely diverse subcellular compartments are the products of evolutionary tinkering, which allowed eukaryotic cells to adapt to life without oxygen. This tinkering resulted in alternative solutions for the same problem, i.e., how to maintain the homeostasis of the cellular metabolism under anaerobic conditions. Consequently, it is not surprising that the various hydrogenosomes are physiologically significantly different – with obvious consequences for symbiotic associations with organisms that rely on the metabolic products provided by the various hydrogenosomes.

2 Hydrogenosomes and Mitochondrial Remnant Organelles Evolved Repeatedly

Initially, the arguments that both mitosomes, the mitochondrial remnant organelles, and hydrogenosomes evolved several times were based on the observation that hydrogenosomes and mitosomes, respectively, were found in a broad spectrum of rather unrelated taxa of unicellular organisms, such as