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An Analysis of Dinoflagellate Metabolism Using EST Data

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The dinoflagellates are an important group of eukaryotic, single celled algae. They are the sister group of the Apicomplexa, a group of intracellular parasites and photosynthetic algae including the malaria parasite *Plasmodium*. Many apicomplexan mitochondria have a number of unusual features, including the lack of a pyruvate dehydrogenase and the existence of a branched TCA cycle. Here, we analyse dinoflagellate EST (expressed sequence tag) data to determine whether these features are apicomplexan-specific, or if they are more widespread. We show that dinoflagellates have replaced a key subunit (E1) of pyruvate dehydrogenase with a subunit of bacterial origin and that transcripts encoding many of the proteins that are essential in a conventional ATP synthase/Complex V are absent, as is the case in Apicomplexa. There is a pathway for synthesis of starch or glycogen as a storage carbohydrate. Transcripts encoding isocitrate lyase and malate synthase are present, consistent with ultrastructural reports of a glyoxysome. Finally, evidence for a conventional haem biosynthesis pathway is found, in contrast to the Apicomplexa, *Chromera* and early branching dinoflagellates (*Perkinsus, Oxyrrhis*).
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Key words: Dinoflagellate; mitochondria; metabolism; EST analysis; alveolate; glyoxysome.

Introduction

Dinoflagellates are unicellular, flagellate protists found in a diversity of ecosystems. Approximately 50% of taxa are photosynthetic, while the remainder have lost the ability to carry out photosynthesis. Photosynthetic dinoflagellates are important primary producers, forming part of both the marine and fresh water phytoplankton. A few species can produce red tides, toxic algal blooms that can lead to shellfish poisoning. Dinoflagellates also form symbioses with corals and a breakdown of this symbiosis, perhaps in response to elevated ocean temperatures, leads to expulsion of the symbionts and coral bleaching (Sanchez-Puerta et al. 2007).

Some of the most unusual genomic organizations of all species are found in the dinoflagellate algae. The nuclear genome is exceptionally large (Holm-Hansen 1969), with multiple copies of many genes, often arranged in tandem repeats (Bachvaroff and Place 2008). The smallest dinoflagellate genome, of *Symbiodinium*, is estimated to be 3×10^9 bp, similar in scale to the human genome (Lin 2006). Therefore, no genome has yet been fully sequenced and instead, extensive EST

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libraries have been created (Bachvaroff et al. 2004; Hackett et al. 2005; Leggat et al. 2007; Slamovits and Keeling 2008).

The chloroplast genome is fragmented and greatly reduced (Koumandou et al. 2004). Recently, significant fragments of the dinoflagellate mitochondrial genome have been sequenced from a number of species including *Alexandrium catenella, Amphidinium carterae, Crypthecodinium cohnii*, *Karlodinium micrum* and *Oxyrrhis marina* (reviewed in Nash et al. 2008). All contain just three protein-encoding genes (*coxI, coxIII, cob*) and fragmentary rRNA-encoding genes, with the majority of genes having been relocated to the nucleus (Jackson et al. 2007; Nash et al. 2007, 2008; Slamovits et al. 2007).

Dinoflagellates are a sister group to the Apicomplexa, a group including a number of obligate parasites which include many important human and animal pathogens such as *Plasmodium* (causative agent of malaria), *Toxoplasma* and *Cryptosporidium* (Walker et al. 2011). Many of the Apicomplexa contain a remnant chloroplast (Dorrell and Smith 2011), but only *Chromera* and closely related species are able to carry out photosynthesis (Moore et al. 2008). The dinoflagellates and Apicomplexa are sister groups to the ciliates, as shown in Figure 1a. Ciliates are a large and diverse group of ciliated protozoa which can be free-living, facultatively parasitic or parasitic. Many species are symbionts. There is no evidence for the presence of a chloroplast in ciliates, although a few genes of possible algal origin have been identified (Archibald 2008). The ciliates, dinoflagellates and Apicomplexa together are referred to as the alveolates.

It has been known for many years that mitochondrial function in *Plasmodium* is unconventional. This has been shown both by biochemical and genome analyses (Bowman et al. 1961; Gardner et al. 2002). In the asexual stage the majority of cellular ATP is synthesized through glycolysis and lactic acid production (Uyemura et al. 2004). There is no evidence for a mitochondrial acetyl-CoA source, as the sole pyruvate dehydrogenase (PDH) is located in the apicoplast (Foth et al. 2005). Despite this, it is clear that the *Plasmodium* mitochondrion is functional (Howe and Purton 2007; Painter et al. 2007). A recent metabolic analysis has shown that the *Plasmodium* TCA cycle is branched, bifurcating at 2-oxoglutarate dehydrogenase, and that malate is produced as a waste product (Olszewski et al. 2010). The mitochondrial electron transport chain is missing a conventional complex I, replacing it with a single-subunit NADH dehydrogenase (Mogi and Kita 2010), and major components

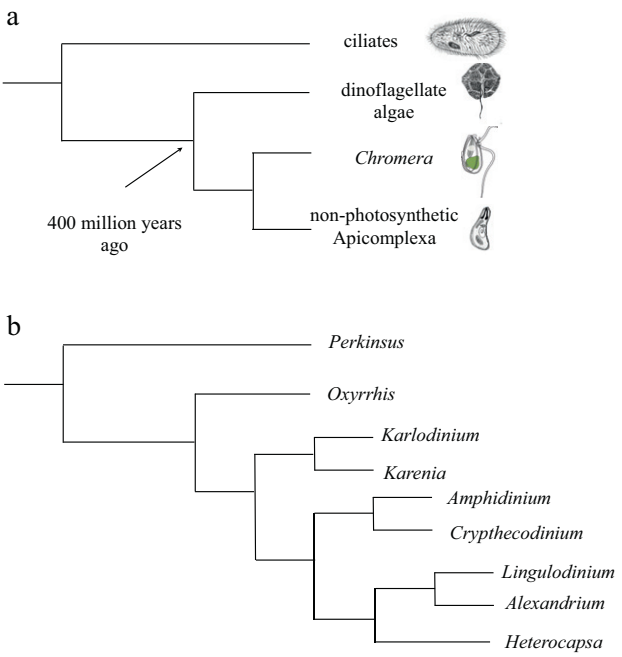

Figure 1. Dinoflagellates, Apicomplexa and ciliate relationships. **a**. Schematic diagram showing relationships within the Alveolata: ciliates (non-photosynthetic), dinoflagellate algae, and the Apicomplexa. *Chromera* is a recently-discovered photosynthetic apicomplexan. A diagram of a model species is shown for each group. **b**. Schematic diagram showing relationships between dinoflagellate species for which EST datasets are available. The diagram is based on two hsp90 and rDNA phylogenies inferred by Hoppenrath and Leander (2010). There is poor phylogenetic support for many dinoflagellate relationships, and so this diagram should be taken as a guide only. However, it is clear that *Perkinsus* and *Oxyrrhis* are early-branching dinoflagellates and the remaining groups are monophyletic.

from complex V (ATP synthase) are also absent. Instead, the electron transport chain may be used for the regeneration of ubiquinone (Painter et al. 2007; van Dooren et al. 2006). Other apicomplexan species have a diversity of mitochondrial metabolic functions, with *Cryptosporidium parvum* containing a mitosome, a derived mitochondrion lacking a genome (Henriquez et al. 2005).

In contrast, the ciliates contain a conventional mitochondrion, undergoing 'textbook style' biochemistry. A proteomic analysis of isolated mitochondria from the ciliate *Tetrahymena thermophila* identified all key components of the TCA cycle (Smith et al. 2007b), and a functional electron transport chain, together with a significant number of proteins (45%) with no known function.

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