

# Bacterial cytochromes *c* structure

from D. R. Thatcher

COMPARISONS of protein structure at the three-dimensional level are able to distinguish similarities, and therefore probable evolutionary connections, which would not be convincing at the amino acid sequence level. The best example of the application of this approach is the discovery of the characteristic super-secondary structure of enzymes which bind dinucleotides. Now that the X-ray crystal structure of four different types of cytochromes *c* is known, a detailed three-dimensional comparison has been made (Dickerson, Timovich and Almasy, *J. molec. Biol.*, **100**, 473; 1976), and the evolutionary implications discussed.

Eukaryotic cytochromes *c* form a clearly homologous group of proteins, both at the three-dimensional level (horse, bonito and tuna crystal structures are available and show an almost identical folding pattern) and at the amino acid sequence level (sequences from over 70 different eukaryotes have similar lengths and have a minimum of 25% of their sequence identical). By contrast bacterial cytochromes *c* show a formidable variation in chemical structure and physical properties; a reflection of the extreme antiquity and diverse modes of energy metabolism in this group of organisms. Dickerson *et al.* have compared the already published three-dimensional structures of tuna cytochrome *c* and *Rhodospirillum rubrum* cytochrome *c*<sub>2</sub> (a purple non-sulphur bacterium) with the new structures of cytochrome *c*<sub>550</sub> from *Paracoccus denitrificans* and *Pseudomonas aeruginosa* cytochrome *c*<sub>551</sub>.

All four cytochromes differ significantly in the length of their polypeptide chains (cytochrome *c*=103 residues; *c*<sub>2</sub>=112 residues; *c*<sub>550</sub>=134 residues and *c*<sub>551</sub>=82 residues).

Although the variation in amino acid sequence between these cytochromes is large (in the case of *c*<sub>551</sub> primary structural similarity can barely be discerned), the overall folding pattern around the haem prosthetic group is recognisable in all four cytochromes. The bacterial cytochromes mainly differ from the tuna cytochrome *c* by additional residues in the external loops around positions 53 and 75 (cytochrome *c* numbering) whilst *c*<sub>550</sub> also has an insertion in a loop in the 20's region and also possesses a 15-residue tail. The small size of *c*<sub>551</sub> is due to a massive deletion (39–58 in tuna cytochrome *c* numbering) of a loop at the bottom of the molecule. The folding of

the rest of the molecule is however conserved and *c*<sub>551</sub> is clearly related to the other cytochromes.

Dickerson *et al.*, go on to propose that this same deletion probably occurs in cytochrome *f* (involved in algal photosynthesis), *c*<sub>555</sub> (a photosynthetic cytochrome of the green sulphur and purple sulphur bacteria), *c*<sub>553</sub> (from the sulphate respirer *Desulphovibrio*) and the *c*<sub>5</sub> of *Pseudomonas mendocina*. This assumption makes the sequence alignment of all these cytochromes with eukaryotic cytochrome *c* much more credible and suggests the existence of a large evolutionarily homologous group of cytochromes whose members all possess a similar polypeptide folding pattern (the cytochrome fold). It is tempting to assume that the different electron transport pathways in which these diverse cytochromes operate also have an evolutionary connection and Dickerson *et al.* explore the way in which their data can be interpreted in terms of the development of bacterial energy metabolism.

Dickerson *et al.*, have drawn attention to the remarkable sequence work of Ambler and colleagues (Ambler *Handbook of Biophysics and Molecular Biology*, 1976; Ambler, Meyer and Kamen, *Proc. natn. Acad. Sci. U.S.A.*, in the press) on other cytochromes *c*<sub>2</sub> in the purple-non sulphur bacteria. Some of these *c*<sub>2</sub>'s align almost exactly with eukaryotic cytochrome *c* (*Rhodomicrobium vannelli*, for example) whilst other *c*<sub>2</sub>'s have, like *Paracoccus c*<sub>550</sub>, additional residues around residues 20, 50 and 70 (such as *Rhodospseudomonas capsulata*). In fact this range of structural variation within *c*<sub>2</sub> has now been extended by the finding of Ambler and Meyer (personal communication) that the *c*<sub>2</sub> of *Rhodospirillum tenue* has the massive deletion characteristic of *c*<sub>551</sub>. We are then left with the intriguing observation that the range of structural variation within cytochromes *c*<sub>2</sub> of the purple non-sulphur bacteria is as great as in all other cytochromes possessing the cytochrome fold.

Dickerson *et al.* consider that the main evolutionary implication of this homology is that bacterial and eukaryotic respiration arose from the dual function cyclic photophosphorylation and respiratory electron transport chain of purple non-sulphur bacteria by loss of the photosynthetic capability.

This interpretation confirms previous schemata for prokaryote evolution (such as Hall, *J. theor. Biol.*, **30**, 429–454; 1971 and in the *Evolution of Bioenergetic Processes*, edit. by Broda, E., 1975) but the evidence really hinges on the question of whether the different cytochromes *c* are evolutionarily representative of the whole electron transport pathways of which they are

members or whether this phylogeny has been muddled by genetic transfer. Physiological studies within the purple non-sulphur bacteria, which have representatives of each major type of cytochrome should resolve this question to some extent. Nevertheless, the purple non-sulphur bacteria could be the key to our understanding the molecular evolution of cytochrome *c*.

# Palaeomagnetic diversity

from Peter J. Smith

PALAEOMAGNETIC studies were begun early this century in an attempt to determine the characteristics of the Earth's magnetic field before the few hundred years of direct observation. By the 1960s, however, they had come to be associated more particularly with the growing evidence in favour of continental drift and seafloor spreading. With the now-widespread acceptance of the principal tenets of the new global tectonics, there has been a tendency for palaeomagnetism to revert more frequently to its original aims, although it is still used widely to elucidate possible continental and/or polar movements (especially those preceding the onset of Wegenerian drift) and has, in addition, become a useful tool for solving particular geological problems (for example, in stratigraphy).

This modern diversity of roles is well illustrated by the many reports that have appeared in the past few months alone. Roy *et al.* (*Geophys. Res. Lett.*, **2**, 537; 1975), for example, have carried out a straight palaeomagnetic directional study of the world's oldest red beds—argillites, 2.3 billion yr old, found in the Huron Supergroup of Ontario. Perhaps 'straight' is hardly the right word in this context, for it is seldom easy to obtain a reliable direction from rocks of such an age. In this case, however, a combination of thermal, chemical and alternating field cleaning appears to give a reliable ancient pole at 67°N, 158°E from a magnetisation acquired at, or within a few tens of millions of years of, the formation of the beds. The new pole is ~100 Myr older than the oldest previous Laurentian poles; and its significance is that in the context of previous poles it provides evidence that the apparent polar wandering path relative to Laurentia from 2.3 to 1.9 billion yr ago was mainly latitudinal and from north to south.

Paradoxically, not only can it be