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ATP synthase, the assembly which makes ATP in mitochondria, chloroplasts and bacteria, uses trans-membrane proton gradients generated by respiration or photosynthesis to drive the phosphorylation of ADP. Its membrane domain is joined by a slender stalk to a peripheral catalytic domain, F1-ATPase. This domain is made of five subunits with stoichiometries of 3 α : 3 β : 1 γ : 1 δ : 1 ϵ , and in bovine mitochondria has a molecular mass of 371 000. We have determined the 3-dimensional structure of bovine mitochondrial F1-ATPase to 6.5 angstrom resolution by X-ray crystallography. It is an approximately spherical globule 110 angstrom in diameter, on a 40 angstrom stem which contains two alpha-helices in a coiled-coil. This stem is presumed to be part of the stalk that connects F1 with the membrane domain in the intact ATP synthase. A pit next to the stem penetrates approximately 35 angstrom into the F1 particle. The stem and the pit are two examples of the many asymmetric features of the structure. The central element in the asymmetry is the longer of the two alpha-helices in the stem, which extends for 90 angstrom through the centre of the assembly and emerges on top into a dimple 15 angstrom deep. Features with threefold and sixfold symmetry, presumed to be parts of homologous alpha and beta subunits, are arranged around the central rod and pit, but the overall structure is asymmetric. The central helix provides a possible mechanism for transmission of conformational changes induced by the proton gradient from the stalk to the catalytic sites of the enzyme.

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