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REVIEW

Organization of the genome and gene expression in a nuclear environment lacking histones and nucleosomes: the amazing dinoflagellates

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Abstract

Dinoflagellates are fascinating protists that have attracted researchers from different fields. The free-living species are major primary producers and the cause of harmful algal blooms sometimes associated with red tides. Dinoflagellates lack histones and nucleosomes and present a unique genome and chromosome organization, being considered the only living knockouts of histones. Their plastids contain genes organized in unigenic minicircles. Basic cell structure, biochemistry and molecular phylogeny place the dinoflagellates firmly among the eukaryotes. They have G1-S-G2-M cell cycles, repetitive sequences, ribosomal genes in tandem, nuclear matrix, snRNAs, and eukaryotic cytoplasm, whereas their nuclear DNA is different, from base composition to chromosome organization. They have a high G + C content, highly methylated and rare bases such as 5-hydroxymethyluracil (HOMeU), no TATA boxes, and form distinct interphasic dinochromosomes with a liquid crystalline organization of DNA, stabilized by metal cations and structural RNA. Without histones and with a protein:DNA mass ratio (1:10) lower than prokaryotes, they need a different way of packing their huge amounts of DNA into a functional chromatin. In spite of the high interest in the dinoflagellate system in genetics, molecular and cellular biology, their analysis until now has been very restricted. We review here the main achievements in the characterization of the genome, nucleus and chromosomes in this diversified phylum. The recent discovery of a eukaryotic structural and functional differentiation in the dinochromosomes and of the organization of gene expression in them, demonstrate that in spite of the secondary loss of histones, that produce a lack of nucleosomal and supranucleosomal chromatin organization, they keep a functional nuclear organization closer to eukaryotes than to prokaryotes.

Keywords: Dinoflagellates; DNA; Dinochromosomes; Nuclear domains; Gene expression; Nucleolus; Cajal bodies; Nuclear matrix

Contents

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Introduction

Dinoflagellates are microscopic, unicellular protists with both prokaryotic and eukaryotic features (Taylor, 1987a, b; Falkowski et al., 2004; Morden and Sherwood, 2002). The most prominent non-eukaryotic features are the lack of histones and nucleosomes; the properties and organization of their DNA with atypical, permanently condensed chromosomes lacking Q, G or C banding; the base composition of their DNA with a high G+C content and modified and rare bases such as 5-hydroxymethyluracil (HOMeU); the persistent nuclear envelope and closed mitosis, etc. Among the main eukaryotic features are the presence of non-coding repetitive DNA sequences in the genome; the existence of a well-defined nucleus and nucleolus, the organization of ribosomal genes in tandem; conservation of snRNAs, etc. Dinoflagellates have eukaryotic G1-S-G2-M cell cycles (Homma and Hastings, 1989; Triemer and Fritz, 1984) with specific checkpoints in both G1 (Yeung and Wong, 2003; Yeung et al., 2000) and G2 phases (Whiteley et al., 1993), and eukaryotic cyclins, cyclin-dependent kinases and their associated histone kinase activity (Levenson et al., 1997; Barbier et al., 2003). Many proteins show cell cycle-specific expression (Kwok and Wong, 2003; Taroncher-Oldenburg et al., 1997; Machabee et al., 1994; ten Lohuis and Miller, 1998; Chan et al., 2002; Bhaud et al., 1999; Levenson et al., 1997). In spite of dinochromosomes lacking direct contact with the extranuclear spindle, dinoflagellates have a spindle checkpoint with anaphase-promoting complex (APC)-mediated activities, that is activated by nocodazole (Yeung et al., 2000). Most of the chloroplastic genes have been transferred to the nucleus and the few remaining are organized in plasmid-like minicircles, containing one gene with a conserved AT-rich core region (Koumandou et al., 2004; Zhang et al., 2002; Bachvaroff et al., 2004; Laatsch et al., 2004). Dinoflagellates possess a unique chromosome organization that will be considered in detail later on (Spector, 1984; Rizzo, 1987, 1991, 2002).

For these reasons dinoflagellates were first considered to be mesokaryotes, a lineage intermediate between prokaryotes and eukaryotes (Herzog et al., 1984; Loeblich, 1984). Molecular phylogeny based on rDNA sequencing data of 5S rRNA (Krishnan et al., 1990), 5.8S rRNA (Maroteaux et al., 1985), small subunit 17S rRNA (Cavalier-Smith, 1993), and large subunit 23–26S rRNA (Daugbjerg et al., 2000) placed the dinoflagellates firmly among the eukaryotes as a monophyletic group, within the Alveolata, along with the Apicomplexa, Ciliata, and Foraminifera, a branch that emerged rather late in evolution, discarding that they could be primitive eukaryotes or mesokaryotes (Sogin, 1991; Lee and Kugrens, 1992).

Primary organization of dinoflagellate DNA

The organization of the dinoflagellate genome is different from other eukaryotes, from base composition to chromosome organization. They are haploid, with a high DNA content from 6 up to 400 pg/n, while eukaryotes usually range between 0.04 and 3 pg and up to 40 pg in some plants (Sparrow et al., 1972; Rizzo, 1987). Their DNA presents a high G+C content (Triplett et al., 1993), contains up to 70% of modified and rare bases non-randomly distributed in the genome, and presents a high substitution of T by HOMeU, characteristic of the phylum, that could confer special binding properties to DNA, of A by N^6-methyladenine, and of C by 5-methyl-C (5-MeC) (Rae and Steele, 1978; Steele and Rae, 1980; Rizzo, 1987). Cytosine methylation by methyltransferases is an evolutionary conserved DNA modification in vertebrates, plants and some fungi. 5-MeC is a component of transcriptionally silent chromatin, essential for development, that may be triggered by small interference RNAs (siRNA) (Tariq and Paszkowski, 2004). The high levels of cytosine methylation in dinoflagellates suggests that major amounts of "heterodinochromatin" may be present in their large genomes, requiring methylation systems to maintain them in a silent state and suggesting the existence of higher plant-like methyltransferases. The levels of 5-MeC in dinoflagellates are also involved in the regulation of gene expression (ten Lohuis and Miller, 1998). Dinoflagellates contain up to a 60%, of repetitive sequences. Their arrangement in the genome is partly eukaryote-like, but a fraction of them present a novel distribution that could be correlated with the atypical organization of this DNA (Hinnebusch et al., 1980; Moreau et al., 1998; Triplett et al., 1993).

Studies on the molecular organization of dinoflagellate genes are very scarce due to lack of information on