star or brown dwarf would also be seen at optical wavelengths. There are potential candidates within the uncertain position of GCRT J1745−3009, so this remains a possible, though unlikely, explanation.

Could GCRT J1745−3009 be a pulsar? Hyman *et al.* note that the five bursts they record appear in rapid succession with a period of about 77 minutes. The rotational energy lost by a normal neutron star (or white dwarf) rotating this slowly would be inadequate to power the observed radio bursts. Thus, by a process of elimination, Hyman and colleagues argue that they have uncovered a new class of coherent emitter.

In our opinion, the claim of a new class is plausible but not beyond doubt. As discussed above, the bursts could still be incoherent emission from an accreting binary star with a whittled-down companion and a relativistic jet but suppressed X-ray emission. If the source turns out to be nearer than the Galactic Centre, it could be one of several previously known types of coherent radio source, including an isolated or binary flaring (brown) dwarf star or magnetized white dwarf, or a nulling radio pulsar (a pulsar that broadcasts pulses only sporadically).

This last seems to us to be the most plausible conventional alternative. PSR 0826−34, for example, is a pulsar that can shut itself off for periods ranging from tens of minutes to eight hours[9]. PSR J1752+2359 is characterized by 45-second bursts of emission that appear roughly every five minutes[10], like GCRT J1745−3009 but speeded up by an order of magnitude.

GCRT J1745−3009 will cause a stampede of further observations: searches for pulsations and quiescent emission in radio, infrared and X-ray bands. But perhaps even more important is the possibility that the radio heavens contain other fast radio transients (which, in anticipation of a trove of discoveries, we nickname 'burpers'). Sensitive radio telescopes and arrays currently lack large fields of view. Fortunately, the construction of several new radio facilities with wider fields of view are being contemplated, and one is already funded[11]. Radio astronomy is poised to deliver new bursts of excitement. ■

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Evolutionary biology

# The hydrogenosome's murky past

Michael W. Gray

The evolution of specialized cellular powerhouses called hydrogenosomes has long confounded biologists. The discovery that in some cases they have their own genome sheds some much-needed light on the issue.

Hydrogenosomes are double-membraned subcellular structures that generate hydrogen while making the energy-storage compound ATP. They are found in certain eukaryotic (nucleus-containing) microbes that inhabit oxygen-deficient environments[1]. The evolution of the hydrogenosome has remained obscure, mainly because these organelles seemed not to have a genome[2,3] — until now. On page 74 of this issue, Boxma *et al.*[4] report the characterization of what seems to be an authentic hydrogenosomal genome in the anaerobic microbe *Nyctotherus ovalis*, an inhabitant of the termite hindgut.

In eukaryotes that live in oxygen-rich (aerobic) environments, organelles called mitochondria are responsible for making ATP. Although an evolutionary relationship between hydrogenosomes and mitochondria has been postulated, this hypothesis remains contentious[2,3]. Mitochondria contain a small genome (mtDNA) that retains traces of their evolutionary origin from a bacterial symbiont[5,6]. Interestingly, the hydrogenosomal DNA isolated by Boxma *et al.* exhibits hallmarks of a bona fide mitochondrial genome.

Adding to this story are two recent papers[7,8] that probe the evolutionary history of the hydrogenosome from another anaerobic microbe, the parasite *Trichomonas vaginalis*. The absence of a hydrogenosomal genome in this organism[9] makes it a challenging task to infer the origin of its hydrogenosome. Indeed, on this point, the two groups[7,8] come to rather different conclusions, even though they analyse the same *Trichomonas* hydrogenosomal proteins.

In animals and fungi, the mitochondrial genome encodes a small number of essential inner-membrane proteins (components of respiratory complexes I–IV and complex V, a specialized type of ATP-synthesizing enzyme) that function in electron transport and ATP production[5]. In addition, mtDNA specifies the RNA components of the mitochondrial protein-synthesis system and, in plants and many algae and protozoa, some of the proteins of this system too[5].

The report by Boxma *et al.*[4] extends their earlier observations[10] — which were provocative but not compelling — that the hydrogenosome of *Nyctotherus* might contain DNA. Having purified *Nyctotherus* hydrogenosomes, the authors isolated a 14-kilobase stretch of DNA and sequenced it[4]. They identified genes that encode

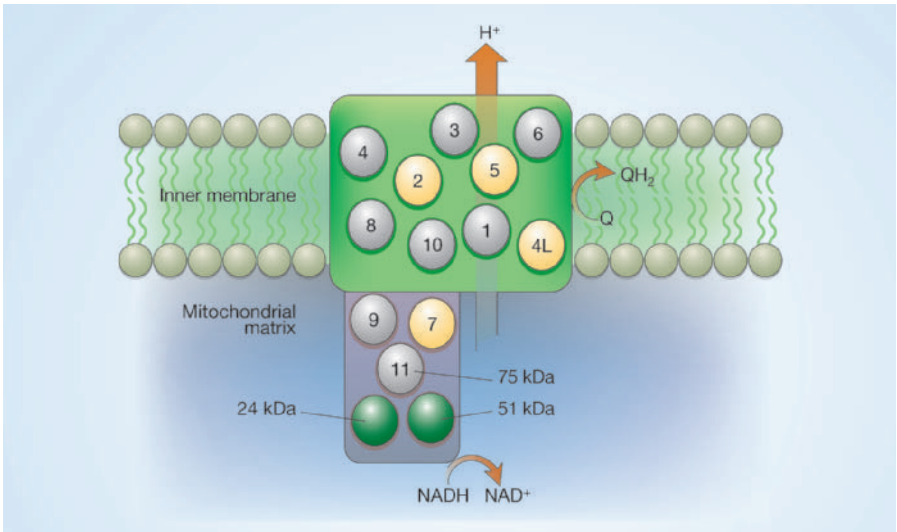


Figure 1 **Subunits of mitochondrial respiratory complex I. The membrane-integrated (green rectangle) and peripheral (purple rectangle) regions include numbered subunits that are encoded in one or more mitochondrial genomes; for example, animal mtDNA specifies seven subunits, 1–6 and 4L. Several subunits (yellow) have been identified in *Nyctotherus ovalis* hydrogenosomal DNA[6]. Genes encoding the 51- and 24-kDa subunits (dark green) have only been found in nuclear genomes. A nucleus-encoded 75-kDa subunit has also been reported in *N. ovalis*[6]. In this step of respiration, the oxidation of nicotinamide adenine dinucleotide (NADH) and reduction of ubiquinone (Q) provide protons and electrons to be passed along the respiratory chain, eventually producing ATP and water.**

homologues of mitochondrial proteins; that is, the mitochondrial and hydrogenosomal counterparts are close relatives with similar sequences. These genes encode four subunits of complex I (Fig. 1), and two proteins and two RNAs from the protein-synthesis system. The properties of these sequences — for instance, characteristic codon-usage patterns and a similarity to mitochondrial genes from aerobic microbes of the same group as *Nyctotherus* (the ciliate protozoa) — make a convincing case that this DNA is part of an mtDNA-like hydrogenosomal genome.

Additionally, Boxma *et al.*[4] identify several proteins in *Nyctotherus* that are encoded by genes in the nucleus but are typically transported to and function in mitochondria; these include three additional subunits of complex I (of molecular mass 24 kilodaltons (kDa), 51 kDa and 75 kDa; Fig. 1) and components of complex II. Phylogenetic reconstructions aimed at inferring the evolutionary history of these proteins show an affiliation with mitochondrial (specifically ciliate) homologues. Not unexpectedly, biochemical analyses suggest that *Nyctotherus* hydrogenosomes do not have complexes III and IV, which are responsible for the final stages of aerobic respiration. Nor is there any evidence of a mitochondrial-type ATP synthase (complex V) in this organism.

These and other observations imply that the *Nyctotherus* hydrogenosome represents an intermediate form between mitochondria, which possess a membrane-bound electron-transport chain, and previously characterized hydrogenosomes, which do not — a "true missing link", in the words of the authors. In parallel, the results suggest that the *Nyctotherus* hydrogenosomal genome, whose total size, shape and gene content have yet to be determined, is probably a reduced ciliate-type mtDNA, lacking those mtDNA-encoded genes that normally specify components required to construct a complete mitochondrial respiratory chain.

The genome-less *Trichomonas* hydrogenosome has been much less forthcoming about its evolution, with sequence-based analysis necessarily limited to nuclear genes that specify the constituent proteins of this organelle. The simultaneous discovery by two groups[7,8] of *Trichomonas* homologues of the 51- and 24-kDa components of mitochondrial complex I (Fig. 1) is a notable development. These proteins (termed Ndh51 and Ndh24, respectively) are the first *Trichomonas* counterparts of components of the mitochondrial respiratory chain to be identified. However, the two groups differ sharply in their conclusions about the evolutionary origin of these proteins, and hence of the hydrogenosome itself.

Both groups used a standard, rigorous approach for reconstructing evolutionary relationships by comparing protein sequences. However, Hrdy *et al.*[8] conclude

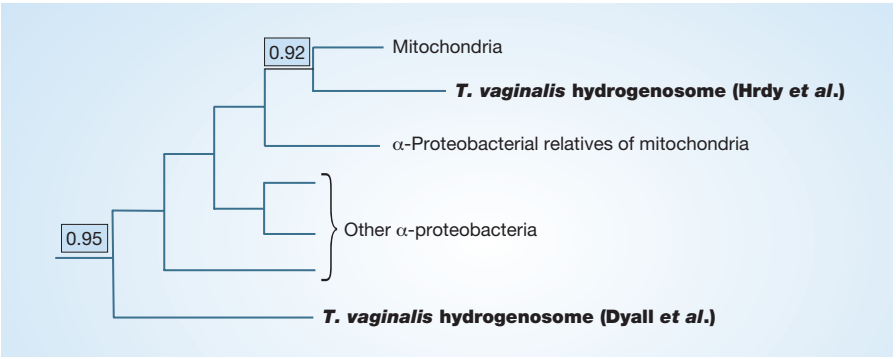


Figure 2 **The conflicting evolutionary positions of the *Trichomonas vaginalis* hydrogenosome. In phylogenetic reconstructions based on an alignment of the Ndh51 (51-kDa subunit) protein sequence, Dyall *et al.*[7] place the *T. vaginalis* hydrogenosome at the base of the α-proteobacterial lineage, not specifically related to mitochondria, whereas Hrdy *et al.*[8] position the hydrogenosome as a specific relative of mitochondria, to the exclusion of α-proteobacteria. Numbers are statistical probabilities that strongly support the associated branches. (Figure courtesy of R. Watkins.)**

that *Trichomonas* Ndh51 shares a specific common ancestry with its mitochondrial counterpart, whereas Dyall *et al.*[7] argue that it does not (Fig. 2). So, why the difference, and who is right?

These conflicting conclusions illustrate a common conundrum in using molecular-sequence data to infer ancient evolutionary events. In parasites such as *Trichomonas*, whose position in the eukaryotic lineage is uncertain to begin with, protein sequences tend to change relatively rapidly in the course of evolution. This can confound their accurate placement in phylogenetic trees, causing so-called long branches. Moreover, *Trichomonas* Ndh51 proved to have a very different amino-acid composition from its counterpart in other organisms, another phenomenon that can severely compromise phylogenetic analysis.

Hrdy *et al.*[8] tried to offset the bias caused by the divergent amino-acid composition by assigning each of the 20 possible amino acids to one of six groups of amino acids that have similar chemistries and commonly replace one another in protein sequences. They then reconstructed the alignment of the Ndh51 and comparison sequences using just the six groups of amino acids and reanalysed the data. This technique has the effect of shortening long branches and homogenizing the amino-acid composition among compared sequences. Using this additional approach, Hrdy *et al.* deduced a common origin for the *Trichomonas* and mitochondrial 51-kDa proteins (Fig. 2).

Several points emerge from these three reports. First, Boxma *et al.*[4] are the first to show that a putative evolutionary relative of the mitochondrion contains (and indeed encodes) homologues of proteins specified by mtDNA. By contrast, although Dyall *et al.*[7] and Hrdy *et al.*[8] also identified and studied two complex I homologues in hydrogenosomes, the genes encoding these two proteins (24 and 51 kDa) have not been found in any mtDNA to date but reside exclusively in the nuclear genome. Admittedly, there is strong evidence that the mitochondrial 24- and 51-kDa subunits of complex I originate from the proto-mitochondrial genome via gene transfer to the nucleus. Nevertheless, their connection (and that of their hydrogenosomal counterparts, Ndh24 and Ndh51) to the proto-mitochondrion is less direct than in the case of proteins whose genes have been retained in at least some extant mitochondrial genomes.

Second, the mitochondrial affiliation demonstrated with Ndh51 by Hrdy *et al.*[8] is consistent with other data — particularly characteristics of the protein import system in hydrogenosomes — that unite these organelles with mitochondria[2,3]. By contrast, there is no solid evidence that specifically affiliates the hydrogenosome of any anaerobic eukaryote with a different eukaryotic bacterial group, in particular an anaerobic hydrogen-producing lineage.

Finally, the sporadic phylogenetic distribution of hydrogenosomes and the intimate phylogenetic intermingling of their anaerobic 'hosts' with aerobic, mitochondrion-containing relatives imply that hydrogenosomes are derived secondarily from mitochondria. Indeed, it seems that nature can evolve a hydrogenosome from a mitochondrion with relative ease.

This story is far from complete, because mitosomes — putative remnant mitochondria that lack the ability to make ATP — have recently been discovered in several microbial lineages that do not have conventional mitochondria[11]. The evolutionary and biochemical connections among mitochondria, hydrogenosomes and mitosomes must be elucidated if we are to truly understand the pathways and mechanisms of eukaryotic cell evolution. ■

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Atmospheric chemistry

# The decay of organic aerosols

Euripides G. Stephanou

The chemistry of organic aerosols has been somewhat neglected on the assumption that they are eliminated from the atmosphere mainly by rainfall. Laboratory studies indicate that a rethink is called for.

Fine particles and droplets suspended in the atmosphere have a key role in environmental issues such as climate and human health. Over the oceans, such aerosols consist mainly of sulphates, but above continents they are mostly organic matter[1]. Organic aerosols come from many sources, including smoke particles from burning fuels and biomass, and the light-induced oxidation of volatile hydrocarbons, both natural and man-made[1]. The main process that removes organic aerosols from the atmosphere has been assumed to be precipitation, but writing in *Geophysical Research Letters* Molina and colleagues[2] suggest that another elimination route could be just as important.

Gaseous organic compounds in the atmosphere interact with oxidants such as ozone and hydroxyl and nitrate radicals, reactions that provide an important sink for their eradication from the atmosphere[3]. For organic aerosols, however, the most common means of removal is by deposition, either sedimentation — simply falling out of the atmosphere — or precipitation[4]. Organic aerosols are usually less than a micrometre in size[5], so it is generally assumed[4] that precipitation is the major process by which they leave the atmosphere; larger particles would be more likely to settle out. Molina and colleagues[2] now identify another removal pathway whereby the organic surface on atmospheric particles is degraded by oxidation initiated by hydroxyl radicals ($OH^{\cdot}$). The efficiency of this process appears to be comparable to precipitation in removing organic aerosols from the atmosphere.

To model the reactions that organic aerosols might undergo in the atmosphere, Molina *et al.*[2] used two organic films deposited on glass slides: a paraffin film to represent aliphatic aerosols (molecules with carbon chains); and a pyrene film to represent aromatic aerosols (having carbon-ring structures). Aliphatic and aromatic hydrocarbons such as paraffin and pyrene have been isolated from organic aerosols from various locations[6].

To examine the oxidation reactions of solid organic compounds, the authors exposed the model aerosol surfaces to an 'atmosphere' of various ratios of $NO_x$:$O_2$:$H_2O$, and then varied the concentration of $OH^{\cdot}$ from $0.1 \times 10^8$ to $100 \times 10^8$ molecules per $cm^3$ (the average global atmospheric $OH^{\cdot}$ concentration[7] is about $10^6$ molecules per $cm^3$). Using state-of-the-art analytical instruments, they then measured the rate of degradation of the organic surface, how quickly the $OH^{\cdot}$ is used up, and the type and speed of formation of the gaseous products.

Molina and colleagues clearly observed the loss of organic carbon from both model substrates. They also observed that, over time, the depletion rate of the organic layer is linearly dependent on the $OH^{\cdot}$ concentration. The aromatic carbon surface degraded more slowly than the aliphatic one, suggesting that the route of decay varies according to the compound. The gaseous products of the degradation reaction are small, volatile, one- and two-carbon species; which particular species are produced depends on the substrate.

From their observations, the authors propose a mechanism for the $OH^{\cdot}$-induced oxidative degradation of organic aerosols. According to this, the reaction leads predominantly to a scission of the carbon–carbon bond in paraffin, and to cleavage of the aromatic ring in pyrene. The authors assume that the rate of carbon loss from the organic film is directly proportional to the $OH^{\cdot}$ concentration, and, given an average $OH^{\cdot}$ concentration of $10^6$ molecules per $cm^3$, they estimate that an aliphatic aerosol of 0.02–0.2 μm will be converted entirely into gaseous products in about six days[2]. The lifetime of an organic aerosol has been estimated from atmospheric measurements and lab experiments to be four to five days[8]. Consequently, this study concludes that oxidative degradation and removal by precipitation occur at comparable rates, and that $OH^{\cdot}$-induced oxidation is a significant mechanism that eliminates organic aerosols from the atmosphere.

Chemical reactions with the $OH^{\cdot}$ radical have been established as the dominant processes by which most gaseous organic compounds are removed from the atmosphere[3]. In fact, $OH^{\cdot}$ reactions occur at environmentally significant rates even for the chemically recalcitrant PCBs (polychlorinated biphenyls), so they are an important atmospheric sink for these pollutants[9,10]. However, there is only very limited information on the reactions of gaseous $OH^{\cdot}$ with organic liquids and solids[2,11], or indeed on any of the chemistry of organic aerosols.

Traditional analytical techniques used to characterize organic aerosols failed to analyse the water-soluble organic compounds (which account for 70–90% of the aerosol mass[12]) and were limited to identifying only the components that could be dissolved in organic solvents (6–20% of aerosol mass[12]). We know now that the water-soluble fraction of total fine particulate aerosol mass contains oxygenated and macromolecular polar organic substances with surface-active properties[12]. But the atmospheric chemistry of these polar species is otherwise relatively unknown and difficult to study. In addition, the association of some species, such as the environmental pollutants polyaromatic hydrocarbons, with black carbon particles seems to show a potential inhibiting effect for their reaction with gaseous $OH^{\cdot}$ (ref. 11).

Molina and colleagues[2] make a strong case that the heterogeneous reactions of organic aerosols with atmospheric oxidants are important for their fate. The results highlight the need for further studies to improve our understanding of the reactions and effects of organic aerosols in the environment. We need a thorough chemical characterization and quantification of the main components, details of their reactions in the presence of atmospheric oxidants, and improved knowledge of their surface properties and water uptake before and after heterogeneous reactions in the atmosphere. Finally, lab experiments are rarely definitive, of course: systematic field studies will also be required. ■

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