gene isolation) that diplomonads may also contain an Hsp60 of mitochondrial origin (*17*). These considerations led to the proposition (6) that the common ancestor of all extant eukaryotes contained mitochondria (and peroxisomes) and was thus aerobic, and that subsequent evolution has been reductive, not acquisitive (with the exception of the chloroplast).

One endeavor these findings should not stimulate is a renewed search for a genome in hydrogenosomes. All characterized mitochondrial genomes are geared solely toward the hallmark function of the organelle—respiration (*18*). Since loss of respiration is a defining feature of hydrogenosomes, one would also expect rapid loss of their mitochondrial genome, making such a search pointless. In contrast, plastid gene products, although geared largely toward photosynthesis—the hallmark function of the chloroplast—are involved in other important metabolic processes as well. Consequently, a residual, functional plastid genome persists in the plants, algae, and other protists that have lost photosynthesis (*19*) (see figure).

Why organelle genomes at all? The present notion is that plastids and respiring mitochondria have kept their genomes because some of the key integral membrane proteins of respiration and photosynthesis are intensely hydrophobic and are therefore unimportable across the organellar outer membranes (*20*). Mitochondrial genome retention may ultimately be driven by the only two proteins (both highly hydrophobic) encoded by all examined mitochondrial genomes (*18, 20*), whereas photosynthetic plastids encode about 10 times as many putatively unimportable proteins (*20, 21*). Unfortunately, this theory fails to account for genome retention in three disparate lineages of nonphotosynthetic plastids, which do not encode any hydrophobic proteins (*19*). Nor does it explain the surprising diversity of organelle genomes in both number and kind of gene products (*18, 21*).

Genomic extinction has also happened repeatedly for the nucleus in many cases of secondary plastid endosymbiosis, the process whereby a protist engulfs a eukaryotic alga and permanently retains part of its prey as a degenerate endosymbiont (*22*). In chlorarchniophytes and cryptomonads, a remnant of the algal endosymbiont's nucleus, termed the nucleomorph (and bearing a tiny genome of 380 to 660 kilobases), persists between the inner and outer pair of membranes surrounding its chloroplast (see figure). But in all other cases, the endosymbiotic nucleus (or nucleomorph) has vanished (*22*). This means that hundreds of ancestrally plastid genes must have been transferred twice during evolution, first from the plastid to the nucleus (then nucleomorph) after primary plastid endosymbiosis, and then again from the nucleomorph to the host nucleus after each of many independent secondary symbioses. All in all, then, the host nucleus seems to be a tremendous magnet, both for organellar genes and for endosymbiotic nuclear genes.

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BIOTECHNOLOGY

DNA Ordering on a Lipid Membrane

Mark S. Spector and Joel M. Schnur

Recent advances in understanding the structure of bioassemblies have suggested their potential use for industrial as well as medical applications (*1*). This has been made possible by the development of tools such as atomic force microscopy (AFM) and near-field optical microscopy, improved synchrotron x-ray sources, and new techniques that permit selective modification of lipids, proteins, and DNA. Theoreticians working with molecular biologists are now using these techniques to gain a much better picture of biological function on the molecular scale. The state of experimental art in this area can been seen on p. 810, where Rädler *et al.* (*2*) present the structure of a bioassembly of DNA and lipid membrane.

Such bioassemblies might be used for the encapsulation and cellular delivery of intact genetic material. Liposomes, micrometer-size hollow spheres, remain the most common lipid-based drug carrier (*3*). Traditional preparations can lead to DNA degradation and low encapsulation efficiency. The use of charged systems has led to improved efficiency in cellular uptake. In 1987, Felgner *et al.* developed a cationic lipid that can be formed into liposomes before the addition of nucleic acids (*4*). Subsequent addition of negatively charged DNA leads to electrostatic binding to the liposome surface, for a 10-fold or greater improvement in cellular uptake (*5*).

The structure and function of these ionic complexes have been the subject of many recent studies. Mixing polyanionic DNA with cationic lipids leads to aggregation of the liposomes and ordering of the DNA (*6*). Similar transformations have long been known to occur in simpler lipid systems when multivalent cations are added to anionic liposomes, causing the bilayers to roll up like a jelly-roll into structures called cochleated cylinders (*7*). However, the structure of the aggregates in the DNA–cationic lipid system has remained unclear.

Using high-resolution x-ray scattering, Rädler *et al.* investigated the structure of these DNA-lipid aggregates (*2*). When DNA is added to small cationic liposomes (less than 0.1 μm in diameter), they collapse into micrometer-sized multilamellar globules. Sur-

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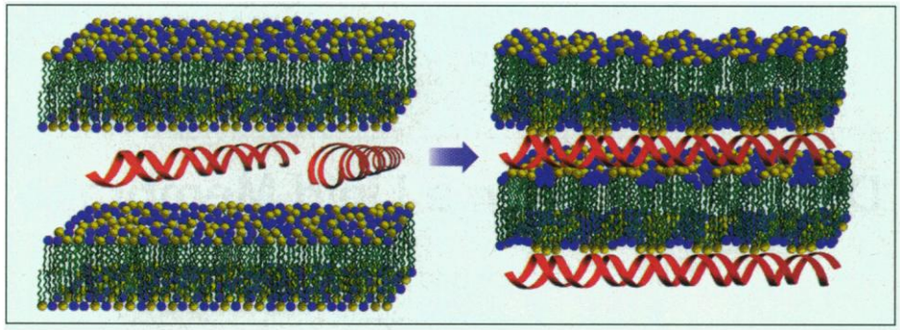
prisingly, they found that the DNA condenses into a highly ordered phase even at large dilutions (*2*). This phase is strongly birefringent and shows defect patterns similar to those of smectic liquid crystals.

The ordering of DNA on a cationic lipid membrane has been predicted with a model that balances the electrostatic repulsion of the DNA molecules with an attractive interaction due to undulations of the bilayer induced by the adsorbed DNA (*8*). This theory predicts an ordered phase of the DNA with interaxial spacings of 2 to 4 nm, depending on the size of the deformation. A condensed phase of DNA on a lipid bilayer has recently been directly imaged with AFM (*9*). By observing plasmid DNA adsorbed onto suspended cationic lipid bilayers, the interaxial DNA spacing was found to increase from 4 to 6 nm with increasing salt concentration. These results are consistent with Dan's model (*8*) and the x-ray scattering reported by Rädler *et al.* (*2*). Similar experiments show the lack of an ordered DNA phase when the lipid bilayer is below the gel transition (*9*), indicating that fluidity of the membrane is essential to DNA condensation, which supports the concept of DNA-induced layer distortions. Current theoretical treatments of single bilayers (*8*) do not consider three-dimensional (3D) ordering of the DNA-lipid system due to undulation-induced coupling of adjacent bilayers. One possibility is a periodic distortion of the bilayer along the long axis of the DNA, leading to layer-to-layer correlation of the DNA (see figure). In addition, the periodicity in the orthogonal direction described by Dan could also lead to 3D ordering.

The structural studies that make use of x-ray scattering (*2*) and AFM (*9*) demonstrate the importance of high-resolution techniques for the characterization of complex fluids. Rädler *et al.* provide important insight into the molecular interactions between DNA and fluid lipid membranes. As we understand more, it is quite possible that new submicrometer assemblies can be engineered to provide enhanced functionality. More work is needed to fully determine the molecular interactions that give rise to these ordered aggregates. By measuring the interaxial spacing as a function of DNA-to-lipid ratio, Rädler and co-workers hope to find an enhanced repulsive interaction due to undulations of the DNA chains. Performing such experiments would provide interesting information on the elastic bending properties of these biopolymers. Further studies on conformational changes of membrane-bound DNA would be useful. It is well established that the helicity of DNA can be reversed at high salt concentrations (*10*). The unique ionic environment provided by the lipid membrane might have important effects on the structure and ultimate function of DNA complexes. Continuing research on the structure of lipid complexes with DNA and proteins should allow for the engineering of novel microstructures from biomolecules for use in medical and nonmedical applications.



DNA-induced ordering. (**Left**) Mixed phospholipid-lipid bilayers, consisting of positively charged (yellow) and neutral (blue) lipids, are initially separated because of electrostatic repulsion when the DNA (red) is added. (**Right**) The DNA condenses between the lipid bilayers, causing multilamellar structures, with the cationic lipids aggregating where the DNA contacts the bilayer. Periodic undulations of the bilayer along the DNA axis may lead to registration of the DNA in the layer below, causing 3D ordering. Ordering in the orthogonal direction is seen in x-ray scattering (*2*). Predicted undulations from this periodicity (*8*) may also lead to inter-bilayer correlations.

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WEBWATCH

Wired rice

http://bioserver.myongji.ac.kr/ricemac.html

Rice is the staple food of over a third of the world's population, and thus understanding the genetics and biotechnology of this plant is useful both scientifically and socially. An information-rich resource is the Korea Rice Genome Database WWW Server, maintained by the Department of Biological Science, Myongji University, Yongin, Korea. Links are provided to the Korea Rice EST (expressed sequence tags) Genome Database, as well as databases in Taiwan, Japan, and the United States. Users can also download a copy of, or sign up for a CD-ROM of the RiceGenes database maintained at Cornell University.

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Edited by David Voss

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